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Identifying predation on rodent teeth through structure and composition: A case from Morocco

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ABSTRACT

Predation by nocturnal birds of prey is one of the most frequent modes leading to the concentration of rodents in fossil assemblages. This mode of accumulation leaves characteristic surface alterations on bones and teeth. In order to evaluate and characterize the effects of these pre-diagenesis alterations on rodent fossil samples, we have carried out microstructural and chemical analyses on incisors collected from present day Moroccan wild animals and owl pellets. The microstructure of both dentine and enamel was well preserved, but chemical changes were evident in pellet samples and depended on the particular tissue and the nature of the predator. The comparison of compositional data obtained from electron microprobe chemical analyses and infrared spectrometry has allowed us to assign a possible predator to an incisor extracted from a pellet of an unknown origin. This method has further implications for the understanding of taphonomy and palaeoecology of archaeological and fossil sites.

1. Introduction

Fossil teeth often present in archaeological and palaeontological sites can be used for phylogenetic, stratigraphic and palaeoenvironmental purposes. Small vertebrate teeth are usually abundant at predation sites, especially Rodent teeth. Unfortunately, the bones and teeth of the prey are frequently mechanically and chemically modified. This first stage of changes precludes and clouds interpretation of subsequent diagenetic alterations. Using the surface bone and teeth damages due to digestion of modern samples, Andrews has distinguished five categories of predators (Andrews, 1990). These parameters have been extensively used in taphonomic studies. However, the classification proposed by Fernandez-Jalvo and Andrews (1992) does not consider the biodiversity of the existing nocturnal and diurnal predators (Denys, 2011), and some taphonomic features are shared by different predators (Fernandez-Jalvo et al., 1998). Moreover, due to the large diversity of geological environments and histories, experimental data show that it is difficult to separate between surperficial abrasion and digestion features (Fernandez-Jalvo et al., 2014). Thus, analyses of the morphological and structural alterations of digested teeth or bones are a major, but only a first step to identify the origin of the modifications.

To improve our understanding of the biological and geological origins of alterations in fossils, it is necessary (i) to enlarge the criteria and to use structural and chemical data, (ii) to compare the diagenetic behaviour of dentine and enamel, (iii) to evaluate the respective contribution of each analytical technique, (iv) to build a modern reference for future archaeological applications, and (v) to understand the effects of gastric juices upon dental tissues and bone microstructure and composition.

Enamel and dentine are apatite biocomposites, but their microstructures, organic/mineral ratios, major and minor element contents, crystallinity, etc. differ.

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For modern samples, most data have been obtained on human, bovine and rodent samples. On large samples, micro-milling permits recovery of powdered dentine and enamel, and numerous data are available in dentistry (Elliott et al., 1985; Boskey, 2007), and in palaeontology to infer their preservation state (Greene et al., 2004; Huang et al., 2007; Wang et al., 2007).

Microstructural and chemical analyses have been done to improve our knowledge of the effects of digestion. A comparison of the compositions of modern bones and teeth from rodents killed and eaten by different predators have shown that despite a well preserved inner microstructure, chemical modifications exist and differ according to the predators and the preys (Dauphin and Denys, 1988, 1992; Denys et al., 1992). Several methods are available to detect diagenetic alterations. Infrared and Raman spectrometries are among the most popular, because they provide data on crystallinity, organic matrices, Ca/P ratios, etc. (Paschalis et al., 1996; Boskey and Mendelsohn, 2005; Pasteris et al., 2008; Beniash et al., 2009; Hollund et al., 2013).

In rodents, which have small ever growing teeth, enamel covers only the labial part of the incisor, and micro-milling does not permit separation of the dentine and enamel. Moreover, digestion induces partial or even total removal of this layer (Fernandez-Jalvo and Andrews, 1992). Teeth of modern and fossil rodents were described by Korvenkontio (1934) who identified three enamel patterns: uniserial, multiserial and pauciserial. The inner layer of Muroidea incisors is built of uniserial enamel (Koenigswald, 1985). Using thin sections of rat incisors, Weber (1965) has described the special structure of the enamel adjacent to the dentine, the "remarkable repeat pattern" of the enamel rod in the inner layer of enamel, and the "highly fibrous appearance" of the outer layer. Then, the two-layered enamel was repeatedly described in modern and fossil rodents (Wahlert, 1968; Boyde, 1978; Martin, 1997). An enamel rod or prism is composed of small elongated crystals (Warshawsky, 1971).

