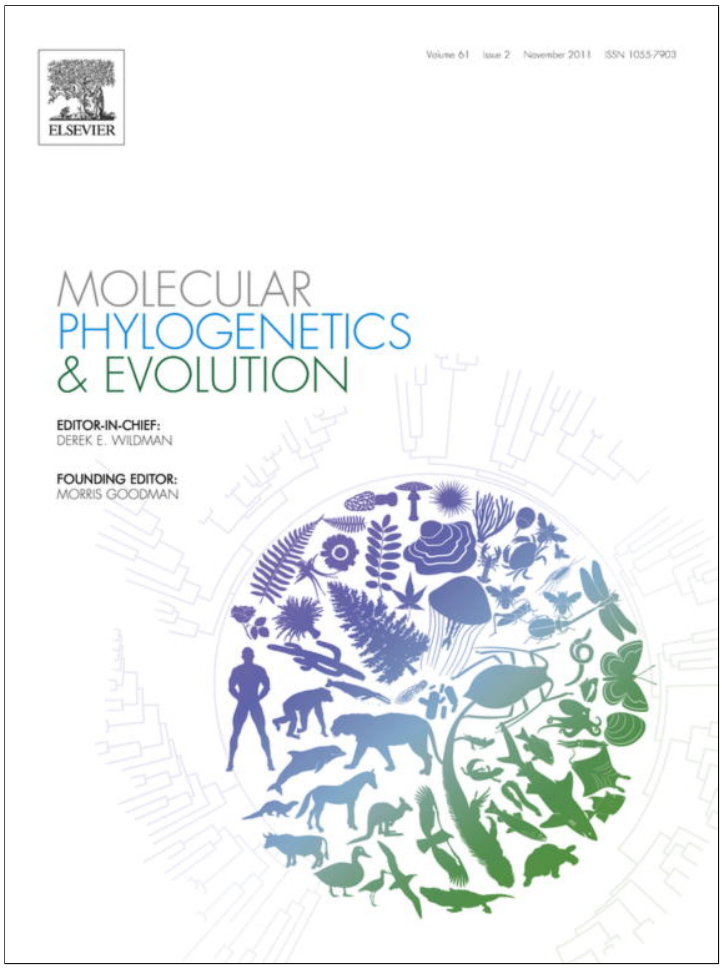

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# A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians

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ABSTRACT

The extant amphibians are one of the most diverse radiations of terrestrial vertebrates (>6800 species). Despite much recent focus on their conservation, diversification, and systematics, no previous phylogeny for the group has contained more than 522 species. However, numerous studies with limited taxon sampling have generated large amounts of partially overlapping sequence data for many species. Here, we combine these data and produce a novel estimate of extant amphibian phylogeny, containing 2871 species (~40% of the known extant species) from 432 genera (~85% of the ~500 currently recognized extant genera). Each sampled species contains up to 12,712 bp from 12 genes (three mitochondrial, nine nuclear), with an average of 2563 bp per species. This data set provides strong support for many groups recognized in previous studies, but it also suggests non-monophyly for several currently recognized families, particularly in hyloid frogs (e.g., Ceratophryidae, Cycloramphidae, Leptodactylidae, Strabomantidae). To correct these and other problems, we provide a revised classification of extant amphibians for taxa traditionally delimited at the family and subfamily levels. This new taxonomy includes several families not recognized in current classifications (e.g., Alsodidae, Batrachylidae, Rhinodermatidae, Odontophrynidae, Telmatobiidae), but which are strongly supported and important for avoiding non-monophyly of current families. Finally, this study provides further evidence that the supermatrix approach provides an effective strategy for inferring large-scale phylogenies using the combined results of previous studies, despite many taxa having extensive missing data.



## 1. Introduction

With over 6800 known species (AmphibiaWeb; http://www.amphibiaweb.org/, accessed April, 2011; hereafter "AW") the extant amphibians (frogs, salamanders, and caecilians) are one of the most diverse radiations of terrestrial vertebrates. The number of known extant amphibians has increased rapidly in recent years, with over 2700 species (~40%) described in the last 26 years (Duellman, 1999; Lannoo, 2005). This newly discovered diversity includes dozens of new species from known genera in poorly studied tropical regions such as Madagascar (Vieites et al., 2009), but also new genera in relatively well-explored regions such as the southeastern United States (Camp et al., 2009), and even new families such as Nasikabatrachidae (Biju and Bossuyt, 2003). Unfortunately, much extant amphibian diversity is currently under extreme threat from pressures such as habitat loss, global climate change, and infectious disease, and many species have gone extinct in the last few decades (Blaustein and Wake, 1990; Stuart et al., 2004).

A phylogenetic framework is critical for discovering, understanding, and preserving extant amphibian diversity, but a large-scale phylogeny for extant amphibians is presently lacking. However, recent molecular and combined-data studies have made important contributions to higher-level phylogeny (Frost et al., 2006; Roelants et al., 2007; Wiens, 2007a, 2011) and to the phylogeny of many major groups, such as caecilians (San Mauro et al., 2009; Zhang and Wake, 2009b), hyloid frogs (Darst and Cannatella, 2004), ranoid frogs (e.g., Bossuyt et al., 2006; Wiens et al., 2009), microhylid frogs (van der Meijden et al., 2007), bufonid frogs (Pauly et al., 2004; Pramuk et al., 2008; Van Bocxlaer et al., 2009), centrolenid frogs (Guayasamin et al., 2009), dendrobatid frogs (Grant et al., 2006; Santos et al., 2009), hemiphractid frogs (Wiens et al., 2007a), hylid frogs (Faivovich et al., 2005, 2010; Wiens et al., 2005b, 2010), terraranan frogs (Hedges et al., 2008; Heinicke et al., 2009), and salamanders (Kozak et al., 2009; Vieites et al., 2011; Wiens et al., 2005a, 2007b; Zhang and Wake, 2009a).

The largest estimate of extant amphibian phylogeny to date is that of Frost et al. (2006). Those authors reconstructed amphibian phylogeny based on relatively intensive sampling of species (522) and characters (up to 4.9 kb of sequence data from 2 mitochondrial and 5 nuclear genes [mean = 3.5 kb], and 152 morphological

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characters). Those authors also proposed extensive changes in taxonomy, especially for taxa delimited at the family and genus level. However, that study has also been criticized on numerous grounds, including concerns about taxon sampling and methodological strategies (Marjanović and Laurin, 2007; Pauly et al., 2009; Wiens, 2007b, 2008). For example, those authors collected up to ~4900 characters per species, but their analysis is apparently based on 15,320 characters, suggesting that their controversial approach to sequence alignment (POY) dominates their results (Wiens, 2008). Although some of the changes made by Frost et al. (2006) have been widely adopted, others are more controversial, such as the partitioning of *Bufo* and *Rana* (Marjanović and Laurin, 2007; Pauly et al., 2009; AW). Indeed, many of these changes are no longer supported, even in Frost's (2011) taxonomic database of extant amphibians (e.g., the families Amphignathodontidae, Batrachophrynidae, Cryptobatrachidae, and Thoropidae recognized by Frost et al. (2006)). Much of the most unstable taxonomy involves the family-level assignment of many of the genera of hyloid frogs, particularly those traditionally assigned to the family Leptodactylidae.

Clearly, extant amphibian phylogeny and classification is still in need of additional study. Fortunately, the numerous studies referenced above (and many others) have produced a massive amount of data that are potentially suitable for a combined, supermatrix approach (e.g., de Queiroz and Gatesy, 2007; Driskell et al., 2004; Pyron et al., 2011; Thomson and Shaffer, 2010; Wiens et al., 2005b). This includes thousands of species represented in GenBank for numerous nuclear and mitochondrial genes, often with substantial overlap of genes among species.

Here, we present a large-scale estimate of amphibian phylogeny, including 2871 species (42% of the 6807 known, extant amphibian species) from 432 of the 504 currently recognized genera (86%), and representatives from every currently delimited, extant family and subfamily. This is 5.5 times more species and nearly twice as many genes as the largest previous study (Frost et al., 2006). The data matrix includes up to 12,712 bp for each species from 12 genes (three mitochondrial, nine nuclear). Importantly, rather than simply reanalyzing published data for relatively well-studied families (e.g., dendrobatids, hylids), we address the monophyly and relationships of many smaller groups that have not been the subject of focused studies (e.g., Ceratophryidae, Cylcoramphidae), as well as relationships among families. We produce a revised classification of extant amphibians, focusing on taxa traditionally ranked as families and subfamilies. This study also provides additional support for the value of the supermatrix approach to large-scale phylogenetic inference (e.g., de Queiroz and Gatesy, 2007; Driskell et al., 2004; Pyron et al., 2011; Thomson and Shaffer, 2010; Wiens et al., 2005b).

## 2. Materials and methods

### 2.1. Taxonomic reference

This analysis has been several years in the making. Our initial taxonomy was based on the September 2009 update of the AmphibiaWeb (AW) database. However, when we refer to current numbers, these are taken from the April, 2011 update. The AW list is fairly current in terms of recently described species, but more conservative than the Amphibian Species of the World (Frost, 2011; hereafter "ASW") regarding some of the more controversial of the recent taxonomic changes (e.g., *Bufo* and *Rana* maintain similar composition as they did prior to Frost et al., 2006). We note some instances where recent updates have modified our original classification. Note that even when not made explicit, we refer in all instances to the known extant diversity of Lissamphibia, given that the clade Amphibia includes numerous extinct stem-group members that are not lissamphibians. The gymnophionans, caudates, and anurans also contain numerous extinct taxa, many of which are grouped in separate genera, subfamilies, and families that are not addressed in our analyses or included in our discussion of phylogeny. See Marjanović and Laurin (2007), Carroll (2009), and Pyron (2011) for an overview of these taxa, their phylogenetic affinities, and the origins of Amphibia and Lissamphibia.

### 2.2. Molecular data

We identified 12 candidate loci that have been broadly sampled and successfully used in amphibian phylogenetics at both lower and higher taxonomic levels. These 12 genes included nine nuclear genes: C-X-C chemokine receptor type 4 (CXCR4), histone 3a (H3A), sodium–calcium exchanger (NCX1), pro-opiomelanocortin (POMC), recombination-activating gene 1 (RAG1), rhodopsin (RHOD), seventh-in-absentia (SIA), solute-carrier family 8 (SLC8A3), and tyrosinase (TYR). Three mitochondrial genes were also included: cytochrome *b* (cyt-b), and the large and small subunits of the mitochondrial ribosome genes (12S/16S; omitting the adjacent tRNAs as they were difficult to align and represented only a small amount of data). This selection of genes includes almost all of those genes used in the higher-level analyses by Frost et al. (2006) and Roelants et al. (2007), and most of those used in other large-scale studies (Faivovich et al., 2005; Grant et al., 2006; Wiens et al., 2009, 2010). However, we did not include the nuclear gene 28S (used by Frost et al. (2006)), as previous analyses of this gene region alone suggest that it contains relatively few informative characters and supports some relationships that are grossly inconsistent with other studies (see Wiens et al., 2006). We conducted GenBank searches by family and subfamily to gather all available sequences, using a minimum-length threshold of 200 bp (a somewhat arbitrary threshold of 1.5% of the total matrix length, to avoid including very short [e.g., <50 bp] fragments), and stopping in August of 2010. Only species in the taxonomic database were included in the sequence matrix, which excluded numerous named taxa of ambiguous status, and many sequences labeled 'sp.' We removed a few (<10) taxa with identical sequence data for all genes (arbitrarily retaining the first in alphabetical order), to avoid potentially misidentified or otherwise confounded specimens or sequences.

For the protein-coding genes, alignment was relatively straightforward. Conceptual translations were used to ensure an open reading frame, and sequences were aligned using the translation-alignment algorithm in the program Geneious v4.8.4 (GeneMatters Corp.), with the default cost matrix (Blosum62) and gap penalties (open = 12, extension = 3). For the ribosomal RNA sequences (12S and 16S sequences), alignment was more challenging. Preliminary global alignments using the MUSCLE (Edgar, 2004) and CLUSTAL (Larkin et al., 2007) algorithms under a variety of gap-cost parameters yielded low-quality results (i.e., alignments with large numbers of gaps and little overlap of potentially homologous characters).

We subsequently employed a two-step strategy for these data. First, we identified sequence clusters of similar length and coverage from the global alignment. These were subsequently aligned separately using the MUSCLE algorithm with the default high-accuracy parameters, which have been shown to outperform CLUSTAL in a variety of settings (Edgar, 2004). These alignments were subsequently refined using the MUSCLE refinement algorithm, and then adjusted manually and trimmed for quality and maximum coverage (i.e., end sequences with low overlap and poor apparent alignment were deleted using the alignment editor in Geneious). These length and position-based sequence groups were then aligned to each other using the profile-profile alignment algorithm in MUSCLE. The resulting final global alignment was

manually adjusted and trimmed again for maximum quality and coverage, and refined a second time. Final adjustments were made by eye for a small number of sequences. This process was repeated for 12S and 16S separately. For 12S, four clusters were produced and combined using profile alignment, with five clusters for 16S.

The final concatenated alignment consists of 12,712 bp for 2871 species. These species included 42% of the currently recognized amphibian species (6807; this and subsequent numbers from AW 2011), representing 41 caecilian species in 23 genera (22% of 189 known extant species and 70% of 33 genera), 436 salamander species in 68 genera (72% of 608 species and 99% of 69 genera), and 2394 frog species from 341 genera (40% of 6010 species and 85% of 402 genera). We selected *Homo* as an outgroup because data were available for *Homo* from all 12 genes, and the sister group to Amphibia is Amniota (e.g., Alfaro et al., 2009; Hugall et al., 2007; Pyron, 2010). The matrix contains data from 2572 species for 16S (90%, 1986 bp), 2312 species for 12S (81%, 1357 bp), 1241 for cyt-b (43%, 1140 bp), 1049 for RAG-1 (37%, 2700 bp), 606 for TYR (21%, 1132 bp), 589 for RHOD1 (21%, 315 bp), 478 for SIA (17%, 397 bp), 445 for POMC (16%, 666 bp), 352 for H3A (12%, 328 bp), 284 for CXCR4 (10%, 753 bp), 220 for NCX1 (8%, 1338 bp), and 175 for SLC8A3 (6%, 1132 bp). The mean length per species is 2563 bp (20% of the total length of the matrix, 12,712 bp), with a range from 249 to 11,462 bp (2–90%), and is available in Dryad repository doi:10.5061/dryad.vd0m7. GenBank numbers are listed in Appendix S1.

Clearly, many taxa had large amounts of missing data (some >97%), and on average each species had 80% missing cells. However, several lines of evidence suggest that these missing data are not problematic. First, two genes (12S/16S) were shared by the vast majority of taxa (90% and 81%, respectively), providing a "backbone" for the placement of most taxa based on overlapping sequence data. Simulations suggest that this sampling design can be critically important for allowing the accurate placement of taxa with extensive missing data, as opposed to having all genes be randomly sampled across species with limited overlap (Wiens, 2003). Second, a large body of empirical and theoretical studies suggests that highly incomplete taxa can be accurately placed in model-based phylogenetic analyses (and with high levels of branch support), especially if a large number of characters have been sampled (recent review in Wiens and Morrill, 2011). Finally, several recent empirical studies have shown that the supermatrix approach (with extensive missing data in some taxa) yields generally well-supported large-scale trees that are in general highly congruent with both existing taxonomies and previous phylogenetic estimates (e.g., Driskell et al., 2004; McMahon and Sanderson, 2006; Pyron et al., 2011; Thomson and Shaffer, 2010; Wiens et al., 2005b).

