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

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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 archaeo-palaeontological 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).

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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

recognized terrestrial small mammal species (<1 kg) belonging to six families; Cricetidae, Caviidae, Ctenomyidae, Octodontidae, Abrocomidae, and Didelphidae (Gardner, 2007; Patton et al., 2015). Some members of these families outweigh 1 kg, thus we only select those taxa below this limit. In this work, some taxa of Cricetidae (Sigmodontinae), Caviidae (Caviinae), Ctenomyidae, Abrocomidae and Didelphidae (Didelphinae, Monodelphini) are taphonomically studied. Their natural histories and their archaeological importance are described in the following paragraphs.

Sigmodontines include the New World rats and mice. With more than 80 genera and 400 species the subfamily Sigmodontinae comprises the most diverse South American rodents, belonging to the family Cricetidae (e.g., D'Elía and Pardiñas, 2015). The earlier fossil records of sigmodontines date from the Late Miocene, but numerous genera appear in the early Pliocene (e.g., D'Elía and Pardiñas, 2015). Sigmodontines are small in size (~12–500 g), mostly nocturnal and occur all the terrestrial environments of South America, from the sea level to nearly 5000 m asl (e.g., D'Elía and Pardiñas, 2015). They present one pair of incisors and three pairs of molars (both upper and lower). The molars can be low-crowned (brachydont) or high-crowned (hypsodont), constitute a complex structure, and exhibit a great variation in size, numbers of roots (from one to six) and morphology related with each group, showing numerous cups, mures, styles, lophs (four or five) and islands (e.g., D'Elía and Pardiñas, 2015). With the exception of the marsh rat Holochilus, sigmodontines are not present in the prehistoric human diet (e.g., Fernández et al., 2011). However, their profuse fossil record are frequently studied for palaeoenvironmental interpretations (e.g., Pardiñas, 1999; Fernández et al., 2009, 2011, 2012, 2015a, 2015b; Fernández, 2012a; Scheifler et al., 2012).

The rodents of the subfamily Caviinae, commonly called cavies, are small to moderate-sized (~150–1500 g), diurnal, colonial, herbivorous and cursorial, belonging to the family Caviidae. They inhabit in nearly all South American environments. Caviinae is composed by three extant genera Cavia, Microcavia and Galea, and its early fossil taxa date from the Mid-Miocene (e.g., Dunnum, 2015). The incisors are narrow. The molariforms are hypsodont, formed for two prisms united by a unique fold giving it V-shaped in lateral view (e.g., Dunnum, 2015). The enamel is thin and non-continuous because of there are dentine tracks with one or two lines without enamel on the tooth column. In addition, the molariforms present rounded protuberances of cementum along the lateral surfaces. In several occasions the presence of Caviinae at archaeological sites has been associated with human consumption and domestication process (e.g., Wing, 1986; Pardiñas, 1999; Quintana, 2005; Fernández et al., 2009). However, these rodents can be hunted by carnivorous mammals and birds of prey (e.g., Redford and Eisenberg, 1992; Bó et al., 2007).

The family Ctenomyidae constitutes of the single recent genus Ctenomys, known as tuco-tucos, with more than 60 species from central and southern South America. Ctenomyidae is closely related to the family Octodontidae (some authors include it within this family), and its history began in the Late Miocene. Ctenomys is a small to moderate-sized (~100–1200 g) fossorial and diurnal rodent. The incisors exhibit wide labial surface and thick enamel. The molariforms are hypsodont and kidney-shaped, with occlusal simplification, thick radial enamel, and wide dentine tracks in anterolingual and posterolingual end of each molar (e.g., Bidau, 2015). Ctenomys is found in nearly all the environments of central and southern South America, but populations in some regions (e.g., Pampean and Patagonian) have declined markedly due to extensive overgrazing and agricultural activities (e.g., Pardiñas and Teta, 2013). Therefore, the abundance of Ctenomys in archaeological sites often is higher than the current times. In addition, the archaeological record of Ctenomys has drawn attention of zooarchaeologists for many reasons:

1) the mentioned abundance in the archaeological context;
2) its fossorial activities produce archaeological and sedimentological disturbances by moving and destroying lithic and bone materials while digging (Durán, 1991);
3) bones could present taphonomic evidences that were exploited by humans (e.g., Pardiñas, 1999);
4) bones and teeth may show evidences of predators activities, including mammalian carnivores and birds of prey (e.g., Pardiñas, 1999).

