The enigmatic history of the European, Asian and American plethodontid salamanders

David B. Wake*

Abstract. Recently published research addressing the question of relationships and biogeography of European plethodontid salamanders has refined time estimates for divergence from American relatives. The recently discovered Korean plethodontid Karsenia is either the sister-taxon of Hydromantes (which has members in Europe and California), or a close relative and co-member of a larger clade that originated in western North America, not eastern North America as formerly thought. The new information strengthens the biogeographical hypothesis that Hydromantes entered Eurasia via the Bering Land Bridge. Arguments are made favoring the placement of European and American relatives in a genus Hydromantes, with an American clade (subgenus Hydromantes) and a European clade (subgenera Atylodes and Speleomantes).

Keywords: Atylodes, biogeography, Hydromantes, morphology, paleogeography, phylogeny, Speleomantes, taxonomy.

Introduction

When the clade of salamanders today bearing the name Plethodontidae was first recognized and named by Gray (1850), it contained species in both Europe and North America. With the passage of time, more and more plethodontids were found in North America, and then the American tropics. The European species, always few in number in comparison to American relatives, were characterized as having a freely projectile tongue and five toes. They were assigned to Geotriton by Gray (1850) (Geotriton later was shown by Dunn, 1923, to be based on a salamandrid and, hence, invalid), and American species with similar traits were placed in Spelerpes (later found to be a junior synonym of Eurycea; Stejneger and Barbour, 1917). A period of taxonomic instability ensued until Strauch (1870) placed European species and American species that had five toes and a projectile tongue in Spelerpes. This taxonomy was adopted in the influential catalogue of Boulenger (1882), but some workers, including Cope (1889), placed species with five toes, partially webbed hands and feet, a projectile tongue, and two premaxillary bones back into Geotriton. Cope remarked on the curious fact that his Geotriton was the only member of a very distinctive and well-marked family that occurred in Europe.

A big change occurred when Camp (1916) described a new species of Spelerpes from the high Sierra Nevada (10 800 ft [3292 m]) of California. Dunn (1923) coined Hydromantes as a replacement name for Geotriton, assigned Camp’s species as the only American representative, and thereby established the fact that that genus had a remarkable distribution, two species in the central Mediterranean region of Europe and one at the heights of the Sierra Nevada of California.

Dunn (1926) thought that Hydromantes italicus was the “most primitive” species of the genus, and that Hydromantes genei was “perhaps closer” to H. platycephalus (see fig. 1) than to H. italicus. He hypothesized that the genus had once been more widely distributed in Europe, and that it had recently become extinct on Corsica. Dunn proposed that continental glaciation and the development of “east-west mountain systems” together were the cause of European extinctions. Furthermore, he hypothesized that Hydromantes had come to Europe through the north, by way of Greenland and Iceland.
Early in my career I noted the following statement in the then new book by Darlington (1957, p. 163): “The *Hydromantes* in Europe is presumably a relict, surviving from a time when plethodontids were widely distributed in Eurasia”. Darlington also noted that herpetologists “apparently agreed” that the European and American species were congeneric. This stimulated me to investigate the zoogeography of the Plethodontidae, a topic that continues to be a focus of research in my laboratory.

It did not take me long to encounter the work of Benedetto Lanza, whose work on *Hydromantes* first started to appear in the mid-1940s. Through the years Dr. Lanza produced many papers dealing with European *Hydromantes*, culminating in such works as the monograph dealing with morphological and genetic studies (Lanza et al., 1995) and the masterful summary of virtually everything known up to the time of publication on the European species (Lanza et al., 2006 [2005]). However, at the time of the latter publication, the first Asian plethodontid, *Karsenia koreana*, had just been described (Min et al., 2005), and the subsequent studies of that species and *Hydromantes*, especially new molecular work, were not available. Here I incorporate new information concerning Californian and Asian species, summarize information published since 2006, and present my views on topics ranging from phylogeny and morphology to taxonomy and biogeography.

### Phylogenetics

When Gray (1850) named the Plethodontidae he included within it species currently considered plethodontids from the Americas, *Hydromantes* (then *Geotriton*) from Europe, but also some present-day ambystomatids and hynobiids. Various familial arrangements were proposed, but following Dunn (1926), the current taxonomy has held, with his *Hydromantes* including two European species as well as the relatively recently described and still poorly known (only from two specimens at that time) *Hydromantes platycephalus*. Cope (1889) recognized two main divisions of plethodontids, Plethodontiae (*Plethodon*, *Hemidactylus*, *Batrachoseps*, *Stereochilus*, and *Autodax* [= present-day *Aneides]*) and Spelerpae (*Geotriton* [= present-day *Hydromantes*], *Gyrinophilus*, *Manculus*