### 2.3. Phylogenetic analyses

We performed phylogenetic inference using maximum likelihood (ML) and assessed support using non-parametric bootstrapping (BS). We assume that Bayesian analysis would yield very similar results (but would be very difficult to implement for so many taxa), and we strongly prefer model-based methods to parsimony (for reasons described in Felsenstein (2004)). We performed ML tree inference and non-parametric bootstrapping using the program RAxMLv7.0.4 (Stamatakis, 2006) with the 12-gene concatenated matrix (species-tree methods were not practical given the large number of taxa). We used the GTRGAMMA model for all genes and partitions because GTR is the only substitution model implemented in RAxML, and all other substitution models are encompassed within the GTR model (Felsenstein, 2004). The GTRGAMMA model in RAxML is recommended over the GTR + Γ + I because the large number of rate categories for Γ (25, as opposed to the usual 4) should adequately account for potentially invariant sites without the need for an extra parameter (Stamatakis, 2006). Even though the GTR + Γ + I model is implemented in some versions of RAxML, its use is explicitly not recommended (Stamatakis, 2006).

Previous phylogenetic analyses of these data show that GTR + Γ + I is generally the best-fitting model for these genes (e.g., Roelants et al., 2007; Wiens et al., 2005a,b, 2009, 2010). These previous analyses also suggest that the protein-coding genes should be partitioned by codon position, whereas the ribosomal genes (12S, 16S) should be partitioned by stems and loops, with separate partitions within and between genes. These secondary structures were identified and coded following the protocol used by Wiens et al. (2005b), based on predicted features from *Pseudacris regilla* (12S; AY819376) and *Rana temporaria* (16S; AY326063) from the European Ribosomal RNA database (http://bioinformatics.psb.ugent.be/webtools/rRNA/). The placement of stems and loops appears to be conserved across most sites, at least within frogs (Wiens et al., 2005b). Our final analysis was partitioned by gene, codon position (for protein-coding genes), and stems and loops (for ribosomal genes).

To find the optimal ML tree, we used a searching strategy that combined the rapid bootstrapping algorithm (100 non-parametric bootstrap replicates) with the thorough ML search option (20 independent searches, starting from every fifth bootstrap replicate). Similar analyses were performed numerous (>10) times as new taxa and sequences were added to the near-final matrix. These analyses collectively represent hundreds of independent searches from random starting points. All of these preliminary analyses showed high congruence with the final ML topology. This concordance strongly suggests that our final ML estimate represents the optimal topology for these data (or close to it). Given that BS values generally appear to be conservative (Felsenstein, 2004), we considered clades with values of 70% or greater to be well-supported. These analyses were performed on a 240-core Dell PowerEdge supercomputing system at the High Performance Computing Center at the City University of New York, and were completed in 16 days using 24 nodes of the CUNY cluster.

### 2.4. Taxonomic revision

A major goal of this study was to revise the higher-level taxonomy of extant amphibians to correspond with the new phylogeny, given several major problems that were discovered. In the Results section below, we compare our results with existing phylogenies and classifications, and describe our proposed solutions to taxonomic problems as we describe them (rather than having a separate section discussing taxonomy). In general, we attempt to alter existing classifications (e.g., AW, ASW) as little as possible, and only when existing groups are not monophyletic. Furthermore, we recognize new groups only if they are strongly supported. Given the size of these phylogenies, we do not detail every congruence and discordance between our phylogeny and all previous studies (especially within families). Instead, we emphasize necessary taxonomic changes revealed by our study. We also focus our phylogenetic comparisons on the largest of the previous analyses (in terms of taxonomic scope and number of species sampled), those of Frost et al. (2006), Roelants et al. (2007), and Wiens (2007a, 2011). The generic composition of all families and subfamilies in our revised classification is provided in Appendix B. Genus names follow our original taxonomic database from the 2009 AW update.

In some cases, our analyses show that higher taxa (i.e., families and subfamilies) are not monophyletic, but not all genera have been included in our tree. Some of these genera are effectively "orphaned" because it is no longer clear to which higher taxon they belong. We generally denote these as *incertae sedis* within the higher taxon in which they were embedded in previous

classifications. Resolving the placement of these taxa in the tree and classification will require additional data and analyses. We consider this a more conservative strategy than simply placing them in the nominate group without data. While in theory this strategy creates more "instability" by removing taxa from named groups, it highlights the need for their study in future analyses, and does not promote the taxonomic burden of heritage (Pyron and Burbrink, 2009) in further propagating classifications with high probability of error based solely on the status quo.

## 3. Results

A summary of the ML tree based on the rapid-bootstrapping analysis from RAxMLv7.0.4 (lnL = −1704992.20) is shown in Fig. 1. This phylogeny is generally well-supported, with 64% of nodes having BS proportions >70. Our analyses support the monophyly of frogs, caecilians, and salamanders, respectively, and weakly support a sister-group relationship between frogs and salamanders, as found in most other studies of extant lissamphibian phylogeny (Frost et al., 2006; Pyron, 2011; Roelants et al., 2007; San Mauro, 2010; Wiens, 2011; Zhang et al., 2005). An alternative grouping of Gymnophiona and Caudata (i.e., Procera) has been supported by some studies (e.g., Feller and Hedges, 1998), and in re-analyses of others (e.g., Zhang et al., 2005; San Mauro et al., 2005; see Marjanović and Laurin, 2007; Pyron, 2011). Many of the family-level relationships within these three groups remain unchanged from recent estimates (Frost et al., 2006; Pyron, 2011; Roelants et al., 2007; San Mauro, 2010; Wiens, 2007a, 2011). However, we find some significant deviations from previous phylogenies and taxonomies, which we describe below along with proposed solutions.

Within caecilians (Fig. 2A), our results agree with other recent studies in supporting clades corresponding to Rhinatrematidae, Ichthyophiidae, and Caeciliidae (Frost et al., 2006; Roelants et al., 2007; San Mauro et al., 2009; Zhang and Wake, 2009b). The traditional family-level classification of caecilians (still used by AW, 2011) is not supported, given that Uraeotyphlidae renders Ichthyophiidae paraphyletic and that Scolecomorphidae and Typhlonectidae render Caeciliidae paraphyletic. Furthermore, we find (Fig. 2A) the caeciliid subfamily Typhlonectinae (recognized by ASW) to be paraphyletic with respect to Caeciliinae (*Cthonerpeton* and *Typhlonectes* are not sister taxa, although this is weakly supported), and also makes Caeciliinae non-monophyletic (i.e., the caeciliines *Caecilia* and *Oscaecilia* are in a strongly supported clade with *Cthonerpeton* and *Typhlonectes,* which excludes all other caeciliine genera such as *Dermophis, Gegeneophis*, and *Siphonops*). Typhlonectinae is synonymized with Caeciliinae in our classification. Within Caeciliidae, we concur with ASW in recognizing the strongly supported subfamily Scolecomorphinae for *Crotaphatrema* and *Scolecomorphus,* which is the sister group to all other caeciliids. Although we could recognize Caeciliinae as the sister group to Scolecomorphinae, this clade is only weakly supported, despite strong support for each subfamily-level clade. Thus, we recognize these two clades as separate subfamilies. We restore the subfamily Herpelinae (Laurent, 1984) for the clade comprising *Herpele* and *Boulengerula*. We recognize the other strongly supported clade as Caeciliinae (Figs. 1, 2A; Appendix B). This arrangement accommodates all taxa included in our tree, though many other genera have not yet been sampled. The following genera are thus considered Caeciliidae *incertae sedis*: *Atretochoana, Brasilotyphlus, Idiocranium, Indotyphlus, Microcaecilia, Mimosiphonops, Nectocaecilia, Parvicaecilia, Potomotyphlus,* and *Sylvacaecilia.*

Within salamanders, the family and subfamily-level relationships are mostly consistent with most recent model-based molecular analyses (Roelants et al., 2007; Wiens, 2011; Wiens et al., 2005a; Zhang and Wake, 2009a) and current classifications (AW, ASW). However, our results differ strongly from Frost et al. (2006) with respect to relationships among the salamander families. Frost et al. (2006) recover a clade comprising Sirenidae, Dicamptodontidae, Ambystomatidae, and Salamandridae. In contrast, we find strong support for a sister-group relationship between Sirenidae and all salamanders exclusive of Cryptobranchidae and Hynobiidae (Figs. 1 and 2B and C), as do Wiens et al. (2005a), Roelants et al. (2007), and Wiens (2007a, 2011). While some classifications recognize only two subfamilies in Plethodontidae (Hemidactylinae and Plethodontinae; AW), we follow most recent authors (Chippindale et al., 2004; Kozak et al., 2009; Vieites et al., 2011; Wiens, 2007a) and ASW in recognizing four subfamilies in Plethodontidae (Bolitoglossinae, Hemidactylinae, Plethodontinae, and Spelerpinae; Figs. 1 and 2D–F). We do not recognize a separate subfamily for *Protohynobius* (contra AW), given that it is likely nested in Hynobiinae (Peng et al., 2010).

Within frogs, strongly-supported higher-level groups and relationships (e.g., among the non-neobatrachian frogs, Neobatrachia, Hyloidea, and Ranoidea) are consistent with most recent studies (Frost et al., 2006; Roelants et al., 2007; Wiens, 2007a, 2011), with some notable exceptions. We find (Fig. 2G) strong support for placing Discoglossoidea (Alytidae + Bombinatoridae + Discoglossidae) as the sister group to all other frogs exclusive of Ascaphidae + Leiopelmatidae (see also Roelants et al., 2007), whereas Frost et al. (2006) and Wiens (2007a, 2011) placed Pipoidea (Pipidae + Rhinophrynidae) in this position. Within Neobatrachia (Fig. 1), we corroborate the placement of Heleophrynidae as the sister taxon to all other neobatrachian frogs (Frost et al., 2006; Roelants et al., 2007; Wiens, 2007a, 2011). We find a weakly supported sister-group relationship between the clade Sooglossidae + Nasikabatrachidae and all neobatrachian frogs to the exclusion of Heleophrynidae (Fig. 1). In contrast, both Roelants et al. (2007) and Wiens (2007a, 2011; Sooglossidae only) placed this clade as the sister-taxon to Ranoidea, whereas Frost et al. (2006) found it to be the sister-group of Hyloidea (including Myobatrachidae + Calyptocephalellidae).

Within Hyloidea, our results suggest that several families currently recognized by both AW and ASW are not monophyletic. All of these problematic taxa were previously placed in the family Leptodactylidae (subdivided extensively by Frost et al., 2006), and include Ceratophryidae, Cycloramphidae, Leptodactylidae, and Strabomantidae. Below we describe the specific problems and our proposed taxonomic solutions. These solutions include recognizing several additional families relative to current classifications (Alsodidae, Batrachylidae, Odontophrynidae, Rhinodermatidae, Telmatobiidae) and synonymizing one (Strabomantidae with Craugastoridae). These newly recognized families are either re-definitions of previously recognized families (Rhinodermatidae, Telmatobiidae), or elevation of existing taxa presently below family rank (Alsodinae, Batrachylinae, Odontophrynini) to the rank of families.

Most of these problematic taxa are contained in a weakly supported clade (Fig. 2Z) that includes the currently recognized families Ceratophryidae, Cycloramphidae, and Hylodidae (note that the content of these families and their subfamilies are the same in both AW and ASW). Under these classifications, Ceratophryidae is presently divided into the subfamilies Batrachylinae (*Atelognathus, Batrachyla*), Ceratophryinae (*Ceratophrys, Chacophrys, Lepidobatrachus*), and Telmatobiinae (*Telmatobius*, including *Batrachophrynus* in AW). Cycloramphidae comprises Alsodinae (*Alsodes, Eupsophus, Hylorina, Insuetophrynus, Limnomedusa, Macrogenioglottus, Odontophrynus, Proceratophrys, Thoropa*) and Cycloramphinae (*Crossodactylodes, Cycloramphus, Rhinoderma, Zachaenus*), and one genus of uncertain placement (*Rupirana*). Hylodidae contains *Crossodactylus, Hylodes,* and *Megaelosia.* With respect to this classification, we find strong support for monophyly of Hylodidae (Fig. 2Z), but the families Ceratophryidae and Cycloramphidae are non-monophyletic, with

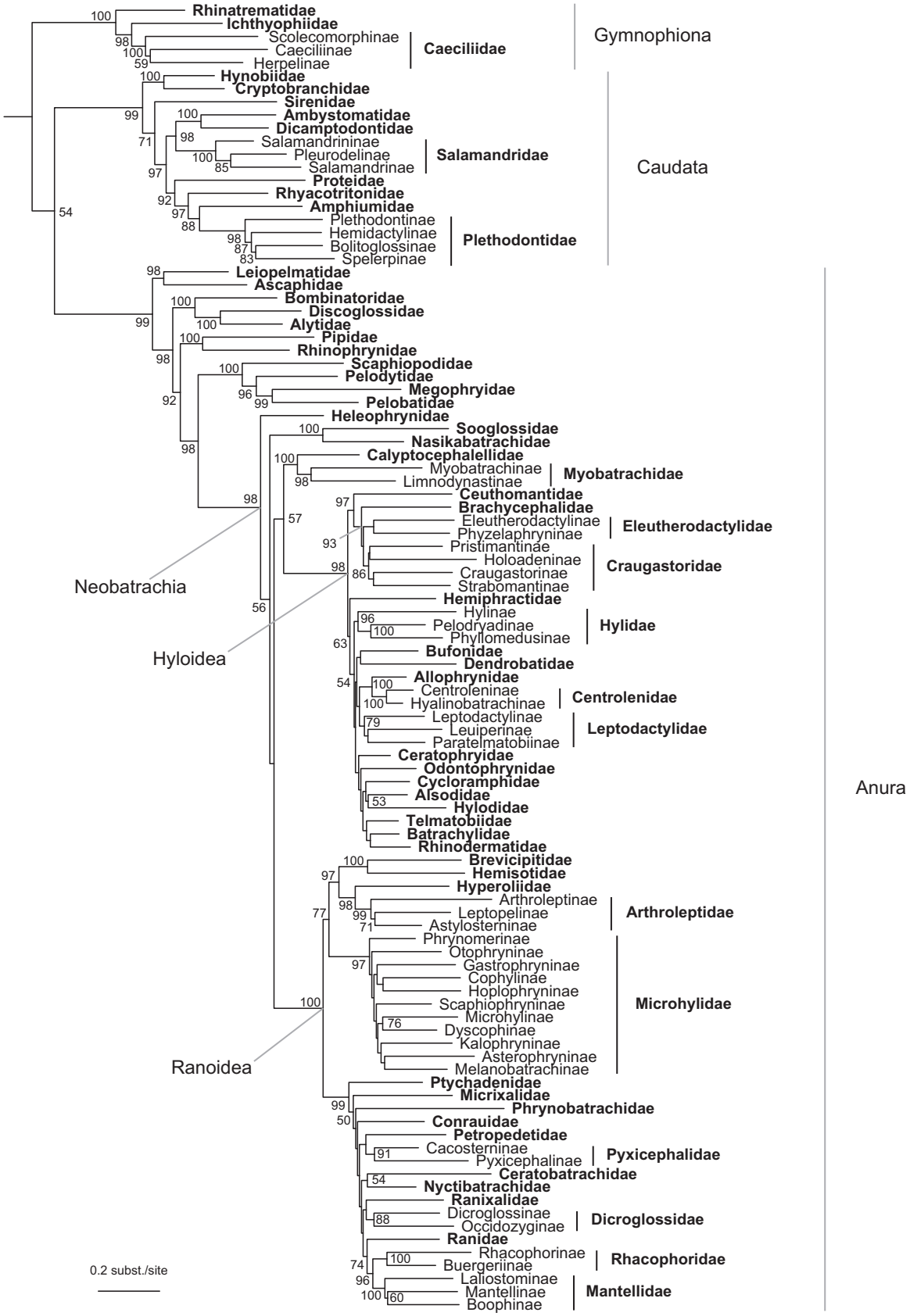



**Fig. 1.** Skeletal representation of the 2871-species tree from maximum likelihood analysis, with tips representing families and subfamilies based on our taxonomic revision. Numbers at nodes are BS proportions greater than 50%. The full version of this tree is presented in Fig. 2, with multiple panels indicated by bold italic letters.

