

Monograph



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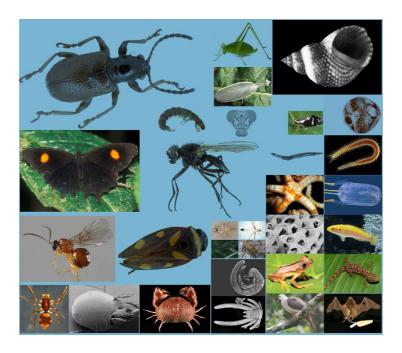


Animal biodiversity:

An outline of higher-level classification and survey of taxonomic richness

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Amphibia incertae sedis

†Albanerpetontidae Fox & Naylor, 1982 (†4)^{4,5}

Order Anura Fischer von Waldheim, 1813 (frogs and toads) (410–466 genera; 6090 species; †~84)⁶

Family Allophrynidae Goin, Goin, & Zug, 1978 (1 genus; 1 species)⁷

Family Alsodidae Mivart, 1869 (3 genera; 32 species)⁸

- 3. Linnaeus (1758) used Amphibia for a different assemblage of taxa than currently recognized, and authorship for the currently understood taxon is either de Blainville, 1816 (Dubois, 2004) or Gray, 1825. Frost et al. (2006) detail reasons for rejecting de Blainville as the authority. Phylogenetic analyses based on molecular data for extant taxa support the monophyly of a clade containing Anura, Caudata, and Gymnophiona (e.g., Zardoya & Meyer, 2001; San Mauro et al., 2005). Phylogenetic analyses of morphological characters, including from a wide-range of extinct taxa, support this clade, with the extinct family Albanerpetontidae included in the crown group (e.g., Sigurdsen & Green, 2011; Ruta et al., 2003; Laurin & Reisz, 1997; Trueb & Cloutier, 1991b). However, some morphology-based analyses support non-monophyly of extant amphibians by placing the Gymnophiona more closely to extant amniotes (e.g., Anderson, 2008; Anderson et al., 2008; but see Marjanović & Laurin, 2008, 2009) than to Anura and Caudata. Often the clade comprising extant amphibians has been referred to as Lissamphibia (Parsons & Williams, 1963; Romer, 1966; Duellman & Trueb, 1986; Bolt, 1991; Trueb & Cloutier, 1991a,b; see also Frost et al., 2006), but we note that this view is not universally held (Dubois, 1983, 2004). We refer to the most exclusive clade containing crown-group amphibians as Class Amphibia, although we recognize that Amphibia is also often applied to extinct tetrapod taxa that are included neither within extant amniotes nor extant amphibians.
- 4. Throughout the manuscript the numbers of genera inclusive of extinct taxa, are listed, followed by the number of extinct (†) genera.
- 5. Historically, the †Albanerpetontidae has been allied to the extant orders of amphibians (Fox & Naylor, 1982; Milner, 2000; McGowan, 2002). Phylogenetic analyses have reaffirmed a close relationship between †Albanerpetontidae, comprising four extinct genera (for recent summary see Sweetman & Gardner, in press), and the extant orders Anura and Caudata, although the precise relationships remain uncertain (Anderson *et al.*, 2008; Ruta *et al.*, 2003).
- 6. Many extinct anuran generic-level taxa exist, but most cannot be assigned with confidence to the families recognized here. A few are demonstrably outside of crown-group Anura (e.g., †*Czatkobatrachus*, †*Mesophryne*, †*Notobatrachus*, †*Prosalirus*, †*Triadobatrachus*, †*Vieraella*, †*Yizhoubatrachus*; Báez & Basso, 1996; Gao & Wang, 1998; Gao & Chen, 2004). When phylogenetic analyses or other evidence allow placement of an extinct genus with some confidence within the crown-group of a family of living species, we have opted to include that extinct taxon within that family. However, because of either a lack of thorough analyses or changing concepts of families, we cannot place many of these extinct taxa within currently recognized families. These extinct taxa include †*Altanulia*, †*Aralobatrachus*, †*Arariphrynus*, †*Avitabatrachus*, †*Aygroua*, †*Comobatrachus*, †*Cordicephalus*, †*Cratia*, †*Elkobatrachus*, †*Eobatrachus*, †*Eopelobates*, †*Eoprhactus*, †*Eorubeta*, †*Estesiella*, †*Estesina*, †*Estesius*, †*Eurycephalella*, †*Hatzegobatrachus*, †*Itemirella*, †*Kizylkuma*, †*Latonia*, †*Liaobatrachus*, †*Liitobatrachus*, †*Liitobatrachus*, †*Itiobatrachus*, †*Polaeophrynos*, †*Paralatonia*, †*Pelophilus*, †*Polaeophrynos*, †*Paralatonia*, †*Pelophilus*, †*Pliobatrachus*, †*Proceratobatrachus*, †*Ranomorphus*, †*Ranavus*, †*Soevesoederberghia*, †*Sunnybatrachus*, †*Thaumastosaurus*, †*Theatonius*, †*Thoraciliacus*, and †*Uldzinia*; see Sanchíz (1998) for a review of most extinct anuran taxa.
- 7. Frost *et al.* (2006), avoiding families with only one genus, treated Allophryninae and Centroleninae as subfamilies of Centrolenidae. Phylogenetic analyses support a sister relationship between these clades (Austin *et al.*, 2002; Faivovich *et al.*, 2005; Wiens *et al.*, 2005; Frost *et al.*, 2006; Guayasamin *et al.*, 2008), but the revision by Guayasamin *et al.* (2009) maintained Allophrynidae and Centrolenidae as separate families. We see either as acceptable and viable taxonomies.
- 8. Pyron & Wiens (2011) were unable to obtain a robust topology of several genera once considered leptodactylids (see also Correa et al., 2006; Frost et al., 2006; Grant et al., 2006) and recognized eight small families: Alsodidae, Batrachylidae, Ceratophryidae, Cycloramphidae, Hylodidae, Odontophrynidae, Rhinodermatidae, and Telmatobiidae. Previously, Grant et al. (2006) refined the taxonomy of Frost et al. (2006) by recognizing Hylodidae as distinct from the Cycloramphidae. Correa et al. (2006) resolved different relationships among these taxa, but used less comprehensive sampling. Both Nuin and do Val (2005) and Heinicke et al. (2009), with limited taxon sampling, showed that Cycloramphidae was likely not monophyletic. Frost et al. (2006) showed that Rhinoderma is nested within their Cycloramphidae; this was also suggested by Correa et al. (2006) who found Rhinoderma to be the sister taxon of Insuetophrynus. Relationships among some of these genera based on morphological data were discussed by Diaz & Valencia (1985), who included Caudiverbera (now Calpytocephalella) in this lineage, and Diaz (1989), with further details on potentially useful diagnostic features within this group provided by Alcalde & Blotto (2006), Cárdenas-Rojas et al. (2007), and Rabanal & Formas (2009). Grant et al. (2006) extended the taxonomy of Frost et al. (2006) by recognizing three subfamilies of Ceratophryidae. However, while several phylogenetic studies have suggested that these subfamilies form a clade (Faivovich et al., 2005; Frost et al., 2006; Grant et al., 2006), others have not (Darst & Cannatella, 2004; Wiens, 2005; Correa et al., 2006; Roelants et al., 2007; Heinicke et al., 2009; Pyron & Wiens, 2011; see also Ruane et al., 2011). Other studies are consistent with monophyly but did not include taxa from all three subfamilies (Wiens et al., 2005). While reporting monophyly, Frost et al. (2006) and Grant et al. (2006) differed in assessments of relationships among the subfamilies: Grant et al. (2006) found a sister relationship between Telmatobiinae and Ceratophryinae whereas Frost et al. (2006) reported a sister relationship between Batrachylinae and Ceratophryinae. Roelants et al. (2007) did not resolve Ceratophryidae as monophyletic, but reported a sister relationship between taxa in the Batrachylinae and Telmatobiinae. Heinicke et al. (2009) also did not resolve Ceratophryidae as monophyletic, but instead found a sister relationship between taxa in the Telamatobiinae and Ceratophryinae. Bossuyt & Roelants (2009) recognized two families, Telmatobiidae and Ceratophyridae, yet did not specify the content of these families, which is crucial given the uncertainty in relationships among the subfamilies. Given that Pyron & Wiens (2011) is the analysis to date with the most complete taxonomic sampling of taxa previously placed in the Ceratophryidae, Cycloramphidae, and Hylodidae, we follow their elevation to family level of the three subfamilies of Ceratophryidae of Grant et al. (2006). Córdova & Descailleaux (2005) provide a cladistic analysis of karyotypic data suggesting that Telmatobius is paraphyletic with respect to Batrachophyrnus. For the families Alsodidae and Batrachylidae, we follow the genus-level revision of Pyron & Wiens (2011) that resulted in placing Hylorhina and several Batrachyla species in Eupsophus.

^{1.} **By** D.C. Blackburn & D.B. Wake (for full contact details, see the list after **References**). The title of this contribution should be cited as "Class Amphibia Gray, 182. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness".

^{2.} The *Amphibian Species of the World* website (Frost, 2011), a continuation of Frost (1985), has guided our work; this site provides detailed information on the taxonomic history of the names we discuss here. Our decisions on which taxa to recognize and at what level are based on current literature and our assessment of current usage. Numbers of species used in our classification are based on the *AmphibiaWeb* website (www.amphibiaweb.org; Accessed 13 October 2011).