Many palaeontological sites in North Africa have yielded numerous rodent remains whose accumulation origins by predation are suggested in absence of taphonomic analyses (Geraads, 1998; Jaeger, 1977; Lopez-García et al., 2013; Reed and Barr, 2010). In the Temara region (Morocco), continuous stratigraphic sequences (~120,000 to ~6000 BP; Nespoulet et al., 2008; Jacobs et al., 2012; Janati et al., 2012; Stoetzel et al., 2014) have yielded an abundant small faunal assemblage whose taphonomic studies have highlighted the importance of predation (Stoetzel et al., 2011) but highlighted the lack of references concerning modern North African predators (Stoetzel and Denys, 2009). The identification of a predation bias in fossil micromammal assemblages is crucial to gain more precise information in the knowledge of the taphonomic history of sites formation as well as palaeoecological reconstructions (Andrews, 1990; Denys and Patou-Mathis, 2014).

To better characterize the diagenetic processes in the archaeological caves located in Morocco, we need to build databases on modern fresh and digested samples before comparing them to fossil material. Some studies have already been undergone on bones (Dauphin et al., 2012; Farre et al., 2014). A first step is to increase references by comparing the enamel and dentine of two modern genera (*Rattus*, *Meriones*). A second step aims to characterize the effects of predation on both microstructure and chemical composition of *Meriones* incisors extracted from modern regurgitation pellets. In rodent incisors the dentine is not covered, not "protected" by the enamel, so that these teeth are a good choice to compare the diagenetic behaviour of the two tissues. In the present work, these comparisons evaluate the ability of infrared spectrometry (FTIR) and chemical analyses to detect the early diagenesis induced by the digestion. A single criterion is not sufficient to infer the state of preservation. Thus, the microstructure, UV fluorescence, quantitative and qualitative chemical analyses, and FTIR observations have been performed.

2. Material and methods

2.1. Material

Incisors were extracted from modern *Rattus sp.* bred at the Museum national d'histoire naturelle (Paris) and *Meriones shawii*. Both genera are Muridae, but *Rattus* is a Murinae and *Meriones* is a Gerbillinae, so that shapes of molars greatly differ. Thus, we used only incisors because they have similar shapes to avoid additional biases. *Meriones* teeth from Morocco have different histories and origins. Two teeth were from wild living animals, while others have been collected in regurgitation pellets. One pellet is from *Bubo ascalaphus* from Guenfouda (near Oujda), another one was from an undetermined owl (*Tyto alba*? from Ouled Boughadi, Central part of Morocco). At last, two other pellets are from unknown predators (Table 1).

2.2. Cleaning – inclusion processes

The residual flesh and possible contaminants (bacteria) were destroyed using Na hypochlorite (dilute commercial solution) at room temperature and an ultrasonic bath. Samples were then rinsed with tap water and air dried. Incisors were mounted in epoxy resin and polished to a 0.25 μm finish using diamond paste. The exposed surface is through the long axis of the tooth, so that enamel and dentine are exposed on the same section. The same teeth were used for microstructural and compositional analyses.

2.3. Scanning electron microscopy

Polished sections and fractured samples were etched to reveal microstructural features. SEM observations were conducted using a Philips SEM XL30 in secondary electron mode (25 kV accelerating voltage), and a Phenom ProX in back scattered electron mode (BSE) (15 kV accelerating voltage). Details of sample preparations are given in the figure legends.

2.4. UV fluorescence

The epifluorescence signal of polished surfaces was observed under ultraviolet light using a Zeiss Standard microscope equipped with Neofluar fluorite objectives, a Zeiss mercury lamp, excitation filter (365 nm), and a transmission cut-off filter (400 nm).

Table 1
Origin of studied samples.

Origin (Morocco)	Predator	Species	Teeth: incisors	Surface modifications
MNHN (bred in captivity)	Fresh material	Rattus sp.	1	No modification
Ben Guerir	Fresh material	*M. shawii*	2 left lower – cut in situ	No modification
Ouled Boughadi	Owl indet.	Meriones	1 isolated right upper	Non digested
Guenfouda	*B. ascalaphus*	Meriones	1 isolated right lower	Broken, non digested
Unknown	Unknown	Meriones	2 isolated left lower	Very light digestion