



## Article

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### Taxonomy of Salamanders of the Family Plethodontidae (Amphibia: Caudata)

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#### Abstract

Several recent publications have made recommendations for changes in the taxonomy of plethodontid salamanders. Here formal taxonomic proposals are made, in accordance with the *Code*, regarding family-group taxa. Subfamilies Hemidactyliinae and Plethodontinae are recognized, the former with four tribes and the latter with five tribes. Genera are assigned to the tribes, and subgenera are recognized in the genera *Batrachoseps*, *Bolitoglossa*, *Hydromantes*, *Oedipina* and *Plethodon*.

**Key words.** Family-group nomina, diagnoses, Batrachosepini new taxon, Aneidini new taxon, Hydromantini new taxon

Recent years have witnessed major changes in our understanding of the phylogenetic relationships of taxa of the largest family of salamanders, the Plethodontidae. These changes have come about in part from generation of new molecular data and their analyses (e.g., Chippindale et al. 2004; Mueller et al. 2004; Vieites et al. 2011), as well as from new discoveries (Camp et al. 2009; Min et al. 2005). However, the taxonomic changes suggested have been done informally, for the most part. Here I offer a formal taxonomy. In this work I have been influenced by the detailed taxonomic treatment of the Family Salamandridae by Dubois and Raffaëlli (2009) and by the critical analysis of Dubois (2008).

The taxonomy based on osteology proposed by Wake (1966) was stable for many years. That taxonomy recognized two subfamilies, Plethodontinae Gray, 1850 and Desmognathinae Gray, 1850. The finding that desmognathines are deeply nested (Chippindale et al. 2004; Mueller et al. 2004) pointed up the need for a taxonomic revision. Chippindale et al. (2004) analyzed some mtDNA sequence data, sequences of a nuclear gene, and some morphological characters; they proposed elevating plethodontine tribes recognized by Wake (1966) to the level of subfamilies (Hemidactyliini to Hemidactyliinae [sic]; Bolitoglossini to Bolitoglossinae; Plethodontini to Plethodontinae, the latter an expansion of Wake's Plethodontinae, now including desmognathines), but they restricted Hemidactyliinae to *Hemidactylum* alone and recognized Spelerpinae for the remainder of Wake's Hemidactyliini. The rank of Desmognathinae was reduced to that of supergenus *Desmognathus* within their Plethodontinae. While Chippindale et al. studied neither *Batrachoseps* nor *Hydromantes*, Mueller et al. included both; *Batrachoseps* was resolved as the sister taxon of *Hemidactylum*, and *Hydromantes* fell within a cluster of taxa including species of the Plethodontinae and the Desmognathinae. Mueller et al. drew no taxonomic conclusions, but indicated the need for multiple independent genetic markers. Dubois (2005) observed that Chippindale et al. had recovered two major lineages and accordingly recognized only two subfamilies, Hemidactyliinae and Plethodontinae; within the Hemidactyliinae he recognized three tribes, Bolitoglossini (including *Batrachoseps* and all tropical genera), Hemidactyliini (only *Hemidactylum*) and Spelerpini. Within the Plethodontinae Dubois recognized two tribes, Desmognathini for the traditional desmognathines as well as *Aneides*, *Ensatina*, *Hydromantes* and *Karsenia*, and Plethodontini for *Plethodon* only. Vieites et al. (2007) presented data from three nuclear genes and found support for a hypothesis of two major plethodontid clades. In an informal taxonomic suggestion in the supplemental on-line materials Vieites et al. (2007) recognized two subfamilies, Plethodontinae and Hemidactyliinae, accepted the supergenus *Desmognathus* within the Plethodontinae, assigned *Hydromantes* to the Plethodontinae, and recognized Spelerpini as a tribe within