Family **Alytidae** Fitzinger, 1843 (2 genera; 12 species; †6)⁹

Subfamily **Alytinae** Fitzinger, 1843 (1 genus; 5 species)

Subfamily **Discoglossinae** Günther, 1858 (1 genus; 7 species)

Family Aromobatidae Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel & Wheeler,

2006 (5 genera; 103 species)¹⁰

Family Arthroleptidae Mivart, 1869 (8 genera; 144 species)¹¹

Family **Ascaphidae** Fejérváry, 1923 (1 genus; 2 species)¹²

Family Batrachylidae Gallardo, 1965 (2 genera; 11 species)¹³

Family **Bombinatoridae** Gray, 1825 (2 genera; 10 species; †1)¹⁴

Family Brachycephalidae Günther, 1858 (2 genera; 49 species)¹⁵

Family **Brevicipitidae** Bonaparte, 1850 (5 genera; 32 species)¹⁶

Family **Bufonidae** Gray, 1825 (~10–~48 genera; 568 species)¹⁷

Family Calyptocephalellidae Reig, 1960 (2 genera; 4 species)¹⁸

Family Centrolenidae Taylor, 1951 (12 genera; 150 species)¹⁹

Subfamily Centroleninae Taylor, 1951 (10 genera; 118 species)

Subfamily **Hyalinobatrachinae** Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada, & Vilà, 2009 (2 genera; 32 species)

^{9.} Analyses of molecular data support a clade containing *Alytes*, *Barbourula*, *Bombina*, and *Discoglossus* (Hay et al., 1995; Hoegg et al., 2004; San Mauro et al., 2004a, 2005; Roelants & Bossuyt, 2005; Frost et al., 2006; Gissi et al., 2006; Roelants et al., 2007; Wiens, 2007; Blackburn et al., 2010). *Alytes* and *Discoglossus* have long been recognized as closely related from morphology-based phylogenetic analyses (e.g., Cannatella, 1985; Gao & Wang, 2001) and molecular phylogenetic analyses agree. Historically, the taxon containing these genera has been referred to as Discoglossidae. Sanchíz (1998) and Dubois (2005) noted the nomenclatural priority of Alytidae. Bossuyt & Roelants (2009) recognize Alytidae and Discoglossidae as separate families based on the extent of "evolutionary time" separating these clades, and this remains an appropriate alternative taxonomy, as would an alternative more inclusive family containing *Barbourula* and *Bombina* (and thus the Bombinatoridae, see below). We tentatively include six extinct taxa in the Alytidae (†*Callobatrachus*, †*Enneabatrachus*, †*Eodiscoglossus*, †*Prodiscoglossus*, †*Scotiophryne*, †*Wealdenbatrachus*, †*Zaphrissa*), although their phylogenetic relationships remain unclear (Sanchíz, 1998; Gao & Wang, 2001; Gao & Chen, 2004; Marjanoviæ & Laurin, 2007).

^{10.} Grant *et al.* (2006) separated a family Aromobatidae (with three subfamilies: Allobatinae, Anomaloglossinae, Aromobatinae) from the Dendrobatidae. While some have rejected this partitioning (Santos *et al.*, 2009; Santos & Cannatella, 2011; Pyron & Wiens, 2011), many in the research community (e.g., Verdade & Rodrigues, 2007; Manzanilla *et al.*, 2009; Brown & Twomey, 2009) have found this partitioning useful and follow the taxonomy of Grant *et al.* (2006). We view either family-level taxonomy as a viable taxonomy. A supplementary document associated with Santos *et al.* (2009) disputes the higher-level taxonomy of Grant *et al.* (2006), but monophyly of the Dendrobatidae and Aromobatidae and the proposed subfamilies of Dendrobatidae receive strong support. The basic topology of generic relationships within Aromobatidae recovered by Santos *et al.* (2009), as well as by Pyron & Wiens (2011), differs little from that of Grant *et al.* (2006). Santos *et al.* (2009) find no support for the Anomaloglossinae. One composite taxon, which combined molecular data for *Allobates alagoanus* with morphological data from *A. olfersioides*, was resolved as sister to the remaining species of *Allobates* by Grant *et al.* (2006). Verdade & Rodrigues (2007) synonymized these two species, with *A. olfersioides* having priority. Santos *et al.* (2009) found this species (referred to in Supplementary Materials as *Colosthethus alagoanus*) to be the sister-taxon of all other species of Aromobatidae. This result renders *Allobates*, and thus Allobatinae, paraphyletic. Pending further analysis of intrafamilial relationships, we list no subfamilies for the Aromobatidae. Grant *et al.* (2006) and Santos *et al.* (2009) provide conflicting views on the number of genera recognized and allocated to the Aromobatidae and Dendrobatidae (see also Brown *et al.*, 2011).

^{11.} The Arthroleptidae (sensu Frost et al., 2006) has been recognized as a morphologically distinctive lineage for decades (Laurent 1941, 1942, 1951; see also Dubois, 1981). This includes recognition that Leptopelis may be more closely related to genera in the Arthroleptidae than to those in the Hyperoliidae, a hypothesis supported by a variety of molecular phylogenetic studies (Emerson et al., 2000; Biju & Bossuyt, 2003; Vences et al., 2003b; Bossuyt et al., 2006; Frost et al., 2006; Roelants et al., 2007). Frost et al. (2006) recognized two subfamilies: Leptopelinae (Leptopelis) and Arthroleptinae (Arthroleptis, Astylosternus, Cardioglossa, Leptodactylodon, Nyctibates, Scotobleps, and Trichobatrachus). However, uncertainty remains in the placement of Leptopelis, including the possibility that the Arthroleptinae sensu Frost et al. (2006) is paraphyletic with respect to Leptopelis (Vences et al., 2003b; Scott, 2005; Frost et al., 2006; Blackburn, 2008), and thus we do not recognize subfamilies of Arthroleptidae.

^{12.} Frost et al. (2006) recognized Ascaphidae and Leiopelmatidae as subfamilies of Leiopelmatidae. Morphology-based hypotheses of phylogeny have either separated these two families as successively branching lineages at the base of anuran phylogeny (e.g., Cannatella, 1985) or resolved them as sister taxa (e.g., Báez & Basso, 1996; Wang et al., 2001). Green et al. (1989) found these taxa to be genetically divergent and suggested that Ascaphus could be more closely related to other clades of extant anurans than to Leiopelma, though recent molecular phylogenetic analyses have recognized these as sister taxa (e.g., Frost et al., 2006; Roelants et al., 2007; Irisarri et al., 2010; Pyron & Wiens, 2011). Bossuyt & Roelants (2009) maintained two families because of the degree of genetic divergence, as did Pyron & Wiens (2011).

^{13.} See footnote 8

^{14.} Monophyly of Bombinatoridae is supported by both molecular (Blackburn *et al.*, 2010) and morphology-based (Cannatella, 1985; Gao & Wang, 2001) phylogenetic studies. We include †*Paradiscoglossus* in the Bombinatoridae (Estes & Sanchíz, 1982). See also footnote 9.

^{15.} Hedges *et al.* (2008) restricted Brachycephalidae to *Brachycephalus* and *Ischnocnema*. Brachycephalidae is one of four recognized families in the unranked taxon Terrarana (Hedges *et al.*, 2008; Heinicke *et al.*, 2009). A viable alternative taxonomy that avoids reliance on unranked taxa would be to recognize the families of Terrarana as subfamilies of Brachycephalidae.

^{16.} Brevicipitidae (sensu Frost *et al.*, 2006), long included in Microhylidae, is now recognized as a member of a larger clade endemic to sub-Saharan Africa (e.g., van der Meijden *et al.*, 2004; Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Kurabayashi *et al.*, 2011). Dubois (2005) enlarged the Brevicipitidae to also contain the taxa recognized here as Arthroleptidae, Hemisotidae, and Hyperoliidae, which is a viable alternative taxonomic arrangement that would produce a taxon with nearly 400 species.

Family Ceratobatrachidae Boulenger, 1884 (5 genera; ~86 species)²⁰

Family Ceratophryidae Tschudi, 1838 (3 genera; 12 species; †3)²¹

Family Ceuthomantidae Heinicke, Duellman, Trueb, Means, MacCulloch & Hedges, 2009 (1 genus; 4 species)²²

Family Conrauidae Dubois, 1992 (1 genus; 6 species)²³

Family Craugastoridae Hedges, Duellman, & Heinicke, 2008 (2 genera; 115 species)²⁴

Family Cycloramphidae Bonaparte, 1850 (2 genera; 33 species)²⁵

Family **Dendrobatidae** Cope, 1865 (13 genera; 182 species)²⁶

Subfamily Colostethinae Cope, 1867 (4 genera; 64 species)

Subfamily **Dendrobatinae** Cope, 1865 (8 genera; 59 species)

^{17.} Generic-level taxonomy within Bufonidae is in a state of flux (Frost et al., 2006, 2009; Pauly et al., 2009). Controversy arises because the many species historically referred to Bufo do not form an exclusive clade with respect to morphologically distinct satellite taxa (e.g., Ansonia, Capensibufo, Nectophrynoides, Pedostibes, Schismaderma, Stephopaedes). In the interests of taxonomic stability, some workers prefer to maintain Bufo for readily recognized "toad"-like taxa, even to the point of reducing morphologically divergent taxa long recognized as genera to subgenera. This would result in a very large genus Bufo, with more than 450 species. Alternatively, approximately 50 genera would be recognized (Frost et al., 2006; Frost, 2011), with many species long placed in Bufo and having extensive literature references being placed in newly (or recently) created genera. Many of the generic-level taxonomic changes have been embraced already by much of the community of amphibian taxonomists (Pramuk et al., 2007; Van Bocxlaer et al., 2009, 2010; Maciel et al., 2010). Pyron & Wiens (2011) recognize 35 genera.