The members of Abrocomidae are called chinchilla rats. This family contains two extant genera, Abrocoma and Cuscomys. The smaller genus Abrocoma (~350 g) occurs in the arid environments from central part of the Andean fringe of South America, and the larger genus Cuscomys (~900 g) is restricted to a small sector in the central Peruvian forest (Patton and Emmons, 2015). The earlier fossil records of Abrocomidae date from the Early Miocene (Verzi et al., 2016). They present narrowed lower incisors; hypsodont and flat-crowned molariforms. Molariforms show a loop-shape occlusal pattern. Lower molariforms are prismatic and angular with two lingual and one labial fold, and upper series show a single lingual and labial folds (e.g., Patton and Emmons, 2015). Members of Abrocoma were found in few archaeological sites throughout their cumulative distributional range, with evidences of raptor activity and human consumption (e.g., Simonetti and Cornejo, 1991; López et al., 2016).

The tribe Monodelphini includes 11 recent genera of American small opossums (~10–250 g), belonging to the family Didelphidae. The recent New World marsupials are known from Late Cretaceous, and currently are found in almost all the environments of South America (Gardner, 2007). The incisors are very small, the canines large, and the molars are tribosfenic. Cheek teeth present a thick and continuous layer of enamel (Gardner, 2007). Bones and teeth of these marsupials are frequent in archaeological sites, but are not present in the prehistoric human diet. On several occasions their archaeological record has been used for palaeoenvironmental reconstructions (Pardiñas, 1999; Fernández et al., 2009, 2011, 2012, 2015a, 2015b; Fernández, 2012a; Scheifler et al., 2012).

2. Materials and methods

Taking into account the remarkable morphological differences between teeth of caviomorph rodents (e.g., Ctenomyidae, Abrocomidae and Caviinae), and teeth of miomorph rodents (Sigmodontinae), the degree to which these teeth are affected by digestive corrosion is also expected to differ, as mentioned earlier by Montalvo et al. (2014, 2015b). The hypsodont and prismatic molars of Caviidae and Abrocomidae could be affected by digestive action faster than those of Sigmodontinae. In addition, the difference in the thickness of the enamel and the type of angle between the edges of the lophs/lophids may be the character that determines how the teeth are affected by digestive action. This scenario allows us to propose that the qualitative and quantitative evidences of digestive corrosion on teeth yield by predators should be evaluated separately for each taxon of prey.

Incisors and molars of Sigmodontinae and Caviomorpha rodents, and marsupials were obtained from pellets of strigiforms (Tyto alba, Bubo virginianus magellanicus, Pseudoscops clamator and Athene cunicularia), falconiforms (Caracara plancus) and accipitriforms (Elanus leucurus, Geranoaetus melanoleucus, Geranoaetus polyosoma and Buteogallus coronatus), and scats of felids (Puma concolor and Leopardus geoffroyi), mustelids (Lontra longicaudis) and mephitid (Conepatus chinga). The selected 15 small mammal

samples from different places of central Argentina had been previously evaluated by different authors (Table 1) using the standard methodology of Andrews (1990) and Fernández-Jalvo and Andrews (1992). In this study, the four categories of digestive corrosion for both digested molars and incisors (light, moderate, heavy and extreme) were redefined according to morphology of teeth of each taxon of prey.

In order to delineate a new and more accurate methodology for the small mammal prey deposited by predators in archaeological and paleontological sites from South America, the results obtained for the degree of digestive corrosion in teeth were compared with data of small mammals prey from North America, Europe and Africa (cf. Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Demirel et al., 2011; Stoetzel et al., 2011; Fernández-Jalvo et al., 2016).

Both taxonomic identification and digestive corrosion on teeth were observed and photographed with a Leica M205A stereomicroscope, two SEM: Jeol 35CF (8 kV) and Jeol JSM-6490LV (10 kV), and two SEM with backscattered detectors to show tooth density changes: FEI-INSPECT (Low Vacuum microscope) and FEI-QUANTA 200 (environmental microscope).