Hemidactyliinae. Vieites et al. (2011) expanded taxon coverage and analyzed a dataset of complete mt genomes and three nuclear genes. They found support for two major clades, Plethodontinae and Hemidactyliinae. However, support for topologies in each clade was not sufficient, in their opinion, to warrant much taxonomic structure within each. Their taxonomic proposal was for five tribes within Plethodontinae: Aneidini, a name suggested informally by Dubois (2008) (whose suggestions were not intended to be formal taxonomic statements), including *Aneides* only; Desmognathini Baird, 1850, including *Desmognathus* and *Phaeognathus*; Ensatinini Gray, 1850, including *Ensatina* only; Hydromantini, another name suggested by Dubois (2008), including *Hydromantes* and *Karsenia*; Plethodontini Gray, 1850, including *Plethodon* only. They proposed recognition of four tribes within Hemidactyliinae: Batrachosepini, another name suggested by Dubois (2008), for *Batrachoseps* only; Bolitoglossini Hallowell, 1856, for twelve tropical genera; Hemidactyliini Hallowell, 1856, for *Hemidactylum* only; Spelerpini Cope, 1859, for six genera. The three new names are *nomina nuda* (International Code of Zoological Nomenclature, 1999, Article 13).

The purpose of this note is to propose a formal taxonomy for Plethodontidae. My points of departure are the recent taxonomic proposal for Amphibia by Blackburn and Wake (2011), and the ergotaxonomy of Salamandridae by Dubois and Raffaëlli (2009). However, my proposal is for a minimal taxonomy, not nearly as detailed as that of Dubois and Raffaëlli (2009), yet following their general strategy. I choose to use the terms “Type Genus” rather than “Nucleogenus,” and “Phylogenetic Definition” rather than “Entexognosis” (alternative terminology was used by Dubois and Raffaëlli 2009). General nomenclature and synonymies follow the Amphibian Species of the World website (<http://research.amnh.org/vz/herpetology/amphibia/>; accessed May 27, 2012).

The taxonomy proposed is intended to coordinate with the clades recovered in the phylogenetic analyses of Vieites et al. (2011) and Pyron and Wiens (2011).

At the time of this writing, 431 species of Plethodontidae are recognized (AmphibiaWeb, 2012); 12 were added so far in 2012 (11 newly named, one raised from synonymy) and more will surely be added. The taxonomy proposed here may well need revision as new knowledge emerges. Content of genera and subgenera is available on AmphibiaWeb.

Class **Amphibia** Gray, 1825  
Order **Caudata** Fischer von Waldheim, 1813  
Family **Plethodontidae** Gray, 1850

Subfamily **Hemidactyliinae** Hallowell, 1856

Type Genus.—*Hemidactylum* Tschudi, 1838: 59.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Hemidactylum scutatum* (Temminck and Schlegel, 1838) and excluding *Plethodon glutinosus* Green, 1818.

Diagnosis.—Salamanders with tongue feeding modes IV (attached or free projectile), V (attached projectile), VI (free projectile) or VIII (attached projectile) (Lombard and Wake 1977, 1986), having short-lived or long-lived larval development, or direct development, and having from 14 to 22 trunk vertebrae. Digits of pes 5, but reduced to 4 in some to all species of *Eurycea*, *Hemidactylum* and *Batrachoseps*. Thirteen or 14 pairs of chromosomes.

Comment.—Vieites et al (2011) found strong support for two major clades within Plethodontidae. Pyron and Wiens (2011) also recovered two major clades, but they explicitly retained the four subfamily taxonomy of Chippindale et al. (2004) and mistakenly cited Vieites et al. (2011) as having used the same taxonomy. Hallowell (1856) used the family-group names Bolitoglossidae and Hemidactylidae in the same paper. I select Hemidactyliinae for the name of this subfamily, following Dubois (2005), Vieites et al. (2011), and Blackburn and Wake (2011), and use Bolitoglossini (see below) for a tribe that contains only the tropical plethodontids.

Tribe **Batrachosepini** new taxon.