^{18.} Calyptocephalellidae is recovered as monophyletic and a sister taxon of our Myobatrachidae (San Mauro et al., 2005; Wiens et al., 2005; Correa et al., 2006; Frost et al., 2006; Pyron & Wiens, 2011). Frost et al. (2006) referred to the clade containing Calyptocephalella and Telmatobufo as the Batrachophrynidae because it was not yet clear that Batrachophrynus is likely embedded within the genus Telmatobius (Aguilar & Pacheco, 2005; Córdova & Descailleaux, 2005; Aguilar & Valencia, 2009).

^{19.} Guayasamin *et al.* (2009) recognized two subfamilies within the Centrolenidae. We follow Pyron & Wiens (2011) in placing the monotypic *Ikakogi* in the Centroleninae. See also footnote 7.

^{20.} Multiple phylogenetic studies have revealed complicated relationships among clades variously assigned to the Ranidae (see Dubois, 1981, 1983, 1992, 2005; Duellman & Trueb, 1986), including clades recognized here as the Arthroleptidae, Mantellidae, and Rhacophoridae (Emerson et al., 2000; Vences et al., 2003bc; Roelants et al., 2004, 2007; Scott, 2005; van der Meijden et al., 2005; Bossuyt et al., 2006; Frost et al., 2006; Wiens, 2007; Wiens et al., 2009; Pyron & Wiens, 2011; see also Ford, 1990; Ruvinsky & Maxson, 1996; Biju & Bossuyt, 2003; Haas, 2003). Dubois (2005) suggested recognizing fourteen subfamilies of Ranidae (Ceratobatrachinae, Conrauinae, Dicroglossinae, Lankanectinae, Mantellinae, Micrixalinae, Nyctibatrachinae, Petropedetinae, Phrynobatrachinae, Ptychadeninae, Pyxicephalinae, Ranixalinae, and Rhacophorinae); for a summary of the taxonomic history of "ranid" frogs, see Frost et al. (2006). The subfamilial taxa of Dubois (2005) were elevated to the family level by Frost et al. (2006), although several were combined into single families; Lankanectinae and Nyctibatrachinae were combined into the Nyctibatrachidae, and Conrauinae, Petropedetinae, and Ranixalinae were combined into the Petropedetidae (although Ranixalidae is recognized as a separate family by subsequent authors; Van Bocxlaer et al., 2006; Bossuyt & Roelants, 2009; Wiens et al., 2009). Some authors (Bossuyt et al., 2006; Wiens et al., 2009) follow the concept of Ranidae advocated by Dubois (2005), but there is growing use of the family-level taxonomy advocated by Frost et al. (2006). As pointed out by Frost et al. (2006), their unranked taxon Natatanura roughly corresponds to what previous workers have referred to as "ranids". There is high support for the Natatanura of Frost et al. (2006) from a variety of phylogenetic studies, although the relationships among these families remain unresolved (Vences et al., 2003bc; Roelants et al., 2004, 2007; Scott, 2005; Bossuyt et al., 2006; Wiens, 2007; Wiens et al., 2009; Pyron & Wiens, 2011). Ceratobatrachidae is supported as monophyletic (Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Roelants et al., 2007; Wiens et al., 2009; Ruane et al., 2011; Pyron & Wiens, 2011; see also Brown, 2004).

^{21.} Based on recent phylogenetic studies (Evans et al., 2008; Ruane et al., 2011), we include three extinct genera in the Ceratophryidae (†Baurubatrachus, †Beelzebufo, †Wawelia). See also footnote 8.

^{22.} Heinicke et al. (2009) described the Ceuthomantidae, as well as its sole genus Ceuthomantis, and showed that it is sister to a clade containing other families placed in the unranked taxon Terrarana.

^{23.} The monophyly of a clade containing *Conraua* and *Petropedetes* (including taxa formerly placed in *Arthroleptides*) is supported in several phylogenetic analyses (Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Roelants *et al.*, 2007; Wiens *et al.*, 2009; Ruane *et al.*, 2011), but not others (van der Meijden *et al.*, 2005; Zimkus *et al.*, 2010; Pyron & Wiens, 2011). Frost *et al.* (2006) resolved this clade to also contain the taxon here recognized as Ranixalidae, but this is not supported by subsequent analyses. Dubois (1992) considered the Conrauini to be a tribe within his subfamily Dicroglossinae (Ranidae of Dubois, 1992) and, by implication, included *Petropedetes* within the Phrynobatrachidae; Dubois (2005) later treated both Conrauinae and Petropedetinae as subfamilies of the Ranidae (sensu Dubois, 2005). In light of the uncertain sister relationship between these two clades and their likely deep divergence (Roelants *et al.*, 2007), we recognize these as two distinct families, Conrauidae and Petropedetidae. For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.

^{24.} Hedges *et al.* (2008) proposed the Craugastoridae for the diverse *Craugastor* and its sister taxon, a new genus *Haddadus*. The Craugastoridae is one of four families in the unranked taxon Terrarana (Hedges *et al.*, 2008; Heinicke *et al.*, 2009; Padial *et al.*, 2009). Pyron & Wiens (2011) found Craugastoridae sensu Hedges *et al.* (2009) to be embedded within the Strabomantidae sensu Hedges *et al.* (2009), and expanded the Craugastoridae to include all taxa previously assigned to Strabomantidae. However, because of low support values among basal nodes in this larger clade, the analysis of Pyron & Wiens (2011) does not reject the hypothesis that Craugastoridae is sister to the Strabomantidae. Higher-level relationships among these clades require further study.

^{25.} See footnote 8.

^{26.} Grant et al. (2006) recognize three subfamilies of Dendrobatidae (for discussion regarding taxa in the Aromobatidae, see footnote 10). The phylogenetic relationships resolved in other studies (Vences et al., 2000, 2003a; Roberts et al., 2006; Santos et al., 2009; Santos & Cannatella, 2011) support the tree topology on which the subfamily taxonomy of Grant et al. (2006) is based. Santos et al. (2009; see also Santos & Cannatella, 2011) argued that the partitioning of Dendrobates into six genera was unnecessary (Adelphobates, Dendrobates, Excidobates, Minyobates, Oophaga, Ranitomeya). Brown et al. (2011) discuss this matter at length and elect to recognize all six genera and describe a seventh genus, Andinobates.

Subfamily **Hyloxalinae** Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel & Wheeler, 2006 (1 genus; 59 species)

Family **Dicroglossidae** Anderson, 1871 (12–14 genera; 177 species)²⁷

Subfamily **Dicroglossinae** Anderson, 1871 (10–12 genera; 155 species)

Subfamily Occidozyginae Fei, Ye, & Huang, 1990 (2 genera; 22 species)

Family Eleutherodactylidae Lutz, 1954 (4 genera; 202 species)²⁸

Subfamily Eleutherodactylinae Lutz, 1954 (2 genera; 195 species)

Subfamily **Phyzelaphryninae** Hedges, Duellman, & Heinicke, 2008 (2 genera; 7 species)

Family †**Gobiatidae** Roček & Nesov, 1993 (†3)²⁹

Family **Heleophrynidae** Noble, 1931 (2 genera; 6–7 species)³⁰

Family Hemiphractidae Peters, 1862 (6 genera; 95 species)³¹

Family Hemisotidae Cope, 1867 (1 genus; 9 species)³²

Family Hylidae Rafinesque, 1815 (42–46 genera; 904 species; †1)³³

Subfamily **Hylinae** Rafinesque, 1815 (36–39 genera 647 species;)

Subfamily **Pelodryadinae** Günther, 1858 (1–2 genera; 198 species)

Subfamily **Phyllomedusinae** Günther, 1858 (5 genera; 59 species)

Family **Hylodidae** Günther, 1858 (3 genera; 42 species)³⁴

Family Hyperoliidae Laurent, 1943 (18 genera; 214 species)³⁵

Family Leiopelmatidae Mivart, 1869 (1 genus; 4 species)³⁶

Family Leiuperidae Bonaparte, 1850 (7 genera; 85 species)³⁷

Family Leptodactylidae Werner, 1896 (6 genera; 105 species)³⁸

36. See footnote 12.

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^{27.} Phylogenetic analyses of molecular data support monophyly of the Dicroglossidae (Kosuch et al., 2001; Roelants et al., 2004, 2007; Kurabayashi et al., 2005; van der Meijden et al., 2005; Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Che et al., 2007; Wiens, 2007; Wiens et al., 2009; Ruane et al., 2011). Two clades, the subfamilies Dicroglossinae and Occidozyginae, also receive strong support (Kosuch et al., 2001; Roelants et al., 2004; Bossuyt et al., 2006; Frost et al., 2006; Che et al., 2007; Wiens et al., 2009; Ruane et al., 2011; Pyron & Wiens, 2011). Generic-level taxonomy and phylogenetic relationships within the Dicroglossinae remain unresolved (Dubois et al., 2001; Jiang et al., 2005; Che et al., 2007, 2009, 2010; Pyron & Wiens, 2011). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.

