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A re-evaluation of the taphonomic methodology for the study of small mammal fossil assemblages of South America





Fernando J. Fernández ^{a, b, *}, Claudia I. Montalvo ^c, Yolanda Fernández-Jalvo ^d, Peter Andrews^{e, f}, José Manuel López^{b, g}

a Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, calle 64 s/n (entre diag. 113 y calle 120), 1900, La Plata, Buenos Aires, Argentina

^c Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, 6300, Santa Rosa, La Pampa, Argentina

^d Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal, 2, 28906, Madrid, Spain

^e The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

^f Blandford Museum, Bere's Yard, Blandford, DT11 7AZ, Dorset, UK

^g Facultad de Filosofía y Letras, Universidad Nacional de Cuyo, Centro de Investigaciones Ruinas de San Francisco, Centro Universitario s/n, Facultad de Filosofía y Letras, Lab. 56, Primer subsuelo, 5500, Mendoza, Argentina

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ABSTRACT

The taphonomic methodology for the study of small mammal fossil was based mainly on actualistic studies of bones and teeth of insectivores (Soricidae, Talpidae, Erinaceidae) and rodents (Arvicolinae, Muridae) recovered from pellets of birds of prey and scats of carnivorous mammals from different places of North America, Europe and Africa. The digestive corrosion patterns on teeth of the South American rodents Sigmodontinae, Caviinae, Ctenomyidae and Abrocomidae, and the marsupials Monodelphini of central Argentina were observed. The comparison between the South American samples with the North American, African and European samples allowed us to establish similarities and differences in the digestive corrosion of the teeth. The main agreements have been recorded in the following groups: Arvicolinae with Caviinae and Abrocomidae; Murinae with Sigmodontinae; Soricidae, Talpidae and Erinaceidae with Monodelphini. However, the particular and simplified configuration of the molars of Ctenomyidae with thicker enamel and dentine exposed has promoted a new description of the categories of digestive corrosion. Likewise Muridae and Sigmodontinae molars, Ctenomyidae presents a delay in the appearance of signs of digestion with regard to other caviomorphs (Caviinae, Abrocomidae). This contribution may, therefore, be useful to know the origin of these South American faunas and the exact taphonomic agent that produced these assemblages. Finally, small mammal samples from an archaeopalaeontological site from Northwestern Patagonia, Argentina, were studied in order to apply the new methodology emerged from the recent samples.

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1. Introduction

The taphonomic methodology for the study of small mammal fossil established by Andrews (1990) is based mainly on actualistic studies of bones and teeth of insectivores and rodents recovered from pellets of raptor birds and scats of carnivorous mammals. Pioneering investigations (Mellett, 1974; Mayhew, 1977; Dodson and Wexlar, 1979; Korth, 1979; Andrews and Evans, 1983; Denys, 1985) showed that digestion could be detected on prey remains. Andrews (1990) established the methodology and distinguished categories of predators according to different grades and intensities of preservation of their small mammal accumulations, and applied the methodology to the Pleistocene site of Westbury (UK). Lately, Fernández-Jalvo and Andrews (1992) could apply this methodology to other fossil and modern sites. Finally, other complementary taphonomic perspective has taken into account the main characteristics of the undigested prey remains (e.g., punctures, crenulated edges, scratches, notches), abandoned by predators (e.g., Hockett, 1995; Lloveras et al., 2009; Montalvo et al., 2016).

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

^{*} Corresponding author. CONICET, Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, calle 64 s/n (entre diag. 113 y calle 120), 1900, La Plata, Buenos Aires, Argentina.

E-mail address: fernandezf77@yahoo.com.ar (F.J. Fernández).

The taphonomic classification proposed by Andrews (1990) makes the distinction between five category of predators [i.e., little (1), intermediate (2), moderate (3), heavy (4) and extreme (5)], that broadly corresponds from low to high degree of digestion modification to strigiforms (categories 1, 2 and 3), falconiforms, accipitriforms (categories 3 and 4) and carnivorous mammals (categories 4 and 5). According to Andrews (1990), these categories are based both on the degree of modification and frequencies of affected elements, considering digestive corrosion marks on the surfaces of teeth (i.e., incisors and molars) and postcranial remains (i.e., proximal epiphysis of femur and distal epiphysis of humerus), the degree of breakage of cranial and postcranial remains (i.e., diaphysis, proximal epiphysis and distal epiphysis), and the relative abundance of skeletal elements. Andrews (1990) developed this methodology using bones and teeth of the small rodents Cricetidae (Arvicolinae) and Muridae, and the small insectivores Talpidae, Soricidae and Erinaceidae from different places of North America, Europe and Africa. Andrews (1990) also noted the distinction in the categories of corrosion, according to the morphology of the molars of the mentioned groups of small mammals. Fernández-Jalvo and Andrews (1992) illustrated Arvicolinae (as this was the most abundant group in the site of Atapuerca) and described the effects of digestion in other groups, but they did not illustrate such taphonomic differences. Subsequently, Demirel et al. (2011) pointed out the disparity in the digestive action between teeth of Muridae and Arvicolinae from an archaeological cave-site located in the southern coast of Turkey. Likewise, Stoetzel et al. (2011) adapted the taphonomic categories of digestive corrosion provided by Andrews (1990) and Fernández-Jalvo and Andrews (1992) for Arvicolinae molars to Muridae (Gerbillinae and Murinae) molars, which constitute the dominant taxa of the small mammal accumulations recovered from an archaeological cave-site located in the northern cost of Morocco. Recently, Fernández-Jalvo et al. (2016) shed light about this issue describing and quantifying different traces of digestion in incisors viewed in lateral and occlusal views of molars of Arvicolinae, Muridae and Soricidae according to traits and degrees of intensity of digestive effects produced by the same predator, and extended the taphonomic observations most frequently used by taxonomists, i.e. the occlusal view of molars. All these authors observed a 'delay' in the categories of digestion in Muridae molars compared with Arvicolinae molars. This is mainly because of the Arvicolinae molars are hypsodont, lophodont, prismatic and have acute salient angles with thin enamel and dentine directly exposed on occlusal surface, against Muridae molars which are brachydont, bunodont with have rounded angles, thicker enamel and closed roots, all of which provide a higher resistance to digestion. Thus, enamel reduction in Muridae molars only occurs in heavy degrees of digestion, whilst in Arvicolinae molars is evident already in light grades of digestion. In addition, Fernández-Jalvo et al. (2016) remarked that in Soricidae, the enamel reduction by digestion mainly extends along the lateral sides in the crown-root junction due to the thicker enamel and more prominent cusps. Murids also show reduction of enamel at the crown-root junction.