---

**Figure 1.** Adult cave salamander from California (*Hydromantes platycephalus*). Photo by Sean Rovito. This figure is published in colour in the online version.
 [= present-day *Eurycea*, in part], *Spelerpes* [= most species of present-day *Eurycea*, *Pseudotriton* and some tropical species, mainly present-day *Pseudoeurycea*], *Oedipus* [= present-day tropical salamanders in several genera], and *Oedipina*). This suggested relationship of *Hydromantes* was based principally on the presence in all species of a freely projectile tongue. Dunn (1926) placed all tropical plethodontids in *Oedipus*, and it and *Hydromantes* were included in his free-tongued *Eurycea* group. *Oedipus* was shown to be a preoccupied name by Taylor (1940), who substituted *Bolitoglossa*, and later Taylor (1944) began the dismantling of *Bolitoglossa* into a number of genera (currently 12; Wake, 2012). Tanner (1952) undertook a comparative study of the hyobranchial musculature of tropical salamanders and compared them with *Hydromantes*. One conclusion was that *Hydromantes* seemed to be a close relative of *Bolitoglossa* and *Magnadigita* (the latter today recognized as a subgenus of *Bolitoglossa*; Wake, 2012). In my first contribution to this question (Wake, 1966), *Hydromantes* was considered to be a relative of the tropical clade and of *Batrachoseps* (from western North America), with *Hydromantes* envisioned as a sister-taxon of the other two taxa. These relationships appeared to be well supported by morphological data, and the same relationship was found by Lombard and Wake (1986). However, this hypothesis required extensive homoplasy, and even the freely projectile tongue and the partially to fully webbed digits, previously the main reasons for associating *Hydromantes* and the tropical genera, were found to be convergently evolved.

No one seemed to question that the American species and the European species of *Hydromantes* were close relatives. For example, Adams (1942) made detailed comparisons of the cranial osteology and head region musculature of *H. genei* and *H. platycephaalus*. He concluded that the two species were “alike” in osteology (but see below), and that while there were great similarities in musculature, there were sufficient differences to indicate that species status was warranted. This was the first detailed demonstration of the close similarity of the European and American species of *Hydromantes*. With respect to morphology, the species of *Hydromantes* possessed many unique features that strongly suggested that they were phylogenetically close relatives.

Subsequent studies only served to substantiate Adams’ conclusions. My doctoral dissertation (see Wake, 1966) treated the comparative osteology of Plethodontidae, sampling *H. brunus*, *H. genei*, *H. italicus*, *H. platycephaalus*, and *H. shastae*. While noting a few differences between the American and European species, those species shared many derived features and they were placed in a supergenus *Hydromantes*, together with a supergenus *Batrachoseps* and a supergenus *Bolitoglossa* (for the then-recognized seven genera of neotropical plethodontids), with *Hydromantes* as the sister-taxon to a clade constituted of the other two. A detailed assessment of the tongue and associated structures (Lombard and Wake, 1977, 1986) showed the species of *Hydromantes* to differ dramatically from all other plethodontids in many aspects of tongue morphology. So, on abundant morphological grounds, European species of *Hydromantes* are not only plethodontids (they have all of the diagnostic characters of the family, including lunglessness), but are close phylogenetic relatives of the three American species.

The era of biochemical systematics began in earnest in the 1970s, when such methods as electrophoretic analysis of allozyme variation and immunological approaches such as micro-complement fixation came into general use. Both of these methods were used by Wake et al. (1978) to study *Hydromantes*. The allozyme data showed small genetic distances among American species (maximum Nei D of 0.553) but the two European species studied, *H. genei* and *H. italicus*, differed greatly (Nei D = 1.135). The difference between the European and American species was even greater,
between 1.276 and 1.399. Immunological distances among the American species were low, between 0 and 9, whereas distances to the European species were 47 and 48. In contrast, immunological distances to outgroup taxa (two species of *Batrachoseps* and three neotropical plethodontids) were from 75 to 105. In combination, these data supported the inferences of relationships from morphology. However, a surprise was the discovery that the Sardinean *H. genei* was greatly differentiated from the mainland *H. italicus*. Subsequent studies by Italian workers (Lanza et al., 1986, 1995; Nascetti et al., 1996) using more allozymes and refined methods revealed even higher levels of variation between European and American salamanders, and Lanza et al. (1986) showed large differences between *H. genei* and the other European species. Furthermore, they showed that Sardinean forms other than *H. genei* were closer relatives of the mainland species than to *H. genei*. In addition to describing a new Sardinean species, they raised former subspecies of *H. genei* to full species rank.