^{28.} Hedges *et al.* (2008) recognized two well-supported clades within the Eleutherodactylidae, one including *Diasporus* and the mega-diverse genus *Eleutherodactylus* and the other including the species-poor *Adelophryne* and the monotypic *Phyzelaphryne*.

^{29.} The †Gobiatidae is an extinct family of three genera (†Cretasalia, †Gobiates, and †Gobiatoides) with obscure relationships to other families of Anura (Roček, 2008). Sanchíz (1998) questioned the validity of †Gobiatoides.

^{30.} Molecular phylogenies have resolved the Heleophrynidae as the sister taxon of all other Neobatrachia (e.g., Hoegg *et al.*, 2004; Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007). Van Dijk (2008) erected *Hadromophryne*, the validity of which is further supported by Pyron & Wiens (2011).

^{31.} Monophyly of the Hemiphractidae has been controversial. Based on molecular phylogenetic analyses, some authors have found the Hemiphractidae to be paraphyletic (Darst & Cannatella, 2004), or polyphyletic (Faivovich *et al.*, 2005; Frost *et al.*, 2006), whereas others resolved it to be monophyletic (Wiens, 2007; Guayasamin *et al.*, 2008; Heinicke *et al.*, 2009; Pyron & Wiens, 2011). Frost *et al.* (2006) recognized three families (Amphignathodontidae, Cryptobatrachidae, Hemiphractidae). Because more recent studies have resolved this family as monophyletic, we maintain the Hemiphractidae for *Cryptobatrachus*, *Flectonotus*, *Gastrotheca*, *Hemiphractus*, and *Stefania*, as well as the resurrected *Fritziana* (Duellman *et al.*, 2011).

^{32.} The family Hemisotidae, containing only the genus *Hemisus*, is assumed to be monophyletic, though we know of no explicit test. Hemisotidae is the sister taxon of the Breviciptidae (Frost *et al.*, 2006; Roelants *et al.*, 2007; van der Meijden *et al.*, 2007b; Wiens, 2007), a relationship previously suggested by morphological phylogenetic studies (Blommers-Schlösser, 1993; Channing, 1995). One viable alternative taxonomic arrangement would be to include Hemisotidae as a subfamily of the Breviciptidae.

^{33.} The content of the Hylidae has been extensively modified in recent years. Those frogs recognized above as the Hemiphractidae were previously considered part of the Hylidae (Duellman, 1970), but they are not necessarily closely related (Darst & Cannatella, 2004; Frost *et al.*, 2006; Wiens, 2007; Heinicke *et al.*, 2009). Most analyses agree in resolving a monophyletic lineage containing three subfamilies (Darst & Cannatella, 2004; Faivovich *et al.*, 2005; Wiens *et al.*, 2005; Frost *et al.*, 2006; Pyron & Wiens, 2011), two of which (Pelodryadinae and Phyllomedusinae) form a clade sister to the third (Hylinae). However, there is some disagreement on the monophyly of Hylidae (Roelants *et al.*, 2007), which, combined with deep genetic divergences, has led some authors to recognize each subfamily as a distinct family (Bossuyt & Roelants, 2009). We recognize a single family with three subfamilies. Faivovich *et al.* (2005) extensively revised the generic-level taxonomy of Hylinae. Generic-level taxonomy of the Pelodryadinae remains in flux with authors recognizing one or two genera (Faivovich *et al.*, 2005; Frost *et al.*, 2006; Rosauer *et al.*, 2009; Tyler *et al.*, 2009; Pyron & Wiens, 2011). For the Phyllomedusinae, Faivovich *et al.* (2010) synonymized *Hylomantis* and *Pachymedusa* with *Agalychnis*. The relationships of †*Australobatrachus* to currently recognized clades remains unclear.

^{34.} The three genera of Hylodidae form a clade (Nuin & do Val, 2005; Frost *et al.*, 2006; Grant *et al.* 2006; see also Pyron & Wiens, 2011) that Grant *et al.* (2006) resolved as the sister taxon of the Dendrobatidae + Aromobatidae (also suggested by morphological and karyological data; e.g., Lynch, 1971; Bogart, 1991; Augiar *et al.*, 2004) and thus removed it from the Cyclorhamphidae, where it had been placed by Frost *et al.* (2006). Pyron & Wiens (2011) resolved Hylodidae as the sister taxon of Alsodidae, and not near the Dendrobatidae + Aromobatidae.

^{35.} The Hyperoliidae is a diverse clade of eighteen genera, many of which have long been recognized as sharing morphological features (Laurent 1986; Drewes, 1984) and both morphological (Drewes, 1984) and molecular phylogenetic analyses support monophyly (Vences *et al.*, 2003b; Frost *et al.*, 2006; Veith *et al.*, 2009). As detailed in footnote 11, the genus *Leptopelis* is now considered part of the Arthroleptidae, which is the sister taxon to Hyperoliidae.

Family Mantellidae Laurent, 1946 (12 genera; 198 species)³⁹

Subfamily Boophinae Vences & Glaw, 2001 (1 genus; 72 species)

Subfamily Laliostominae Vences & Glaw, 2001 (2 genera; 4 species)

Subfamily Mantellinae Laurent, 1946 (9 genera; 122 species)

Family **Megophryidae** Bonaparte, 1850 (10 genera; 160 species)⁴⁰

Family Micrixilidae Dubois, Ohler, & Biju, 2001 (1 genus; 11 species)⁴¹

Family Microhylidae Günther, 1858 (68 genera; 495 species)⁴²

Subfamily **Asterophryinae** Günther, 1858 (22 genera; 252 species)

Subfamily **Cophylinae** Cope, 1889 (7 genera; 58 species)

Subfamily **Dyscophinae** Boulenger, 1882 (1 genus; 3 species)

Subfamily **Gastrophryninae** Fitzinger, 1843 (13 genera; 59 species)

Subfamily **Hoplophryninae** Noble, 1931 (2 genera; 3 species)

Subfamily **Kalophryninae** Mivart, 1869 (1 genus; 17 species)

Subfamily Melanobatrachinae Noble, 1931 (1 genus; 1 species)

Subfamily Microhylinae Günther, 1858 (9 genera; 71 species)

Subfamily Otophryninae Wassersug & Pyburn, 1987 (2 genera; 6 species)

Subfamily Phrynomerinae Noble, 1931 (1 genus; 5 species)

Subfamily **Scaphiophryninae** Laurent, 1946 (2 genera; 12 species)

Family Myobatrachidae Schlegel, 1850 (20 genera; 127 species; †1)⁴³

Subfamily **Limnodynastinae** Lynch, 1969 (8 genera; 44 species)

Subfamily Myobatrachinae Schlegel, 1850 (12 genera; 83 species; †1)

Family Nasikabatrachidae Biju & Bossuyt, 2003 (1 genus; 1 species)⁴⁴

Family **Nyctibatrachidae** Blommers-Schlösser, 1993 (2 genera; 29 species)⁴⁵

Family **Odontophrynidae** Lynch, 1969 (3 genera; 36 species)⁴⁶

Family †**Palaeobatrachidae** Špinar, 1972 (†4)⁴⁷

^{37.} Grant *et al.* (2006) recognized Leiuperidae for a clade of seven genera that Frost *et al.* (2006) included within the Leptodactylidae. Frost *et al.* (2006) did not resolve the Leiuperidae as monophyletic but both Correa *et al.* (2006) and Grant *et al.* (2006) did. Leiuperidae is treated as a subfamily of Leptodactylidae by Pyron & Wiens (2011).

^{38.} Ruvinsky & Maxson (1996) showed that Leptodactylidae sensu Lynch (1971, 1973) is polyphyletic (see also Darst & Cannatella (2004), Faivovich et al. (2005), Wiens et al. (2005), and Carrera et al. (2006). Frost et al. (2006) partitioned Leptodactylidae into multiple families; Grant et al. (2006) modified this scheme by further partitioning (see also Pyron & Wiens, 2011). Based in part on previous work of Heyer (1998) and Kokobum & Giaretta (2005) and finding that Adenomera and Lithodytes form a clade sister to Leptodactylus, Frost et al. (2006) considered these genera to be synonyms of Leptodactylus. However, subsequent authors have provided evidence that these genera are morphologically distinct (Ponssa & Heyer, 2007), and both molecular (Pyron & Wiens, 2011) and morphology-based (de Sá et al., 2005; Ponssa et al., 2010) phylogenetic analyses suggest that Adenomera and Lithodytes are not nested within Leptodactylus.