In spite of the fact that South American samples were not included by Andrews (1990) and Fernández-Jalvo and Andrews (1992), the empirical application of this methodology for interpreting the origin of micromammal assemblages from palaeontological and archaeological sites has been very useful in many parts of the world (e.g., Weissbrod et al., 2005; Matthews, 2006; Reed and Denys, 2011; Stoetzel et al., 2011; Pokines, 2014), including South America, and especially Argentina (e.g., Pardiñas, 1999; Fernández et al., 2009, 2011, 2012, 2015a, 2015b; Fernández, 2012a, 2012b; Verzi et al., 2008; Montalvo, 2002; Montalvo et al., 2008a, 2012a, 2015a; Scheifler et al., 2012; Fernández and De Santis, 2013). In addition, many small mammal predators that inhabit Argentina have already been taphonomically evaluated using this methodology (Iglesias, 2009; Álvarez et al., 2012; Ballejo et al., 2012; Carrera and Fernández, 2010; Fernández, 2012a; Gómez, 2005, 2007; Gómez and Kaufmann, 2007; Montalvo et al., 2007, 2008b, 2012b, 2014, 2015b, 2015c, Montalvo and Tallade, 2009, 2010; Montalvo and Tejerina, 2009; Quintana, 2015; Rudzik et al., 2015). Nonetheless, a re-evaluation of the taphonomic methodology for the study of small mammal fossil teeth assemblages digested and deposited by predators in South America is needed. In addition, the fact that most of the aforementioned actualistic researches were performed by our work group implies an important accumulated knowledge for observing predator samples.

In order to do this, we develop a qualitative and quantitative study of the digestive corrosion on incisors and cheek teeth of the small rodents Ctenomyidae, Abrocomidae, Caviidae Cricetidae Sigmodontinae, and the small marsupials Didelphidae Monodelphini recovered from modern samples of pellets of raptor birds and scats of carnivorous mammals of central Argentina.

1.1. Digestive corrosion on teeth of small mammals

Predation is one of the most recurring causes of small mammal accumulations, and digestive corrosion is the greatest evidence of this (Andrews, 1990; Fernández-Jalvo et al., 2016). The evidences of digestive corrosion on incisors and molars is based both on the degree of modification and proportion of the affected (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). The corrosion is more noticeable at the extremes of the teeth, primarily affecting the enamel, with a mineralized prismatic ultrastructure that facilitates penetration of digestive acids (Dauphin et al., 2015). Later, digestion extends to dentine, because it has an organic content with a more homogeneous ultrastructure than enamel (Andrews, 1990; Dauphin et al., 2015). Isolated incisors could show the entire surface digested, whereas the *in situ* incisors display alteration only in the crown (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Breakage during ingestion increases the effects of digestion as gastric acids penetrate into tooth, resulting in thin and rounding broken edges (Andrews, 1990; Fernández-Jalvo et al., 2016). The greatest variability of molars due to morphology and thickness of enamel can also yield differences in the way they are affected by digestion (Andrews, 1990).

The digestive acids of predators produce differential corrosion effects on bones and teeth, mainly because of the level of digestive acids varies between strigiforms, falconiforms, accipitriforms, carnivorous mammals and humans (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). On the one hand, avian raptors have a distinctive digestion related with their glandular and muscular stomach. Non-digestible remains such as teeth, bones, claws, hair. feathers and chitin are regurgitated forming a pellet. The pH of gastric acids of strigiforms is 2.5 to 2.2, whilst in falconiforms and accipitriforms range from 1.8 to 1.3 (Duke et al., 1975). In consequence, strigiforms cause light to moderate degrees of digestion and falconiforms and accipitriforms yield strong degree of digestive corrosion (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). On the other hand, both carnivorous mammals and humans may chew their prey before ingestion, and the indigestible remains are ejected in the scats. Thus, they can produce extreme levels of digestive corrosion due to gastric and bile acids (Andrews and Evans, 1983; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Crandall and Stahl, 1995; Lupo and Schmitt, 2005; Dewar and Jerardino, 2007).

1.2. South American small mammals

Within the South America there are currently numerous

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