With the advent of DNA sequencing, the relationships of *Hydromantes* were re-investigated, always with the goal of determining whether the European species and American species of the genus were truly more closely related to each other than to members of other taxa. Jackman et al. (1997) obtained 555 basepairs of the mitochondrial gene cytochrome b from samples of *Hydromantes* (one sample each of four European species, three from Sardinia and *H. italicus*; five samples of the three American species) and *Batrachoseps* (five samples of three species of subgenus *Batrachoseps*; three samples of three species of subgenus *Plethopsis*), as well as samples of *Bolitoglossa, Aneides, Plethodon*, and *Aneides*. The most important result is that European and American species of *Hydromantes* were each other’s closest relatives. Furthermore, and surprisingly, the differences between the two groups were less than between the two subgenera of *Batrachoseps* (which occur in Oregon, California, and Baja California Norte in western North America). But another unremarked result was that *Batrachoseps* and *Bolitoglossa* did not form the sister taxon of *Hydromantes*. With respect to genetic distances (Kimura 2 parameter), *Hydromantes* and either *Batrachoseps* (0.178-0.252) or *Bolitoglossa* (0.191-0.242) tended to be more differentiated than members of the tribe Plethodontini (0.142-0.222), and the phylogenetic analysis found ambiguity with respect to the closest relative of *Hydromantes*. These results served notice that the long-maintained view that *Hydromantes*, *Batrachoseps* and the tropical species (supergenus *Bolitoglossa*) form a clade should be tested.

The first strong evidence that *Hydromantes* was not a bolitoglossine came from analysis of complete mitochondrial genes (Mueller et al., 2004). While the two species of *Hydromantes* studied (the American *H. brunus* and the European *H. italicus*) formed a strongly supported clade, it was nested within a clade containing *Aneides, Desmognathus, Ensatina, Phaeognathus*, and *Plethodon*. There were three major surprises in this result: 1. The long-standing view that desmognathines formed a sister-taxon to other plethodontids was rejected (a result confirmed by Chippindale et al. [2004] using a nuclear gene [Rag1], portions of two mitochondrial genes, and traditional morphological characters; they did not study *Hydromantes*); 2. *Desmognathus* and *Phaeognathus* were nested within the plethodonines (members of the tribe Plethodontini – *Aneides, Ensatina*, and *Plethodon*); 3. *Hydromantes* was also nested within the plethodonines with high statistical confidence, and its closest relative was *Aneides* (although this result had low statistical confidence).

When Min et al. (2005) announced the discovery of the first Asian plethodontid, *Karsenia* from Korea, they included the new form in a phylogenetic analysis based on the nuclear gene Rag1. Both were members of a clade that included *Aneides, Desmognathus, Ensatina, Phaeognathus* and *Plethodon*, with
high statistical support; *Hydromantes* was found to be sister to *Ensatina*, but with low statistical support.

Roelants et al. (2007) studied one mitochondrial and four nuclear genes in a subset of plethodontids that included both American (*H. platycepha*lus) and European (*H. italic*us) species. Among relevant taxa they had only *Ensatina, Desmognathus*, and *Plethodon*, but again *Hydromantes* was found to be monophyletic and to be nested within the plethodontine + desmognathine clade, as a sister-taxon of a *Desmognathus + Ensatina* clade (with weak statistical support for both relationships).

This study was followed by that of Vieites et al. (2007), which used three nuclear genes; they again found that *Hydromantes* and *Karsenia* were nested within the plethodontines + desmognathines, with high statistical support. *Hydromantes* and *Karsenia* were found to be sister-taxa, and in turn to form a sister-taxon relationship with a clade including *Aneides, Desmognathus*, and *Ensatina*. *Plethodon* was the sister to the combined clade of the other species.

A complete mitochondrial genome of *Karsenia* and data for three nuclear genes were added by Vieites et al. (2011). The results support the earlier molecular work in finding a monophyletic *Hydromantes*, two major clades of plethodontids, and inclusion of *Hydromantes* in the subfamily Plethodontinae. There is also statistical support for a sister-taxon relationship of *Hydromantes* and *Karsenia*, and this clade is sister to a clade including *Aneides, Desmognathus, Ensatina* and *Phaeognathus*. *Plethodon* is the sister-taxon of all other plethodontines.

Pyron and Wiens (2011) added no new data for plethodontids, but included data from GenBank for nine nuclear and three mitochondrial genes and included all taxa for which data were available. However, complete data were not available for any taxon, and some taxa were represented by as little as 3% of the possible total of 12,712 base pairs. The mitochondrial gene 16S was available, at least in part, for 90% of the taxa, but 10 of the genes were available, in part, from as many as 43% of the taxa to as few as 6%. Despite its limitations, this work contains the most comprehensive analysis of amphibian relationships. Important findings include: 1. *Hydromantes* is monophyletic; 2. *Hydromantes* is the sister-taxon of a clade that includes *Aneides, Ensatina, Desmognathus, Karsenia, Phaeognathus* and *Plethodon*. These taxa constitute the subfamily Plethodontinae. However, it must be kept in mind that they did not include the majority of available data for the mitochondrial genome (Mueller et al., 2004).