^{39.} Phylogenetic analyses provide strong support for the monophyly of the Mantellidae (Emerson *et al.*, 2000; Vences *et al.*, 2003bc; Roelants *et al.*, 2004, 2007; Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Vieites *et al.*, 2009; Wiens *et al.*, 2009; Ruane *et al.*, 2011). The subfamilies (Boophinae, Laliostominae, and Mantellinae) are also strongly supported (Vences *et al.*, 2003c; Roelants *et al.*, 2004; Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Glaw *et al.*, 2006; Kurabayashi *et al.*, 2008; Vieites *et al.*, 2009; Wiens *et al.*, 2009; Pyron & Wiens, 2011). Frost *et al.* (2006) included the Laliostominae in the Mantellinae, but the taxonomic community has not accepted this proposal (e.g., Glaw & Vences, 2006; Glaw *et al.*, 2006; Hiobiarilanto *et al.*, 2010) and these clades may not be sister to one another (Pyron & Wiens, 2011). The relationship of the monotypic *Tsingymantis* to the recognized subfamilies remains a point for future research (Glaw *et al.*, 2006; Kurabayashi *et al.*, 2008). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.

^{40.} The monophyly of the Megophryidae is widely accepted (e.g., Ford & Cannatella, 1993; Frost *et al.*, 2006). The most significant recent taxonomic change is the recognition that *Leptobrachium* is paraphyletic with respect to *Vibrissaphora* (Rao & Wilkinson, 2008; Brown *et al.*, 2009). We refrain from recognizing subfamilies within Megophryidae (Leptobrachiinae, Leptolalaginae, Megophryinae, as advocated by Delorme *et al.*, 2006) until phylogenetic analyses with more inclusive taxon sampling are available. However, the molecular phylogenetic analysis by Pyron & Wiens (2011) generally supports the subfamilies of Delorme *et al.* (2006), but lacks sampling for *Leptobatrachella*; their analysis also suggests that *Xenophrys* may be paraphyletic with respect to both *Megophrys* and *Brachytarsophrys*.

^{41.} The monophyly of the Micrixalidae, containing only the genus *Micrixalus*, is supported by phylogenetic analyses (Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Frost *et al.*, 2006; Wiens *et al.*, 2009; see also Dubois *et al.*, 2001). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.

^{42.} Following recognition of the Brevicipitidae (see footnote 16), there is strong support for the monophyly of the Microhylidae (Ford & Cannatella, 1993; Haas, 2003; van der Meijden *et al.*, 2004, 2007b; Frost *et al.*, 2006; Roelants *et al.*, 2007; Kurabayashi *et al.*, 2011). Based in part on the substantial divergences between subfamilies observed in DNA sequence data, Bossuyt & Roelants (2009) elevated each subfamily to family rank. However, Bossuyt & Roelants (2009) did not mention the Otophryninae, leaving its status uncertain, and failed to provide any details on the many taxa not assigned to subfamilies within the classification scheme of Frost *et al.* (2006). At this point, adopting a strategy in which each subfamily of Microhylidae is elevated to family would lead to many genera of unclear affinities being orphaned. Thus, we advocate recognizing the family Microhylidae with multiple subfamilies and leaving certain genera without subfamily designation. Based on Greenbaum (2006), we suggest that *Altigius, Melanophryne, Myersiella*, and *Syncope* should be included in the Gastrophryninae. Following Pyron & Wiens (2011) and Trueb *et al.* (2011), we tentatively include *Synapturanus* in the Otophryninae.

Family **Pelobatidae** Bonaparte, 1850 (1 genus; 4 species)⁴⁸

Family **Pelodytidae** Bonaparte, 1850 (1 genus; 3 species; †2)⁴⁹

Family Petropedetidae Noble, 1931 (1 genus; 12 species)⁵⁰

Family Phrynobatrachidae Laurent, 1941 (1 genus; 84 species)⁵¹

Family Pipidae Gray, 1825 (4-5 genera; 33 species; †7)⁵²

Family **Ptychadenidae** Dubois, 1987 (3 genera; 51 species)⁵³

Family Pyxicephalidae Bonaparte, 1850 (13 genera; 67 species)⁵⁴

Subfamily Cacosterninae Noble, 1931 (11 genera; 61 species)

Subfamily **Pyxicephalinae** Bonaparte, 1850 (2 genera; 6 species)

Family **Ranidae** Rafinesque, 1814 (10–16 genera; 369 species)⁵⁵

Family Ranixalidae Dubois, 1987 (1 genus; 10 species)⁵⁶

Family **Rhacophoridae** Hoffman, 1932 (15 genera; 333 species)⁵⁷

Subfamily **Buergeriinae** Channing, 1989 (1 genus; 5 species)

- 44. The monotypic family Nasikabatrachidae (Biju & Bossuyt, 2003) is nearly universally accepted, although Frost *et al.* (2006) included the sole genus in the Sooglossidae. We follow the generally accepted practice of maintaining these as two distinct families (e.g., Frost, 2011; Pyron & Wiens, 2011).
- 45. Frost *et al.* (2006) subsumed the Lankanectinae and Nyctibatrachinae of Dubois (2005) into a single family, Nyctibatrachidae. The monophyly of this family, containing the two genera *Lankanectes* and *Nyctibatrachus*, receives high support from phylogenetic analyses (van der Meijden *et al.*, 2005; Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Wiens *et al.*, 2009; Ruane *et al.*, 2011; Pyron & Wiens, 2011; see also Dubois & Ohler, 2001). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.
- 46. Pyron & Wiens (2011) found strong support for the monophyly of a clade of three genera (*Macrogenioglottus*, *Odontophrynus*, and *Proceratophrys*), which they recognized as the Odontophrynidae. See also footnote 8.
- 47. †Palaeobatrachidae contains four recognized extinct genera (†Albionbatrachus, †Messelobatrachus, †Palaeobatrachus, and †Pliobatrachus) and is generally allied to the extant Pipidae although the phylogenetic relationships of this family remain obscure (Sanchíz, 1998). The phylogenetic analyses of Gao & Wang (2001) and Gao & Chen (2004), which included †Palaeobatrachus, suggest that †Palaeobatrachidae may nest within the Pipidae, but a phylogenetic analysis with greater taxonomic sampling of extinct pipoid taxa supports the monophyly of Pipidae to the exclusion of †Palaeobatrachus (Trueb & Báez, 2006; see also Roček, 2003).
- 48. The well-supported Pelobatidae contains a single genus (*Pelobates*) with four species (Cannatella, 1985; Ford & Cannatella, 1993; Lathrop, 1997; García-París *et al.*, 2003; Roelants & Bossuyt, 2005; Frost *et al.*, 2006; Veith *et al.*, 2006). Based in part on the morphological phylogenetic analysis of Cannatella (1985), Ford & Cannatella (1993) defined Pelobatidae to include *Pelobates* as well as *Scaphiopus* and *Spea* (see also, e.g., Noble, 1925). Analyses of morphological data by Lathrop (1997), Henrici & Haynes (2006), and Henrici (2009) further support this result as well as including the extinct taxa †*Elkobatrachus*, †*Macropelobates*, and †*Eopelobates* in the Pelobatidae. However, subsequent molecular phylogenetic analyses, as well as a combined analysis of larval and adult morphology (Pugener *et al.*, 2003) indicate that *Pelobates*, *Scaphiopus*, and *Spea* do not form a clade exclusive of Pelodytidae and Megophryidae (see also footnote 39). We follow the results of these recent studies by recognizing Pelobatidae and Scaphiopodidae to be distinct families, although the relationships of the extinct taxa now remain uncertain and we consider these Anura *incertae sedis*.
- 49. The monophyly of the Pelodytidae, which contains a single genus (*Pelodytes*) with three species, is supported by phylogenetic analysis of mitochondrial DNA sequence data (García-París *et al.*, 2003). Analyses of both morphological and molecular data support the Pelodytidae as a member of a larger clade containing the Pelobatidae, Scaphiopodidae, and Megophryidae (Cannatella, 1985; Ford & Cannatella, 1993; Hay *et al.*, 1995; García-París *et al.*, 2003; Pugener *et al.*, 2003; Roelants & Bossuyt, 2005; San Mauro *et al.*, 2005; Frost *et al.*, 2006; Veith *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Ruane *et al.*, 2011). †*Miopelodytes* and †*Tephrodytes* have been included in the Pelodytidae based on the fusion of the tibiale and fibulare (unique among archaeobatrachians; Cannatella, 1985), but the precise relationships of these two genera to *Pelodytes* remains unclear (Taylor, 1941; Henrici, 1994).
- 50. See footnote 23.
- 51. The monophyly of the Phrynobatrachidae, containing the single diverse genus *Phrynobatrachus*, is well supported by phylogenetic analyses (Scott, 2005; Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Roelants *et al.*, 2007; Wiens *et al.*, 2009; Ruane *et al.*, 2011; Zimkus *et al.*, 2010). While combined molecular and morphological data of Scott (2005) suggested paraphyly of *Phrynobatrachus* with respect to *Natalobatrachus*, the recent phylogenetic analysis of van der Meijden *et al.* (2011) demonstrate *Natalobatrachus* to be within the Pyxicephalidae. For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.

