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Evolution of venom across extant and extinct eulipotyphlans

L'évolution du venin chez les eulipotyphles modernes et éteints

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ABSTRACT

Orally delivered venom in animals is found in distantly related invertebrate and vertebrate taxa, but is relatively rare in overall abundance. The trait would appear to be highly adaptive for prey capture and defence, and has been suggested to be a key innovation that led to the diversification of the venomous snakes. In extant mammals, oral venom is only found in the Eulipotyphla (which includes solenodons, shrews, moles and hedgehogs), and is only known to be present in four species. The phylogenetic distribution of venom across extant mammals suggests that venom evolved independently three times in the Eulipotyphla. In extant shrews, grooved teeth are not associated with venomousness; only the solenodon has both grooved lower incisors and salivary venom. Given these data, recent inferences of widespread venomous abilities in extinct eulipotyphlans on the basis of grooved teeth are not justified.

RÉSUMÉ

Le venin administré avec les dents est un caractère relativement rare chez les vertébrés. Le caractère semble être hautement adaptif pour la capture de proie ou la défense ; il a été considéré comme une innovation majeure qui a conduit à la diversification des serpents venimeux. Chez les mammifères modernes, le venin oral n'est connu que chez quatre espèces d'Eulipotyphla (qui comprend les solénodontes ou almiquis, les musaraignes, les taupes et les hérissons). La distribution phylogénétique de venin chez les mammifères modernes suggère que l'acquisition de venin a évolué de façon indépendante, trois fois, chez les eulipotyphles. Chez les musaraignes, les dents rainurées ne sont pas associées à la présence de venin, et seul la solénodonte comporte à la fois des dents cannelées et de la salive venimeuse. Compte tenu de ces données, les inférences récentes de capacités venimeuses chez des eulipotyphles éteints sur la base de la présence de dents cannelées ne sont pas justifiées.

1. Introduction

In animals, venom is found in a wide variety of taxa, including: spiders, wasps, scorpions, octopuses, amphibians, teleosts, snakes, lizards and a few mammals (Büchler et al., 1968). The ability to subdue prey with venom and defend against predators would appear to be a highly adaptive trait, and thus it is puzzling that venom and venom delivery systems are not more common among animals. The delivery of venom from modified salivary glands has two components – the secretion of modified

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salivary proteins (the venom) and the delivery apparatus (the teeth). The manufacture of venom proteins and the architecture of the associated dental structures are complex, and have been extensively documented elsewhere (Fry et al., 2010; Ligabue-Braun et al., 2012). Venom delivered through hollow teeth is a highly specialized weapon nearly completely restricted to the toxicoferan reptiles (Fry et al., 2006); only the solenodon, an extant eulipotyphlan mammal, also possesses a duct-like tooth as well as salivary venom. Most other venomous vertebrates (e.g. the short-tailed shrew and the Komodo dragon) have sharp teeth for puncturing, after which venomous saliva bathes the wound produced by the puncturing teeth.

The discovery that several species of varanid lizard produce salivary venom (Fry et al., 2006) led to a transformation in how researchers think about the evolutionary history of venom. Fry et al. (2006) proposed the name Toxicofera for the common ancestor of anguimorph and iguanian lizards and snakes, as they believe the origin of venom to predate the split between those clades. This suggests that the capacity to develop venomous saliva may be more widespread than previously believed; in fact, Dufton (1992) and Hurum et al. (2006) posited that venomousness might have been a primitive trait for Mammalia.

Recently, several papers have suggested that venom may have been more widely distributed across mammals in the past, partly based on descriptions of fossil mammals with teeth hypothesized to be adapted for venom delivery (e.g. Cuenca-Bescós and Rofes, 2007; Fox and Scott, 2005; Furió et al., 2010; Hurum et al., 2006; Peigné et al., 2009; Rofes and Cuenca-Bescós, 2009; Turvey, 2010). Since orally delivered venom in extant mammals is restricted to only a few eulipotyphlans (*Blarina brevicauda*, *Neomys fodiens*, *Neomys anomalus*, and *Solenodon paradoxus*), the proposed widespread prevalence of oral venom delivery systems in extinct mammals begs the question: if venom was widespread across fossil mammals, and if it is an adaptive trait, why was it lost in most living mammals? Possible explanations include that venom may be costly to produce, venom may not be an adaptive trait, or purportedly “venomous” fossil mammals were not actually venomous. When phylogeny, current function and comparative anatomy are assessed, it is clear that venom delivery is not the ancestral condition for mammals, and it is therefore highly unlikely that venom was widespread in fossil mammals. In fact, there is no strong evidence for an inference of venom in any fossil mammal.

