References


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Are Salamandra atra and S. lanzai sister species?

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In 1988 Nascetti and co-authors described a new species of Alpine salamander, S. lanzai, from the Monviso Massif in the south-western Alps. Like S. atra this species is black and viviparous. Grossenbacher (1994) concluded that both species are monophyletic and represent the western and eastern descendants of an ancestral form that formerly inhabited the whole Alpine ridge.
In 1994 Joger and Steinfartz published an investigation of the evolutionary history of western Mediterranean Salamandra populations which included a cladistical re-analysis of Olivieri’s (1991) allozyme data on several species and subspecies of Salamandra. Subsequently both papers are cited only by their authors’ names.

In her thesis Olivieri presented data on allelic divergence of 24 Salamandra populations at 33 allozyme loci, including populations of S. algira, S. atra, S. corsica and S. lanzai. Her phenetic analyses gave rise to the hypothesis that S. lanzai and S. corsica are sister taxa, whereas the two species of Alpine salamanders, S. atra and S. lanzai, turned out to be paraphyletic. Consequently, viviparity and obligate melanism, both characterising the latter two, seemed to have evolved convergently within the genus. Joger and Steinfartz added plasma protein data to Olivieri’s allozyme data. Using both character sets they performed a cladistic re-analysis of Olivieri’s data. In their opinion synapomorphic allele substitutions support the assumption of monophyly of the two black salamander species.

A closer examination of Joger and Steinfartz’ cladogram makes apparent that their plasma protein data (mainly albumin phenotypes) represent only autapomorphic characters of the five species (including S. salamandra). Thus, they are not informative in a cladistic sense. Synapomorphies are only present in Olivieri’s allozyme data. In addition Joger and Steinfartz did not show alleles solely present in S. corsica and S. lanzai (e.g. α-Gpdh-2103, Pt-2103) that could have been treated as synapomorphies of both taxa.

Using the program PAUP, version 3.1.1, of Swofford (1993) I analysed the allozyme data of Olivieri cladistically under the parsimony criterion, resulting in a tree that explains the observed pattern of character states by the lowest number of evolutionary steps (e.g. Swofford and Olson, 1990). Each allele was treated as a character with two possible states, presence (1) or absence (0). To test the robustness of tree topologies alleles were resampled 1000 times by bootstrapping the original data set (Felsenstein, 1985).

Like Olivieri’s phenetic analysis the resulting maximum parsimony tree supports paraphyly of the Alpine salamanders and contradicts Joger and Steinfartz’ cladistic re-analysis (fig. 1): S. lanzai forms a separate clade with S. corsica, whereas S. atra stands together with the S. salamandra clade. This topology is supported by bootstrap values of 60% for the S. corsica/S. lanzai clade. In contrast, monophyly of S. atra and S. lanzai, the hypothesis of Joger and Steinfartz, is only supported by 37%. Even if only a single S. salamandra taxon is included in the maximum parsimony analysis (as well as only one population of each S. algira, S. atra, S. corsica and S. lanzai) there is no significant support for either monophyly or paraphyly of S. atra and S. lanzai. This holds also true when further phenetic analyses using different distance estimates and tree constructing algorithms are performed.

It can be concluded that the allozyme data of Olivieri do not provide sufficient support for either her or for Joger and Steinfartz’s hypotheses. Bootstrap values for each of the concurring hypotheses are too low to allow for an exclusion of the alternative one. However, all analyses provide at least higher support for Olivieri’s hypothesis of paraphyly