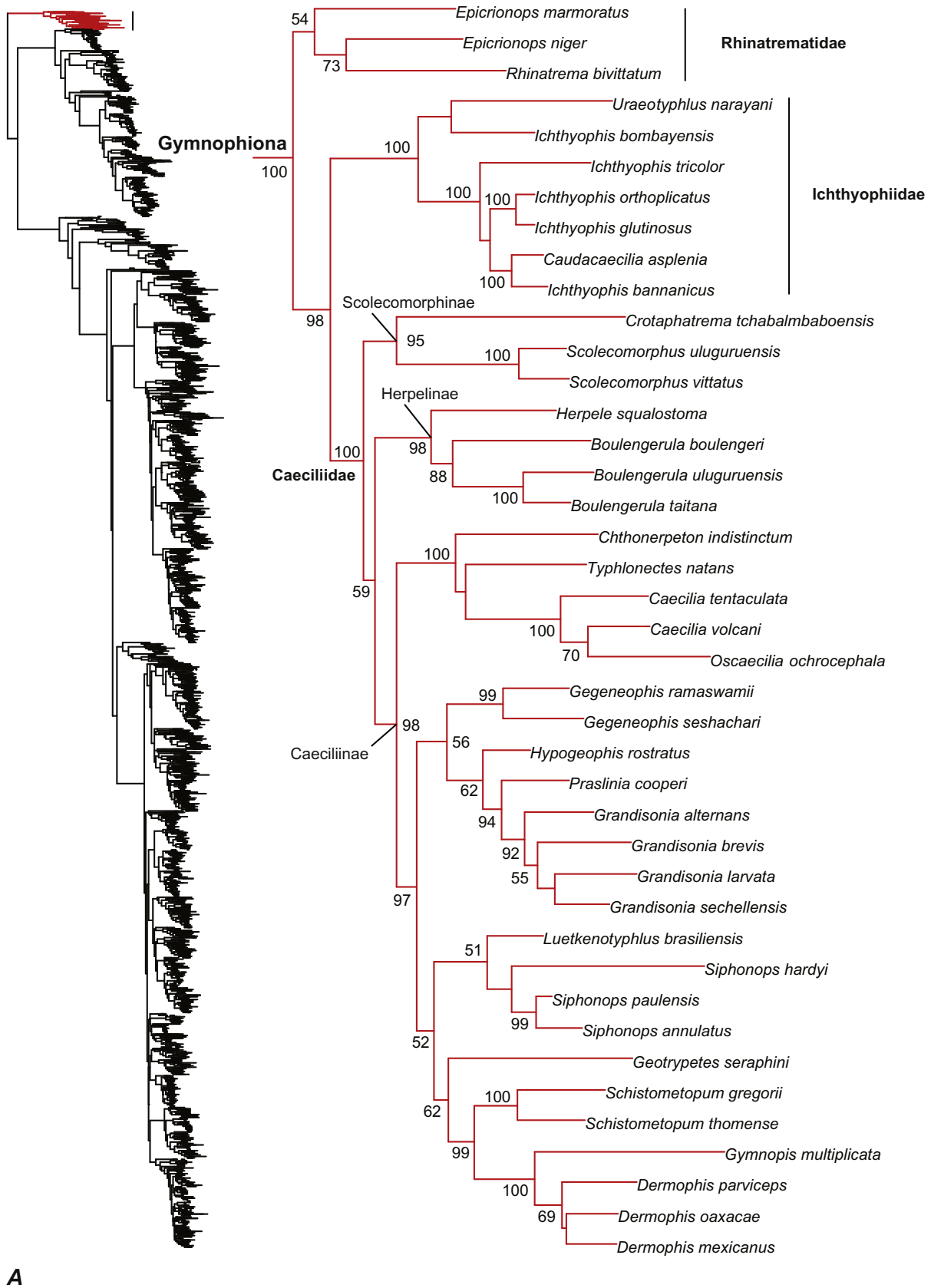



**Fig. 2.** Large-scale maximum likelihood estimate of amphibian phylogeny, containing 2871 species represented by up to 12,871 bp of sequence data from 12 genes (three mitochondrial, nine nuclear). Numbers at nodes are maximum likelihood BS proportions greater than 50%. A skeletal version of this tree at the subfamily level is presented in Fig. 1. Bold italic letters indicate figure panels.

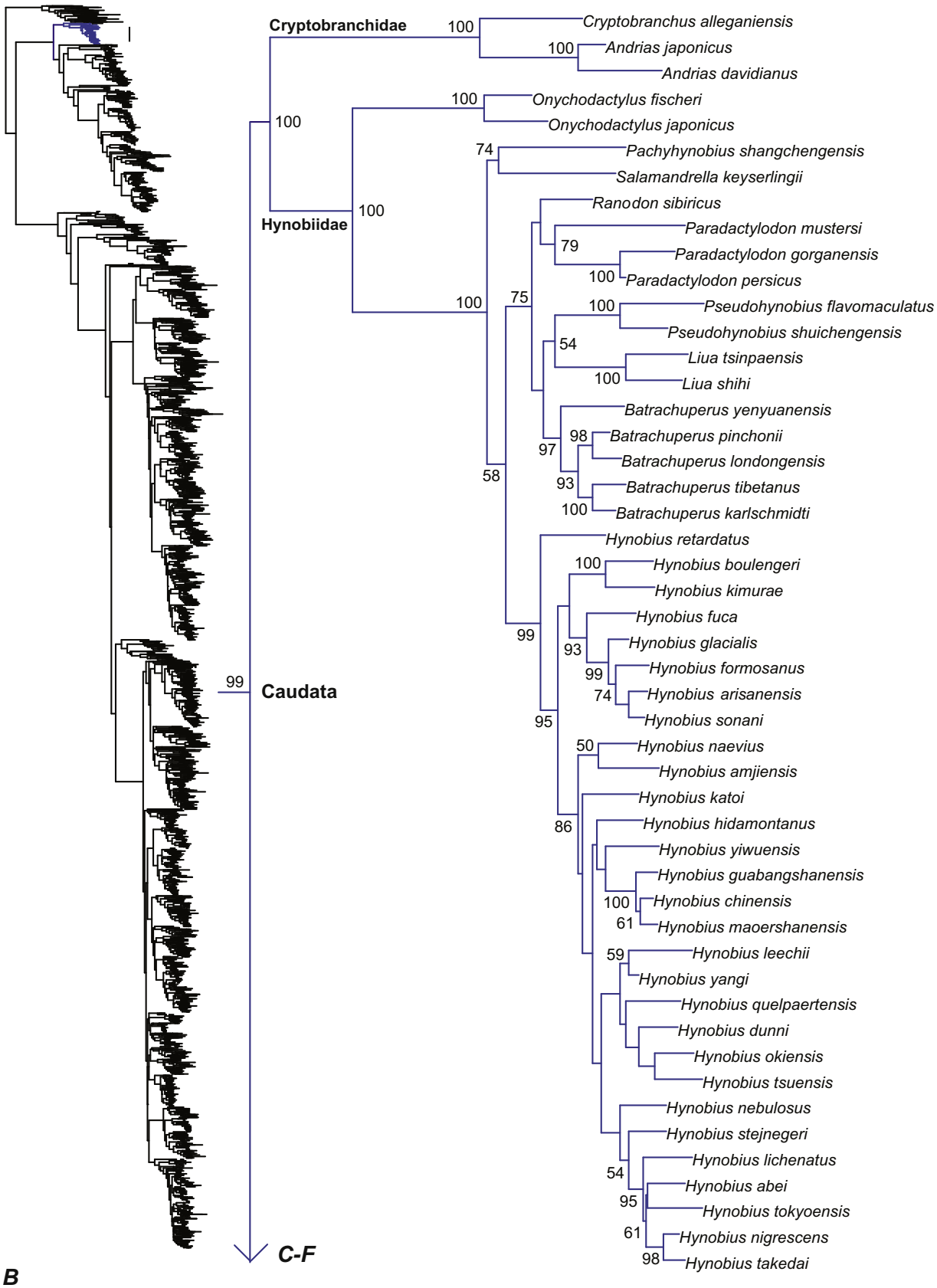



**Fig. 2** (*continued*)

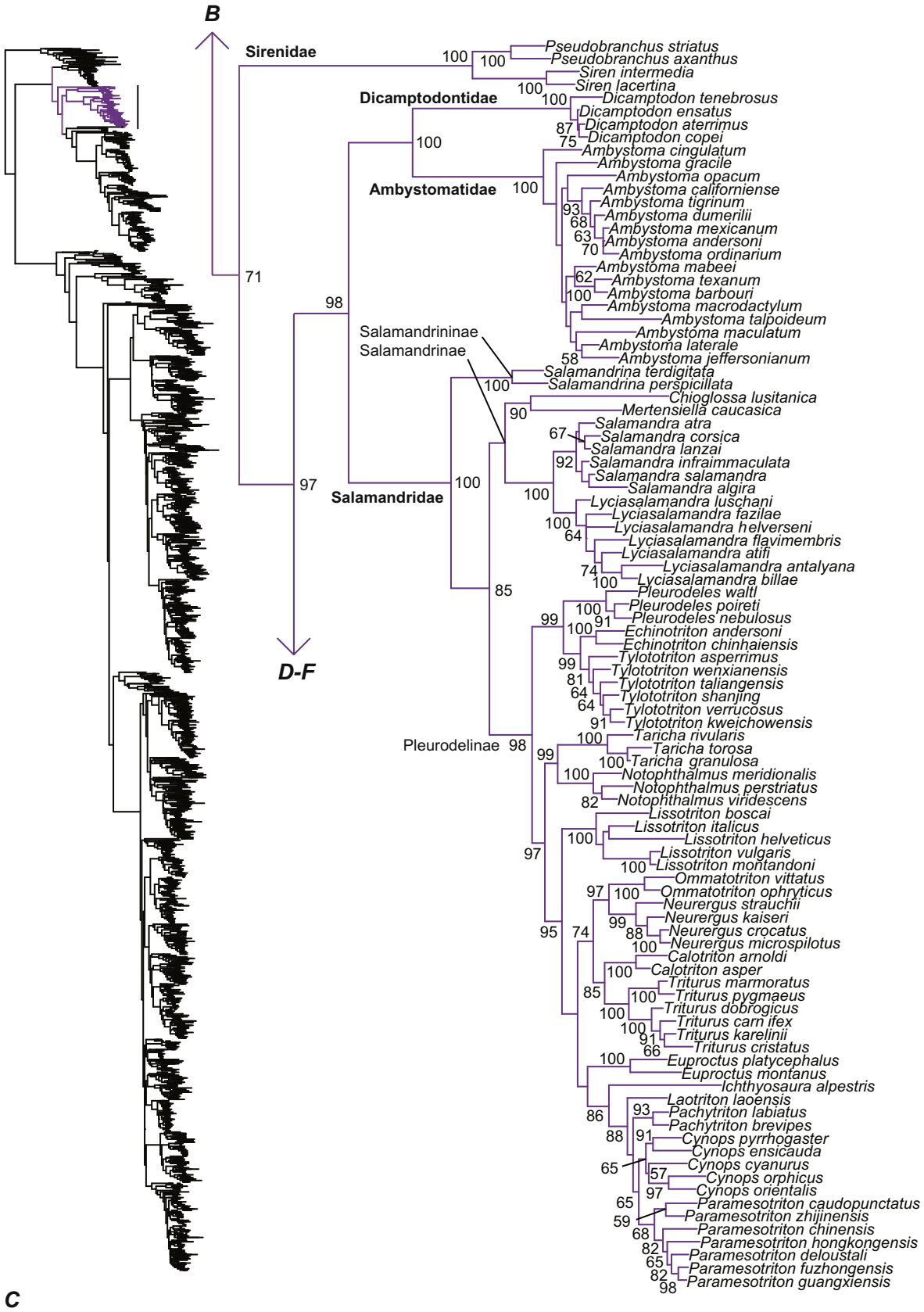



**Fig. 2** (*continued*)

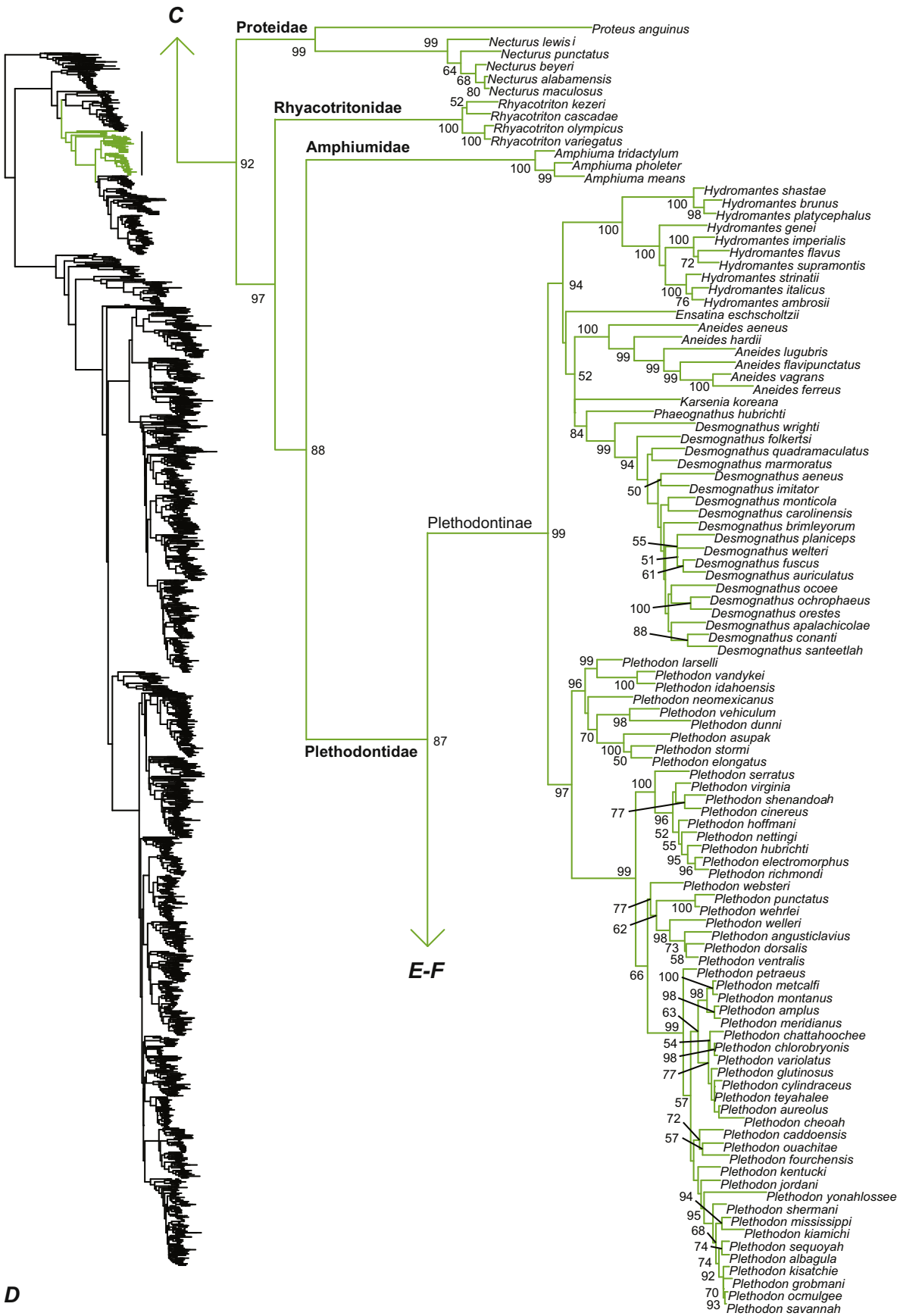
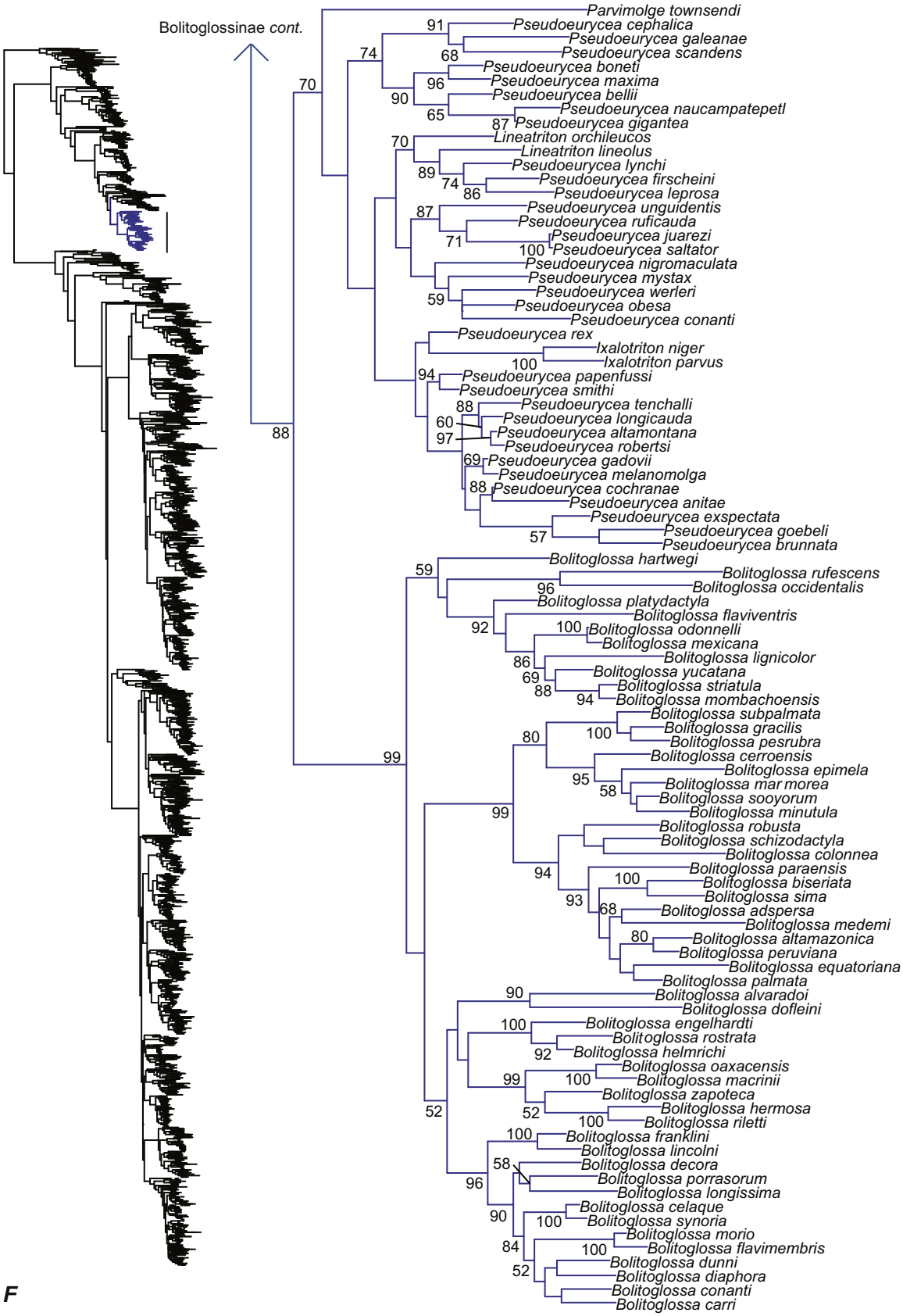



