

Evidence of tail autotomy in the European plethodontid *Hydromantes (Atylodes) genei* (Temmick and Schlegel, 1838) (Amphibia: Urodela: Plethodontidae)

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Abstract. Caudal autotomy is a defensive mechanism widely adopted by lungless salamanders (Plethodontidae) from the New World. In contrast, in Europe, this mechanism was not described until very recently for just one Sardinian species, *Hydromantes (Speleomantes) sarrabusensis*. We report on tail autotomy observed in another species from the same island, *Hydromantes (Atylodes) genei*. In Europe, self-amputation of the tail seems to be restricted to some plethodontids inhabiting Sardinia, while continental species do not exhibit analogous antipredator strategies.

Keywords. Autotomy, *Hydromantes*, Plethodontid.

Autotomy is the ability to cast off, spontaneously or by reflex, a part of the body and, in herpetology, it usually refers to the breakage and loss of the tail. Autotomy is a widespread defence against predators among invertebrates and vertebrates (see references in Cooper et al., 2004).

Salamander antipredator strategies include autotomy among the suites of behavioural and morphological traits employed against predators and competitors (Brodie, 1983; Stebbins and Cohen, 1995). Such anatomical adaptation evolved in some plethodontids and salamandrids from an initial strategy based on redirecting the attack by predators to the body and/or the head to the tail by means of adopting a defensive posture (Brodie, 1977).

Morphological diversification in skeletal, tongue and digital characteristics have all played an important role as diversification drivers in the large adaptive radiation of the family Plethodontidae, the most remarkable among salamanders, embracing from troglodytic species to entirely arboreal ones (Wake and Larson, 1987). There is some evidence that supports a complex pattern of independent origins of coevolved traits (Wake, 1991). One of the most surprising traits, the ability to autotomize and regenerate the tail as defensive behaviour, has received little attention in evolutionary studies (Mueller et al., 2004). Among plethodontids, which are distributed predominantly in the Americas (Wake, 1966; AmphibiaWeb, 2010), all members of the tropical radiation, including the neotropical genus *Bolitoglossa*, and a few species of other American genera (*Ensatina*, *Hemidactylium* and *Batrachoseps*) have specialized region at the base of the tail that is related to autotomy but many plethodontids that do not have specialized autotomy zones nevertheless are capable of autotomy (for a detailed account see Wake and Dresner, 1967).

The genus *Hydromantes* occurs in western North America (California; see USGS National Amphibian Atlas, 2009) and in central Mediterranean Europe. In particular, European plethodontids occur on the Mediterranean island of Sardinia (five species) and in peninsular Italy and a small southern-eastern portion of France (three species; Sindaco et al., 2006; Carranza et al., 2008). The North American *Hydromantes* belong to the subgenus *Hydromantes*, the mainland Europe species and four of the five Sardinian species are ascribed to the subgenus *Speleomantes* and a species inhabiting the southwest of Sardinia to the subgenus *Atylodes*. All three subgenera have sometimes been considered as full genera as a result of the large geographical disjunction that exists between western North America and Italy, but according to both the morphological differences and especially the low level of genetic differentiation that exists within the genus *Hydromantes* it is considered here that it is more appropriate to treat them as subgenera (see et al., 2005 for the taxonomic debate; Lanza et al., 2006; Wake; Crochet, 2007 for the alternative use of both terms; Carranza et al., 2008 and van der Meijden et al., 2009 for genetic differentiation within *Hydromantes*).

Autotomy has been reported for European species only recently (Favelli et al., 2007) in the Sardinian *Hydromantes* (*S.*) *sarrabusensis* (Lanza, Leo, Forti, Cimmaruta, Caputo and Nascetti, 2001).

During fieldwork carried out in Sardinia in 2006, we studied a population of *Hydromantes* (*A.*) *genei* (Temminck and Schlegel, 1838), inhabiting a mine gallery near S. Giovanni's cave (Domusnovas, Carbonia-Iglesias). Each animal was measured and sexed and immediately released at the sampling site. During the handling of the specimens, tail autotomy was recorded in a subadult salamander (Fig. 1). The salamander, after twisting movements of the tail, lost a small portion of its distal part without losing blood. In the same population we observed other salamanders with regenerated tails.