^{43.} From one to three families of myobatrachids (Myobatrachidae, Limnodynastidae, Rheobatrachidae) have been recognized. Ford & Cannatella (1993) questioned the monophyly of a single family (e.g., Heyer & Liem, 1976) and proposed that †Rheobatrachus may be most closely related to the Myobatrachinae (sensu Heyer & Liem, 1976). Several molecular phylogenetic analyses did not test the monophyly of each family (e.g., Read et al., 2001; Morgan et al., 2007). Frost et al. (2006) found that twenty genera variously assigned to the three families form a clade, yet chose to recognize two families (Limnodynastidae and Myobatrachidae, the latter containing Mixophyes and †Rheobatrachus). Much of the uncertainty of higher-level taxonomy in this clade relates to Mixophyes and †Rheobatrachus, the relationships of which remain uncertain (Heyer & Liem, 1976; Farris et al., 1982; Frost et al., 2006; Roelants et al., 2007; Ruane et al., 2011; Pyron & Wiens, 2011). In several analyses, Mixophyes and †Rheobatrachus are not sister taxa and the relationships of these two genera to the other taxa in the Limnodynastidae and Myobatrachidae (sensu Frost et al., 2006) remain unclear (Roelants et al., 2007; Pyron & Wiens, 2011; Ruane et al., 2011). Bossuyt & Roelants (2009) recognized Rheobatrachidae, Limnodynastidae, and Myobatrachidae but mentioned neither †Rheobatrachus nor Mixophyes explicitly. To date, the most complete relevant analyses are those of Frost et al. (2006) and Pyron & Wiens (2011), which largely agree with one another, yet disagree on whether Rheobatrachus and Mixophyes form a clade. Because of remaining uncertainties in the placement of †Rheobatrachus and Mixophyes, we follow Pyron & Wiens (2011) by using two subfamilies for the single family Myobatrachidae. The genus †Rheobatrachus became extinct in the late 20th century.

Subfamily **Rhacophorinae** Hoffman, 1932 (14 genera; 327 species)

Family Rhinodermatidae Günther, 1858 (2 genera; 3 species)⁵⁸

Family **Rhinophrynidae** Günther, 1859 (1 genus; 1 species; †2–3)⁵⁹

Family **Scaphiopodidae** Cope, 1865 (2 genera; 7 species)⁶⁰

Family Sooglossidae Noble, 1931 (2 genera; 4 species)⁶¹

Family Strabomantidae Hedges, Duellman, & Heinicke, 2008 (17–19 genera; 572 species)⁶²

Subfamily **Holoadeninae** Hedges, Duellman, & Heinicke, 2008 (6 genera; 47 species)

Subfamily **Strabomantinae** Hedges, Duellman, & Heinicke, 2008 (11–13 genera; 525 species)

Family **Telmatobiidae** Fitzinger, 1843 (2 genera; 60 species)⁶³

Order Caudata Fischer von Waldheim, 1813 (salamanders) (67–68 genera; 614 species; †~66)⁶⁴

- 53. The monophyly of the Ptychadenidae receives strong support from phylogenetic analyses (Scott, 2005; Bossuyt *et al.*, 2006; van Bocxlaer *et al.*, 2006; Wiens *et al.*, 2009). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.
- 54. Phylogenetic analyses of molecular data provide strong support for the monophly of the African endemic family Pyxicephalidae (van der Meijden et al., 2005, 2011; Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Roelants et al., 2007; Wiens, 2007; Wiens et al., 2009; Zimkus et al., 2010; Pyron & Wiens, 2011) and its component subfamilies Cacosterninae and Pyxicephalinae (Scott, 2005; van der Meijden et al., 2005, 2011; Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Roelants et al., 2007; Wiens et al., 2009; Zimkus et al., 2010; Pyron & Wiens, 2011). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.
- 55. Phylogenetic analysies of molecular data provide strong support for the monophly of the African endemic family Pyxicephalidae (van der Meijden et al., 2005, 2011; Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Roelants et al., 2007; Wiens, 2007; Wiens et al., 2009; Zimkus et al., 2010; Pyron & Wiens, 2011) and its component subfamilies Cacosterninae and Pyxicephalinae (Scott, 2005; van der Meijden et al., 2005, 2011; Bossuyt et al., 2006; Frost et al., 2006; Van Bocxlaer et al., 2006; Roelants et al., 2007; Wiens et al., 2009; Zimkus et al., 2010; Pyron & Wiens, 2011). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.
- 56. The Ranixalidae, containing only the genus *Indirana*, a well supported clade (Roelants *et al.*, 2004, 2007; Bossuyt *et al.*, 2006; Van Bocxlaer *et al.*, 2006; Wiens *et al.*, 2009; Ruane *et al.*, 2011; Pyron & Wiens, 2011). For further details on taxonomy of taxa placed in the Ranidae of Dubois (2005), see footnote 20.
- 57. Rhacophoridae and its two subfamilies are clades (Emerson *et al.*, 2000; Haas, 2003; Kurabayashi *et al.*, 2005; Scott, 2005; van der Meijden *et al.*, 2005; Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Vences *et al.*, 2003bc; Van Bocxlaer *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Li *et al.*, 2009; Wiens *et al.*, 2009; Yu *et al.*, 2009; Ruane *et al.*, 2011; Pyron & Wiens, 2011). Phylogenetic analyses led to the recognition of several additional rhacophorine genera (Biju *et al.*, 2010; Meegaskumbura *et al.*, 2010). For further details on taxa placed in the Ranidae by Dubois (2005), see footnote 20.
- 58. See footnote 8.
- 59. The Rhinophrynidae, represented today only by the monotypic *Rhinophrynus*, is the sister taxon of the extant Pipidae (Cannatella, 1985; Hay *et al.*, 1995; Haas, 2003; Pugener *et al.*, 2003; Roelants & Bossuyt, 2005; Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Ruane *et al.*, 2011). The phylogenetic analyses of Gao & Wang (2001) and Gao & Chen (2004) support a sister relationship of *Rhinophrynus* with †*Palaeobatrachus*, but analyses with greater sampling of extinct pipoid taxa do not support this relationship (Trueb *et al.*, 2005; Trueb & Báez, 2006; Marjanović & Laurin, 2007). We follow Henrici (1998) by including the fossil taxa †*Chelomophrynus* and †*Rhadinosteus*, and possibly †*Eorhinophrynus*, in the Rhinophrynidae.
- 60. The genera *Scaphiopus* and *Spea* form the monophyletic Scaphiopodidae (Cannatella, 1985; Lathrop, 1997; García-París *et al.*, 2003; Roelants & Bossuyt, 2005; Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Ruane *et al.*, 2011), which Ford & Cannatella (1993) included in the Pelobatidae. While the phylogenetic analyses of morphological data by Henrici & Haynes (2006) and Henrici (2009) did not resolve *Scaphiopus* and *Spea* as sister taxa to the exclusion of *Pelobates*, other phylogenetic analyses present evidence that these two genera form a clade. The phylogenetic relationships and family-level taxonomy of fossil taxa previously allied to *Pelobates*, *Scaphiopus*, and *Spea* remain unclear (Zweifel, 1956; Henrici & Haynes, 2006; Henrici, 2009) and we thus leave these unassigned to family. See also footnote 48.
- 61. Sooglossidae is a well supported clade (Nussbaum, 1982; Ford & Cannatella, 1993; Nussbaum & Wu, 2007; Frost *et al.*, 2006; van der Meijden *et al.*, 2007a; Pyron & Wiens, 2011). Partitioning of the diversity of this family into genera is supported by morphological, molecular, and acoustic data (Nussbaum & Wu, 2007; van der Meijden *et al.*, 2007a; see also Nussbaum *et al.*, 1982).
- 62. Hedges *et al.* (2008) proposed the Strabomantidae and its two subfamilies (Holoadeninae and Strabomantinae) for a diverse clade of Central and South American genera. Strabomantidae is one of four families in the unranked taxon Terrarana (Hedges *et al.*, 2008; Heinicke *et al.*, 2009). Subsequent molecular phylogenetic analyses with less taxon sampling have not resolved the two subfamilies as monophyletic (Heinicke *et al.*, 2007, 2009), or even as forming a clade (Padial *et al.*, 2009), but because these are based on substantially less sampling of taxa and/or genetic loci, we follow the subfamily taxonomy proposed by Hedges *et al.* (2008). See also footnote 24.
- 63. See footnote 8.

^{52.} Phylogenetic analyses of morphological and molecular data support the monophyly of the Pipidae (Cannatella, 1985; Cannatella & Trueb, 1988ab; Ford & Cannatella, 1993; Haas, 2003; Pugener et al., 2003; Evans et al., 2004; Roelants & Bossuyt, 2005; San Mauro et al., 2005; Frost et al., 2006; Trueb & Báez, 2006; Marjanović & Laurin, 2007; Roelants et al., 2007; Wiens, 2007; Irisarri et al., 2011; Ruane et al., 2011). The relationships of Hymenochirus and Pseudhymenochirus are unclear; some studies find these genera (typically represented only by Hymenochirus) to be more closely related to extant Xenopus (including Silurana; Roelants & Bossuyt, 2005; San Mauro et al., 2005; Roelants et al., 2007; Wiens, 2007; Irisarri et al., 2011; Ruane et al., 2011), or to Pipa (Cannatella, 1985; Cannatella & Trueb, 1988ab; Evans et al., 2004; Pugener et al., 2003; Báez & Harrison, 2005; Trueb et al., 2005; Marjanović & Laurin, 2007), or possibly sister to a clade containing both Xenopus and Pipa (Frost et al., 2006); see also de Sá & Hillis (1990). Because of these uncertainties, we refrain from recognizing subfamilies within the Pipidae. Cannatella & Trueb (1988a) recognized the genus Silurana as distinct from Xenopus, although one of these authors states that this was an unsound decision (Pauly et al., 2009). Diverse extinct taxa of the Pipidae include †Eoxenopoides, †Llankibatrachus, †Pachycentrata (Pipinae; Báez & Harrison, 2005; Trueb & Báez, 2006), †Saltenia, †Shelania, †Singidella (Pipinae; Báez & Harrison, 2005), and †Vulcanobatrachus. Other extinct taxa that may be more closely related to Pipidae than to Rhinophrynidae include †Avitabatrachus, †Cordicephalus, and †Thoraciliacus, and possibly the Palaeobatrachidae (Báez et al., 2000; Trueb et al., 2005; Trueb & Báez, 2006), but we do not include these taxa within the Pipidae.