In addition, small mammal samples from an archaeological and palaeontological site from Northwestern Patagonia, Argentina were studied in order to apply the new methodology emerged from the recent samples. Cueva Huenul 1 site (CH1 hereafter) is a large cave located in Northwestern Patagonia (Neuquén Province, Argentina) at east of the Andes mountain range, near the southern margin of the Colorado River (36°56′45″S, 69°47′32″W, 1008 m asl). Research being conducted at the CH1 site provided stratified sequences of paleontological and archaeological remains spanning the late Pleistocene-late Holocene (~16-04 kyr BP). Late Pleistocene layers correspond to paleontological deposit, and Holocene layers to archaeological ones. The paleontological and archaeological materials recovered from squares A1, B1, C1 and D1 include lithic artifacts, pottery, archaeobotanical remains, hearths, coprolites and bones of megafaunal taxa, bones of large birds, bones and teeth of large and medium mammals, and small vertebrates remains (e.g., Barberena et al., 2015). The small mammals recovered from square A1 were taphonomically studied by Fernández et al. (2012), but without distinguishing between taxa. Subsequently, the small mammals recovered from squares C1 and D1 were taphonomically analyzed considering the new methodology presented here for Sigmodontinae, Caviinae, Ctenomyidae, and Monodelphini. In both studies the taphonomic analyses of the small mammals showed that most of the small mammal fauna from late Pleistocene to late Holocene was probably accumulated as the prey assemblage of the common owl T. alba.

The generated information is presented in qualitative and quantitative mode. When the categories of modification of the small mammals are evaluated, qualitative and quantitative aspects of several attributes should be considered, with digestive corrosion as the greatest evidence of predation (e.g., Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 2016). Here, based on the study of small mammal samples (Table 1), it is possible to arrive to definition of categories of teeth digestion for the South American small mammals.

Samples are housed in the Facultad de Ciencias Exactas y Naturales (UNLPam, La Pampa Province, Argentina), laboratory of Anatomía Comparada, Facultad de Ciencias Naturales y Museo (UNLP, La Plata, Buenos Aires Province, Argentina), Centro de Investigaciones Ruinas de San Francisco, Facultad de Filosofía y Letras (UNCuyo, Mendoza Province, Argentina) and IADIZA-CONICET (Mendoza Province, Argentina).

3. Results and discussion

3.1. Taphonomic model for small mammal's teeth

The morphology of the incisors of Caviinae, Abrocomidae,

Table 1
Main features of the studied samples.