Some questions remain concerning the relationships of *Hydromantes* to other plethodontines, but the closest relationship with the best support to date is with *Karsenia*. These questions doubtless will be pursued using rapidly developing next generation sequencing methods to obtain enlarged databases.

**Morphological, ecological and behavioral comparisons**

Lanza et al. (2006 [2005]) usefully summarized information concerning the biology of European *Hydromantes* and also included references to the American species. I will build on this foundation. Vastly more information is available for the European than for the American species, which remain poorly known biologically, largely because they are, in general, less common and more difficult to study than the European species.

The great morphological similarity between European and American species was documented by Adams (1942), whose work was not cited by Lanza et al. (2006 [2005]). The head morphology, including the skull and musculature, of *H. platycepha*lus was compared with that of *H. genei*. While Adams’ intent was to show that the species differed and that species status was warranted, his main result was the demonstration that the two species closely resemble each other and differ only in relatively minor details. For example, the skull is shorter...
and flatter in male *H. platycephalus* than in *H. genei*, and there are a few minor differences in the origin and insertion of muscles. The relatively poorly developed skull of *H. platycephalus* and especially its much larger cranial fontanelle are illustrated but not mentioned. Furthermore, the elongated *pars frontalis* of the maxilla in *H. platycephalus* and the contrasting low profile of the process in *H. genei* are illustrated. Also shown are elongated teeth that extend laterally out of the mouth and beyond the margins of the head in male *H. platycephalus*. These are derived morphological traits that characterize the American species and distinguish them from the European species. Septomaxillary bones are always present in American species, but may be absent in some specimens in some but not all of the European species. Among the notable derived similarities are the absence of prefrontal bones of the skull, the presence of long maxillaries, and a wide gap between the paravomerine tooth patches and the anterior vomerine teeth.

In contrast to the close similarity of the European and American *Hydromantes*, *Karsenia* differs dramatically from both groups and more closely resembles other American genera, especially *Plethodon*, because *Karsenia* retains the generalized morphology inferred for the family as a whole (Buckley et al., 2010). The skull of *Hydromantes* is weakly ossified and flattened, with incomplete articulations, relative to most members of the subfamily Plethodontidae, whereas *Karsenia*, also a plethodontine, has a relatively well ossified, domed skull characterized by strong jaws. The genera differ dramatically with respect to the tongue and hyobranchial apparatus. *Karsenia* has a tongue similar to those of *Plethodon* and *Aneides*, whereas that of *Hydromantes* is the most specialized of all salamanders (Lombard and Wake, 1977; Deban et al., 1997). In short, nothing in the osteology or general morphology of *Karsenia* suggests that it is a close relative of *Hydromantes*.

The European and American species of *Hydromantes*, while overwhelmingly similar in morphology, do differ in some respects, as noted above (see also Wake, 1966; Lanza and Vanni, 1981). In addition, the trunks of the European species are slightly shorter than those of the American species, the consequence of having on average fewer vertebrae (mode 13 vs. mode 14; Lanza et al., 1995). The vertebrae bear transverse processes that separate distally on the first few vertebrae of all species, but after the fourth vertebrae in the European species the transverse processes are fused and become reduced in length, whereas in the American species they remain separated. The central and posterior ribs of the European species are unicipital, whereas those of the American species retain the ancestral bicipital anatomy (this is another way of presenting the information in the preceding sentence). The tails of American species are bluntly tipped whereas those of European species are more sharply tipped and a little longer. Basal tail autotomy does not occur in *Hydromantes*, although tails are known to break near their tips in the European species. American species of *Hydromantes* are well known for using their tails in locomotion, in the manner of a fifth leg, especially when walking on smooth or wet sloping surfaces, and they have specialized tail tip cells (Serra et al., 1991); this behavior is not known in the European species. Differences in tail musculature have been reported (Serra and Stefani, 1974), but no detailed comparative analysis has been conducted.

*Hydromantes* has 14 pairs of chromosomes (as in most plethodontids) but the European species differ from the American in some details (e.g., they have a more asymmetrical 14th chromosome), and *H. (A.) genei* differs from other European species in some respects (it and the American species lack XY sex chromosomes), but in most respects all species have similar karyotypes (in having all biarmed chromosomes) (Nardi, 1991; Sessions and Kezer, 1991).
Taxonomy

While there is little discussion of which species taxa of *Hydromantes* should be recognized, there is controversy over which generic names should be applied.