**Fig. 2** (*continued*)


**Fig. 2** (*continued*)

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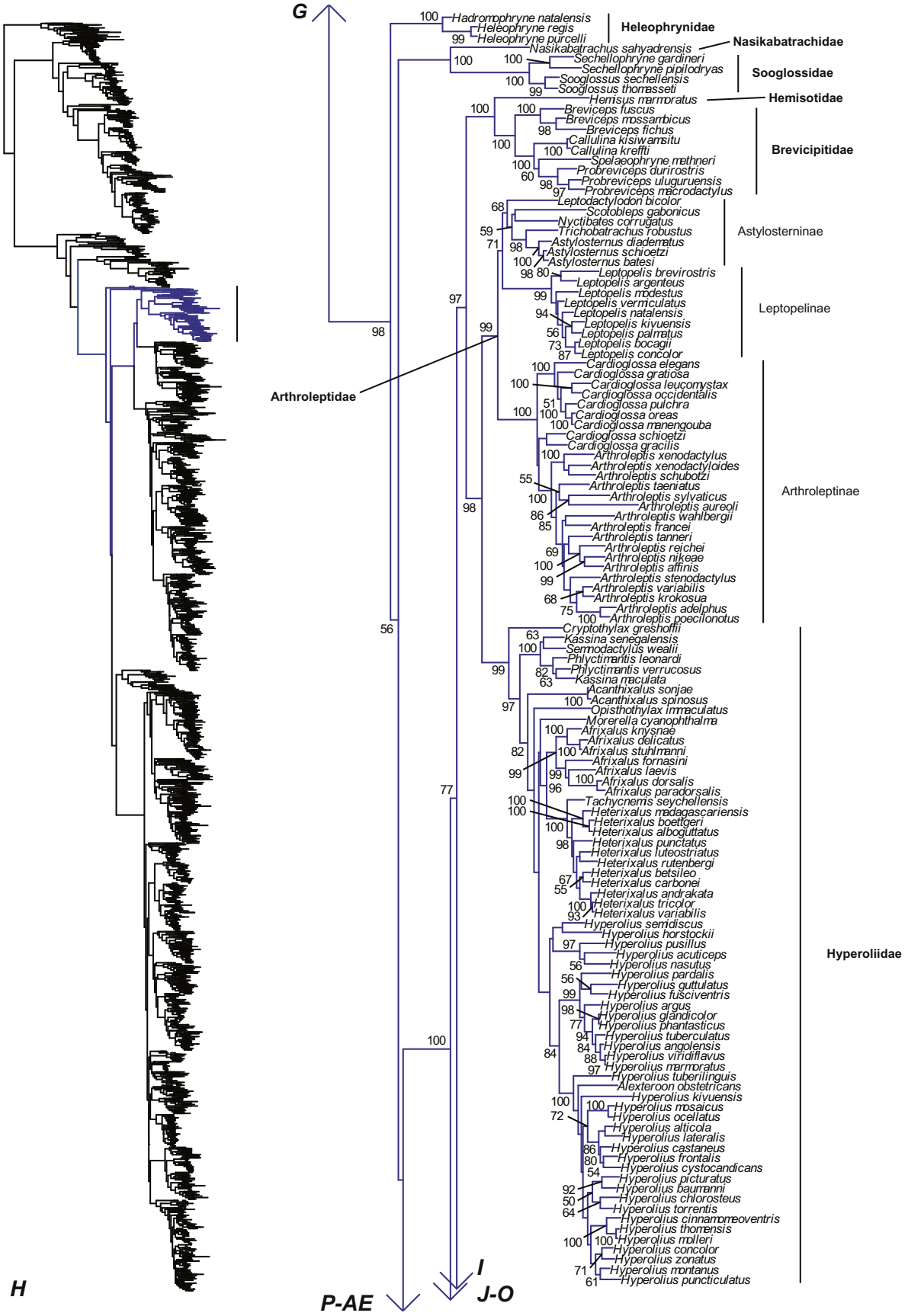


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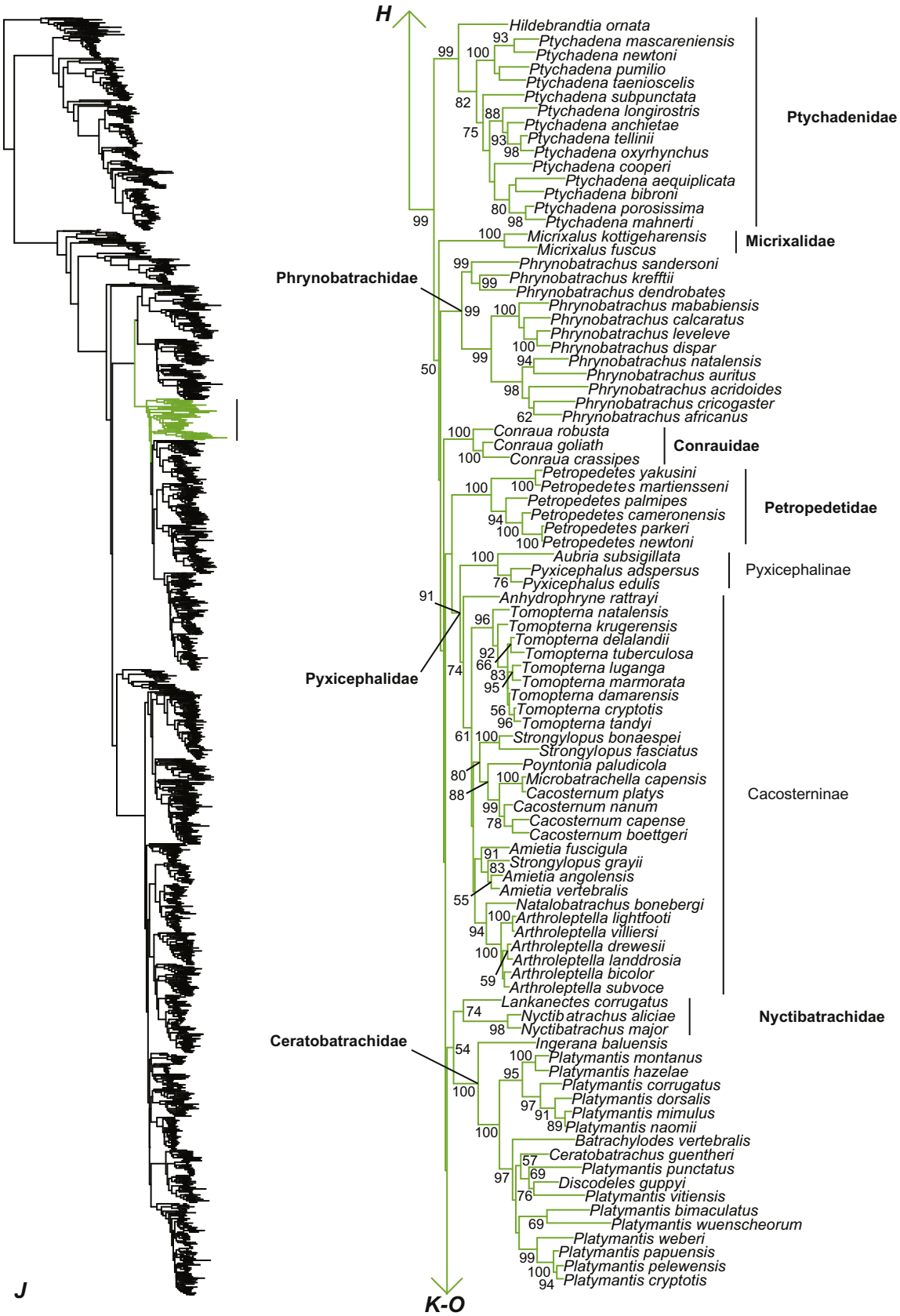


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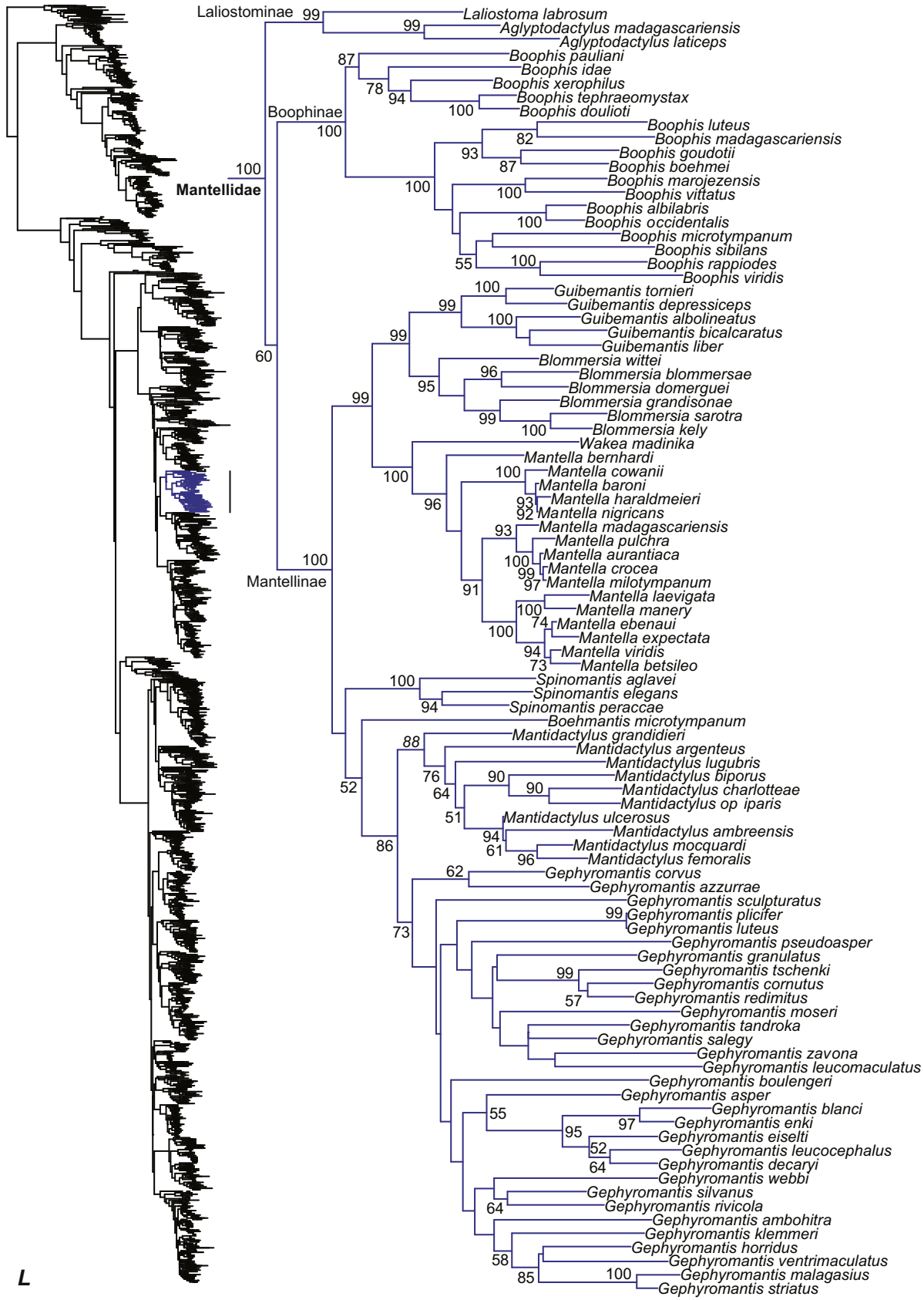