Type Genus.—*Batrachoseps* Bonaparte, 1839 Fasc. 2: Folio 131.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Batrachoseps attenuatus* (Eschscholtz, 1833) and excluding *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854, *Eurycea lucifuga* Rafinesque, 1822, and *Hemidactylum scutatum* (Temminck and Schlegel, 1838).

Diagnosis.—Slender salamanders with only 4 digits comprising the pes, tongue feeding mode VIII (attached projectile)(Lombard and Wake 1977, 1986), and a skull with a large dorsal fontanelle between the frontal and parietal bones. Sixteen to 23 trunk vertebrae. Direct development with no larval stage. Thirteen pairs of chromosomes.

Comment.—Wake (1966) identified a clade, Bolitoglossini, including three taxa treated as supergenera: *Batrachoseps*, *Bolitoglossa* and *Hydromantes*. Analyses of molecular data place *Hydromantes* within the Plethodontinae, and fail to recover strong support for a sister taxon relationship of *Batrachoseps* and *Bolitoglossa*. However, there are seven morphological synapomorphies related to the tongue feeding system (Wake et al. 2012) shared by *Batrachoseps* and the tropical American taxa grouped here in a more restricted Bolitoglossini. All of the morphological synapomorphies are shared with *Hydromantes* and are almost certainly homoplasies (Lombard and Wake 1986, Wake et al. 2012). A unique synapomorphy of *Batrachoseps* + tribe Bolitoglossini is reduction in the number of chromosomes from 14 to 13 pairs. In some molecular analyses *Hemidactylum* and *Batrachoseps* are sister taxa (summarized in Vieites et al. 2011); accordingly, the taxonomy proposed is conservative in only recognizing well-supported clades. Should new information strongly support a sister-group relationship with members of the tribe Bolitoglossini, a single tribe would be appropriate.

Content.—

Genus *Batrachoseps* Bonaparte, 1839 (22 currently recognized species).

Subgenus *Batrachoseps* Bonaparte, 1839 (19 species).

Subgenus *Plethopsis* Bishop, 1937 (3 species).

#### Tribe **Bolitoglossini** Hallowell, 1856.

Type Genus.—*Bolitoglossa* Duméril, Bibron and Duméril, 1854 9:88.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854 and excluding *Batrachoseps attenuatus* (Eschscholtz, 1833), *Eurycea lucifuga* Rafinesque, 1822, and *Hemidactylum scutatum* (Temminck and Schlegel, 1838).

Diagnosis.—Salamanders of diverse habitus with 5 digits comprising the pes, tongue feeding mode VI (free projectile)(Lombard and Wake 1977, 1986), and skull with fully articulated frontal and parietal bones or with a fontanelle between the parietal bones. Either 14 or 18–22 trunk vertebrae. Direct development with no larval stage. Thirteen pairs of chromosomes.

Comment.—This is by far the largest tribe of Plethodontidae and all treatments (e.g. Wiens et al. 2007, Vieites et al. 2011) recover it as a clade. See comment under *Batrachosepini*.

Content.—

Genus *Bolitoglossa* Duméril, Bibron and Duméril, 1854 (121 species).

Subgenus *Bolitoglossa* Duméril, Bibron and Duméril, 1854 (13 species).

Subgenus *Eladinea* Miranda-Ribeiro, 1937 (57 species).

Subgenus *Magnadigita* Taylor, 1944 (35 species).

Subgenus *Mayamandra* Parra-Olea, García-París and Wake, 2004 (4 species).

Subgenus *Nanotriton* Parra-Olea, García-París and Wake, 2004 (4 species).

Subgenus *Oaxakia* Parra-Olea, García-París and Wake, 2004 (5 species).

Subgenus *Pachymandra* Parra-Olea, García-París and Wake, 2004 (3 species).

Genus *Bradytriton* Wake and Elias, 1983 (1 species).

Genus *Chiropterotriton* Taylor, 1944 (12 species).

