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SHORT COMMUNICATION

First evidence of poisonous shrews with an envenomation apparatus

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Abstract Herein, we report evidence of an envenomation apparatus (EA) in two different species of extinct "giant" shrews, *Beremendia* and an indeterminate soricine (Mammalia, Eulipotyphla, Soricidae), documented by very well preserved fossil specimens recovered from two Early Pleistocene cave deposits of the Sierra de Atapuerca in Burgos, Spain. The two soricine taxa from Atapuerca have evolved specialized teeth as EAs, which differ from those of recently reported mammals of the Paleocene age, being more similar to the ones described in the modern *Solenodon*. This discovery reveals the first instance of shrews possessing what appears to be an EA, an evolutionary adaptation that, in these species, was probably related to an increase in body mass and hunting of a larger-sized prey. The Atapuerca specimens would have a highly specialized EA, one of the very few reported for an extinct or living mammal of any time. In addition to the presence of a gutter-like groove along the medial side of the crown of the lower incisors, these two species also present stout jaws and a modified mandibular symphysis with a conspicuous cavity, which in life would likely contain large amounts of connective tissue. The strong mandible architecture of these large shrews would be, in this way, reinforced by a more immovable symphysis, increasing the bite force exerted over a potential prey. This adaptation, together with the grooved incisors, would ensure a rapid and efficient transmission of the poisonous saliva to paralyze relatively large-sized prey.

Keywords Envenomation apparatus · Poisonous shrews · Atapuerca specimens

Introduction

Predation using a salivary venom apparatus is not common in mammals, although it seems to have a deeper and more diverse evolutionary history than previously thought, as some Paleocene remains from North America have recently shown (Fox and Scott 2005). Eulipotyphlans (Waddell et al. 1999) are the only instance of living mammals with poisonous saliva, but no evident venom apparatus has been previously described for the group, with the exception of the Caribbean genus *Solenodon* (Pournelle 1968; Dufton 1992; Dannelid 1998). The possibility of multiple origins of salivary venoms and envenomation apparatuses (EAs) during mammalian history, suggested by Fox and Scott (2005), has now been reassessed. We report here the first evidence of EAs in shrews, documented in specimens of *Beremendia fissidens* and a large indeterminate soricine from the cave deposits of the Pleistocene sites of the Sima del Elefante (ca. 1.25–1.5 Ma; Cuenca-Bescós and Rofes 2004) and Gran Dolina (ca. 0.78–0.9 Ma; Parés and Pérez-González 1995), respectively. Both sites are located in the Sierra de Atapuerca, Spain (Arsuaga et al. 1997; Carbonell et al. 1999).

Description

B. fissidens is a widely reported and well-studied, large-sized soricine known from the earliest Pliocene to the early Middle Pleistocene, and showing a wide Euroasiatic distribution (Rzebik-Kowalska 1998; Storch et al. 1998). Although its dentition has been exhaustively described

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(Rzebik-Kowalska 1976; Reumer 1984), no attention was given to the purpose of the narrow, but conspicuous, groove running from shortly before the tip to the crown-root junction on the medial side of the lower incisor crowns. The lower incisors of *B. fissidens* resemble those of other soricids, but are more elongate, robust and strongly upturned, and bear sharply pointed apices. The indeterminate soricine from Gran Dolina, even larger in size than *Beremendia*, shows the same type of dental adaptations (Fig. 1). The surface of the groove is enamel-covered, and it is almost uniformly C-shaped in cross section (Figs. 2 and 3a). The channel in these teeth likely functioned as a gutter, conducting poisonous saliva generated in some kind of enlarged submandibular salivary glands along the crown of the incisor. Although the teeth involved in the EA of the Atapuerca shrews are not the same, the mechanism of envenomation was probably similar to that described in modern solenodons (Rabb 1959; Dufton 1992). The structure of the groove itself vaguely resembles that observed in the lower canine of the indeterminate Paleocene mammal reported by Fox and Scott (2005), although the latter is placed on the lateral side. It is noteworthy that the location of the grooves on the medial side of the lower incisors of *Beremendia* and the indeterminate soricine leave them absolutely free from occlusion, ensuring an unobstructed flow of venom when the mandible is adducted.