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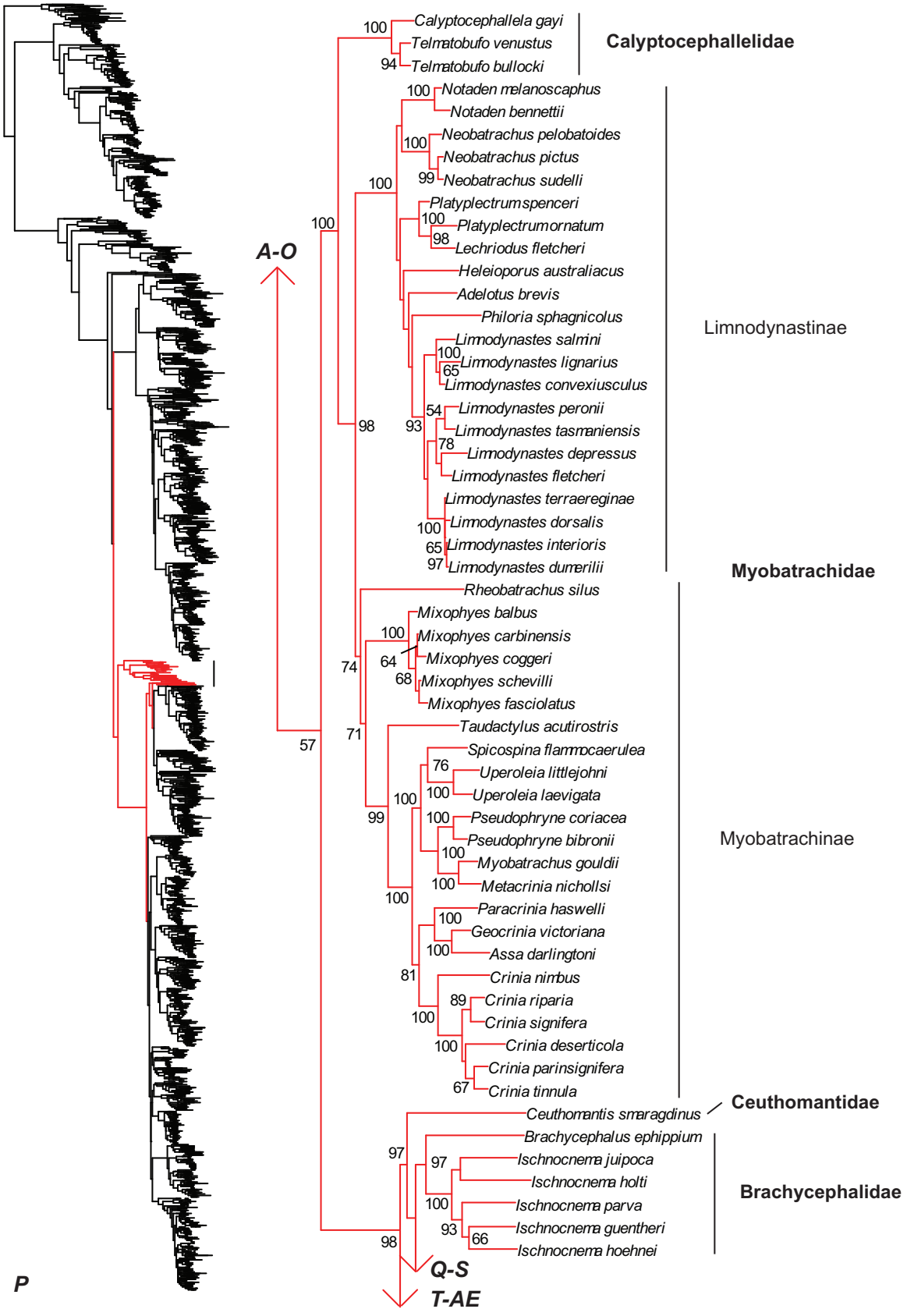


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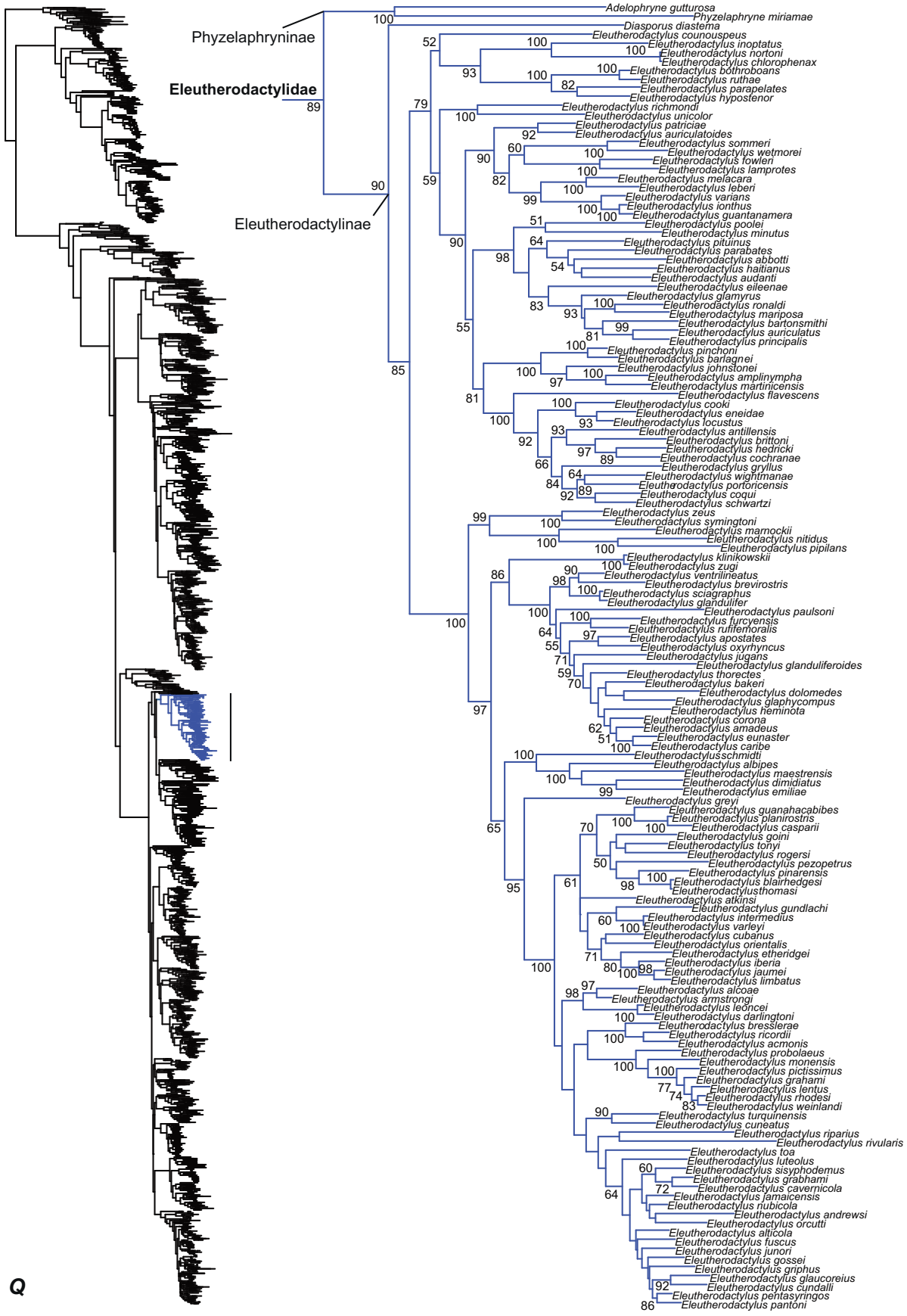


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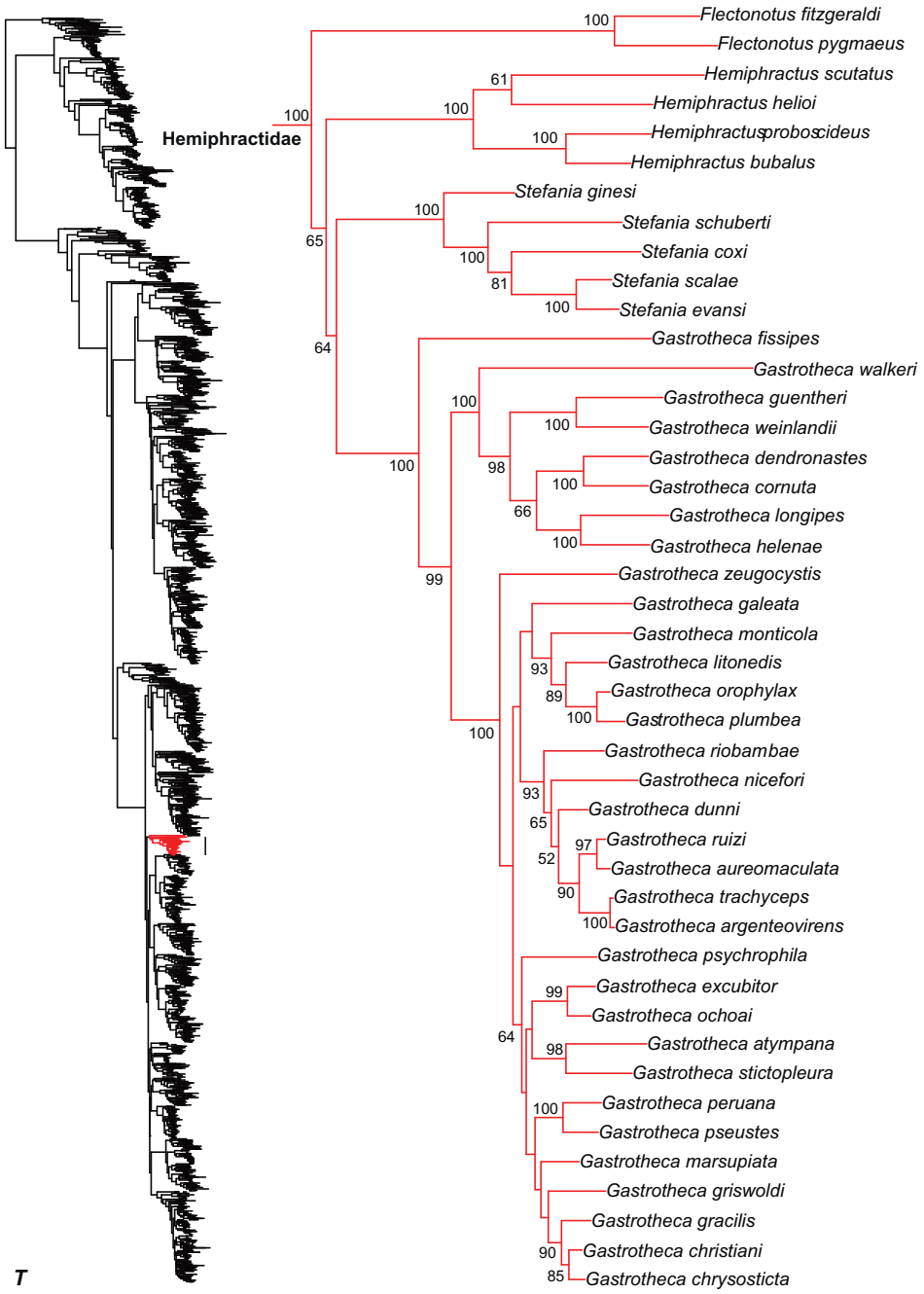


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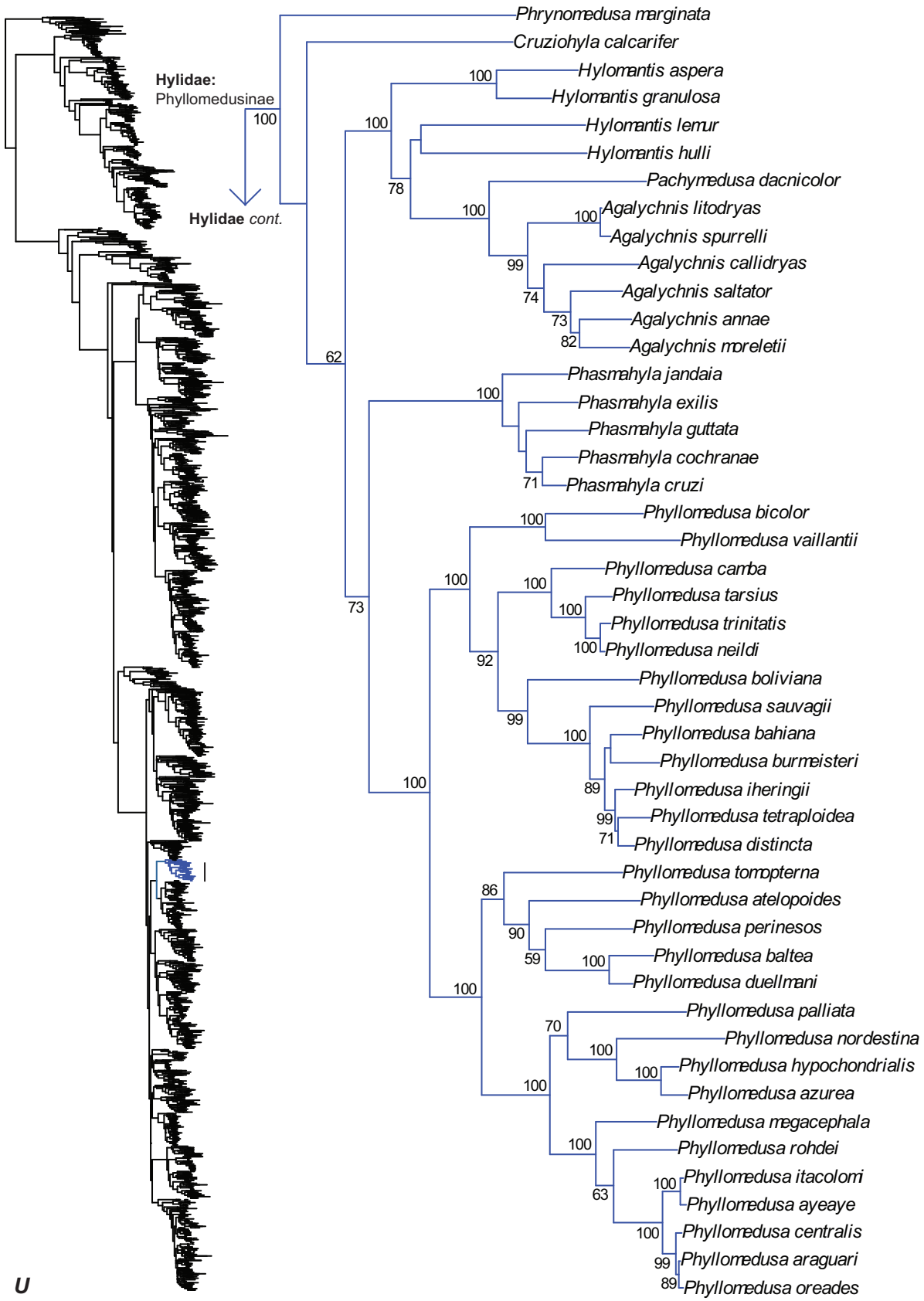
genera interdigitating amongst each other and with Hylodidae. Because relationships amongst these groups are weakly supported, we split these clades into multiple, strongly supported families, rather than recognizing larger, weakly supported families that would possibly be found non-monophyletic in future studies.

The subfamily Ceratophryinae is the sister group to all other members of this clade (Fig. 2Z). Although this placement of the group is weakly supported, monophyly of Ceratophryinae is well supported. We restrict the family Ceratophryidae to include only this subfamily. Within the sister group to ceratophryids is a strongly supported clade (BS = 100%) that includes the cyclorhamphid alsodine genera *Macrogenioglottus*, *Odontophrynus*, and *Proceratophrys*. This clade is here named Odontophrynidae, corresponding to the former telmatobiine leptodactylid tribe Odontophrynini (Lynch, 1971). Within the larger sister-group of Odontophrynidae is a weakly supported clade comprising the genera *Insuetophrynus*, *Rhinoderma*, *Batrachyla* (*B. leptopus*), *Atelognathus*, and *Telmatobius*. Within this clade, the cycloramphid genera *Insuetophrynus* and *Rhinoderma* are strongly supported as sister taxa, for which we resurrect the family Rhinodermatidae (Günther, 1858). This family was widely recognized prior to revision by Frost et al. (2006), but containing only *Rhinoderma* (e.g., Duellman and Trueb, 1994).