Genus *Cryptotriton* García-París and Wake, 2000 (7 species).

Genus *Dendrotriton* Wake and Elias, 1983 (8 species).

Genus *Ixalotriton* Wake and Johnson, 1989 (2 species).

Genus *Nototriton* Wake and Elias, 1983 (16 species).

Genus *Nyctanolis* Elias and Wake, 1983 (1 species).

Genus *Oedipina* Keferstein, 1868 (36 species).

Subgenus *Oedipina* Keferstein, 1868 (21 species).

Subgenus *Oeditriton* McCranie, Vieites and Wake, 2008 (3 species).

Subgenus *Oedopinola* Hilton, 1946 (12 species).

Genus *Parvimolge* Taylor, 1944 (1 species).

Genus *Pseudoeurycea* Taylor, 1944 (49 species).

Genus *Thorius* Cope, 1869 (23 species).

#### Tribe **Hemidactyliini** Hallowell, 1856.

Type Genus.—*Hemidactylum*, Tschudi, 1838: 59, 94.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Hemidactylum scutatum* (Temminck and Schlegel, 1838) and excluding *Batrachoseps attenuatus* (Eschscholtz, 1833), *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854, and *Eurycea lucifuga* Rafinesque, 1822.

Diagnosis.—Small salamanders with 4 digits comprising the pes, tongue feeding mode V (attached projectile) (Lombard and Wake 1977, 1986), and skull with fully articulated frontal and parietal bones with no fontanelle. Mean number of trunk vertebrae 15. Short-lived larval stage. Fourteen pairs of chromosomes.

Comment.—See comment under *Batrachosepini*.

Content.—

Genus *Hemidactylum* Tschudi, 1838 (1 species).

#### Tribe **Spelerpini** Cope, 1859.

Type Genus.—*Spelerpes* [currently *Eurycea*] Rafinesque, 1832: 22.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Eurycea lucifuga* Rafinesque, 1822 and excluding *Batrachoseps attenuatus* (Eschscholtz, 1833), *Bolitoglossa mexicana* Duméril, Bibron and Duméril, 1854, and *Hemidactylum scutatum* (Temminck and Schlegel, 1838).

Diagnosis.—Salamanders of diverse habitus, mostly with 5 digits (two species with 4 digits) comprising the pes, tongue feeding mode IV (attached or free projectile) (Lombard and Wake 1977, 1986), and with skull of metamorphosed species with fully articulated frontal and parietal bones with no dorsal fontanelle. Numbers of trunk vertebrae vary in mean values per species from 13 to 21. Long-lived larval stage which may be the permanent condition in many species. Fourteen pairs of chromosomes.

Comment.—This is a well-supported clade that is recovered as sister to the remainder of the Hemidactyliini (e.g., *Batrachoseps*, tribe *Bolitoglossini*, and *Hemidactylum*), but sometimes not well supported. Given uncertainties in the resolution of relationships, I recognize four tribes within Hemidactyliinae. An alternative would be to recognize two infra-families, one including only Spelerpini and the other including the remaining two (see comment under *Batrachosepini*) or three tribes.

Content.—

Genus *Eurycea* Rafinesque, 1822 (26 species).

Genus *Gyrinophilus* Cope, 1869 (4 species).

Genus *Haideotriton* Carr, 1939 (1 species).

Genus *Pseudotriton* Tschudi, 1838 (2 species).

Genus *Stereochilus* Cope, 1869 (1 species).

Genus *Urspelerpes* Camp, Peterman, Milanovich, Lamb, Maerz and Wake, 2009 (1 species).

#### Subfamily **Plethodontinae** Gray, 1825.

Type Genus.—*Plethodon* Tschudi, 1838: 92.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Plethodon glutinosus* (Green, 1818) and excluding *Hemidactylium scutatum* (Temminck and Schlegel, 1838).