Family Ambystomatidae Gray, 1850 (1 genus; 32 species; †2)⁶⁵

Family **Amphiumidae** Gray, 1825 (1 genus; 3 species; †1)⁶⁶

Family †Batrachosauroididae Auffenberg, 1958 (†7)⁶⁷

Family Cryptobranchidae Fitzinger, 1826 (2 genera; 3 species; †6)⁶⁸

Family **Dicamptodontidae** Tihen, 1958 (1 genus; 4 species; †5)⁶⁹

Family **Hynobiidae** Cope, 1859 (9 genera; 53 species; †1)⁷⁰

Family †Karauridae Ivachnenko, 1978 (†2–3)⁷¹

Family Plethodontidae Gray, 1850 (27 genera; 418 species)⁷²

Subfamily **Hemidactyliinae** Hallowell, 1856 (20 genera; 322 species)

Subfamily **Plethodontidinae** Gray, 1850 (7 genera; 96 species)

Family **Proteidae** Gray, 1825 (2 genera; 6 species; †2)⁷³

Subfamily **Proteinae** Gray, 1825 (1 genus; 1 species; †2)

- 64. We consider Caudata and Urodela to be synonyms and follow the argumentation of Frost *et al.* (2006) by recognizing Caudata as the appropriate name (for a contrasting view, see Dubois, 2004). Family-level assignment is currently not possible for ~25 extinct genera. Of these, †*Karaurus* and †*Kokartus* may be outside crown-group Caudata. Unassigned taxa, some of which are based on very limited material (e.g., †*Galverpeton*), are †*Apricosiren*, †*Batrachosauroides*, †*Bishara*, †*Chrysotriton*, †*Comonecturoides*, †*Galverpeton*, †*Hemitrypus*, †*Hylaeobatrachus*, †*Iridotriton*, †*Jeholotriton*, †*Kiyatriton*, †*Laccotriton*, †*Liaoxitriton*, †*Marmorerpeton*, †*Mynbulakia*, †*Nesovtriton*, †*Paleoamphiuma*, †*Pangerpeton*, †*Prosiren*, †*Ramonellus*, †*Regalerpeton*, †*Seminobatrachus*, †*Sinerpeton*, †*Triassurus* (possibly not within Caudata; Estes, 1981; Milner, 2000), and †*Valdotriton*.
- 65. The monophyly is well established for Ambystomatidae and Dicamptodontidae, and the clades are sister taxa (Larson, 1991; Larson & Dimmick, 1993; Frost et al., 2006; Roelants et al., 2007; Vieites et al., 2007, 2009; Wiens, 2007; Zhang & Wake, 2009a; Pyron & Wiens, 2011). Frost et al. (2006) reduced Dicamptodontidae to a subfamily of Ambystomatidae to avoid two taxa each with only one genus. Significantly, the decision by Frost et al. (2006) to place the Dicamptodontidae in the Ambystomatidae because "each contain[s] a single genus" (p. 118) disregards the long recognition of extinct genera as belonging to these families (e.g., Estes, 1981). In light of the deep separation of the taxa (probably in excess of 100 my: Roelants et al., 2007; Zhang & Wake, 2009a; Vieites et al., 2009), the long fossil record of dicamptodontids, documentation of their former occurrence in Europe (Venczel, 2008), and substantial biological differences between the two clades, we recognize these as two distinct families. We follow Estes (1981) by including five extinct genera (†Ambystomichnus [an ichnotaxon; Peabody, 1954], †Bargmannia, †Chrystotriton, †Geyeriella, and †Wolterstorffiella) in the Dicamptodontidae. While we agree with Milner (2000) that the inclusion of these in Dicamptodontidae is based on very limited data (i.e., vertebral morphology; Estes, 1981), it is the only evidence at hand and serves as a hypothesis to be tested with additional data. Rogers (1976) described †Amphitriton as an extinct genus of Ambystomatidae; Estes (1981) and Milner (2000) have shown that the morphological features of this extinct taxon fall within the diversity observed in Ambystoma.
- 66. The monophyletic Amphiumidae contains three extant species of *Amphiuma*. Amphiumidae is the sister-taxon of the Plethodontidae (Larson & Dimmick, 1993; Frost *et al.*, 2006; Roelants *et al.*, 2007; Vieites *et al.*, 2007, 2009; Wiens, 2007; Zhang & Wake, 2009a; Pyron & Wiens, 2011). We include †*Proamphiuma*, and refrain from including †*Paleoamphiuma* because of disagreements as to its affinities (Rieppel & Grande, 1998; Gardner, 2003).
- 67. The †Batrachosauroididae is an extinct, enigmatic family of uncertain phylogenetic affinity with seven currently recognized genera (†Batrachosauroides, †Mynbulakia, †Opisthotriton, †Palaeoproteus, †Parrisia, †Peratosauroides, and †Prodesmodon; Estes, 1969; Denton & O'Neill, 1998; Milner 2000). Estes (1981) considered batrachosauroidids to be closely related to extant proteids. Other enigmatic genera such as †Hylaeobatrachus and †Prosiren may also belong to this lineage (Milner, 2000)
- 68. The monophyletic Cryptobranchidae (e.g., Wiens, 2007; Zhang & Wake, 2009a; Pyron & Wiens, 2011) contains two extant genera (Andrias and Cryptobranchus) and two extinct genera (†Aviturus and †Ulanurus). Gubin (1991) placed †Aviturus and †Ulanurus in the subfamily †Aviturinae within the Cryptobranchidae, but we refrain from recognizing this subfamily taxonomy pending cladistic analyses. Four other extinct genera (†Chunerpeton, †Jeholotriton, †Pangerpeton, and †Regalerpeton) form a clade with extant cryptobranchids exclusive of other salamanders but these have not been formally included within the Cryptobranchidae (Zhang et al. 2009; Skutschas & Gubin, in press; see also Wang & Evans, 2006). Estes (1981) provides details on other taxa considered junior synonyms of Andrias. Skutschas (2009) also includes both †Eoscapherpeton and †Horezmia in the Cryptobranchidae.
- 69. See footnote 65.
- 70. Hynobiidae is monophyletic (e.g., Frost et al., 2006; Zhang & Wake, 2009a; Zheng et al., 2011; Pyron & Wiens, 2011) and sister to the Cryptobranchidae (Larson, 1991; Larson & Dimmick, 1993; Frost et al., 2006; Roelants et al., 2007; Vieites et al., 2007, 2009; Wiens, 2007; Zhang & Wake, 2009a; San Mauro, 2010; Pyron & Wiens, 2011). A close relationship between the Hynobiidae and Cryptobranchidae is supported by morphological data (Noble, 1925; Larsen, 1963; Larson & Dimmick, 1993). Molecular phylogenetic analysis of the recently rediscovered Protohynobius puxiongensis reveals that it is closely related to Pseudohynobius and nested well within Hynobiidae (Peng et al., 2010), thus invalidating the former subfamily Protohynobinae (Fei & Ye, 2000). We follow Venczel (1999) by including the extinct †Parahynobius in the Hynobiidae.
- 71. †Karauridae is an extinct family comprising two genera (†*Karaurus* and †*Kokartus*) from the Jurassic of middle Asia (Ivachnenko, 1978; Nessov, 1988). The †Karauridae is believed to be the sister taxon of extant salamanders (Evans & Milner, 1996; Evans *et al.*, 2005; Skutschas & Martin, 2011; Skutschas & Gubin, in press). Another extinct genus, †*Marmorerpeton*, may be allied to the †Karauridae (Milner, 2000).
- 72. Evidence for two major clades within the Plethodontidae is strong (Vieites *et al.*, 2007, 2011; Camp *et al.*, 2009) and two subfamilies, Hemidactyliinae and Plethodontinae, are recognized (contra Pyron & Wiens, 2011). Vieites *et al.* (2011) recognized four tribes in the Hemidactyliinae and five in the Plethodontinae; their Bolitoglossini and Spelerpini were treated as subfamilies by Chippindale *et al.* (2004) and Pyron & Wiens, (2011). Each subfamily and each tribe is well resolved as monophyletic in molecular phylogenetic analyses (e.g., Chippindale *et al.*, 2004; Mueller *et al.*, 2004; Macey, 2005; Min *et al.*, 2005; Frost *et al.*, 2006; Wiens, 2007; Kozak *et al.*, 2009; Vieites *et al.*, 2011, Pyron and Wiens, 2011). However, inferred relationships among the tribes have changed over time with increases in phylogenetic data (Hedges & Maxson, 1993; Hay *et al.*, 1995; Chippindale *et al.*, 2004; Mueller *et al.*, 2004; Macey, 2005; Min *et al.*, 2005; Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Kozak *et al.*, 2009; Vieites *et al.*, 2011).

