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Taxonomy of the Plethodontid Salamander Genus *Hydromantes* (Caudata: Plethodontidae)

David B. Wake[1], Alfredo Salvador[2], Miguel A. Alonso-Zarazaga[3]

[1]Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720-3160
e-mail: wakelab@uclink.berkeley.edu

[2]Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

[3]Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

The plethodontid salamanders that occur in Europe are included in the taxon *Speleomantes* Dubois 1984, which is treated either as a genus (e.g., Lanza, 1999), or as one of two subgenera of *Hydromantes* Gistel 1848 (e.g., Jackman et al., 1997). In the latter case, the subgenus *Hydromantes* includes only North American (i.e., Californian) species. The taxonomic history of *Hydromantes* (*sensu lato*) is complicated. The species currently assigned to *Hydromantes* and/or *Speleomantes* were placed in various genera (e.g., *Geotriton*, *Spelerpes*) prior to 1923, when Dunn made a proposal that stabilized taxonomy (all species placed in *Hydromantes*) for over 60 years, until Lanza and Vanni (1981) placed the American species (by this time, three in number) in a new genus *Hydromantoides* on the basis of morphological and genetic data (see also Lanza et al., 1995). Dubois (1984) showed that Dunn had erred in technical but significant details of taxonomic procedure in using the name *Hydromantes*, and proposed a new name, *Speleomantes*, for the European species. His suggestion for the taxonomy of the group was to recognize a single genus, *Hydromantoides*, with two subgenera, *Hydromantoides* and *Speleomantes*. Lanza (1986) subsequently raised *Speleomantes* to generic level.

The name *Hydromantes* had been widely used, and the demonstration by Dubois (1984) that it was a substitute name for a taxon whose type species is a member of the Salamandridae had serious implications. Dubois reduced *Hydromantes* to the synonymy of *Triturus* Rafinesque, 1815, which of course made it unavailable for plethodontids. This led Smith and Wake (1993) to offer a possible solution to the International Commission on Zoological Nomenclature. They suggested that *Salamandra genei* Temminck & Schlegel, 1838 be designated as the type species of *Hydromantes*, thereby preserving the name for species of the Plethodontidae. Discussion followed (Dubois,

1995; Salvidio, 1995; Smith et al., 1995, 1996), and a modification of the proposal was offered that would retain *Speleomantes* for European species and restore *Hydromantes* for American species (Dubois, 1995). This proposal was accepted, and the International Commission on Zoological Nomenclature issued Opinion 1866 (1997) designating *Spelerpes platycephalus* Camp, 1916 as the type species of *Hydromantes* Gistel, 1848.

Although Gistel (1848) had used *Hydromantes* originally as a replacement name for *Geotriton* (i.e., *Triturus*), twenty years later (Gistel, 1868) he reverted to use of *Geotriton* and the name *Hydromantes* did not appear. The two species he assigned to *Geotriton* in 1868 were identified as " *fuscus* Bonap." and "*cinereus*? Merr.". The intention of Gistel (1868) is clear, because following the entry "G e o t r i t o n Bonap." the vernacular name is given: "Höhlenmolch", or Cave Salamander, the widely used term for the biological entity that he referred to *Geotriton fuscus* and that currently is known as either *Hydromantes (Speleomantes) italicus* or *Speleomantes italicus*.

Gistel (1868) listed a number of genera under the general heading "Salamandrini (Salamanderartige Lurche)". The first genus listed is "LIII A t y l o d e s Gistel (Ohndrüser)", and its only species is "103 G e n e i", from "Sardinien". The brief description of *Atylodes*, in German, is accurate for the taxon today known as *Hydromantes (Speleomantes) genei*, which occurs only on the southwestern part of the island of Sardinia. The next genus listed is "LIV, *Salamandra*", and from context it is apparent that Gistel was distinguishing *Atylodes* from *Salamandra*. The vernacular name he chose for *Atylodes* translates into English as the glandless salamander, and Gistel explicitly emphasized the lack of parotoid glands ("Keine Parotiden"). *Geotriton* appears later in the list, as genus number LVIII.