The sister group to Rhinodermatidae (Fig. 2Z) is a strongly supported clade consisting of *Atelognathus* and *Batrachyla leptopus* (type species of the genus; ASW), a clade corresponding primarily to the ceratophryid subfamily Batrachylinae. We recognize this clade as a distinct family (Batrachylidae). The other two *Batrachyla*

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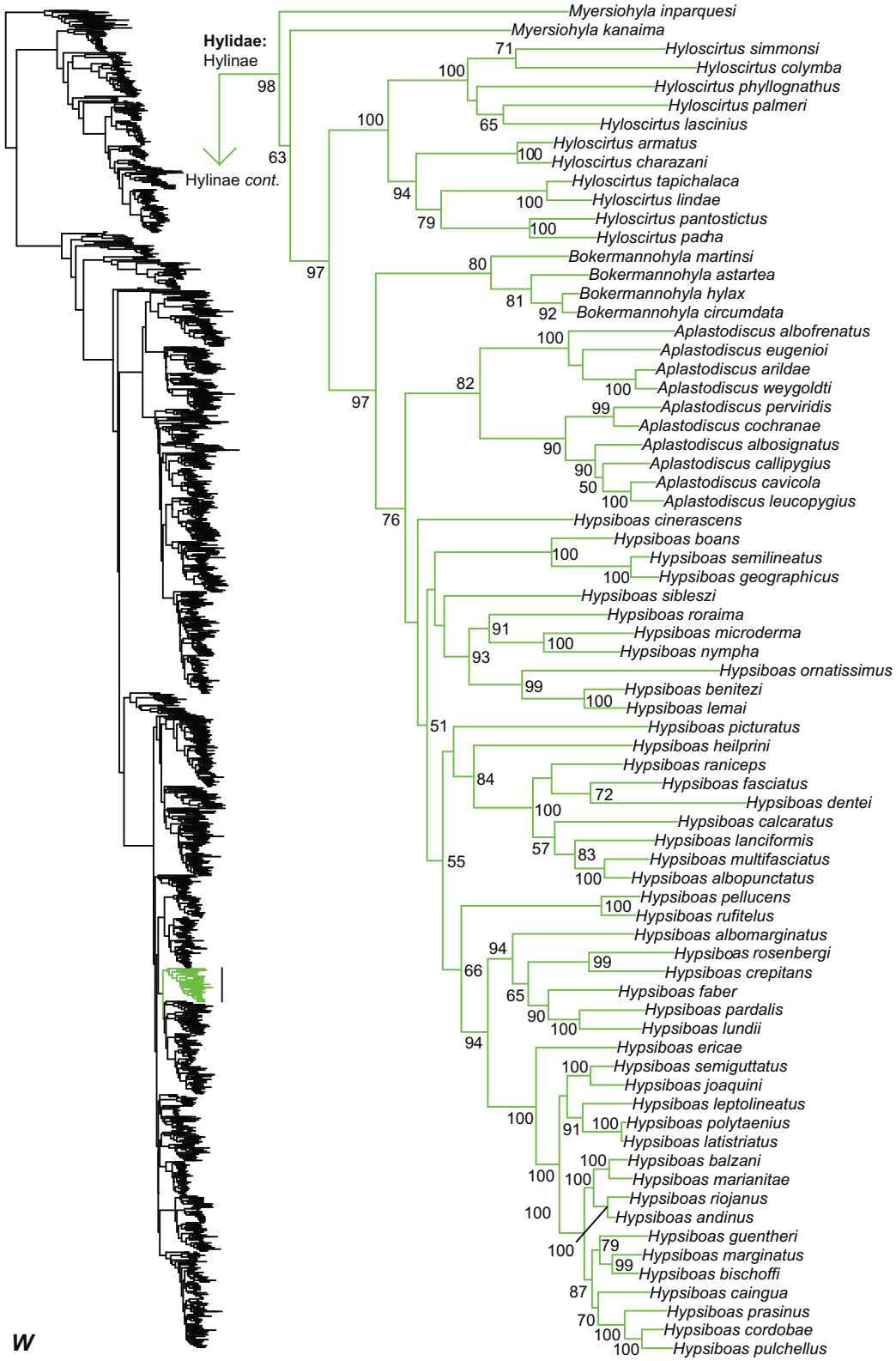


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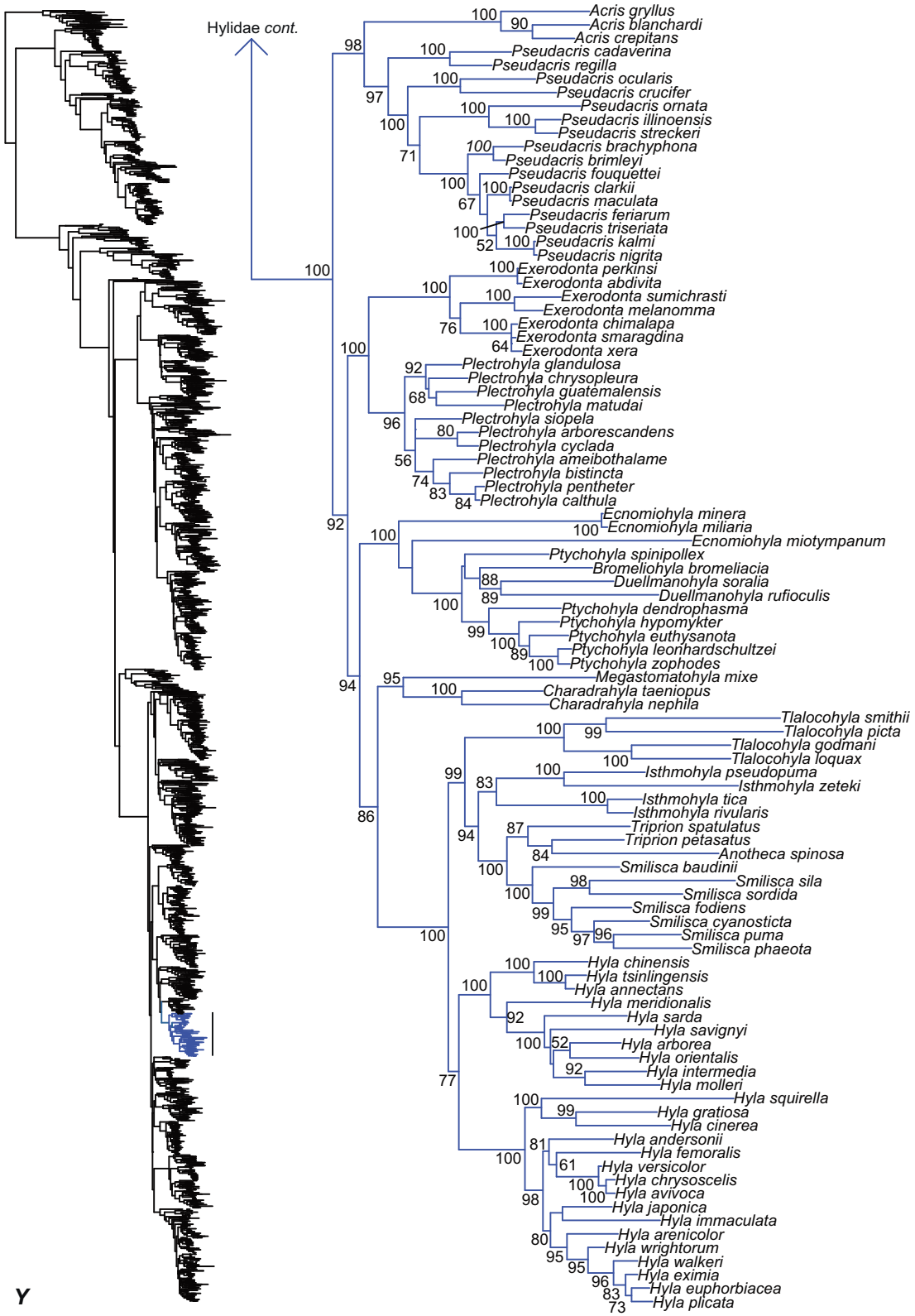
species included in our analysis are placed in a clade with *Alsodes*, *Eupsophus*, and *Hylorina* (see below). The sister group to the clade of Rhinodermatidae + Batrachylidae is the ceratophryid genus *Telmatobius* (Fig. 2Z). We resurrect the family Telmatobiidae (Miranda-Ribeiro, 1920) for this strongly supported clade (containing only *Telmatobius*, which likely contains *Batrachophrynus*; ASW), which was previously recognized as a ceratophryid subfamily (Telmatobiinae) by ASW and AW. Next up the tree is a moderately well supported clade (BS = 79%) consisting of two cycloramphid genera, the cycloramphine genus *Cycloramphus* and the alsodine genus *Thoropa*. We recognize this clade as the family Cycloramphidae (a greatly restricted version relative to current classifications).


**Fig. 2** (*continued*)

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The sister group to Cycloramphidae consists of Hylodidae (strongly supported as monophyletic), and a clade consisting of some of the former alsodine cycloramphid genera (*Alsodes*, *Eupsophus*, *Hylorina*, *Limnomedusa*) and two species of the ceratophryid genus *Batrachyla*. Support for the monophyly of this group is relatively weak (54%) including *Limnomedusa* but is strong (91%) without it. We tentatively recognize this clade as a distinct family (Alsodidae), comprising *Alsodes*, *Eupsophus*, *Hylorina*, and *Limnomedusa*. This is the only family that we recognize (that was not included in previous classifications) that is not strongly supported, but we prefer this taxonomy as opposed to recognizing a monotypic family containing only *Limnomedusa*. While we generally

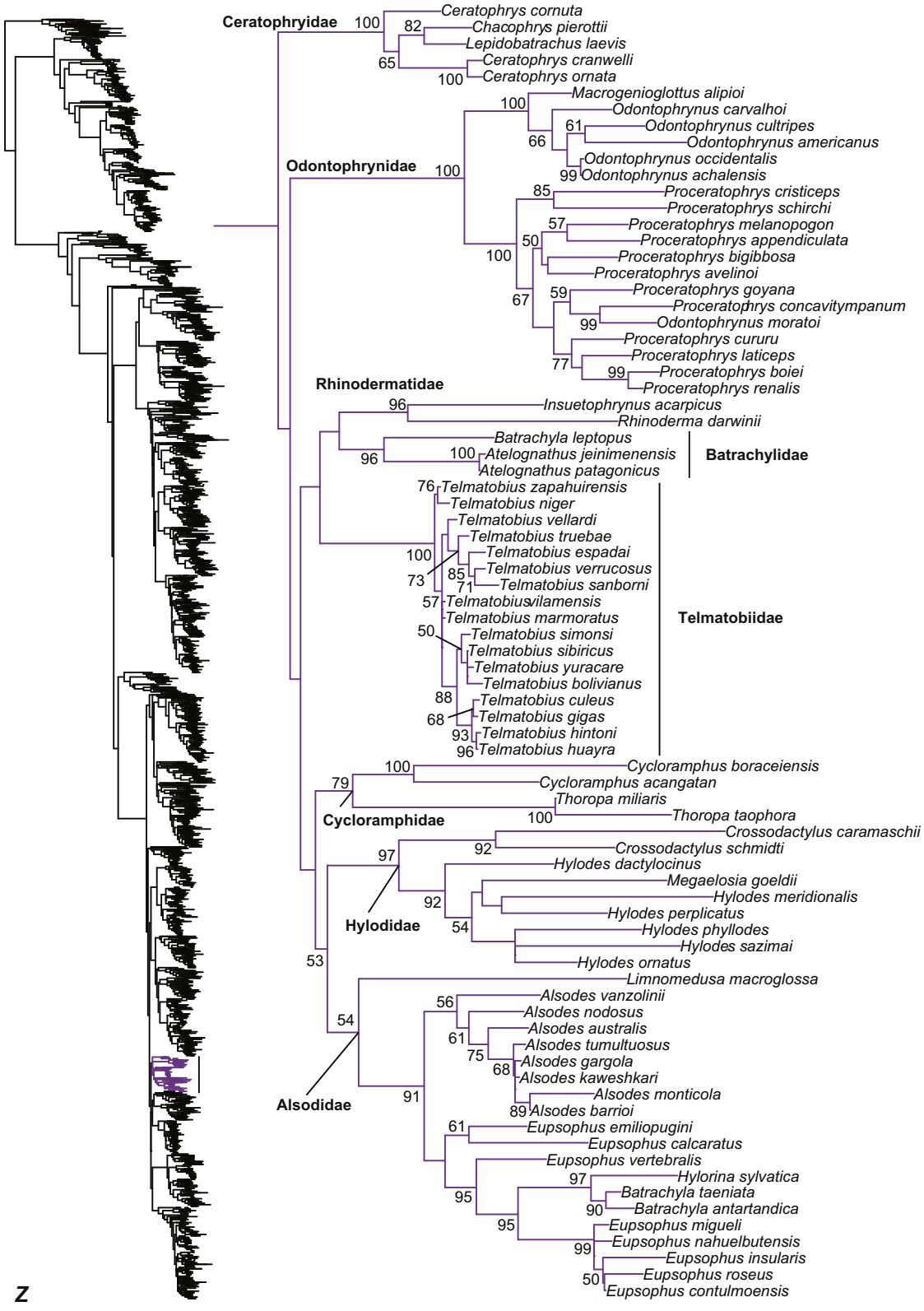
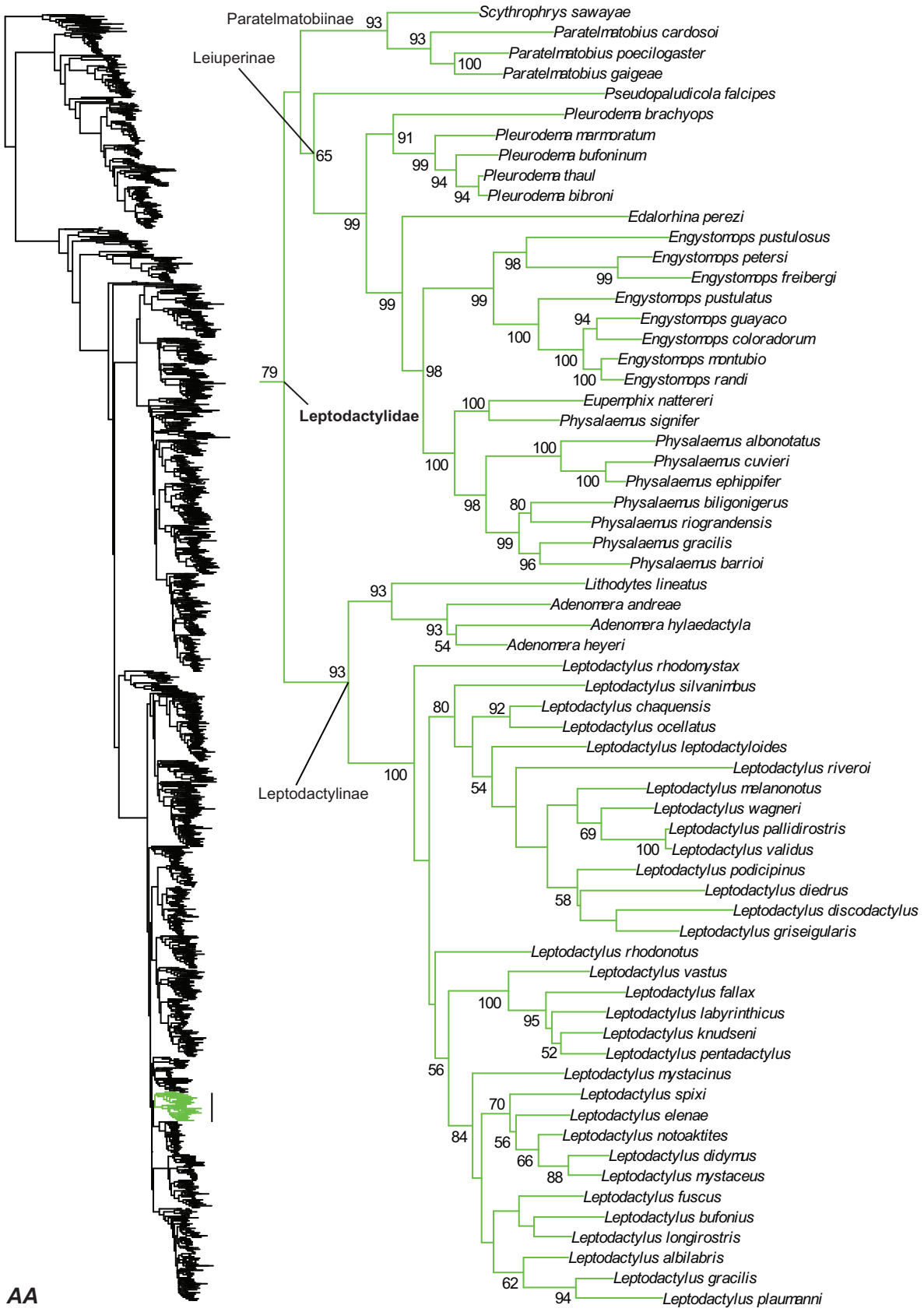



**Fig. 2** (*continued*)

refrain from addressing generic-level taxonomy here, the genus *Batrachyla* represents a special case, being split between two families. As *Batrachyla taeniata*, *Batrachyla antartandica*, and *Hylorina sylvatica* are strongly placed within *Eupsophus*, we synonymize those three species with *Eupsophus*. We keep the other two *Batrachyla* species (*Batrachyla fitzroya* and *Batrachyla nibaldoi*) in *Batrachyla* with the type species *B. leptopus* in Batrachylidae.

