

PHYLOGENETIC AND TAXONOMIC ISSUES RELATING TO SALAMANDERS OF THE FAMILY PLETHODONTIDAE

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THE occasion of the third decennial Conference on the Biology of Plethodontid Salamanders, and the first publication of the proceedings of the conference, is a propitious time to take stock concerning diverse phylogenetic and taxonomic issues. As background, the monograph of Cope (1889) is used as a point of departure. Cope recognized a family Desmognathidae (for *Desmognathus*) and a family Thoriidae (for *Thorius*), both distinguished from the Plethodontidae by having opisthocelous vertebrae. Within the Plethodontidae he recognized two groups of genera: Plethodontae [*Plethodon*, *Hemidactylum*, *Batrachoseps*, *Stereochilus*, and *Autodax* (= *Aneides*)], and Spelerpes [*Geotriton* (= *Hydromantes*), *Gyrinophilus*, *Manculus* (now included in *Eurycea*), *Spelerpes* (*Eurycea* and *Pseudotriton*), *Oedipina*, and *Oedipus* (supergenous *Bolitoglossa*, minus *Oedipina* and *Thorius*)]. The fundamental distinction was that the Plethodontae has a tongue attached anteriorly, while Spelerpes has a free tongue. Cope thought that "The generic relationships of the above-named groups are exceedingly simple, and the ease with which the animals can be analyzed renders the case free from the doubts which constantly arise in discussions of generic relationships as to the probable omission of characters from the argument" (Cope, 1889:121–122).

The famous monograph of Dunn (1926) remains useful today. Dunn documented the unique features of the family, discussed relationships to other families, and included a lengthy treatment of relationships of species within some of the genera (e.g., *Desmognathus*), and of the genera to each other. Only 16 genera and 72 species were recognized. Dunn noted that *Desmognathus* and *Leurognathus* differed from the other genera in many re-

spects, but he chose not to recognize any taxa between genus and family. Dunn envisioned two "main groups" of genera along the lines of Cope's groups—a *Plethodon* group with attached tongues and a *Eurycea* group with free tongues, "connected by three intermediate genera which hardly belong to either group" (Dunn, 1926:22)—*Stereochilus*, *Typhlotriton*, and *Typhlomolge*. Apart from the recognition of many more species and a few novel new genera, the largest difference between the taxonomy of today and that of Dunn is his treatment of tropical salamanders. He recognized only 31 tropical species (about 44% of the total number of species of plethodontids; tropical species constitute more than 65% today), all placed in *Oedipus*.

While workers such as Noble (1927, 1931) quibbled with some of Dunn's ideas, the monograph remained authoritative for several decades. Taylor (1944) described many tropical species and sorted them into a number of genera. Several new genera (e.g., *Phaeognathus*, *Haideotriton*) and many new species were named in North America as well, but it was not until my comparative osteological study (Wake, 1966) that there was a major change in taxonomy and phylogenetic perspective. That work was published on the eve of the cladistic revolution, and while most taxa are monophyletic and based on shared derived character states, there are some inconsistencies with respect to modern cladistic methodology (e.g., in the brief discussion of familial relationships). The main results of that study have remained surprisingly robust and find wide acceptance to this day.

Wake (1966) thought that plethodontids were derived from an ambystomatid ancestral stock (in 1966 the Ambystomatidae included the three subfamilies Ambysto-

matinae, Dicamptodontinae, and Rhyacotritoninae, all currently recognized as families), that the genera of plethodontids could be placed in two subfamilies, Desmognathinae and Plethodontinae, both with ancestral and derived characters, and that the Plethodontinae could be segregated into three tribes, the Hemidactyliini, the Plethodontini, and the Bolitoglossini. A major departure from prior work was the grouping of *Hydromantes*, *Batrachoseps*, and all of the tropical salamanders (super-genus *Bolitoglossa*) as a monophyletic tribe Bolitoglossini. Another novel feature was the placement of *Hemidactylium* with the *Eurycea* group of genera of Dunn (1926). I envisioned the Hemidactyliini as the central evolving stock, giving rise first to the desmognathines, next to the bolitoglossines, then to the plethodontines, and finally to *Hemidactylium* on the one hand and the remaining hemidactyliines on the other, but I was uncertain on the placement of *Hemidactylium*, which ended up with the *Eurycea* group mainly by default. I use the 1966 taxonomy and phylogenetic interpretation as a point of departure for my re-evaluation.