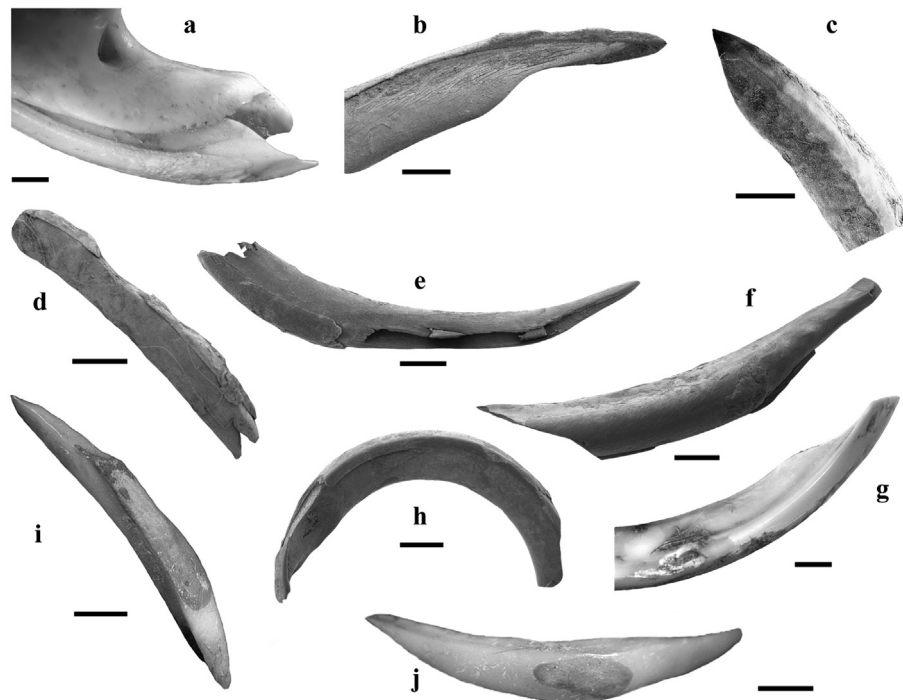| N	Predator	Location	Prey	Total sample (pellets/scats)	References
1	*Tyto alba* (barn owl)	35°25'S, 64°29'W La Pampa Province, Argentina	Sigmodontinae	59	Gorordo et al., 2006
2	*Tyto alba*	32°35'S, 69°02'W Mendoza Province, Argentina	Abrocomidae, Caviinae	210	López et al., 2016
3	*Bubo virginianus magellanicus* (Magellanic horned owl)	34°56'45″S, 69°50'55″W Mendoza Province, Argentina	Sigmodontinae, Ctenomyidae, Monodelphini	84	Montalvo et al., 2015b
4	*Pseudoscops clamator* (striped owl)	34°36'6″S, 58°21'33″W Buenos Aires Province, Argentina	Sigmodontinae, Caviinae	21	Rudzik et al., 2015
5	*Athene cunicularia* (burrowing owl)	36°37'10″S, 64°19'45″W La Pampa Province, Argentina	Sigmodontinae, Ctenomyidae Caviinae	132	Montalvo and Tejerina, 2009
6	*Caracara plancus* (southern caracara)	36°37'10″S, 64°19'45″W La Pampa Province, Argentina	Sigmodontinae, Ctenomyidae Caviinae	67	Montalvo and Tallade, 2009; Montalvo et al., 2011
7	*Elanus leucurus* (white-tailed Kite)	36°43'S, 64°16″W La Pampa Province, Argentina	Sigmodontinae, Caviinae	118	Montalvo et al., 2014
8	*Geranoaetus melanoleucus* (black-chested buzzard-eagle)	32°35'S, 69°02'W Mendoza Province, Argentina	Abrocomidae, Caviinae	25	Abraham, 2012; López et al., 2016
9	*Geranoaetus polyosoma* (red-backed hawk)	34°56'6″S, 69°50'42″W Mendoza Province, Argentina	Sigmodontinae, Ctenomyidae Caviinae	50	Iglesias, 2009
10	*Buteogallus coronatus* (crowned solitary eagle)	36-37°S, 67-65°W La Pampa Province, Argentina	Ctenomyidae	42	Galmes et al., 2015
11	*Puma concolor* (Puma)	36°55'S, 64°16'W La Pampa Province, Argentina	Sigmodontinae, Ctenomyidae, Caviinae	76	Montalvo et al., 2007
12	*Leopardus geoffroyi* (Geoffroy's cat)	37°57' S, 65°33' W La Pampa Province, Argentina	Sigmodontinae, Caviinae	179	Montalvo et al., 2012b
13	*Leopardus* cf. *L. geoffroyi/L. pajeros* (Pampas cat)	34°02'S, 67°58'W Mendoza Province, Argentina	Abrocomidae, Ctenomyidae, Caviinae, Monodelphini	86	Tabeni et al., 2012
14	*Lontra longicaudis* (Neotropical otter)	31°30'52″S, 60°29'51″W Santa Fé Province, Argentina	Sigmodontinae, Caviinae	320	Montalvo et al., 2015c
15	*Conepatus chinga* (Andean hog-nosed skunk)	36°55'S, 64°16'W La Pampa Province, Argentina	Sigmodontinae, Ctenomyidae	59	Montalvo et al., 2008b

Sigmodontinae is similar than those rodent groups of North America, Europe and Africa (Arvicolinae and Muridae). Thus, the observed modifications in each of the categories are also similar (Table 2, Fig. 1a—f). In this context the categories of digestive corrosion of these South American rodents present equal characteristics than those obtained by Andrews (1990), Fernández-Jalvo

Table 2
Categories of digestion of incisors for small mammals of South America compared with African and European preys (taken from Fernández-Jalvo and Andrews, 1992, p. 413; Fernández-Jalvo et al., 2016).