Also meaningful is the presence of a conspicuous fossa within the mandibular symphysis on each half of the mandible (Fig. 1). The fossae are long depressions with a smooth basin and a large number of nutrient foramina. Each of these fossae is surrounded by a thick wall or crest to which the symphyseal cartilage would have attached (Fig. 3b). The resulting cavity formed by the union of the two fossae would probably have housed a large amount of connective tissue in live, reinforcing the architecture of an already strongly built mandible itself. The presence of a stronger, more immovable symphysis to improve the bite force exerted by the Atapuerca shrews could be a specialized character developed in order to ensure a rapid and efficient toxic saliva transmission.

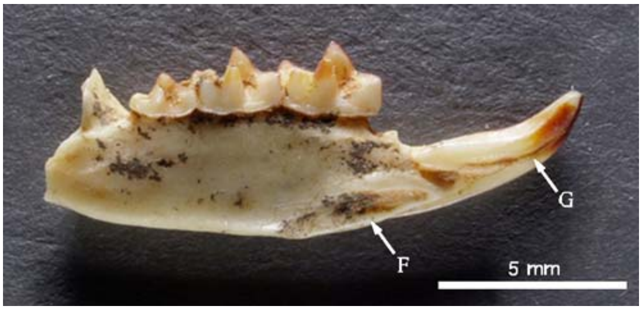

Fig. 1 Indeterminate soricine, specimen MPZ 2005/590. Incomplete left mandible in medial view showing the EA. *G* groove, *F* fossa

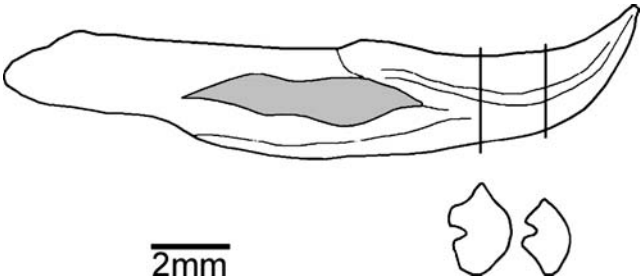

Fig. 2 Indeterminate soricine, MPZ 2006/336. Drawing of the complete left lower incisor in medial view showing cross sections of the envenomation groove along its crown. Sections taken from broken specimens

Discussion

The proposal of Fox and Scott (2005) regarding the independent origins of venomous saliva in different groups of mammals would be reinforced by the two large shrews from Atapuerca. More than 55 my after *Bisonalveus browni* and the other Paleocene mammal reported by Fox and Scott (2005), these shrews developed a sophisticated EA, which may be directly related to the marked increase in body mass of the two species. Given that *B. browni* belongs to the Order Cimolesta, the Atapuerca shrews would be the first fossil members of the Eulipotyphla to show evidence of the use of venomous saliva through a described EA.