FAMILY PLETHODONTIDAE

There has been no proposal to include plethodontids as members of any other currently recognized family of salamanders since the admission of *Typhlomolge* to the Plethodontidae (Fowler and Dunn, 1917). Dunn (1926) showed that *Typhlomolge* was a plethodontid; his conclusions were foreshadowed by Emerson's (1905) demonstration that the genus was not a proteid. There have been no shifts of genera from other families into the Plethodontidae since that time. While Soler (1950) proposed recognition of a family Desmognathidae, he acknowledged close relationship with the Plethodontidae.

The Plethodontidae is well supported by character data—lunglessness is universal, all metamorphosed individuals have a nasolabial groove, only adult plethodontids lack an ossified pterygoid bone, plethodontids have a unique arrangement of vomerine and postvomerine teeth, there are a number of unique features associated

with the hyobranchial apparatus and the nervous system, and there are unique features of courtship. Recently Larson and Wilson (1989) and Larson (1991) have provided characters from rRNA sequences that further support the monophyly of the family, and Sever (1991) has presented some characters from the morphology of the cloacal region.

When I argued for a phylogenetic relationship between the plethodontids and the ambystomatids (Wake, 1966), I had *Rhyacotriton* very much in mind. With the breakup of the Ambystomatidae, the possibility of a sister taxon relationship with the Rhyacotritonidae (fide Good and Wake, 1992) must be seriously considered. Larson and Wilson (1989) and Larson (1991) have shown that plethodontids are very distinct from other families, and occupy a rather basal position. Rhyacotritonids also are rather basal, and remote from both ambystomatids and dicamptodontids (Good and Wake, 1992; Larson, 1991; Sever, 1991, 1992). The rRNA sequence data have supported some traditional groupings (notably the monophyly of the Hynobiidae + Cryptobranchidae), while they have challenged others (the widely accepted grouping of the Plethodontidae with the Ambystomatidae, or alternatively with the Salamandridae). Further resolution of relationships of the families of salamanders is likely to come with additional sequence data, and by combining sequence data with traditional characters (such work is in progress, Larson and Dimmick, personal communication).

SUBFAMILY DESMOGNATHINAE

This is a well supported, monophyletic group (Schwenk and Wake, 1993; Soler, 1950; Wake, 1966). *Phaeognathus* has many autapomorphies, and it seems to be a basal derivative within the subfamily. All remaining species fit well within *Desmognathus*, although *Leurognathus*, which contains a single species with a few autapomorphies, is universally recognized. This may well render *Desmognathus* paraphyletic. This problem may be solved by DNA sequence data (Titus, 1992). A special phylogenetic puzzle of the subfamily is the

number of times that direct development has evolved. Direct development is found in *Phaeognathus*, *D. aeneus*, and *D. wrighti*. It seems unlikely that aquatic larvae have re-evolved in the subfamily (for one thing, a more ancestral hyobranchial system is present in desmognathine larvae than in the remaining plethodontids: Wake, 1966). However, *Phaeognathus* is a sister taxon of *Desmognathus*, and if one or both of the species of *Desmognathus* that have direct development should prove to be basal within the genus, that possibility must be considered.

SUBFAMILY PLETHODONTINAE

Wake (1966) recognized three tribes of genera: Plethodontini (for *Plethodon*, *Aneides*, and *Ensatina*), Bolitoglossini (for *Bolitoglossa*, *Chiropterotriton*, *Lineatriton*, *Oedipina*, *Parvimolge*, *Pseudoeurycea*, *Thorius*, *Batrachoseps*, and *Hydromantes*), and a catch-all Hemidactyliini (all other genera). The Plethodontini and Hemidactyliini were treated as sister taxa, and this group was the sister taxon of the Bolitoglossini. While there has been general acceptance of these three groups, there has been a low level of debate about the reality of the Hemidactyliini and about which two of these three groups are sister taxa. Lombard and Wake (1986) accepted the three tribes and the desmognathines as four primary taxa and analyzed relationships of them, concluding that Desmognathinae was basal and that Bolitoglossini and Plethodontini were terminal sister taxa. Presch (1989) objected to using these four taxa as OTU's. He attempted a reanalysis of the data set, but recorded some characters in ways that I find to be unacceptable. Presch showed that no hypothesis of relationships is robust, but Lombard and Wake had made the same point. New neurological evidence adds support for the sister group relationship of the Plethodontini and Bolitoglossini (Wake et al., 1987).