Had the work of Gistel (1868) been known to Dubois (1984), we believe that he would have adopted the name *Atylodes* rather than proposing the new name *Speleomantes*. Gistel's work has been cited rarely in the herpetological literature and the name *Atylodes*, mentioned by Neave (1939) in his list of generic and subgeneric taxa, remained undiscovered until now. Mertens (1936) was the first to mention Gistel's book when he revalidated the taxon *Podarcis muralis* var. *wagleriana* Gistel, 1868 and elevated it to species rank in combination with *Lacerta*, *Lacerta wagleriana* (Gistel, 1868). In later years, this taxon and Gistel's book were mentioned by Mertens and coworkers in two checklists of the European herpetofauna (Mertens & Müller, 1940, Mertens & Wermuth, 1960), and more recently, Arnold (1973) transferred *Lacerta wagleriana* to *Podarcis wagleriana* and again cited Gistel's book. Mertens (1936) explicitly lists *Atylodes* among the new taxa in Gistel (1868), as follows: "Caudata. S. 158 *Atylodes*, Typus: *Salamandra genei* SCHLEGEL: - *Hydromantes* GISTEL 1848." THE latest edition of the International Code of Zoological Nomenclature (1999) protects *Speleomantes*, which has been cited extensively since it was first proposed. Our proposal is that the name *Atylodes* also should be preserved and herein we present our argument.

Molecular and morphological studies of *Hydromantes* (*sensu lato*) have shown that the genus is monophyletic and that it includes three, not two, subclades. Wake (1966) presented morphological evidence of monophyly for the genus, and those characters have not been challenged. Especially compelling is the unique hyobranchial apparatus and tongue (see also Lombard and Wake, 1973, 1986; Lanza et al., 1995; Jackman et al., 1997). Molecular data also support monophyly (sequences of the

mitochondrial gene cytochrome b), as does a combined analysis of morphological and molecular data (Jackman et al., 1997).

Within *Hydromantes* Wake (1966) showed that the European and American species differed in some osteological features (shape of facial process of maxilla, most ribs bicipital in American species but unicipital in European species), and there are also some other morphological and behavioural differences (Lanza and Vanni, 1981; Lanza et al., 1995). Wake et al. (1978) measured albumin immunological distances between the two groups and obtained distances of 47 and 48. They suggested on the basis of these and allozymic data that the European and American lineages had been diverging for about 28 million years (using a molecular evolutionary clock calibration of 1.7 albumin immunological distance units equals roughly one million years). Immunological distances between species within the American group were from 1-9, but distances between the European species were not measured because antiserum was available only for the American species *Hydromantes shastae*.

Wake et al. (1978) presented a limited study of allozymes (18 loci in 70 specimens, including all American species plus one population each of *H. genei* and *H. italicus*) and reported large genetic distances between the European and American species (averaging D_{Nei} of about 1). Surprisingly, Wake et al. also found a genetic distance of about 1 between the two European species studied (*Hydromantes genei* and *Hydromantes italicus*).

Extensive electrophoretic investigations of the European species by Lanza et al. (1995) and Nascetti et al. (1996) using 33 loci in nearly 500 specimens reported genetic distances between European and American species so great as to be essentially

unmeasureable. The three species from eastern Sardinia (*H. flavus, H. imperialis, H. supramontis*) are more closely related to the species on the European mainland (*H. ambrosii, H. italicus, H. strinatii*) than they are to *H. genei*, which is limited in distribution to the southwestern part of the island. Genetic distances between *H. genei* and the other European species are greater than 1.47 (Wake et al., 1978, reported a distance of 1.135 with their limited sample). Nascetti et al. (1996) also reported substantial geographic differentiation within the limited range of *H. genei* (D_{Nei} as great as 0.25), raising the possibility that more than a single species should be recognized and suggesting that the taxon is relatively old.

Nardi (1991) showed that morphologically differentiated sex chromosomes of the XX/XY type occur in the continental species, as well as in the eastern Sardinian species. However, sex chromosomal dimorphism is absent in *H. genei*. The American species of *Hydromantes* also lack morphologically differentiated sex chromosomes, and this is generally thought to be an ancestral feature in the Plethodontidae (Sessions and Kezer, 1991). The 14th pair of chromosomes of the American species is metacentric (presumed to be the ancestral state) whereas that of *H. genei* and the other European species is subtelocentric. Nardi (1991) also reported differences between *H. genei* and the other European species with respect to the distribution of centromeric satellites on chromosomes, and furthermore found that *H. genei* differed from the others in having more pericentric heterochromatin and more restriction sites for a particular marker in ribosomal genes. In a later study, Nardi et al. (1999) report a number of differences between *H. shastae, H. genei,* and the other European species with respect to repetitive DNA. The results, too technical to be easily summarized here, suggest that *H. genei*

retains some ancestral elements, and it consistently differs from other European species as well as from *H. shastae.*

Lanza and Leo (2001) reported that one population of *Hydromantes imperialis* gives birth to living young, but the data, although based on independent observations by two observers, were scanty. Early reports of live-bearing in continental species are suspect, and although reproductive habits of the different species of European plethodontids are not fully known, the American species are all oviparous, as is *H. genei,* and clutches of eggs are known for some but not all of the remaining European species (Lanza, 1999). Thus, all of the provocative accounts of live-bearing are for mainland or eastern Sardinian species (Lanza, 1999; Lanza and Leo, 2001).