Diagnosis.—Salamanders with tongue feeding modes I (attached protrusible), II (attached protusible), III (attached projectile) or VII (free projectile)(Lombard and Wake 1977, 1986), having short-lived or long-lived larval development, or direct development, and having from 13 to 24 trunk vertebrae. Five digits in pes. Fourteen pairs of chromosomes.

#### Tribe **Aneidini** new taxon.

Type Genus.—*Aneides* Baird, 1851: 2, 257.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Aneides lugubris* (Hallowell, 1849) and excluding *Desmognathus fuscus* (Rafinesque, 1820), *Ensatina eschscholtzii* Gray, 1850, *Hydromantes platycephalus* (Camp, 1916) and *Plethodon glutinosus* (Green, 1818).

Diagnosis.—Salamanders of moderate to large size that lower the mandible to open the mouth and feed with tongue feeding mode II (attached protrusible)(Lombard and Wake 1977, 1986), having well ossified, solidly articulated skull with single premaxillary bone, and from 15 to 18 trunk vertebrae. Tail base unconstricted. Direct development with no larval stage.

Comment.—Relationships within Plethodontinae are not fully resolved and so I elect to recognize five tribes. An alternative would be to include *Aneides* in Ensatini, but a sister taxon relationship between *Aneides* and *Ensatina* is not well supported (Vieites et al. 2011). Another alternative would be to recognize infrafamilies for Plethodontini, on the one hand, and for *Aneides* and all other members of Plethodontinae, on the other (but see comment under Hydromantini, below).

Content.—

Genus *Aneides* Baird, 1851 (6 species).

#### Tribe **Desmognathini** Baird, 1850.

Type Genus.—*Desmognathus* Baird, 1850: 252.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Desmognathus fuscus* (Rafinesque, 1820) and excluding *Aneides lugubris* (Hallowell, 1849), *Ensatina eschscholtzii* Gray, 1850, *Hydromantes platycephalus* (Camp, 1916) and *Plethodon glutinosus* (Green, 1818).

Diagnosis.—Very small to large terrestrial or aquatic salamanders that raise the skull to open the mouth and feed with tongue feeding mode I (attached protrusible)(Lombard and Wake 1977, 1986), having a compact, fully ossified skull with single premaxillary bone and from 15 to 23 trunk vertebrae. Tail base unconstricted. Short-lived to long-lived larvae, or direct development with no larval stage.

Comment.—The species of *Desmognathus* and *Phaeognathus* are always recovered as a clade (Kozak et al. 2009; Vieites et al. 2011) that is relatively deeply nested within the Plethodontinae. Because it has for long been recognized as a distinctive, readily identifiable group, I recommend restricting Desmognathini to members of the two included genera.

Content.—

Genus *Desmognathus* Baird, 1850 (21 species).

Genus *Phaeognathus* Highton, 1961 (1 species).

#### Tribe **Ensatini** Gray, 1850.

Type Genus.—*Ensatina* Gray, 1850: 48.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Ensatina eschscholtzii* Gray, 1850 and excluding *Aneides lugubris* (Hallowell, 1849), *Desmognathus fuscus* (Rafinesque, 1820), *Hydromantes platycephalus* (Camp, 1916) and *Plethodon glutinosus* (Green, 1818).

Diagnosis.—Terrestrial salamanders of moderate size that lower the mandible to open the mouth and feed with tongue feeding mode III (attached projectile)(Lombard and Wake 1977, 1986), having a lightly ossified but well-articulated skull with paired premaxillary bones. Short bodied, with 14–15 trunk vertebrae. Autotomy constriction at base of tail. Direct development with no larval stage.

Comment.—See comment under Aneidini.

Content.—

Genus *Ensatina* Gray, 1850 (1 species).