Extensive morphological homoplasy in plethodontids makes it likely that molecular characters will be needed to resolve the relationships of higher taxa. Paedomorphosis is a factor to be taken seriously in the family, and organismal-wide (so-

called global) heterochrony could affect many characters at once, leading to an inflated impression of the extent of homoplasy, but so far it has not proven possible to sort coevolving complexes of characters that might be unconnected functionally from independently evolving characters. I personally like to use new data sets to test hypotheses based on old data, and so I have long advocated the use of molecular and other kinds of data. Linda Maxson and I started a collaboration with the goal of testing alternative morphologically based phylogenetic hypotheses, but the taxa are too differentiated for microcomplement fixation of albumin to be effective. Protein electrophoresis is useful for comparing closely related species and even genera, but the higher taxa are beyond the limit of effectiveness of the technique. On the other hand, the taxa are not sufficiently distinct to be in the range of resolution using the ribosomal RNA sequences studied to date (Larson and Wilson, 1989). I am confident that in time molecules with the appropriate rates of molecular evolution will be identified, and that comparative sequence analysis will contribute positively to our understanding of cladistics in plethodontids. Episodes of reciprocal illumination obtained by testing phylogenetic hypotheses with different data sets will lead to deeper understanding of the nature and degree of independence of characters, and at that point a total evidence approach to understanding phylogenetics of the family will be appropriate.

TRIBE HEMIDACTYLIINI

There is reason to question if this is a monophyletic taxon. The problem is with *Hemidactylum*, which does not fit comfortably with the other genera, as Wake (1966) acknowledged. Historically, *Hemidactylum* was considered to be a close relative of *Plethodon* (Dunn, 1926). The genus was grouped with the other hemidactyliines almost by default, for it lacked the derived direct development of the Bolitoglossini and Plethodontini, it lacked the derived morphological traits of the Desmognathinae, and I was reluctant to establish a fourth tribe that included only a

single monotypic genus. However, subsequently Wake and Lombard (1972) did suggest that *Hemidactylium* might best be placed in its own tribe, but failed to make this move in their later analysis (Lombard and Wake, 1986). The remaining genera of the Hemidactyliini appear to form a monophyletic group.

Stereochilus, *Gyrinophilus*, *Pseudotriton*, and *Hemidactylium* are relatively noncontroversial as far as their generic status is concerned, although there have been attempts to combine *Gyrinophilus* and *Pseudotriton* (Grobman, 1959; countered by Martof and Rose, 1962). However, the remaining genera are difficult. I included *Manculus quadridigitata* in *Eurycea*, as had Dunn (1926), but argued for separate generic status for *Typhlotriton*, *Haideotriton*, and *Typhlomolge*. The last genus, in particular, has been controversial (e.g., Mitchell and Reddell, 1965; Mitchell and Smith, 1972; Potter and Sweet, 1981). The two species currently assigned to *Typhlomolge* differ osteologically from perennibranchiate species assigned to *Eurycea*, but it may be that these traits have been derived within the framework of a monophyletic group of species, and if so all of these may eventually be combined in a single genus. Molecular studies in progress by Chippindale and Hillis (presented at this conference) suggest that *Typhlotriton* and *Haideotriton* also require renewed attention, and they, too, might fall within the framework of an expanded *Eurycea*.