In summary, our new taxonomy replaces the non-monophyletic interdigitating families Ceratophryidae and Cycloramphidae with a somewhat larger set of families that are each generally strongly

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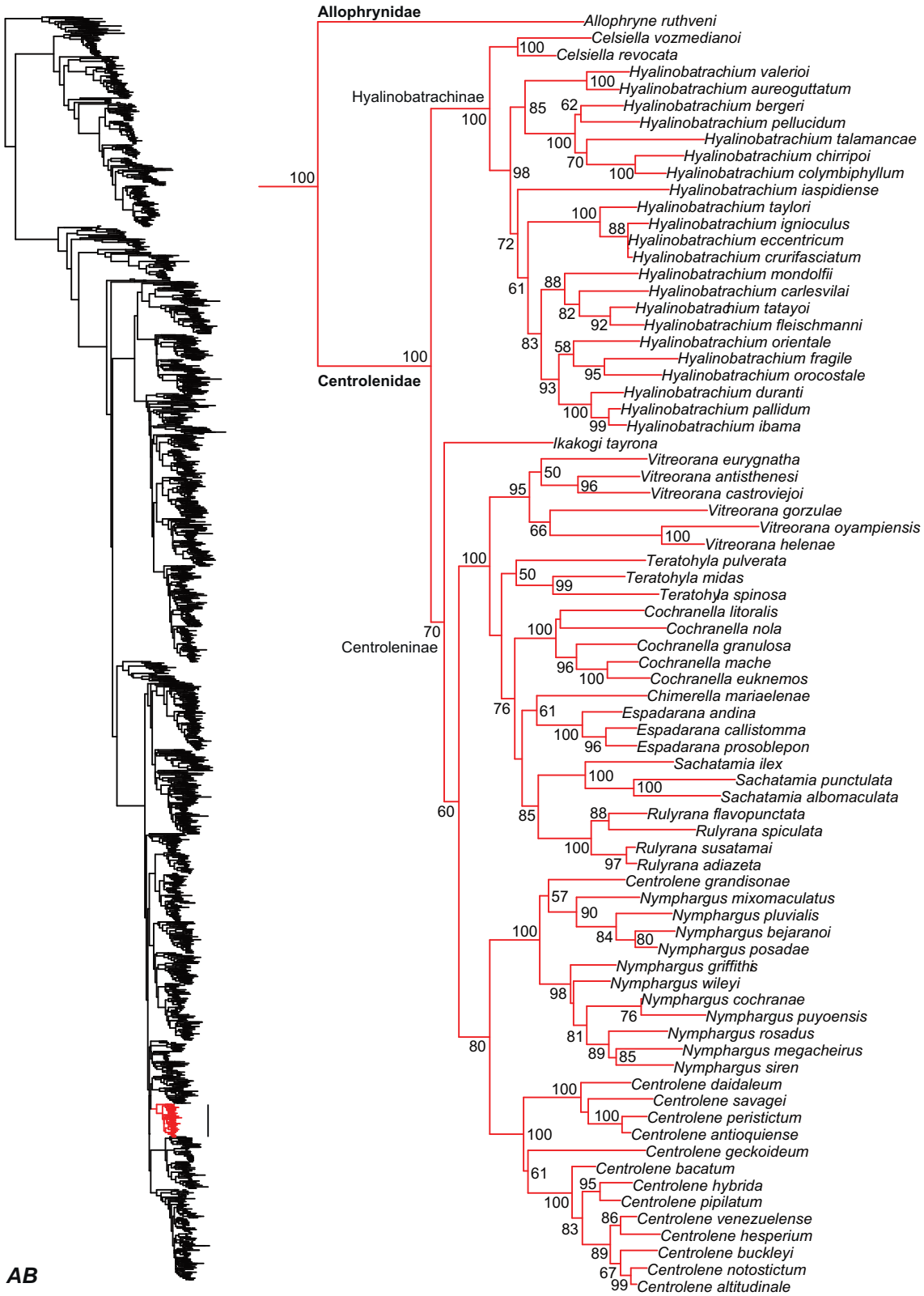


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supported. However, we acknowledge that the family-level placement of the cycloramphid genera *Rupirana* (no subfamily assigned by AW or ASW), *Zachaenus*, and *Crossodactylodes* (both previously Cycloramphinae; AW; ASW) are uncertain in our classification (Hyloidea *incertae sedis*), given the lack of molecular data for these genera and the apparent problems in the previous taxonomy (Figs. 1 and 2Z). Assuming that they are cycloramphids as the family is defined here (Figs. 1 and 2; Appendix B) may be incorrect.

We also find that the currently recognized families Leiuperidae and Leptodactylidae are also problematic (Fig. 2AA). Our results


**Fig. 2** (*continued*)


**Fig. 2** (*continued*)


**Fig. 2** (*continued*)

(Fig. 2AA) show that Leptodactylidae is paraphyletic with respect to Leiuperidae, given that the leptodactylid genera *Paratelmatobius* and *Scythrophrys* are more closely related to leiuperids than they are to other leptodactylids (although this is not strongly supported). We solve this taxonomic problem by expanding Leptodactylidae to again include all leiuperid genera, and recognizing Leiuperinae and Leptodactylinae as subfamilies. This arrangement treats Leptodactylidae as the strongly supported clade (BS = 79%) of mostly foam-nesting frogs that has long been recognized as behaviorally and morphologically distinctive (as the leptodactyline leptodactylids; Lynch, 1971; Duellman and Trueb, 1994). We consider this preferable to recognizing a new family for *Paratelmatobius* and *Scythrophrys*, genera for which we recognize a new subfamily (Paratelmatobiinae *subfam. nov.*; Appendix A), to avoid a paraphyletic Leptodactylinae.

According to our results, the family Strabomantidae (sensu AW, ASW) is also paraphyletic (Fig. 2R). Strabomantidae is a recently described family (Hedges et al., 2008) that includes many species that were traditionally classified as *Eleutherodactylus* (in the family Leptodactylidae; see ASW). Specifically, we find that the strabomantid genera *Hypodactylus* and *Strabomantis* are more closely related to craugastorids (*Haddadus*, *Craugastor*) than they are to the other sampled strabomantid genera (e.g., *Barycholos*, *Bryophryne*, *Holoaden*, *Lynchius*, *Noblella*, *Oreobates*, *Phrynopus*, *Pristimantis*, *Psychrophrynella*). To resolve this problem (and to reduce the proliferation of terraranan families), we subsume Strabomantidae into Craugastoridae, given that Craugastoridae occurs first in Hedges et al. (2008), though we recognize that this is an arbitrary criterion. Within Craugastoridae, we recognize a subfamily Craugastorinae (Fig. 2R) that corresponds to the previously recognized family (e.g., Hedges et al., 2008; AW, ASW).

The former members of Strabomantidae are apportioned among three strongly supported clades (which we recognize as subfamilies within Craugastoridae) and one weakly supported clade (which we consider *incertae sedis*). One of the strongly supported clades consists solely of the genus *Strabomantis*, for which we recognize a restricted subfamily Strabomantinae (Appendix B). Another comprises the genera *Barycholos*, *Bryophryne*, *Holoaden*, *Noblella*, and *Psychrophrynella*, for which we use the previously recognized subfamily Holoadeninae (e.g., ASW). The third strongly supported clade comprises the genera *Lynchius*, *Oreobates*, *Phrynopus*, and *Pristimantis*. We recognize this clade as a new subfamily, Pristimantinae *subfam. nov.* (see Appendix A for formal definition). The weakly supported clade is the genus *Hypodactylus*. Rather than recognizing a new subfamily for this genus (or allowing it to render other subfamilies non-monophyletic), we consider this genus *incertae sedis*, along with several other genera of the former Strabomantidae that were not included in this (or other molecular phylogenies), including *Atopophrynus*, *Dischiodactylus*, *Geobatrachus, Mucubatrachus, Niceforonia,* and *Paramophrynella*. In theory, some of these closely related subfamilies could be combined (e.g., Craugastorinae and Strabomantinae or Holoadeninae and Pristimantinae), but the resulting subfamilies would then not be strongly supported.

As in most previous studies (Darst and Cannatella, 2004; Roelants et al., 2007; Wiens, 2007a, 2011), we find strong support for monophyly of Hyloidea, but relationships among the families are weakly supported (Figs. 1 and 2P-AE). Therefore, we do not present extensive comparison of among-family relationships between our study and previous studies. Nevertheless, there are some intriguing patterns that occur in multiple studies, such as placement of bufonids with dendrobatids (e.g., this study, Frost et al., 2006; Roelants et al., 2007; Wiens, 2011). We also corroborate the monophyly and current composition of Brachycephalidae (Hedges et al., 2008), Hemiphractidae (Wiens et al., 2007a,b; Wiens, 2011), Hylidae (with subfamilies Hylinae, Phyllomedusinae, and Pelodryadinae; Wiens et al., 2010), Bufonidae (Pramuk et al., 2008; Van Bocxlaer et al., 2009), Allophrynidae and Centrolenidae. Within Centrolenidae (Fig. 2AB), we support the subfamilies Centroleninae and Hyalinobatrachinae, and we place the previously *incertae sedis* genus *Ikakogi* in Centroleninae with strong (70%) bootstrap support. We do not recognize a family Aromobatidae separate from Dendrobatidae, as there is no phylogenetic justification for splitting Dendrobatidae (Fig. 2AC). We follow Santos et al. (2009) in recognizing a single family Dendrobatidae, including the former aromobatids and containing no subfamilies (see also AW).

Our higher-level phylogeny within Ranoidea is generally similar to other recent estimates (e.g., Frost et al., 2006; Roelants et al., 2007; Wiens, 2011), and many of these relationships are well supported in our study and previous studies (e.g., among brevicipitids, hemisotids, microhylids, hyperoliids, arthroleptids). Our results also support current delimitation of subfamilies (Figs. 1 and 2H–I; see Appendix B) in Microhylidae (van der Meijden et al., 2007) and Arthroleptidae (including Astylosterninae; see ASW). Some previous taxonomies (e.g., Bossuyt et al., 2006; Wiens et al., 2009) and current taxonomies (including AW) recognize a large (>1400 species) family Ranidae (with 13 subfamilies) as the sister group to all other ranoids. Other recent authors have considered these subfamilies distinct families (Bossuyt and Roelants, 2009; Frost et al., 2006; Roelants et al., 2007). We follow this latter arrangement here, recognizing the families Ptychadenidae, Micrixalidae, Phrynobatrachidae, Conrauidae, Petropedetidae, Pyxicephalidae, Nyctibatrachidae, Ceratobatrachidae, Ranixalidae, Dicroglossidae, Ranidae, and Rhacophoridae, and Mantellidae, all of which are strongly supported (Figs. 1 and 2J–O). Within these families, subfamilies follow Frost (2011): within Pyxicephalidae, we recognize Cacosterninae and Pyxicephalinae; Dicroglossidae comprises Occidozyginae and Dicroglossinae; Rhacophoridae consists of Buergeriinae and Rhacophorinae; and Mantellidae is composed of Laliostominae, Boophinae, and Mantellinae (Figs. 1 and 2J–O). Relationships among many of these families remain poorly supported, as in previous studies (Roelants et al., 2007; Wiens et al., 2009). Given the extensive sampling of taxa in this clade, resolving their relationships may instead require adding many more characters (i.e., more genes).

## 4. Discussion

### 4.1. Systematics of extant lissamphibians

Here, we provide a large-scale estimate of amphibian phylogeny, containing over 2800 species (42% of the known extant diversity). This phylogeny is largely congruent with those of several recent molecular analyses (Frost et al., 2006; Roelants et al., 2007; Wiens, 2007a, 2011). Nevertheless, our increased sampling of taxa and characters (especially among former leptodactylid frogs) reveals that several currently recognized families are not monophyletic as currently delimited (i.e., Ceratophryidae, Cycloramphidae, Leptodactylidae, Strabomantidae). To correct these problems, we present a new classification of extant amphibians. We have been as conservative as possible in our taxonomic changes, such that deviations from current taxonomy are made only when necessitated by non-monophyly of higher taxa, and in such a way that newly recognized taxa are strongly supported (with the exception of Alsodidae as described above). It is possible that future phylogenies might reveal some of our changes to be unnecessary (e.g., in cases where there was weak support for non-monophyly of families, future analyses might strongly resolve them as monophyletic). However, by focusing on only strongly supported clades, the higher taxa that we recognize should not be misleading, even as new data are added. We are also conservative in that we only address taxonomy at the subfamily level and above, given that our sampling of genera is mostly complete whereas our sampling of species is not. Nevertheless, our study

corroborates previous studies showing the paraphyly of numerous genera (e.g., *Bufo, Rana*) and shows many additional genera to be non-monophyletic (e.g., *Batrachyla*). Importantly, our study also provides a framework to which additional sequences can be readily added. Our data matrix is available at Dryad repository doi:10.5061/dryad.vd0m7. It should thus be relatively straightforward to add more taxa to this tree.

### 4.2. Supermatrices and large-scale phylogenetic inference

This analysis corroborates several recent studies suggesting that the supermatrix approach is a powerful strategy for large-scale phylogenetic inference (e.g., Driskell et al., 2004; McMahon and Sanderson, 2006; Thomson and Shaffer, 2010; Pyron et al., 2011; Wiens et al., 2005b). For example, even though each taxon had (on average) 80% missing data, we found that most species were placed in the families and genera expected based on previous taxonomy, often with very strong support. In cases where we found that currently recognized families were not monophyletic, this was not due to species being randomly placed on the tree, but rather due to differences in the placement of strongly supported clades of species and genera. Moreover, all of our 67 families and all but two of the 50 subfamilies are strongly supported.

Despite the overall strong support for most of the tree (i.e., 64% of all nodes have BS >70), certain clades remain poorly supported. Therefore, a potential criticism of the supermatrix approach is that this poor support may have arisen due to missing data in many taxa. However, several lines of evidence suggest that this is not the case. First, many previous studies have shown that there is typically little relationship between the support for clades and the amount of missing data in the included species (e.g., Pyron et al., 2011; Wiens et al., 2005b, and for an analysis of multiple datasets see Wiens and Morrill, 2011). Second, we find that most of the clades that are weakly supported in our study are also weakly supported in other studies that have more limited missing data (and the same is true for strongly supported clades). For example, in their study of extant amphibian phylogeny based on multiple nuclear and mitochondrial genes (with little missing data), Roelants et al. (2007) showed weak support for relationships among hyloid families, microhylid subfamilies, and the families of former ranids, but strong support for relationships among the major clades of frogs, salamanders, and caecilians. These same patterns of weak and strong support appear in our study (Fig. 1). Previous studies suggest that these patterns of support are more likely to reflect underlying branch lengths, such as weak support for short branches (Wiens et al., 2008), rather than impacts of missing data.