Since the plethodontid tail has locomotor, respiratory, behavioural and food storage functions (Wake and Dresner, 1967), its autotomy can be highly costly and therefore it plays an important role in the survival of the salamanders. Tail autotomy represents a loss of fat and protein (energy), both that are stored in the tail and represent the main source of energy in the tail regrown process, however making possible constraints, for instance, to the reproductive input (Maynard Smith and Parker, 1976; Bernardo and Agosta, 2005) and may impose other social costs, such as reduction in fighting ability (Wise and Jaeger, 1998). Indeed, even in species which are highly specialised for caudal autotomy these very

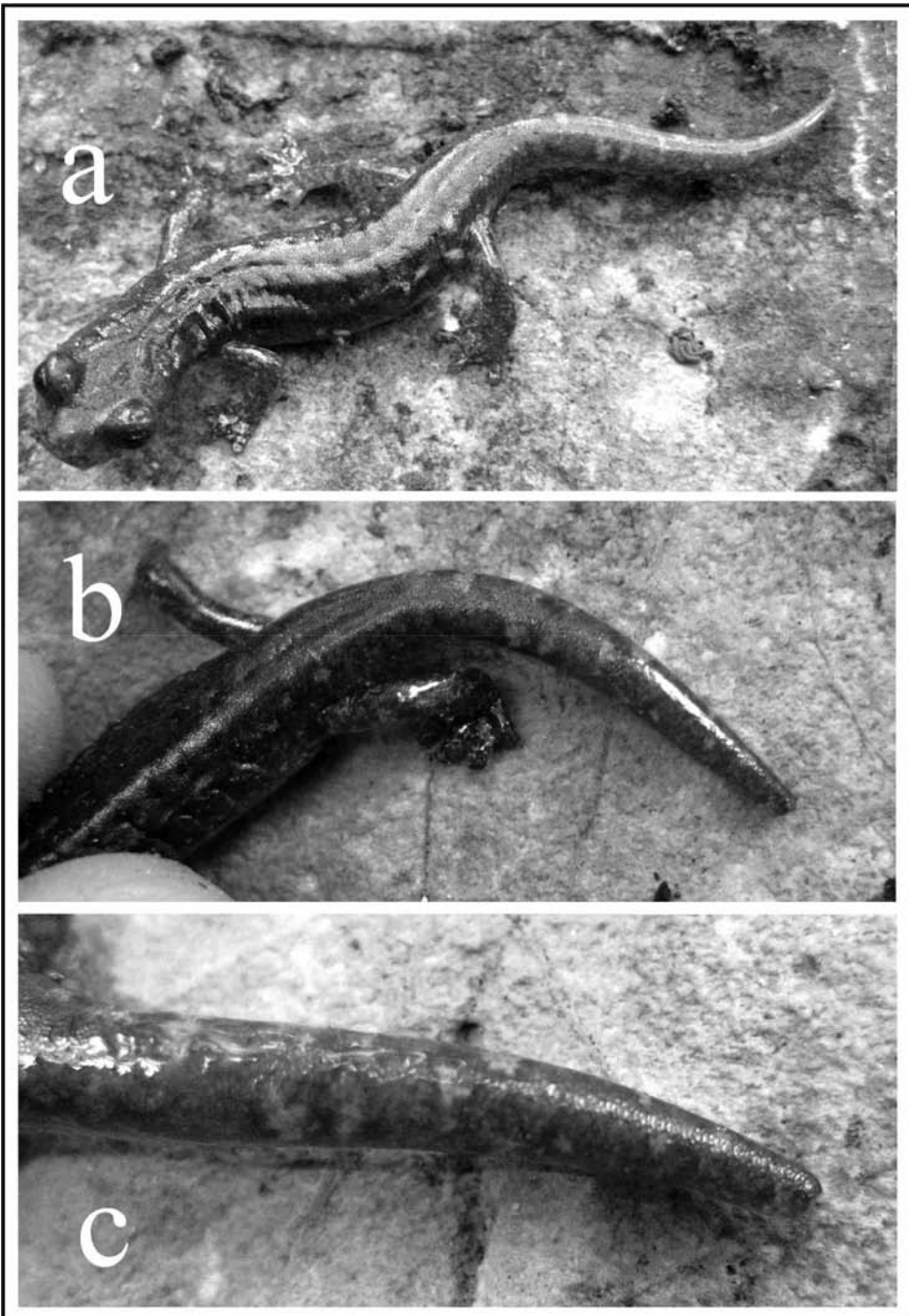


Figure 1. Specimen of *Hydromantes (A.) genei*, showing tail autotomy: *a.* the salamander before autotomy; *b.* the same salamander after caudal autotomy; *c.* close-up of the autotomised tail; note that just the tail tip was shed.

rarely drop their tails unless the situation is life threatening (Beneski, 1989). An autotomic plethodontid observed by Favelli et al. (2007) used the fingers of the person handling the animal as a fulcrum to break its tail. To the contrary, the salamander we observed was free on the palm when autotomised its tail. Furthermore, as may be noted in Fig.1, the shed portion of the tail was very small. The loss of small portion of distal part of the tail reduces the disadvantage previously mentioned. The modality of caudal autotomy that was observed could be considered a case of “economy of autotomy”, which has been known for many years also in some reptiles (e.g., Woodland, 1920; Bustard, 1968; Cooper et al., 2009).