Dubois (1984b) raised a point relating to taxonomic priority. He argued that an older and more appropriate name for the tribe Hemidactyliini is the Mycetoglossini, based on the argument that Bonaparte (1839) had used the name *Mycetoglossa* as a substitute name (invalid) for *Pseudotriton*, and had later used the term Mycetoglossina as a subfamilial category (Bonaparte, 1850). Dunn (1926) and other workers ignored this family-group name, recognizing the priority of the name Plethodontidae (Gray, 1850), listed by Bonaparte (1850) as a synonym of his Mycetoglossina. The name Hemidactyliini (based on Hallowell, 1856) has become well established, and the rules on zoological no-

menclature are in a state of transition, so the case is not so simple as Dubois (1984b) implies. Recently an appeal has been made to the International Commission on Zoological Nomenclature to suppress the name Mycetoglossina and to conserve the Hemidactyliini (Smith and Wake, 1993b), and I recommend maintaining the traditional taxonomy until the matter receives formal action.

TRIBE PLETHODONTINI

This grouping of three genera is supported by a variety of morphological and molecular evidence (Jackman, this conference; Larson et al., 1981; Wake, 1963, 1966), and *Ensatina* is acknowledged as the sister taxon of *Plethodon* + *Aneides*. *Aneides* is a monophyletic group, but molecular evidence (Jackman, in progress; Larson et al., 1981) increasingly points to *Plethodon* as being paraphyletic, with western members of the genus having a sister group relationship to *Aneides*. One solution is to place all species in the tribe in a single genus *Plethodon*, because *Ensatina* includes only a single species and is apparently the sister taxon of the others, but such a genus would be large and inconvenient. An alternative is to place just the species of *Plethodon* and *Aneides* in a single genus *Plethodon*, but such a taxon would still be large. Another alternative would be to expand *Aneides* to include western *Plethodon*, but I know of no morphological character evidence for such a grouping. A final alternative is to name a new genus for the western species of *Plethodon*, but I know of only weak morphological or molecular character evidence for such a move. Ideally, while I would like to see genera to be monophyletic, I would also like them to be diagnosed by morphological characters, because I think that a major goal of taxonomy is convenience.

I would like to comment briefly on newly discovered information concerning the curious name *Ensatina eschscholtzii platensis*. The status of this taxon, which is based on a single specimen purportedly collected near Montevideo, Uruguay (Jiménez de la Espada, 1875) (and hence the name, derived from Rio de la Plata), has

been considered by Dunn (1926) and Myers and de Carvalho (1945). The latter authors suggested that a specimen from the Sierra Nevada of California had been carried by a miner back to Uruguay, where it eventually reached a traveling companion of Jiménez de la Espada, who in turn first noticed the specimen as he was packing his third shipment in Chile for transportation to Spain. Savage (1978) presented a brief summary of the "Comisión Científica del Pacífico", 1862–1865. He stated that Jiménez de la Espada visited the "countries of Central America" on two different occasions. He also noted that a zoologist on the expedition, Fernando Amor, died in December 1863, in San Francisco, California, of an illness contracted in the Atacama Desert. Savage did not mention that at least one ship from the expedition went as far north as San Francisco while the "Comisión" was in progress. This fact has been vividly illustrated by the recent publication of a remarkable set of photographs by Rafael Castro Ordóñez (Calatayud Arinero and Puig-Samper, 1992), a photographer with the "Comisión". What particularly struck me were three plates (75, 85, 86) taken in present-day Calaveras Big Trees State Park, in the central Sierra Nevada of California, where I have been conducting a field study of *Ensatina eschscholtzii platensis* for the past eight years. The salamanders are abundant in this area, and I suggest that it was this previously unrecorded visit by members of the "Comisión" that accounts for the specimen that was mislabeled as being from Uruguay and that ultimately was sent to Madrid.

TRIBE BOLITOGLOSSINI

I know of no challenges to the monophyly of this taxon, which includes about one-half of all the species of salamanders of all families. Currently there are three recognized supergenera—*Hydromantes*, in Europe and western North America, *Batrachoseps*, in western North America, and *Bolitoglossa*, which occurs in mainly tropical America from northeastern Mexico to Brazil, Bolivia and Peru. Morphological evidence favors the hypothesis of a

sister group relationship of *Batrachoseps* and *Bolitoglossa*, with *Hydromantes* being an earlier derivative (Lombard and Wake, 1986), and this hypothesis is favored by cytological evidence as well (Sessions and Kezer, 1991). The problem with this hypothesis is that it requires that completely free tongues have evolved twice within the Bolitoglossini, assuming that the genioglossal muscle of *Batrachoseps* has not reappeared, which seems highly unlikely (Lombard and Wake, 1977; Roth and Wake, 1985). However, the prevailing hypothesis of phylogenetic relationships of the plethodontid genera already requires that fully free tongues have evolved independently in the *Eurycea* group, so this homoplasy is not so unexpected as it might seem (Lombard and Wake, 1986; Wake, 1991).