	Light	Moderate	Heavy	Extreme
North American, African and European rodents **Arvicolinae Muridae** South American rodents **Caviinae Abrocomidae Sigmodontinae**	Digestion affects the whole enamel surface showing slight to moderate pitting and matt surfaces. In some cases, digestion is concentrated at the tips of the incisors, where the enamel is totally removed and indicating digestion while the incisors are still retained in the jaws.	The surface of the enamel is more intensively affected, and the dentine is also modified with a wavy surface. Enamel remains along the length of the tooth, except sometimes when it is removed from the tip.	Digestion occurs on both enamel and dentine, producing a wavy surface on the latter and reducing the enamel to small island on the surface of the dentine. Sometimes the enamel is almost entirely eaten away, and the dentine can take on an appearance similar to effects of weathering (cracked).	Damage is extensive on both the enamel and the dentine, some teeth having all of the enamel removed, leaving a narrow and dentine core, while others also have much of the dentine removed so that the edges of the dentine, or of the enamel if still remaining, collapses in on itself. Where the enamel remains on these teeth it is restricted to small islands separated by areas of dentine.
South American rodents: **Ctenomyidae**	Digestion affects part of the enamel surface showing slight pitting. Digestion could concentrate at the tips of the incisors, where the enamel is totally removed. The dentine is not affected.	The surface of the enamel is more intensively affected. Dentine has a wavy surface.	Digestion occurs on both enamel and dentine, producing a wavy surface on the latter and reducing the enamel to small island on the surface of the dentine.	Damage is extensive on both the enamel and the dentine, some teeth having all of the enamel removed, leaving a narrow and dentine core, while others also have much of the dentine removed so that the edges of the dentine, or of the enamel if still remaining, collapses in on itself.
North American, African and European insectivores **Talpidae Soricidae Erinaceidae** South American marsupials **Monodelphini**	No digestion can be seen. No damage.	Matt surface enamel.	Enamel form islands.	Small island of enamel or enamel completely removed. Dentine highly rounded.

Fig. 1. Examples of rodent digested incisors from South America. a: light corrosion in Sigmodontinae incisor (sample 14); b: light corrosion in Sigmodontinae incisor (sample 12); c: moderate corrosion in Sigmodontinae incisor (sample 9); d: heavy corrosion in Sigmodontinae incisor (sample 9); e: extreme corrosion in Caviidae incisor (sample 13); f: extreme corrosion in Caviidae incisor (sample 13); g: light corrosion in Ctenomyidae incisor (sample 11); h: moderate corrosion in Ctenomyidae incisor (sample 13); i: heavy corrosion in Ctenomyidae incisor (sample 10); j: extreme corrosion in Ctenomyidae incisor (sample 10). Scales = 1 mm.

and Andrews (1992), Demirel et al. (2011), Stoetzel et al. (2011) and Fernández-Jalvo et al. (2016). However, for Ctenomyidae, because incisors have a wider labial surface and thicker enamel, a delay in the appearance of digestion (Fig. 1g—j) was observed when compared to other rodent incisors (Tables 2 and 3).

The categories of digestive corrosion of Monodelphini teeth (Fig. 2a—d) display similar characteristics than those obtained by Andrews (1990), Fernández-Jalvo and Andrews (1992), and Fernández-Jalvo et al. (2016) for the insectivores Talpidae, Soricidae and Erinaceidae (Tables 2 and 4). Although a reduced number of Monodelphini teeth were revised, a delay of evidence of digestion was recorded (Tables 3 and 5), as it was observed by Fernández-

Jalvo et al. (2016) in Soricidae molars, which is consistent with the presence of a thick and continuous layer of enamel, all of which provide resistance to corrosion.

Considering the comparable morphological patterns of the molars, the categories of digestive corrosion of Caviinae and Abrocomidae (mainly lower molars) show similar features than those obtained by Andrews (1990), Fernández-Jalvo and Andrews (1992), Demirel et al. (2011) and Fernández-Jalvo et al. (2016) for Arvicolinae (Tables 4 and 5, Fig. 3a—i). However, the molars of Caviinae present abundant interprisms cementum and protuberances of this tissue placed on the enamel in the groove mainly between the prisms. In fact, digestive corrosion easily removes the protuberances

Table 3
Percentages of incisors digested for studied predator samples. Abbreviations: L: light; M: moderate; H: heavy; E: Extreme.