2. Venom in extant mammals

Venom is rare across mammals. The most famous example of venom in mammals is the male platypus (*Ornithorhynchus anatinus*), which the animal delivers from a spur on the calcaneus. Since the tarsal spur is a sexually dimorphic trait, it likely functions for mate defence in the platypus (Ligabue-Braun et al., 2012). The slow loris (genus *Nycticebus*) secretes a protein from the brachial gland near its elbow, which, when mixed with saliva and injected via a bite, produces anaphylaxis in a victim. Lorises apply their brachial secretions to the fur around their head, and appear to use them primarily as warning signals to conspecifics (Hagey et al., 2007). The toxin seems to be a secondary function of the exudate, and presumably affects only susceptible species like humans (Hagey et al., 2007).

In extant eutherian mammals, the only order containing members with venomous saliva is the Eulipotyphla (hedgehogs, shrews, moles & solenodons) – this order contains about 452 species (Wilson and Reeder, 2005). Within Eulipotyphla, only four species have been shown to be venomous: the Hispaniolan solenodon (*Solenodon paradoxus*) [the Cuban solenodon (*S. cubanus*) is possibly also venomous, although it has not been tested] and three of 376 species of shrews (Soricidae) (*Blarina brevicauda*, *Neomys fodiens* and *N. anomalus*) (Dufton, 1992; Pucek, 1968). There is some evidence that other species of *Blarina* (*B. carolinensis* and *B. hylophaga*) and the Canarian shrew (*Crocidura canariensis*) (Lopez Jurado and Mateo, 1996) may be venomous; prey bitten by these animals reacts in a similar fashion to prey bitten by known venomous animals, but their saliva has not been tested experimentally (Lopez Jurado and Mateo, 1996). Many other species are as yet untested (including the American shrew, *Sorex cinerus*, and the European mole, *Talpa europaea*) (Dufton, 1992; Ligabue-Braun et al., 2012). Nussbaum and Maser (1969) observed the water shrew *Sorex palustris* immobilize a large vertebrate prey by grasping it by the head and interpreted this as evidence of venom; however, Pearson (1956) reported no significant toxicity in *S. palustris* saliva.

However, a number of species of eulipotyphlans and rodents have been tested and found to lack venom. These include: the European hedgehog (*Erinaceus europaeus*) (Mebs, 1999), the common mole (*Scalopus aquaticus*), the white-footed mouse (*Peromyscus leucopus*), meadow mouse (*Microtus pennsylvanicus*) (Pearson, 1942), a number of long-tailed shrews (*Sorex fumeus*, *S. pacificus*, *S. palustris*, *S. sinuosus*, *S. trowbridgii*, *S. personatus* and *S. vagrans*), the least shrew (*Cryptotis parva*), the shrew-mole (*Neurotrichus gibbsi*) (Pearson, 1950, 1956), and the greater white toothed shrew (*Crocidura russulla*) (Bernard, 1960). These observations suggest that, while not all species have been evaluated, venom is relatively rare across Eulipotyphla.

Of the 376 species of living shrews, only three are known to be venomous (0.8%). Even if we include species that are reasonably likely to be venomous – *B. carolinensis*, *B. hylophaga*, *Crocidura canariensis* – the proportion of venomous shrew species only increases to 1.6%. If we look at the proportion of all eulipotyphlans that are or may be venomous (including the solenodon), there are four known venomous species out of 452 (or eight if we extend it to the possibly venomous species, including *S. cubanus*). This means that 0.9% (at most 1.8%) of eulipotyphlans are venomous. If we assume that the proportion of modern venomous taxa accurately represents the distribution of venom in extinct species (and there is no good reason to assume that venom was more common in the past), we would predict that a similarly tiny fraction (less than 2%) of extinct species of shrew should be venomous.

Assessing the phylogenetic relationships among venomous shrews might shed light on how the trait evolved. Is it, as some have suggested (e.g. Hurum et al., 2006), a primitive trait that was lost in non-venomous lineages? Or is it an evolutionary novelty in a few eulipotyphlans?