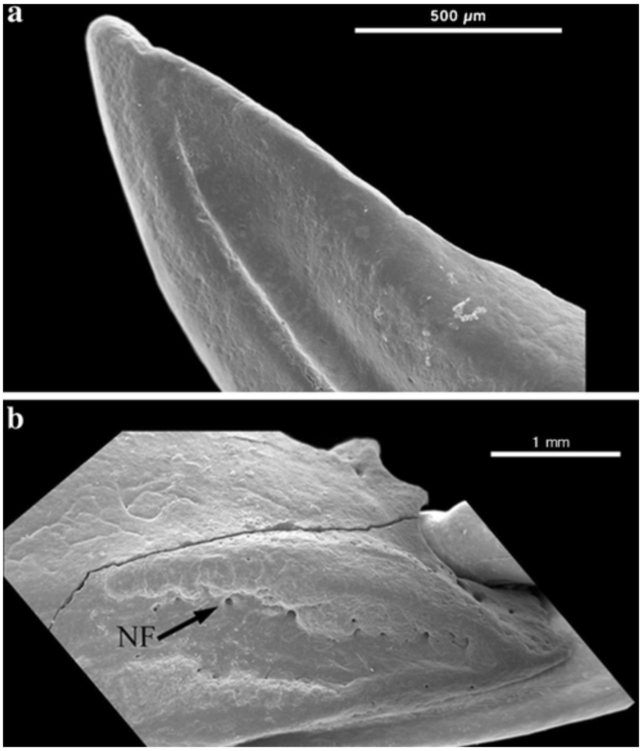

Fig. 3 **a** *B. fissidens*, MPZ 2005/454. SEM detail of the incisor tip in medial view showing the C-shaped, enamel-covered groove. **b** Indeterminate soricine, MPZ 2005/590. Detail of the fossa surrounded by the symphyseal wall. *NF* nutrient foramen

The large size attained by these shrews, approximately 40–45 g for *Beremendia* and 55–60 g for the indeterminate soricine [calculated using the methods of Bou et al. (1987)], could have been an adaptation for the hunting and handling of ever larger prey species, whose immobilization would have required the development of a stronger and more efficient EA. Additionally, the bite force also increases with shrew body size (Carraway and Verts 1994), a general trait that could have turned advantageous in these particular cases.

The saliva of modern *Blarina* (a moderately large species of venomous shrew) for instance, is toxic and enables the animal to deal with a rather large prey, which is immobilized by the fluid, thereby reducing the struggling of the prey (Dannelid 1998). This also enables *Blarina* to store food, which is living but comatose, paralyzed by the toxin (Merritt 1986; Dufton 1992). We parsimoniously assume a similar behavior for the Atapuerca shrews.

Our own inspections of recent soricids *Blarina*, *Neomys*, *Sorex*, and *Crocidura* mandibles clearly confirm the absence, in these taxa, of grooved incisors like those observed in the Atapuerca specimens. However, *Blarina* shows a quite similar, but smaller and inconspicuous, cavity at the symphyseal region to the one observed in the large fossil forms reported in this paper. Very shallow and incipient fossae are also present in *Neomys* and *Crocidura*. These traits have not been described in previous anatomical studies (e.g., Pearson 1950; Pournelle 1968).

The living mammals that produce venomous saliva (*Blarina*, *Neomys*, and *Solenodon*) have been reported to capture prey species more than double their body size, e.g., small rodents, amphibians, reptiles, fishes, and birds (Aitchison 1987; Churchfield 1990; Dufton 1992; Haberl 2002). Although the saliva is highly toxic (Pucek 1959; Kita et al. 2004), neither *Blarina* nor *Neomys* possesses teeth with clearly specialized structures to transmit the venom to the flesh of the prey, other than incisors with concave inner surfaces (Pournelle 1968; Churchfield 1990). Additionally, two other shrew species (*Sorex palustris* and *Crocidura canariensis*) have been reported to be venomous (Nussbaum and Maser 1969; López-Jurado and Mateo 1996). However, a specialized structure for the injection of concentrated venom has been described only for the Caribbean *Solenodon*, the largest of them all (Dufton 1992). The two giant shrew species from Atapuerca, with a body mass approximately three to four times that of the extant water shrew (*Neomys fodiens*), could have ventured to take even larger and more dangerous prey species, with the help of injection by a potent venom, which their complex EA would transmit quickly and efficiently.

It would be of great interest to reexamine the eulipotyphlans of different paleontological localities, which include *Beremendia* and other taxa of extinct large shrews (e.g., *Lunanosorex*, *Blarinoides*, *Shikamainosorex*), from this new perspective. The possibility of finding evidence of the use of venoms in the buccal region or elsewhere (Hurum et al. 2006) should be, at least, considered from now on when studying mammalian fossil predators, in particular the small ones. We are convinced that over time, new studies and discoveries will join the venomous mammals of the Paleocene and the giant shrews of the Plio-Pleistocene, allowing for a greater understanding of the evolution of salivary venom apparatuses in mammals.

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