Our results and those of other studies suggest that extensive missing data need not be an impediment to constructing large-scale phylogenies with the supermatrix approach. Nevertheless, one aspect of our sampling design may have greatly facilitated the integration of the different genes used in this study. Specifically, 90% of the species had sequence data for the 16S gene and 81% had data for 12S. Thus, most species had comparable data for at least one gene, which may have greatly facilitated placing them on the tree with only a limited amount of character data (Wiens et al., 2005b). Although it is possible to reconstruct a phylogeny when missing and non-missing data are randomly distributed among characters, the number of genes and characters required to obtain accurate phylogenies may be much higher than when the non-missing data are all in the same characters (e.g., Wiens, 2003). A clear lesson for future studies is that adding taxa to this large-scale phylogeny will be greatly facilitated if researchers include these same 12S and 16S genes, along with widely sampled nuclear genes such as RAG-1. Increasing sampling of the other nuclear genes may be advantageous as well.

## Acknowledgments

We thank the many researchers who made this study possible through their detailed studies of amphibian phylogeny with a (mostly) shared set of molecular markers, and uploading their sequence data to GenBank. We would like to thank F.T. Burbrink (CUNY-CSI), J. Lombardo (CUNY-CSI), and T.J. Guiher (CUNY-CSI) for computational assistance, and D.R. Frost (AMNH) and A.M. Bauer (Villanova) for advice on taxonomy. This research was supported in part by US National Science Foundation grants to R.A.P. (DBI-0905765), J.J.W. (EF 0334923), and the CUNY HPCC (CNS-0958379 and CNS-0855217). We would like to thank A. Larson, and two anonymous reviewers for helpful comments that substantially improved this manuscript.

## Appendix A. Description of new subfamilies

Pristimantinae *subfam. nov.* (family Craugastoridae)
*Type:* genus and species *Pristimantis galdi* Jiménez de la Espada, 1870.
*Content:* four genera, >465 species; *Lynchius, Oreobates, Phrynopus, Pristimantis.*
*Phylogenetic Definition:* this subfamily consists of the most recent common ancestor of *Lynchius, Oreobates, Phrynopus,* and *Pristimantis*, and all descendants thereof.
*Distribution:* these frogs are primarily restricted to the Andes and Amazon Basin of South America (Hedges et al., 2008).
*Remarks:* The four genera of this subfamily are grouped with strong support (81% BS proportion; Fig. 2R), and we find weak support for their placement as the sister group to Holoadeninae (Fig. 2R).

Paratelmatobiinae *subfam. nov.* (family Leptodactylidae)
*Type:* genus and species *Paratelmatobius lutzii* Lutz and Carvalho 1958.
*Content:* two genera, eight species; *Paratelmatobius* and *Scythrophrys.*
*Phylogenetic Definition:* this subfamily consists of the most recent common ancestor of *Paratelmatobius* and *Scythrophrys*, and all descendants thereof.
*Distribution:* these frogs are primarily restricted to southern and eastern Brazil (AW; ASW).
*Remarks:* The two genera of this subfamily are grouped with strong support (93% BS proportion), and we find weak support for placing them as the sister group of Leiuperinae (Fig. 2AA).

## Appendix B. Generic content of families and subfamilies

The list below accounts for all extant amphibian genera currently recognized by AW and ASW, with family and subfamily classification updated to reflect our phylogenetic estimate and taxonomic changes. The 72 genera not sampled in our phylogeny are either included in their previously delimited groups (when these were found to be strongly supported), or considered *incertae sedis* (along with any sampled taxa explicitly delimited as such) when their placement was ambiguous due to non-monophyly of previously recognized higher taxa. As noted above, Lissamphibia also contains numerous extinct taxa, including gymnophionans, caudates, and anurans, which are not considered here (Marjanović and Laurin, 2007).

### B.1. Gymnophiona

**Caeciliidae**: *incertae sedis:* (*Atretochoana, Brasilotyphlus, Idiocranium, Indotyphlus, Microcaecilia, Mimosiphonops, Nectocaecilia, Par-*

*vicaecilia, Potomotyphlus, Sylvacaecilia*); Caeciliinae (*Caecilia, Chthonerpeton, Dermophis, Gegeneophis, Geotrypetes, Grandisonia, Gymnopis, Hypogeophis, Luetkenotyphlus, Oscaecilia, Praslinia, Typhlonectes, Schistometopum, Siphonops*), Herpelinae (*Herpele, Boulengerula*), Scolecomorphinae (*Crotaphotrema, Scolecomorphus*); **Ichthyophiidae**: *Caudacaecilia, Ichthyophis, Uraeotyphlus*; **Rhinatrematidae**: *Epicrionops, Rhinatrema.*

*B.2. Caudata*

**Ambystomatidae**: *Ambystoma*; **Amphiumidae**: *Amphiuma*; **Cryptobranchidae**: *Andrias, Cryptobranchus*; **Dicamptodontidae**: *Dicamptodon*; **Hynobiidae**: *Batrachuperus, Hynobius, Liua, Onychodactylus, Pachyhynobius, Paradactylodon, Protohynobius, Pseudohynobius, Ranodon, Salamandrella*; **Plethodontidae**: Bolitoglossinae (*Batrachoseps, Bolitoglossa, Bradytriton, Chiropterotriton, Cryptotriton, Dendrotriton, Ixalotriton, Lineatriton, Nototriton, Nyctanolis, Oedipina, Parvimolge, Pseudoeurycea, Thorius*), Hemidactylinae (*Hemidactylium*), Plethodontinae (*Aneides, Desmognathus, Ensatina, Hydromantes, Karsenia, Phaeognathus, Plethodon*), Spelerpinae (*Eurycea, Gyrinophilus, Haideotriton, Pseudotriton, Stereochilus, Urspelerpes*); **Proteidae**: *Necturus, Proteus*; **Rhyacotritonidae**: *Rhyacotriton*; **Salamandridae**: Pleurodelinae (*Calotriton, Cynops, Echinotriton, Euproctus, Ichthyosaura, Laotriton, Lissotriton, Neurergus, Notophthalmus, Ommatotriton, Pachytriton, Paramesotriton, Pleurodeles, Taricha, Triturus, Tylototriton*), Salamandrinae (*Chioglossa, Lyciasalamandra, Mertensiella, Salamandra*), Salamandrininae (*Salamandrina*); **Sirenidae**: *Siren, Pseudobranchus.*

*B.3. Anura*

*Incertae sedis* in Hyloidea (*Crossodactylodes, Rupirana, Zachaenus*).

**Allophrynidae**: *Allophryne*; **Alsodidae**: *Alsodes, Eupsophus, Limnomedusa*; **Alytidae**: *Alytes*; **Arthroleptidae**: Arthroleptinae (*Athroleptis, Cardioglossa*), Astylosterninae (*Astylosternus, Leptodactylodon, Nyctibates, Scotobleps, Trichobatrachus*), Leptopelinae (*Leptopelis*); **Ascaphidae**: *Ascaphus*; **Batrachylidae**: *Atelognathus, Batrachyla*; **Bombinatoridae**: *Barbaroula, Bombina*; **Brachycephalidae**: *Brachycephalus, Ischnocnema*; **Brevicipitidae**: *Balebreviceps, Breviceps, Callulina, Probreviceps, Spelaeophryne*; **Bufonidae**: *Adenomus, Altiphrynoides, Andinophryne, Ansonia, Atelopus, Bufo, Bufoides, Capensibufo, Churamiti, Crepidophryne, Dendrophryniscus, Didynamipus, Frostius, Laurentophryne, Leptophryne, Melanophryniscus, Mertensophryne, Metaphryniscus, Nectophryne, Nectophrynoides, Nimbaphrynoides, Oreophrynella, Osornophryne, Parapelophryne, Pedostibes, Pelophryne, Pseudobufo, Rhamphophryne, Sabahphrynus, Schismaderma, Spinophrynoides, Stephopaedes, Truebella, Werneria, Wolterstorffina*; **Calyptocephalellidae**: *Calyptocephalella, Telmatobufo*; **Centrolenidae**: Centroleninae (*Centrolene, Chimerella, Cochranella, Espadarana, Ikakogi, Nymphargus, Rulyrana, Sachatamia, Teratohyla, Vitreorana*), Hyalinobatrachinae (*Celsiella, Hyalinobatrachium*); **Ceratobatrachidae**: *Batrachylodes, Ceratobatrachus, Discodeles, Ingerana, Palmatorappia, Platymantis*; **Ceratophryidae**: *Ceratophrys, Chacophrys, Lepidobatrachus*; **Ceuthomantidae**: *Ceuthomantis*; **Conrauidae**: *Conraua*; **Craugastoridae**: *incertae sedis* (*Atopophrynus, Dischiodactylus, Geobatrachus, Hypodactylus, Mucubatrachus, Nicefo roni a, Paramophrynella*), Craugastorinae (*Craugastor, Haddadus*), Holoadeninae (*Barycholos, Bryophryne, Euparkerella, Holoaden, Noblella, Psychrophrynella*), Pristimantinae (*Lynchius, Oreobates, Phrynopus, Pristimantis*), Strabomantinae (*Strabomantis*); **Cycloramphidae**: *Cycloramphus, Thoropa*; **Dendrobatidae**: *Allobates, Ameerega, Anomaloglossus, Aromobates, Colostethus, Dendrobates, Epipedobates, Hyloxalus, Mannophryne, Phyllobates, Rheobates, Silverstoneia*; **Dicroglossidae**: Dicroglossinae (*Chaparana, Chirixalus, Euphlyctis, Fejervarya, Hoplobatrachus, Limnonectes, Nannophrys, Nanorana, Paa, Sphaerotheca*), Occidozyginae (*Ingerana, Occidozyga*); **Discoglossidae**: *Discoglossus*; **Eleutherodactylidae**: Eleutherodactylinae (*Diasporus, Eleutherodactylus*), Phyzelaphryninae (*Adelophryne, Phyzelaphryne*); **Heleophrynidae**: *Hadromophryne, Heleophryne*; **Hemiphractidae**: *Cryptobatrachus, Flectonotus, Gastrotheca, Hemiphractus, Stefania*; **Hemisotidae**: *Hemisus*; **Hylidae**: Hylinae (*Acris, Anotheca, Aparasphenodon, Aplastodiscus, Argenteohyla, Bokermannohyla, Bromeliohyla, Charadrahyla, Corythomantis, Dendropsophus, Diaglena, Duellmanohyla, Ecnomiohyla, Exerodonta, Hyla, Hyloscirtus, Hypsiboas, Isthmohyla, Itapotihyla, Megastomatohyla, Myersiohyla, Nyctimantis, Osteocephalus, Osteopilus, Phyllodytes, Plectrohyla, Pseudacris, Pseudis, Ptychohyla, Scarthyla, Scinax, Smilisca, Sphaenorhynchus, Tepuihyla, Tlalocohyla, Trachycephalus, Triprion, Xenohyla*), Pelodryadinae (*Litoria*), Phyllomedusinae (*Agalychnis, Cruziohyla, Hylomantis, Pachymedusa, Phasmahyla, Phrynomedusa, Phyllomedusa*); **Hylodidae**: *Crossodactylus, Hylodes, Megaelosia*; **Hyperoliidae**: *Acanthixalus, Afrixalus, Alexteroon, Arlequinus, Callixalus, Chlorolius, Chrysobatrachus, Cryptothylax, Heterixalus, Hyperolius, Kassina, Kassinula, Morerella, Opisthothylax, Paracassina, Phlyctimantis, Semnodactylus, Tachycnemis*; **Leiopelmatidae**: *Leiopelma*; **Leptodactylidae**: Leptodactylinae (*Adenomera, Hydrolaetere, Leptodactylus, Lithodytes*), Leiuperinae (*Edalorhina, Engystomops, Eupemphix, Physalaemus, Pleurodema, Pseudopaludicola, Somuncuria*), Paratelmatobiinae (*Paratelmatobius, Scythrophrys*); **Mantellidae**: Boophinae (*Boophis*), Laliostominae (*Aglyptodactylus, Laliostoma*), Mantellinae (*Blommersia, Boehmantis, Gephyromantis, Guibemantis, Mantella, Mantidactylus, Spinomantis, Tsingymantis, Wakea*); **Megophryidae**: *Borneophrys, Brachytarsophrys, Leptobrachella, Leptobrachium, Leptolalax, Megophrys, Ophryophryne, Oreolalax, Scutiger, Vibrissaphora, Xenophrys*; **Micrixalidae**: *Micrixalus*; **Microhylidae**: *incertae sedis* (*Gastrophrynoides, Paramophrynella*), Asterophryninae (*Albericus, Aphantophryne, Asterophrys, Austrochaperina, Barygenys, Callulops, Choerophryne, Cophixalus, Copiula, Genyophryne, Hylophorbus, Liophryne, Mantophryne, Oreophryne, Oxydactyla, Pherohapsis, Sphenophryne, Xenorhina*), Cophylinae (*Anodonthyla, Cophyla, Madecassophryne, Platypelis, Plethodontohyla, Rhombophryne, Stumpffia*), Dyscophinae (*Dyscophus*), Gastrophryninae (*Adelastes, Altigius, Arcovomer, Chiasmocleis, Ctenophryne, Dasypops, Dermatonotus, Elachistocleis, Gastrophryne, Hamptophryne, Hyophryne, Hypopachus, Melanophryne, Myersiella, Nelsonophryne, Relictivomer, Stereocyclops, Syncope*), Hoplophryninae (*Hoplophryne, Parhoplophryne*), Kalophryninae (*Kalophrynus*), Melanobatrachinae (*Melanobatrachus*), Microhylinae (*Calluella, Chaperina, Glyphoglossus, Kaloula, Metaphrynella, Microhyla, Micryletta, Ramanella, Uperodon*), Otophryninae (*Otophryne, Synapturanus*), Phrynomerinae (*Phrynomantis*), Scaphiophryne (*Paradoxophyla, Scaphiophryne*); **Myobatrachidae**: Limnodynastinae (*Adelotus, Heleioporus, Lechriodus, Limnodynastes, Mixophyes, Neobatrachus, Notaden, Philoria, Platyplectrum, Pseudophryne*), Myobatrachinae (*Arenophryne, Assa, Crinia, Geocrinia, Metacrinia, Myobatrachus, Paracrinia, Rheobatrachus, Spicospina, Taudactylus, Uperoleia*); **Nasikabatrachidae**: *Nasikabatrachus*; **Nyctibatrachidae**: *Lankanectes, Nyctibatrachus*; **Odontophrynidae**: *Macrogenioglottus, Odontophrynus, Proceratophrys*; **Pelobatidae**: *Pelobates*; **Pelodytidae**: *Pelodytes*; **Petropedetidae**: *Petropedetes*; **Phrynobatrachidae**: *Phrynobatrachus*; **Pipidae**: *Hymenochirus, Pipa, Pseudhymenochirus, Silurana, Xenopus*; **Ptychadenidae**: *Hildebrandtia, Lanzarana, Ptychadena*; **Pyxicephalidae**: Cacosterninae (*Amietia, Anhydrophryne, Arthroleptella, Cacosternum, Ericabatrachus, Microbatrachella, Natalobatrachus, Nothophryne, Poyntonia, Strongylopus, Tomopterna*), Pyxicephalinae (*Aubria, Pyxicephalus*); **Ranidae**: *Amnirana, Amolops, Huia, Hylarana, Meristogenys, Odorrana, Pseudoamolops, Pterorana, Rana, Staurois*; **Ranixalidae**: *Indirana*; **Rhacophoridae**: Buergeriinae (*Buergeria*), Rhacophorinae (*Chiromantis, Dendrobatorana, Feihyla, Ghatixalus, Gracixalus, Kurixalus, Liuixalus, Nyctixalus, Philautus, Polypedates, Rhacophorus, Theloderma*), **Rhinodermatidae**: *Insuetophrynus,*

*Rhinoderma*; **Rhinophrynidae**: *Rhinophrynus*; **Scaphiopodidae**: *Scaphiopus, Spea*; **Sooglossidae**: *Sechellophryne, Sooglossus*; **Telmatobiidae**: *Batrachophrynus, Telmatobius.*

## Appendix C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.06.012.

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