Studies of sequences of the mitochondrial gene cytochrome b (Jackman et al., 1997) showed that the European and American species group were well differentiated from each other, with each forming a clade. A basal polytomy in the European clade left relationships between *H. italicus, H. genei,* and two species from eastern Sardinia unresolved (however *H. supramontis* and *H. flavus* were close relatives with high support). The Kimura 2-parameter distance between *H. genei* and the other European species was the highest recorded in the European clade (13.7-15%). More extensive studies of DNA sequence evolution in *Hydromantes* are in progress.

Larson et al. (2003) summarized available data for *Hydromantes* and suggested an approximate early Eocene divergence of the American and European lineages and an Oligocene divergence of the two European lineages from each other. In turn, they suggest an Early Miocene divergence of the eastern Sardinian and mainland lineages. The weight of all available evidence (as hypothesized by Lanza et al., 1995, and

critically evaluated by Delfino et al., 2004) is that the European and American lineages separated very long ago, possibly associated with the separation of the continental masses that gave rise to North America and Europe around 50 ma.

Lanza (1983), Nardi (1991), Lanza et al. (1995), Nascetti et al. (1996) and Delfino et al. (2004) all discuss historical biogeography of the European species. Progenitors of *H. genei* are thought to have separated from a continental ancestral stock (fossil *Hydromantes* are known from the Middle Miocene of Slovakia, Venczel and Sanchíz, 2004) during the late Oligocene (27-30 Myr) when a Sardinian-Corsican microplate was detached from the main European plate. Lanza (1983; see also Lanza et al., 1995) hypothesized that the microplate that became Sardinia may have formed from two parts, which migrated separately with ancestors of *H. genei* occupying a small "Iglesiente block", a fossil island that definitively joined the larger block for form the present island of Sardinia in the Pliocene. Ancestors of the present-day species of eastern Sardinian are thought to have migrated from the mainland to the larger of the two parts of the microplate during the latest Miocene (Messinian, about 6 Myr), when desiccation restored a land connection to the continent. Although Nascetti et al. (1996) also considered a more recent alternative, the new molecular data (Jackman et al., 1997, not cited by Nascetti et al.) and the analysis of Larson et al. (2003) are more compatible with the scenario of Lanza et al. (1995).

All available data agree that *H. genei* is widely divergent from the other European species in proteins, mitochondrial DNA, sex chromosomes, and perhaps even in reproduction, and to a minor extent in morphology. Accordingly, because we think that the phylogenetic information is most readily reflected taxonomically through the use of

subgenera (see arguments in Jackman et al., 1997, and Parra-Olea et al., 2004), we propose the following taxonomy:

Genus *Hydromantes* Gistel, 1848

Subgenus *Hydromantes* Gistel, 1848

Included species: *Hydromantes (Hydromantes) platycephalus* (Camp, 1916); *Hydromantes (Hydromantes) brunus* Gorman, 1954; *Hydromantes (Hydromantes) shastae* Gorman and Camp, 1953

Subgenus *Atylodes* Gistel, 1868

Included species: *Hydromantes (Atylodes) genei* (Temminck and Schlegel, 1838).

Subgenus *Speleomantes* Dubois, 1984

Included species: *Hydromantes (Speleomantes) italicus* Dunn, 1923; *Hydromantes (Speleomantes) ambrosii* Lanza, 1955; *Hydromantes (Speleomantes) flavus* Stefani, 1969; *Hydromantes (Speleomantes) supramontis* Lanza, Nascetti et Bullini, 1986; *Hydromantes (Speleomantes) imperialis* Stefani, 1969; *Hydromantes (Speleomantes) strinatii* Aellen, 1958.

Because this is also a phylogenetic classification it is readily convertable to alternative classification systems, such as the phylocode. In a phylogenetic classification

the generic level clade would be *Hydromantes*. If *Atylodes* and *Speleomantes* are sister taxa, as all available morphological and biochemical evidence suggests, the name of the subordinate clade would be *Atylodes*, which has priority over *Speleomantes.*

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