All agree that *Hydromantes* is a plethodontid, and all recent molecular phylogenetic analyses indicate that it is allied with taxa in the subfamily Plethodontidae. Recently Wake (2012) formally named a tribe Hydromantini to contain *Hydromantes* and *Karsenia*. Beyond this there is some controversy. However, I will argue in favor of the following classification:

Family Plethodontidae
Subfamily Plethodontinae
Tribe Hydromantini
Genus *Hydromantes* Gistel, 1848
Subgenus *Hydromantes* Gistel, 1838
Species: *platycephalus* (Camp, 1916); *brunus* Gorman, 1954; *shastae* Gorman & Camp, 1953
Subgenus *Atylodes* Gistel, 1868
Species: *genei* (Temminck & Schlegel, 1838)
Subgenus *Speleomantes* Dubois, 1984
Species: *italicus* Dunn, 1923; *ambrosii* Lanza, 1955; *flavus* Stefani, 1969; *imperialis* Stefani, 1969; *sarrabuseonis* (Lanza, Leo, Forti, Cimmaruta, Caputo, & Nascetti, 2001); *strinatii* Aellen, 1958; *supramontis* Lanza, Nascetti, & Bullini, 1986.

This taxonomy (Wake, 2012) is followed by the Amphibian Species of the World (Frost, 2013) and the AmphibiaWeb (AmphibiaWeb, 2013) websites. The taxonomic history of *Hydromantes* has been treated by Dubois (1984), Wake et al. (2005), and Lanza et al. (2006 [2005]), and is abbreviated here. A confusing early history ended when Dunn (1923) replaced the invalid name *Geotriton* with *Hydromantes*, and named the mainland Italian species, which curiously had been without a legal name, as *Hydromantes italicus*. For many years there was agreement that European and American species were congeneric until Lanza and Vanni (1981) proposed splitting the genus, placing the American species in a new genus *Hydromantoides*; type species *platycephalus*. Dubois (1984) was concerned with procedures followed by Dunn and proposed a single genus with two subgenera, the American species being assigned to *Hydromantoides* (*Hydromantoides*) and the European species being assigned to *Hydromantoides* (*Speleomantes*); type species *italicus*. The International Commission on Zoological Nomenclature (1997) ultimately resolved this matter by changing the type species of *Hydromantes* to *platycephalus*, thereby rendering *Hydromantoides* a strict junior synonym. Wake et al. (2005) resurrected *Atylodes* as a subgeneric name for *genei* and suggested that if European species were to be considered a separate genus or subgenus, the appropriate name is *Atylodes*, but Crochet (2007) argued in favor of *Speleomantes* and his argument has been accepted by Speybroeck et al. (2010), who recommended against use of *Atylodes* at any level (see below).

Currently, there are five alternative, equally valid taxonomic options in my view:

1. Recognize no subgenera and place all of the species in *Hydromantes*. This is a commonly used option in general texts.
2. Recognize a genus *Hydromantes*, with two subgenera, *Hydromantes* for the American species and *Speleomantes* for the European species.
3. Recognize three subgenera of *Hydromantes*: *Hydromantes*, *Speleomantes*, *Atylodes*.
4. Recognize two genera, with two subgenera of *Speleomantes*, *Speleomantes* and *Atylodes*.
5. Recognize three genera.

In the following, I treat each of these options:

1. The monophyly of *Hydromantes* is no longer questioned. I recommend this option for authors whose work deals with fields such as physiology, develop-
ment, anatomy and functional morphology, and biomechanics.

2. While clearly forming a clade, European and American species do differ in allozymes, DNA sequences, and in some anatomical and behavioral details. To recognize this by using subgenera is appropriate, and this is a taxonomy that I find acceptable.

3. A case can be made that *H. genei* differs in substantive ways from other European species in some morphological and cytological details, as well as in allozymes, but some ambiguity exists with respect to support for two European clades in the available DNA sequence data (van der Meijden et al., 2009). This is the taxonomy I prefer and recommend.

4. My arguments for rejecting this option are essentially the same as for option 5, below.

5. The fundamental reason for the initial split of *Hydromantes* by Lanza and Vanni (1981) was their suspicion that European and American clades had been convergently derived. Substantial evidence of monophyly has been obtained from mitochondrial and nuclear gene sequences, and by 2006, even Lanza et al. (2006 [2005], p. 30) largely, but not completely, conceded: “Almost certainly *Speleomantes* and *Hydromantes* belong to a monophyletic supergenus (*Hydromantes*), although a very remote possibility exists that it may be polyphyletic –”.

Although my support for option 3 and rejection of options 4 and 5 may seem to devolve to a hollow argument over ranks, I think more important issues are at stake. I would like to be able to derive phylogenetic information from taxonomic ranks, without resorting to an alternative, non-Linnaean taxonomic system. One effective way of attaining such a goal is through the use of subgenera. I think this is especially effec-

ative when there is strong evidence of monophyly from diverse sets of biologically significant traits. I will present three case studies from Plethodontidae.