The genus *Hydromantes* has many autapomorphies (Lombard and Wake, 1977, 1986; Wake, 1966). Lanza and Vanni (1981) separated the European and American species of *Hydromantes* into two formal taxa, using the name *Hydromantoides* for the American species. Wake (1966) presented osteological evidence that the European and American species could be distinguished, and Wake et al. (1978) showed that the two groups differed in biochemical characters as well. Consequently, the only debate is whether it is useful to separate a clearly monophyletic genus into two genera. I find the two groups to be very similar in terms of morphology, ecology, and behavior, and they share an absolutely unique food-capturing system (Lombard and Wake, 1977). Furthermore, if one compares degree of molecular divergence and accepts a general molecular evolutionary clock, the two groups of *Hydromantes* are about as different from each other (Wake et al., 1978) as are the species of *Aneides* from each other (Larson et al., 1981), and in general the degree of genetic differentiation relative to that in other plethodontid genera is low (cf. Larson, 1984). So this is very much a matter of personal choice, and I choose to recognize a single genus. A new twist was added when Dubois (1984a) published one of a series of papers on the nomenclature of

amphibians. Dunn (1923) argued that *Geotriton* was preoccupied by a salamandrid, and he assumed that *Hydromantes* was the next available name. This is a very complicated story, discussed in detail by Dubois, who claims that Dunn erred, on technical grounds, when he selected the name *Hydromantes*. The name is credited to Gistel (1848), who apparently thought that he was applying the name to the species known today as *Hydromantes italicus*. According to Dubois, the name *Hydromantes* was a substitute name for *Geotriton*, a name first used by Bonaparte (1831) (but lacking a diagnosis or a list of included species, it is a nomen nudum). In 1832, Bonaparte again used the name and associated it only with a single species, *Salamandra exigua* Laurenti, 1768. This taxon is now considered to be a synonym of *Triturus vulgaris*. Dubois claims that this species must be considered to be the type species of *Geotriton*, even though Bonaparte (1837) clearly applied the name to a species that is included in present-day *Hydromantes*. On narrow, technical grounds, which I do not have the space to present here, Dubois argued that *Hydromantes* was invalid for plethodontid salamanders and that the appropriate name for the genus was the new name of Lanza and Vanni (1981), *Hydromantoides*. Dubois briefly considered the biological evidence and concluded that it might be appropriate to recognize subgenera for the European and American species. Because Lanza and Vanni had designated *Spelelperes platycephalous* Camp, 1916, as the type species of *Hydromantoides*, Dubois proposed a new subgeneric name for the European species, *Hydromantoides (Speleomantes)*, with *Hydromantes italicus* Dunn, 1923, as the type species. Thus, if one accepts the nomenclatural argument of Dubois and the taxonomic argument of Lanza and Vanni, the correct generic name for the California *Hydromantes* is *Hydromantoides*, and the correct generic name for the European *Hydromantes* is *Speleomantes*. I reject both arguments. *Hydromantes* has been used almost universally in a large literature since 1923, and I see no useful purpose in dredging up technical

arguments dating back 90 years earlier. We have had stability for 70 years, and pending a formal decision on a recent appeal to the International Commission on Zoological Nomenclature (Smith and Wake, 1993a), I recommend continued use of *Hydromantes* for the European and American species traditionally associated with this name. *Batrachoseps* is another problematic genus that might well be separated into subgenera or genera. The two major groups in the genus are differentiated by many biochemical characters, but the morphological data are not easily interpreted (Wake, 1989). The name *Plethopsis* is available for *Batrachoseps wrighti* and its relatives (*B. campi* and an undescribed species). However, the monophyly of *Batrachoseps*, as currently recognized, is unquestioned, so the only reason to divide the genus would be for convenience (the genus will soon be larger; there are several undescribed species: Wake and co-workers, in preparation).