N	Predator	% incisors digested																		
		Sigmodontinae				Caviinae				Abrocomidae				Ctenomyidae				Monodelphini			
		L	M	H	E	L	M	H	E	L	M	H	E	L	M	H	E	L	M	H	E
1	*Tyto alba* (n = 184)	26.1	3.8	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	*Tyto alba* (n = 30)	—	—	—	—	9.5	0	0	0	—	—	—	—	—	—	—	—	—	—	—	—
3	*Bubo virginianus magellanicus* (n = 45)	69.6	4.4	0	0	—	—	—	—	—	—	—	—	32.7	1.1	0	0	10	0	0	0
4	*Pseudoscops clamator* (n = 190)	37.6	28.8	10.2	0	40.1	27	8.9	0	—	—	—	—	—	—	—	—	—	—	—	—
5	*Athene cunicularia* (n = 31)	61.5	26	12.5	0	65.1	24.2	11.4	0	—	—	—	—	33.3	0	0	0	—	—	—	—
6	*Caracara plancus* (n = 34)	22.1	42.5	30.2	5.2	18.3	44.5	33.3	3.9	—	—	—	—	29.8	15.2	6.2	0	—	—	—	—
7	*Elanus leucurus* (n = 64)	38.1	39.7	20.6	1.6	34.9	41.1	23.1	0.9	—	—	—	—	—	—	—	—	—	—	—	—
8	*Geranoaetus melanoleucus* (n = 38)	—	—	—	—	17.5	56.5	20.5	0	—	—	—	—	—	—	—	—	—	—	—	—
9	*Geranoaetus polyosoma* (n = 94)	21.7	49.3	29	0	38.5	33.8	33.8	0	—	—	—	—	58.3	33.3	0	0	—	—	—	—
10	*Buteogallus coronatus* (n = 4)	—	—	—	—	—	—	—	—	—	—	—	—	0	0	75	25	—	—	—	—
11	*Puma concolor* (n = 48)	21.8	21.5	24.8	27.3	23.3	24.8	25.2	26.7	—	—	—	—	25	75	0	0	—	—	—	—
12	*Leopardus geoffroyi* (n = 64)	9.3	35.4	35.6	19.7	7.4	37.5	38.8	16.3	—	—	—	—	—	—	—	—	—	—	—	—
13	*Leopardus* cf. *L. geoffroyi/L. pajeros* (n = 48)	15.1	42.2	35.4	5.9	27.1	39.3	27.4	5.3	—	—	—	—	35.2	42.1	8.6	0	0	0	0	0
14	*Lontra longicaudis* (n = 31)	47.1	41.2	11.8	0	71.4	28.6	0	0	—	—	—	—	—	—	—	—	—	—	—	—
15	*Conepatus chinga* (n = 30)	17.1	37.1	22.9	22.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
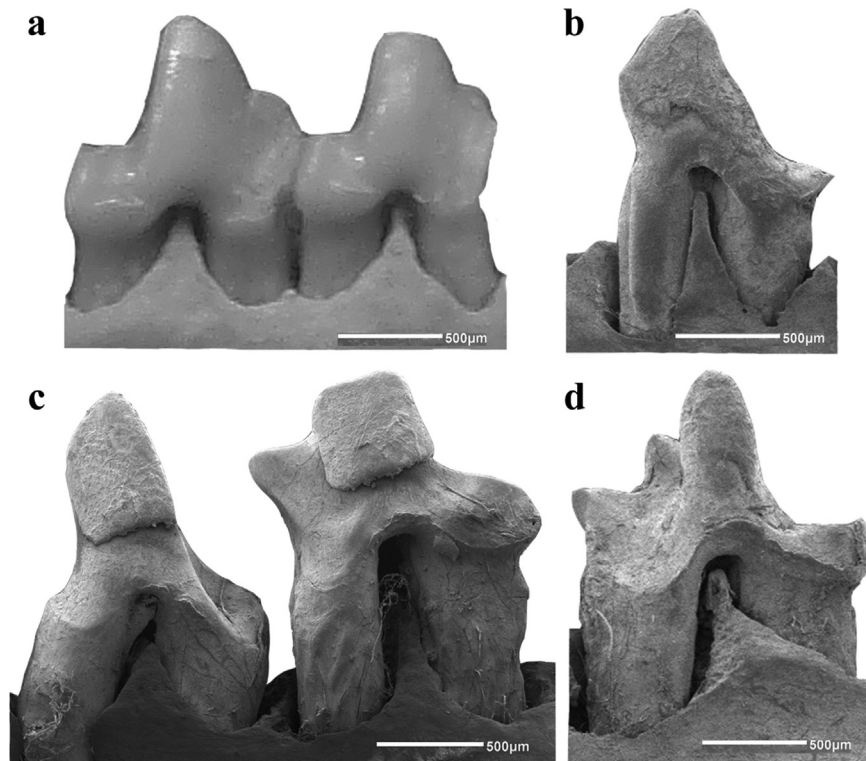
Fig. 2. Examples of digested molars of Monodelphini from South America. a: light corrosion (sample 3); b: moderate corrosion (sample 13); c: heavy corrosion (sample 13); d: extreme corrosion (sample 13).