*Bolitoglossa* contains more species than all the members in any other family of salamanders (at present, 128). The taxon has distinctive osteology and external morphology (e.g., all species have partially to fully webbed digits) and is immediately identifiable in the field. It has a unique tongue that is one of the most specialized in the Bolitoglossini. *Bolitoglossa* is always differentiated in DNA sequences, and Parra-Olea et al. (2004) recognized seven subgenera. While these are based primarily on molecular data, there is some supporting morphological data, and most of subgenera have unique distributions. However, there are some questions about the monophyly of at least two of the subgenera (*Mayamandra*, *Pachymandra*). In short, there is no reason break up this genus at this time, and good reasons not to do so.

*Batrachoseps* is a relatively speciose (21-22 species) group of plethodontid species from the west coastal region of North America. The species are immediately identifiable in the field by having only four digits on the hind limb and by being slender, with long tails. They have a unique tongue, and they differ from all except tropical plethodontids in having only 13 pairs of chromosomes. Based on some osteological details, allozymes and DNA sequences, two clades are recognized; these were treated as subgenera by Jackman et al. (1997) and subsequent authors. The DNA sequence differences are the same magnitude as those separating European and American species of *Hydromantes* (Vieites et al., 2007, 2011).

*Oedipina* is a deeply tropical clade of 36 species. Species are immediately identifiable because they are slender with elongate bodies (four or more trunk vertebrae than any other tropical salamander) and long, slender tails, with short to diminutive limbs. Three clades have been identified using DNA sequences, but only one of them has morphological characters
and even those are somewhat equivocal. Accordingly, the three clades have been assigned to three subgenera.

In each of these cases the depth of divergence, measured by DNA sequences, is roughly equivalent to that between European and American species of *Hydromantes*, and there are some morphological characters. Yet, the clades share so much in common that all interests are served by using a subgeneric classification. *Hydromantes* is a fourth instance. However, in the case of *Hydromantes* the degree of shared specialization and high level of synapomorphic morphology and behavior is even greater than in the other three cases. Furthermore, the very fact that the clade is present in Europe and western North America and presents a unique zoogeographic enigma for salamanders argues in favor of retaining a single genus for these species. The taxonomy draws attention to the puzzle and elevates its significance, spurring action in search of a solution to the question as to how this distribution can be explained.

**Biogeography**

*Hydromantes* is a biogeographic enigma among salamanders, but there are some informative comparisons to be made with other amphibians. Holarctic distributions are not unusual; *Rana* and bufonids are two notable examples. The western North American *Rana* are members of a clade widespread in Eurasia, and North American bufonids are closely related (although no longer considered congeneric) with Eurasian toads. Salamandrids are represented in both North America and Eurasia, and proteids are found in Europe and North America (but the proteid split is much older than the others – Early Cretaceous [Zhang and Wake, 2009]). What is unique about the plethodontids is representation in Korea and the Sardinian and Italian mainland-SE France, and nowhere else in Eurasia.

Even before discovery of *Karsenia* there was controversy over the biogeographic history of *Hydromantes*. Acceptance that *Hydromantes* is a clade and the availability of time trees advances us beyond the analysis of Lanza et al. (2006 [2005]), which concluded that while *Karsenia* may well have dispersed from western North America via a Beringian connection, *Hydromantes* was likely to have arrived at its present distribution as a result of a vicariant event following break-up of the North American-European connection via Greenland. Delfino et al. (2006 [2005]) also discussed what they term the “*Hydromantes* problem”, concluding that direct spread from North America onto Europe via a North Atlantic connection and a subsequent break-up of the land connection “was less unlikely than a dispersal requiring the crossing of the Beringian Bridge and the whole of Asia” (p. 57) (note that this was written before the discovery of the Asian *Karsenia*). Lanza et al. (2006 [2005]) do discuss *Karsenia*, but are not convinced that it has much to offer with respect to understanding the biogeographic history of *Hydromantes*. What most concerns both sets of authors is the absence of plethodontids across vast stretches of Eurasia and no fossil record (although Delfino et al. note that plethodontid fossils are, in general, rare and relatively recent).

Time trees are now available for the North American-European divergence of salamandrids and plethodontids. Available evidence suggests a divergence of about 60-70 MYA (Zhang et al., 2008; Vieites et al., unpublished data). However, this is not a “clean” separation of Europe and America, but of Eurasia and America, because the eastern Asian salamandrids (Cynops, Laotriton, Pachytriton, Parmesotriton) are nested internally within the clade of modern European newts, which in turn is the sister clade to the North American genera (Notopthalmus, Taricha). In contrast to the long separation of *Karsenia + Hydromantes* from other plethodontids (see below), the divergence of European and American *Hydromantes* is dated at about 41 MYA (Vieites et al., 2007). Available molecular evidence suggests...
that *Karsenia* and *Hydromantes* are sister taxa (Vieites et al., 2007, 2011), but some analytical treatments of the data, especially those that use no mitochondrial sequences (some treatments in Vieites et al., 2011) or only a fraction of the available mitochondrial sequences (Pyron and Wiens, 2011) do not find support for such a clade. Assume, for the moment, that the relationship is real. The estimated time of divergence of *Karsenia* + *Hydromantes* in relation to the other plethodontines is 74-77 MYA, a little earlier than the estimated age of the salamandrid split (the error estimates overlap). The estimate of the divergence of *Karsenia* from *Hydromantes* is 67-69 MYA (Vieites et al., 2007).