Subfamily Necturinae Fitzinger, 1843 (1 genus; 5 species)

Family Rhyacotritonidae Tihen, 1958 (1 genus; 4 species)⁷⁴

Family Salamandridae Goldfuss, 1820 (21–22 genera; 86 species; †9)⁷⁵

Subfamily Pleurodelinae Tschudi, 1838 (16–17 genera; 69 species; †7)

Subfamily Salamandrinae Goldfuss, 1820 (4 genera; 15 species; †1)

Subfamily Salamandrininae Fitzinger, 1843 (1 genus; 2 species)

Family †Scapherpetontidae Auffenberg & Goin, 1959 (†3)⁷⁶

Family **Sirenidae** Gray, 1825 (2 genera; 4 species; †3)⁷⁷

Order **Gymnophiona** Müller, 1832 (caecilians) (31 genera; 188; †3)⁷⁸

Family Caecilidae Rafinesque, 1814 (2 genera; 42 species)⁷⁹

Family **Dermophiidae** Taylor, 1969 (4 genera; 14 species; †1)⁸⁰

Family Herpelidae Laurent, 1984 (2 genera; 9 species)81

Family Ichthyophiidae Taylor, 1968 (3 genera; 50 species)82

Family Indotyphlidae Lescure, Renous & Gasc, 1986 (7 genera; 21 species)83

Family **Rhinatrematidae** Nussbaum, 1977 (2 genera; 11 species)⁸⁴

Family Scolecomorphidae Taylor, 1969 (2 genera; 6 species)⁸⁵

- 76. The extinct family †Scapherpetontidae includes three genera: †Lisserpeton, †Piceoerpeton, and †Scapherpeton (Estes, 1969; Naylor & Krause, 1981). Following Estes (1981), we recognize this as a distinct taxon instead of subsuming these genera within the Dicamptodontidae based on vertebral morphology (i.e., Edwards, 1976). The relationship of the †Scapherpetontidae to other salamander families remains unclear.
- 77. The phylogenetic relationship of the two genera of the Sirenidae (*Pseudobranchus* and *Siren*) to other salamanders has long been enigmatic (e.g., Boyden & Noble, 1933; Larsen, 1963; Estes, 1965). Its monophyly is well established, with most studies resolving it as the sister to a large clade (Salamandroidea) containing Ambystomatidae, Dicamptodontidae, Plethodontidae, Proteidae, Rhyacotritonidae, and Salamandridae (Wiens *et al.*, 2005; Roelants *et al.*, 2007; Wiens, 2007; Pyron & Wiens, 2011), although Zhang & Wake (2009a), using complete mitochondrial genomes, found Sirenidae to be sister to all other salamanders. We follow Evans *et al.* (1996) by including three extinct genera in the Sirenidae (†*Habrosaurus*, †*Kababisha*, and †*Noterpeton*), though we note that the affinities of these taxa remain enigmatic (Rage *et al.*, 1993; Milner, 2000).
- 78. Doubts about monophyly led Frost *et al.* (2006) to recognize only three families: Caeciliidae, Typhlonectidae, and Rhinatrematidae. In order to resolve apparent paraphyly, Wilkinson *et al.* (2011) recognized nine familes. Their classification is compatible with the results of the most comprehensive molecular phylogenetic analyses (Roelants *et al.*, 2007; Zhang & Wake, 2009b; Pyron & Wiens, 2011), yet many taxa remain unsampled. We adopt the classification of Wilkinson *et al.* (2011), which identifies major clades and presents detailed justifications for recognizing these as families (rather than subfamilies as in Pyron & Wiens, 2011); because of this recent presentation, we do not go into detailed summaries for each family of caecilians. The Caeciliidae (sensu Nussbaum & Wilkinson, 1989; see also Wilkinson & Nussbaum, 2006) is the family-level taxon most affected by changes proposed by Wilkinson *et al.* (2011); it is divided into five families (Caeciliidae, Dermophiidae, Herpelidae, Indotyphlidae, and Siphonopidae). †*Apodops*, described by Estes & Wake (1972) as a caeciliid based on stated similarities to *Dermophis*, *Gymnophis*, and *Geotrypetes*, is tentatively placed in the Dermophiidae (M. Wake, pers. comm.). Of the three extinct genera of Gymnophiona, only †*Apodops* is within crown-group Gymnophiona; †*Eocaecilia* and *Rubricaecilia* are likely sister to extant caecilians (Jenkins & Walsh, 1993; Evans & Sigogneau-Russell, 2001; Jenkins *et al.*, 2007).
- 79. See footnote 78.
- 80. See footnote 78.
- 81. See footnote 78.
- 82. Most phylogenetic analyses agree in finding a close relationship between the Icthyophiidae and the former Uraeotyphlidae (Wilkinson & Nussbaum, 1996; Gower et al., 2002; Wilkinson et al., 2003; San Mauro et al., 2004b, 2009; Frost et al., 2006; Loader et al., 2007; Roelants et al., 2007; Gower et al., 2008; Gower & Wilkinson, 2009; Zhang & Wake, 2009b), although most of these studies are based on a single representative of each taxon. Frost et al. (2006) subsumed the Uraeotyphlidae within the Ichthyophiidae based on data for three specimens, one of which was unidentified to species. In studies with richer taxon sampling, Gower et al. (2002), Zhang & Wake (2009b), and Pyron & Wiens (2011) found *Ichthyophis* to be paraphyletic with respect to *Uraeotyphlus*, and *Ichthyophis* is paraphyletic with respect to *Caudicaecilia* (Roelants et al., 2007; Zhang & Wake, 2009b; Pyron & Wiens, 2011). The validity of genera in the Ichthyophiidae requires further research (i.e., Wilkinson et al., 2011).

^{73.} Monophyly of the Proteidae has long been debated (e.g., Larsen & Guthrie, 1974; Hecht & Edwards, 1976). Molecular phylogenetic studies recover a monophyletic Proteidae but with very long internal branches and a split likely in excess of 120 my (Frost *et al.*, 2006; Roelants *et al.*, 2007; Wiens, 2007; Zhang & Wake, 2009a). While we recognize a single family, there are extinct taxa assigned to Proteinae and a reasonable alternative would be to raise the subfamilies (Proteinae and Necturinae) to family level (Zhang & Wake, 2009a). The extinct taxa †*Mioproteus* and †*Orthophyia* are morphologically similar to *Proteus* (Estes, 1981; Milner, 2000) and we place these genera in the Proteinae.

^{74.} The Rhyacotritonidae, containing only the genus *Rhyacotriton*, is sister to the clade comprising the Amphiumidae and Plethodontidae (Mueller *et al.*, 2004; Min *et al.*, 2005; Frost *et al.*, 2006; Wiens *et al.*, 2005; Roelants *et al.*, 2007; Vieites *et al.*, 2007, 2011; Wiens, 2007; Zhang & Wake, 2009a; Pyron & Wiens, 2011; Zheng *et al.*, 2011).

^{75.} Monophyly of the Salamandridae is well established based on morphological and molecular evidence (Wake & Özeti, 1969; Titus & Larson, 1995; Frost et al., 2006; Wiens, 2007; Roelants et al., 2007; Zhang et al., 2008; Zhang & Wake, 2009a; Pyron & Wiens, 2011). Molecular phylogenetic analyses reveal three well resolved clades of salamandrids (Weisrock et al., 2006; Zhang et al., 2008; Pyron & Wiens, 2011) that are each now recognized as a subfamily (Dubois & Raffaëlli, 2009). Following Estes (1981) and Dubois & Raffaëlli (2009), we recognize nine extinct genera in the Salamandridae, with seven in the Pleurodelinae (†Brachycormus, †Carpathotriton, †Chelotriton, †Koallelia, †Oligosemia [considered a possible synonym of Triturus by Estes, 1981], †Palaeopleurodeles, and †Procynops) and one in the Salamandrinae (†Megalotriton). Unlike Dubois & Raffaëlli (2009), we consider the extinct †Archaeotriton as Salamandridae incertae sedis because its affinities remain unclear (Estes, 1981; Venczel, 2008).

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- 84. Rhinatrematidae is monophyletic (Wilkinson & Nussbaum, 1996; Frost *et al.*, 2004; Roelants *et al.*, 2007; Zhang & Wake, 2009b) and is the sister taxon of all other living Gymnophiona (Hedges *et al.*, 1993; Wilkinson & Nussbaum, 1996; San Mauro *et al.*, 2004b, 2009; Frost *et al.*, 2006; Loader *et al.*, 2007; Roelants *et al.*, 2007; Gower *et al.*, 2008; Gower & Wilkinson, 2009; see also Wake, 1993).
- 85. The Scolecomorphidae is a morphologically distinctive clade (Frost et al., 2006; Pyron & Wiens, 2011; Wilkinson et al., 2011).
- 86. See footnote 77.
- 87. While Pyron & Wiens (2011) suggest paraphyly of the aquatic Typhlonectidae with respect to the terrestrial Caeciliidae of Wilkinson *et al.* (2011), their analysis includes but two typhlonectid genera. The morphological similarities among typhlonectids and their distinctiveness in relation to other caecilians are well established (Wilkinson & Nussbaum, 1997, 1999).

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