#### Tribe **Hydromantini** new taxon.

Type Genus.—*Hydromantes* Gistel, 1848: xi.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Hydromantes platycephalus* (Camp, 1916) and excluding *Aneides lugubris* (Hallowell, 1849), *Desmognathus fuscus* (Rafinesque, 1820), *Ensatina eschscholtzii* Gray, 1850 and *Plethodon glutinosus* (Green, 1818).

Diagnosis.—Terrestrial salamanders of small to moderate size that raise the skull to open the mouth with tongue feeding mode II (attached protrusible) or VII (free projectile)(Lombard and Wake 1977, 1986), having a well articulated skull or a weakly articulated skull always with paired premaxillary bones (Buckley et al. 2011). Short bodied, 13–16 trunk vertebrae. Tail base unstricted. Direct development with no larval stage.

Comment.—This clade is usually recovered but it is sometimes not well supported (Vieites et al. 2007, 2011). I recognize this clade as a tribe. It includes all Old World plethodontids. Should *Karsenia* + *Hydromantes* be found not to constitute a clade, some taxonomic revision would be in order. Because I think that *Desmognathini* is usefully set apart from other members of *Plethodontinae*, other tribes should be recognized, exactly which depending on the nature and robustness of future phylogenetic hypotheses (see comments under *Aneidini* and *Desmognathini*).

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Genus *Hydromantes* Gistel, 1843 (11 species).

Subgenus *Atylodes* Gistel, 1868 (1 species).

Subgenus *Hydromantes* Gistel, 1843 (3 species).

Subgenus *Speleomantes* Dubois, 1984 (7 species).

Genus *Karsenia* Min, Yang, Bonnet, Vieites, Brandon and Wake, 2005 (1 species).

#### Tribe **Plethodontini** Gray, 1850.

Type Genus.—*Plethodon* Tschudi, 1838: 92.

Phylogenetic Definition.—The most inclusive monophyletic taxon including the species *Plethodon glutinosus* (Green, 1818) and excluding *Aneides lugubris* (Hallowell, 1849), *Desmognathus fuscus* (Rafinesque, 1820), *Ensatina eschscholtzii* Gray, 1850 and *Hydromantes platycephalus* (Camp, 1916).

Diagnosis.—Terrestrial salamanders of small to moderate size that lower the mandible to open the mouth and use tongue feeding mode II (attached protrusible)(Lombard and Wake 1977, 1986), having a moderately articulated skull with paired premaxillary bones, and 14–24 trunk vertebrae. Tail base unstricted. Direct development with no larval stage.

Comment.—*Plethodon* is always recovered as a clade in analyses of molecular data, and it may be the sister taxon of all other members of *Plethodontinae* (Kozak et al. 2009, Vieites et al. 2011). Should this sister-group relationship be found to be well supported, an alternative taxonomy would be to place *Plethodon* in its own infrafamily and place the remaining genera in a coordinated infrafamily containing several tribes (see comments under *Aneidini*, *Desmognathini* and *Hydromantini*).

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*Plethodon* Tschudi, 1838 (55 species).

Subgenus *Hightonia* Vieites, Nieto-Román, Wake and Wake, 2011 (9 species).

Subgenus *Plethodon* Tschudi, 1838 (46 species).

## Summary

Following is a summary of the suprageneric taxonomy and general geographic distribution of the family Plethodontidae, as treated herein:

### Family Plethodontidae

#### Subfamily Hemidactyliinae

Tribe Batrachosepini (West Coast Region of North America)

Tribe Bolitoglossini (New World Tropics)

Tribe Hemidactyliini (Eastern and Central North America)

Tribe Spelerpini (Eastern and Central North America)

#### Subfamily Plethodontinae

Tribe Aneidini (Eastern and Western North America, and New Mexico)

Tribe Desmognathini (Eastern and Central North America)

Tribe Ensatinini (West Coast Region of North America)

Tribe Hydromantini (California, South Korea, Southwestern France, Italian Mainland, and Sardinia)

Tribe Plethodontini (Eastern, Central and Western North America).

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