These time estimates led Vieites et al. (2007) to propose a biogeographic scenario in which a common ancestor of *Karsenia* + *Hydromantes* dispersed from western North America to Eurasia. The Western Interior Seaway separated eastern from western North America from the mid-Cretaceous well into Paleocene and was likely responsible for the origin of the two main plethodontid clades (plethodontines in the west and hemidactyliines in the east). When the dispersal to Asia began (Late Cretaceous), the earth was warm and the salamanders would have lived far north, where distances between continents are relatively short. The Turgai Sea separated Asia from Europe at the time, and it was continuous with the Western Interior Seaway in North America. The split between *Karsenia* and *Hydromantes* took place near the end of Cretaceous. A long period of evolution of *Hydromantes* ensued, during which time it evolved many morphological and behavioral specializations, followed by a split between the *H. (Atylodes + Speleomantes)* clade and the *H. (Hydromantes)* clade, the former (which retains more ancestral traits) dispersing west to Europe following closure of the Turgai Sea, and the latter dispersing back into North America, leaving no trace in eastern Asia. The split between the two European clades is dated at 16-17 MYA, whereas the first split in North America was more recent (ca. 8 MYR). The only relevant fossil, a trunk vertebra (diagnostable as *H. (Speleomantes)* sp. from Slovakia) is dated at 13.75 Ma (±1.25 Ma) (Venczel and Sanchíz, 2005), a date compatible with the dates obtained from analyses of molecular data (for detailed analysis see Vieites et al., 2007).

The paleogeography of the northern regions of Earth is undergoing nearly constant revision (e.g., Jones, 2011). Three possible land bridges are relevant to the discussion of historical biogeography of *Hydromantes*: Bering Land Bridge, Thulean Land Bridge and De Geer Land Bridge. One must keep in mind that there is much circularity in interpreting the evidence for and against land bridges at particular times. Distributions of organisms, usually land mammals, “demand” that a dispersal route have been present, and the geological evidence is sought. Thus the paleogeographic reconstructions are based on some amalgam of distributional and geological evidence. The Bering Land Bridge is widely accepted as having been in existence at least (although perhaps intermittently at first) from the Late Cretaceous (ca. 100-65 Ma) well into the Oligocene. Various American mammals are thought to have dispersed into Eurasia via this bridge from the Early Eocene into the Early Oligocene (ca. 34-28 Ma); additional dispersals are postulated for Late Oligocene to earliest Miocene (28-20 Ma), and Late Early to early Middle Miocene (20-14 Ma) (Briggs, 1995; Eberle and Greenwood, 2012). The bridge was again in place when three-toed horses dispersed from America into Eurasia and Africa in the Vallesian European Land Mammal Age (Miocene; 11-9 Ma).

In contrast to the dating of the Bering route, the Thulian Land Bridge is thought to have been an intermittent connection across the North Atlantic (North America to Greenland, Iceland, the Faeroes to Scotland) only in the Early Eocene (Eberle and Greenwood, 2012). A De Geer Land Bridge, further to the north, thought to have connected North America through Greenland and Svalbard to present-day northern Norway, is more problematic. There are
significant problems with both possible bridges (summarized by Jones, 2011), not the least of which is the high probability of some deep sea-ways (hundreds of meters in depth!) at points in both the Thulian and De Geer bridges. However, there is some new evidence that a short-lived Thulian Bridge was in place 55-53.5 Ma (earliest Eocene; Jones, 2011), although Storey et al. (2007) argue on the basis of radiometric dates, that the opening of the northeast Atlantic took place 55.5 (± 0.5 Ma). There is, in general, far less evidence of the Thulian and De Geer bridges than of the Bering Bridge, and they appear to have been intermittent and relatively short-lived, which would hardly have been favorable for the dispersal of salamanders.

From the above data, I conclude that the likeliest scenario for the current disjunct distribution of *Hydromantes* is that salamanders dispersed by way of the Bering Land Bridge and reached Europe sometime following the closure of the Turgai Strait (also known as the Obik Sea). That seaway connected the Peri-Tethyan basins, the West Siberian Boreal basins and the Western Interior Seaway in North America, producing a landmass in western North America/eastern Eurasia, where the ancestors of *Hydromantes* (or of *Hydromantes* and *Karsenia*) originated (for discussion of the once-favored Appalachian origin of plethodontids, see Mueller et al., 2004; Vieites et al., 2007). The Turgai Strait closed starting in the Late Eocene or Oligocene, when the two major clades of *Hydromantes* had already diverged; the clade retaining the greater number of ancestral morphological and behavioral traits was then able to move westward into central/southern Europe, where they certainly were present as early as 13.75 Ma (Miocene). There are problems with any postulated history, but I think there are fewer with this one than with others. For example, the estimated 41 Ma separation of European and American clades of *Hydromantes* fits well with the likely existence of a broad and long-lasting Bering Bridge, that seems to have persisted from at least the Late Cretaceous well into the Miocene.