Table 4
Categories of digestion of molars for small mammals of South America compared with African and European preys (taken from Fernández-Jalvo and Andrews, 1992, p. 412; Fernández-Jalvo et al., 2016).

|	Light	Moderate	Heavy	Extreme
North American, African and European rodents **Arvicolinae** South American rodents **Caviinae Abrocomidae**	Digestion is restricted to the occlusal corners of the salient angles of the teeth and does not penetrate below the alveolar margins. Also it does not usually penetrate through the enamel and into the dentine, so that the corners of the teeth are rounded and the salient angles flattened. Narrow enamel gaps in occlusal view. In Caviinae molars, saliences of cementum along the side surfaces are easily removes.	The enamel has been removed along the half or the entire length of the salient angles, leaving a smooth edge. More flattened salient angles in occlusal view.	Corners are strongly rounded with deeply penetrated salient angles and enamel extensively removed from the entire length of the salient angle. Dentine exposed removed and flattened in occlusal areas.	The damage is so great that only rarely are the teeth identifiable. The damage of the enamel again extends along the salient angles but there is considerable digestion of the dentine, which undermines the enamel shell and causes it to collapse inwards along the length of the salient angles. This produces a characteristic curled appearance of the tooth and gaps in the dentine. Dentine collapsed inwards in occlusal view.
South American rodents **Ctenomyidae**	Digestion affects part of the enamel surface showing slight pitting, which it is easily seen from the occlusal and side views. The dentine is not affected.	Enamel thickness is thinned and removed, which it is easily seen from the occlusal and side views. The dentine can take on an appearance similar to effects of weathering.	Digestion reaches the base of the tooth. Enamel presents a narrow layer, in many areas disappears. Dentine is depressed in the center of the tooth.	Enamel is removed in the most part of the tooth, and small island on the surface of the dentine is observed. Dentine is depressed and collapsed in the center of the tooth.
North American, African and European rodents **Muridae** South American rodents **Sigmodontinae**	Rounded cusps smoother in occlusal view. Matt enamel in lateral view.	Show a pitted enamel surface. The surface of the enamel is more intensively affected, reaching the half of the crown. Reduction of enamel at the crown-root junction. In Sigmodontinae molars, dentine can be affected, but not wavy.	The surface is heavily pitted and the enamel partly removed along the edge of the wear facets on occlusal view. In lateral view the enamel is removed. In both views the dentine is not affected. In Sigmodontinae molars, the dentine is exposed and melted.	More of the enamel is removed. It formed small islands, with or without dentine hollowed out and etched. In Sigmodontinae molars dentine is collapsed and loses its diagnostic features.
North American, African and European insectivores **Talpidae Soricidae Erinaceidae** South American marsupials **Monodelphini**	Insectivore molars do not show any alteration.	Only matt surface is observed.	Enamel heavily pitted and removed, dentine exposed at the edge contact between the crown and the roots. Dentine is not affected.	The enamel may be largely removed, leaving islands of cracked and scored enamel, or it may be entirely missing and the dentine hollowed out and etched so that only the bare outlines of the teeth remains.