The degree of specialisation for defensive tail loss varies among different Plethodontids lineages. Some of them have highly specialised tail morphologies with basal constrained tails (*Ensatina* and *Hemidactylium*) associated with adult terrestrial life. In those species, the breakage includes almost the entire tail to ensure a large portion of food, discouraging predators to attack the salamander (Wake and Dresner, 1967). Other lineages do not possess a localised breakage plane in their tail but have just developed wound healing capabilities. Finally, other lineages have no specialisation for caudal loss and their tails simply break mechanically as found in semi aquatic desmognathines and non-neotenic spelelpines (Wake and Dresner, 1967).

In the genus *Hydromantes* (i.e., European cave salamanders and the three Californian species) tail autotomy is rare. In all American plethodontids exhibiting autotomy, rupture occurs between, rather than through, vertebrae as in lizards (see Stebbins and Choens, 1995). Intervertebral breakage was confirmed also for the Sardinian species *H. (S.) sarrabusensis* (Favelli et al., 2007) and, likely, intervertebral breakage occurs also in *H. (A.) genei*. Despite the fact that tail regeneration after accidental breakage has been reported for some European mainland populations of *Hydromantes* (Salvidio, 1997), tail autotomy is only known to occur in the Sardinian species *H. (S.) sarrabusensis* (Favelli et al., 2007) and *H. (A.) genei* (this note). This difference among continental and island plethodontids cannot be tested due to absence in research effort on *H. ambrosii*, *H. italicus*, and *H. strinatii* because these mainland species are more studied than their island congeners (cf. Lanza et al., 2006) and specific tests conducted to assess the occurrence of tail autotomy in continental plethodontids gave always negative results (Lanza et al., 2006).

The tail plays an important role for climbing as it has been demonstrated for arboreal and saxicolous American salamanders of medium sizes (Wake, 1966) but not for small sized species (Alberch, 1981). With respect to the body dimension, in *Hydromantes (A.) genei* and *H. (S.) sarrabusensis* the largest sex presents an adult size of up to 124 mm, which is smaller than other Sardinian plethodontids (up to 127 mm for the smaller sex and up to 150 for the largest one) and comparable to the size of mainland species (up to 128 mm) (see Lanza et al., 2007). However the actual differences in size among *Hydromantes* species (less than 20%) are not comparable to size differences that exist among medium size and miniaturised salamanders (more than 100%) of the supergenus *Bolitoglossa* (Alberch, 1981).

European *Hydromantes* are cave-adapted species [with the exception of *H. (S.) sarrabusensis*] characterised by possessing large and webbed hands and feet that most probably are an adaptation to manoeuvre on the wet, smooth walls of caves (Lanza, 1991), as has been reported for other plethodontids species adapted to similar environmental condition (e.g., *Chiropterotriton magnipes*, Jaekel and Wake, 2007). Furthermore, the positive allom-

etric lengthening of the tail (meaning that larger individuals have proportionately longer tail), has a similar adaptive significance because Cave salamanders use their prehensile and sensitive tail largely during climbing (Lanza, 1991). The loss of the tail can thus likely affect their climbing performance. It would be of particular interest to investigate if the two Sardinian taxa exhibiting caudal autotomy [*H. (A.) genei* and *H. (S.) sarrabusensis*] are more terrestrial than climbers or if they are too small to be affected by the loss of the tail on their climbing abilities. However little ecological information is available to allow any preliminary conclusions. *Hydromantes (S.) sarrabusensis* is a terrestrial salamander living on the ground in a granitic area without caves of south-eastern Sardinia (Lanza et al., 2006) and, consequently, it can be hypothesised that it climbs less than the other European cave-adapted species. Thus, in this species, the tail loss would affect its movement capacity less than in a cavernicolous species. On the contrary, *Hydromantes (A.) genei*, although it also inhabits humid forested areas in the vicinity of streams, it is mainly a cavernicolous species, but no data are available to establish if this salamander spends more time on the ground than other European plethodontids.

Hydromantes (A.) genei is the sister and basal clade to all the other European cave salamanders and its ancestor colonised Sardinia in the late Miocene (9 Million of year ago, Ma), while *H. (S.) sarrabusensis* belongs to a different lineage of eastern Sardinian plethodontids and originated approximately 5 Ma (Carranza et al., 2008; van der Meijden et al., 2009).

Studies on the evolution of the caudal autotomy, could elucidate if this defensive trait was acquired independently by these two species and therefore can be considered a convergence. In *Hydromantes (A.) genei* two distinct lineages (A and B), showing a deep genetic divergence, have been recognised (Lanza et al., 1995; Carranza et al., 2008; van der Meijden et al., 2009). We only observed tail autotomy in members of lineage A. Further studies need to verify the existence of tail autotomy in the other lineage and in other Sardinian plethodontid species, whose ecological traits are substantially unknown. Indeed, consideration should be given to conspecific populations, or populations of closely related species, which are exposed to diverse predator pressures and may exhibit different level of tail autotomy as defensive behaviour (Cooper et al., 2004).

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