The alternative route, favored by Delfino et al. (2006 [2005]), Lanza et al. (2006 [2005]), and Lanza et al. (2009), is based on use of either the Thulian or De Geer bridges, which were less long lasting than the Bering Bridge, and far less well-documented. Furthermore they were separated from the western North American place of likely origin of a *Karsenia* + *Hydromantes* ancestral clade, or a *Hydromantes* ancestral clade, by the Western Interior Seaway. These authors were writing when it was still thought that the European and American clades of *Hydromantes* had separated 28 Ma (Wake et al., 1978) or 50 Ma (Lanza and Vanni, 1981), rather than the new estimate of 41 Ma and the much older estimate of 74-77 Ma for *Karsenia* + *Hydromantes*. Furthermore, the 41 Ma timing estimate for the divergence within *Hydromantes* is considerably more recent than the radiometrically determined opening of the North Atlantic (55.5 Ma; Storey et al., 2007).

The two amphibian taxa most relevant for contributing some understanding of plethodontid history are the newts, Salamandridae (Pleurodelinae), and the ranid frogs of the genus *Rana* (which I recognize as containing two subgenera, *Rana* in western North America and across northern Eurasia, and *Lithobates*, mainly central and eastern North America into the tropics as far as Bolivia). I earlier noted that the age of separation of the North American from the Eurasian salamandrids is 60-70 Ma, which times span the uppermost Cretaceous to the mid-Paleocene. The salamandrids most likely moved eastward into North America across the Bering Bridge, while plethodontids initially moved from westward into Asia across the same bridge, although perhaps a little earlier. Bossuyt et al. (2006), using molecular phylogenetic inferences, estimate that ancestral *Rana* began differentiating on the order of 31-32 Ma, in Early Oligocene, while the separation of *Rana* (Rana) and *Rana* (Lithobates) dates to about 21-22 Ma, Early Miocene. The
ranids underwent a major divergence in North America, and the ancestors of *Rana (Rana)* dispersed westward back into Eurasia, leaving a small part of that clade and all of *R. (Lithobates)* behind. The first *Rana* appear in the European fossil record in Late Eocene (lower Headonian stage, standard level MP 16; Rage and Roček, 2003, Rage, 2012). According to the latest estimates (International Commission on Stratigraphy, 2013), the age of this record is between 38-41 Ma, which is difficult to reconcile with the molecular timing estimate and the Bossuyt et al. (2006) scenario. Perhaps ancestral *Rana* were present earlier than estimated in Europe, and they may have made their way into North America at about the same time (sometime a little more recent than 41 Ma) that *H. (Hydromantes)* was moving east. However, the Bering Land Bridge was present at various times from the Cretaceous well into the Tertiary, and was most likely available for plethodontid and salamandrid salamanders between 60-74 Ma and again for ranids and *Hydromantes* in late Eocene to early Oligocene. If the Thulian and De Geer bridges existed at all, they occurred in the Early Eocene, too late for the salamandrid and plethodontid initial dispersal, and too early for *Hydromantes* and *Rana*. Thus, an eastern route from North America to Europe for amphibians appears to be highly unlikely because it was short-lived and did not exist during the times of inferred dispersals.

Not only are fossil plethodontids rare, but plethodontids themselves are rare in Eurasia. Yet, the existence of a single fossil in the Miocene of Slovakia bears witness to the previously more widespread distribution of *Hydromantes*. The surprisingly recent discovery of *Karsenia* in Korea gives hope that other plethodontids remain to be discovered in the vast reaches across the Eurasian land mass. Each year numerous species of plethodontid salamanders are discovered and described (see AmphibiaWeb, 2013), and it will not surprise me if there are more to be discovered in Asia that could shed light on the enigma of plethodontids in the Old World.

**Acknowledgements.** Benedetto Lanza has been an inspiration to me since I began my work on plethodontid salamanders and I am pleased to dedicate this paper to him. He showed me how to find *Hydromantes* near Firenze and welcomed me into his home, always in a spirit of cordiality and generosity, and I am grateful to him. I thank William Clemens and Jaelyn Eberle for discussion of Arctic and sub-Arctic paleobiogeography, and Sebastiano Salviodo and Antonio Romano for answering questions. I thank Marvalee Wake for discussion and comments on the manuscript. My research has long been supported by the National Science Foundation.

**References**