There are old records of *Batrachoseps* from Alaska (Cope, 1889; Dunn, 1926) and from Nevado de Colima, Jalisco, Mexico (Gadow, 1905). I have examined all of the specimens involved and agree with previous authors (Hendrickson, 1953; Stebbins, 1951; Stebbins and Lowe, 1949) that there are reasons to question the records from Alaska. Ron Crombie (in litt.) has studied letters from Lt. Nichols, who sent the Alaskan specimen to the National Museum. The ship "Hassler" moved between southeastern Alaska and Mare Island (Vallejo, San Francisco Bay Region), California. Much of Nichols' material was from Alaska, but perhaps he inadvertently mixed a specimen from Mare Island or vicinity, where *Batrachoseps* is abundant, with his Alaskan material. I think it unlikely that *Batrachoseps* is in Alaska, especially because species with similar morphology are not known to occur north of extreme southeastern Oregon.

The Mexican specimen, a juvenile, is less readily dismissed. Gadow (1908) recounted in detail the circumstances of capture. Stebbins (1951), who examined the specimen, considered it to be correctly assigned to *Batrachoseps*. However, I suspect that

it is a member of the supergenus *Bolitoglossa*, some members of which occasionally have four rather than five toes (Wake, 1991), because the specimen appears to have a free tongue (it is possible that the specimen has been damaged, however).

The supergenus *Bolitoglossa* has been very difficult to analyze phylogenetically because the group as a whole is highly derived morphologically, and there are relatively few characters (Wake and Elias, 1983). Some large, well defined genera (*Thorius* and *Oedipina*) have been widely but not universally recognized for over 100 years. Homoplasy is so great in the supergenus that Dunn (1926) reacted by simply recognizing a single genus (*Oedipus*, later shown to be preoccupied by an insect). Taylor (1944) accomplished a significant advance by breaking this genus into seven, and Tanner (1950) added an eighth. Wake and Brame (1963) showed that Taylor's genus *Magnadigita* was not valid, and Elias and Wake (1983), Wake and Elias (1983), and Wake and Johnson (1989) added four genera, for a present-day total of eleven. Major problems remain, for five of these (*Bradytriton*, *Ixalotriton*, *Lineatriton*, *Nyctanolis*, and *Parvimolge*) are monotypic, one (*Pseudoeurycea*) is suspected to be paraphyletic, and one (*Bolitoglossa*) is very large (containing about a quarter of all species of salamanders). There has been recent progress in developing phylogenetic hypotheses for the group (Sessions and Kezer, 1991; Wake and Elias, 1983; Wake and Johnson, 1989), but the effort is hampered by the vast amount of homoplasy and the fact that many of the species are poorly known. Doubtless molecular data will help in testing alternative hypotheses based on morphological and karyological data, and such work is underway in my laboratory.

There is a worrisome old record of a tropical salamander, *Spelerpes infuscatus* (Peters, 1879), from Haiti. Dunn (1924) did not examine the unique holotype, but he nonetheless considered the taxon to be a synonym of present-day *Lineatriton lineola*. I agree with Dunn in considering the locality to be in error (the specimen, in the Berlin Museum, was obtained from the

Museum Godeffroy, associated with an animal dealer in Hamburg). However, I have examined the type specimen and on the basis of its having a subocular groove that intercepts the lip, an autapomorphy of *Thorius*, I assign it to that genus, possibly as a synonym of *T. narisovalis* of Oaxaca, which has nostrils of similar size and shape.

CONCLUSIONS

Many opportunities exist for developing and testing phylogenetic hypotheses for plethodontid salamanders. Robust phylogenetic hypotheses have been difficult to obtain, mainly because of the extent of morphological homoplasy. As we come to understand the nature of homoplasy and the biological basis for homoplasy in particular characters (Wake, 1991; Wake and Larson, 1987), I expect more progress in solving the phylogenetic problems that I have outlined. Cytological (e.g., Sessions and Kezer, 1991) and molecular (e.g., Larson, 1991) data not only will add to the data base, but should also help to sort homoplasy from synapomorphy, and help us to determine how independent the currently recognized morphological characters are from one another. In another decade, I hope that we will have achieved robust phylogenetic hypotheses for the genera and suprageneric taxa, and a stable, phylogenetic taxonomy.

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