Table 5
Percentages of molars digested for studied predator samples. Abbreviations: L: light; M: moderate; H: heavy; E: Extreme.

N	Predator	% molars digested																			
		Sigmodontinae				Caviinae				Abrocomidae				Ctenomyidae				Monodelphini			
		L	M	H	E	L	M	H	E	L	M	H	E	L	M	H	E	L	M	H	E
1	*Tyto alba* (n = 308)	35.1	1.3	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	*Tyto alba* (n = 70)	–	–	–	–	–	–	–	–	5	0	0	0	–	–	–	–	–	–	–	–
3	*Bubo virginianus magellanicus* (n = 49)	35.1	4.1	8	0	–	–	–	–	–	–	–	–	74.7	9.6	4.3	0	5	0	0	0
4	*Pseudoscops clamator* (n = 671)	28.1	0	0	0	51.3	39.8	8.9	0	–	–	–	–	–	–	–	–	–	–	–	–
5	*Athene cunicularia* (n = 62)	70	10	0	0	66.7	13.9	0	0	–	–	–	–	65.3	0	0	0	–	–	–	–
6	*Caracara plancus* (n = 68)	30.4	18.2	16.2	0	4	34.3	30.4	31.3	–	–	–	–	18.2	27.7	20.5	17.4	–	–	–	–
7	*Elanus leucurus* (n = 220)	27.4	32.6	34.7	5.3	9.8	28.9	39.8	21.5	–	–	–	–	–	–	–	–	–	–	–	–
8	*Geranoaetus melanoleucus* (n = 156)	–	–	–	–	5.6	31.5	45.4	2.8	0	50	50	0	–	–	–	–	–	–	–	–
9	*Geranoaetus polyosoma* (n = 326)	37.6	28.1	1.7	0	0	0	66.6	33.3	–	–	–	–	25	42.9	32.1	0	–	–	–	–
10	*Buteogallus coronatus* (n = 16)	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	100	–	–	–	–
11	*Puma concolor* (n = 122)	13.3	13.4	10.5	2.1	3.7	21	30.5	44.8	–	–	–	–	14.3	33.6	24.8	27.3	–	–	–	–
12	*Leopardus geoffroyi* (n = 144)	12.5	33.3	25	3.9	3.3	34.7	45.3	16.7	–	–	–	–	–	–	–	–	–	–	–	–
13	*Leopardus* cf. *L. geoffroyi/L. pajeros* (n = 96)	18.6	21.8	20.5	0	5.3	39.6	49.2	5.9	0	100	0	0	5.4	15.4	38.3	3.9	0	33.3	33.3	33.3
14	*Lontra longicaudis* (n = 40)	14.8	33.3	29.6	22.2	0	15.4	53.8	30.8	–	–	–	–	–	–	–	–	–	–	–	–
15	*Conepatus chinga* (n = 45)	36.2	21.3	12.8	29.8	–	–	–	–	–	–	–	–	0	0	100	0	–	–	–	–

of cementum along the side surfaces of the molars, leaving numerous striated depressions. On the one hand, the absence of saliences of cementum in the upper part of the crown may indicate that the molars were *in situ* during the digestion (Fig. 3j and k), while the absence of these protuberances along the entire crown may suggest the molars were *ex situ* during the digestion.

The categories of digestive corrosion of Sigmodontinae molars present similar characteristics than those obtained by Andrews (1990), Fernández-Jalvo and Andrews (1992), Demirel et al. (2011), Stoetzel et al. (2011) and Fernández-Jalvo et al. (2016) for Muridae (Tables 4 and 5, Fig. 4). However, there are some exceptions within this group should be highlighted and explored in greater detail in future work. For instance, the hypsodont and pseudo-prismatic molars of *Reithrodon auritus* could be affected by digestive action faster than other Sigmodontinae, in similar way of those of Caviinae and Arvicolinae (Fig. 4c). Another example the
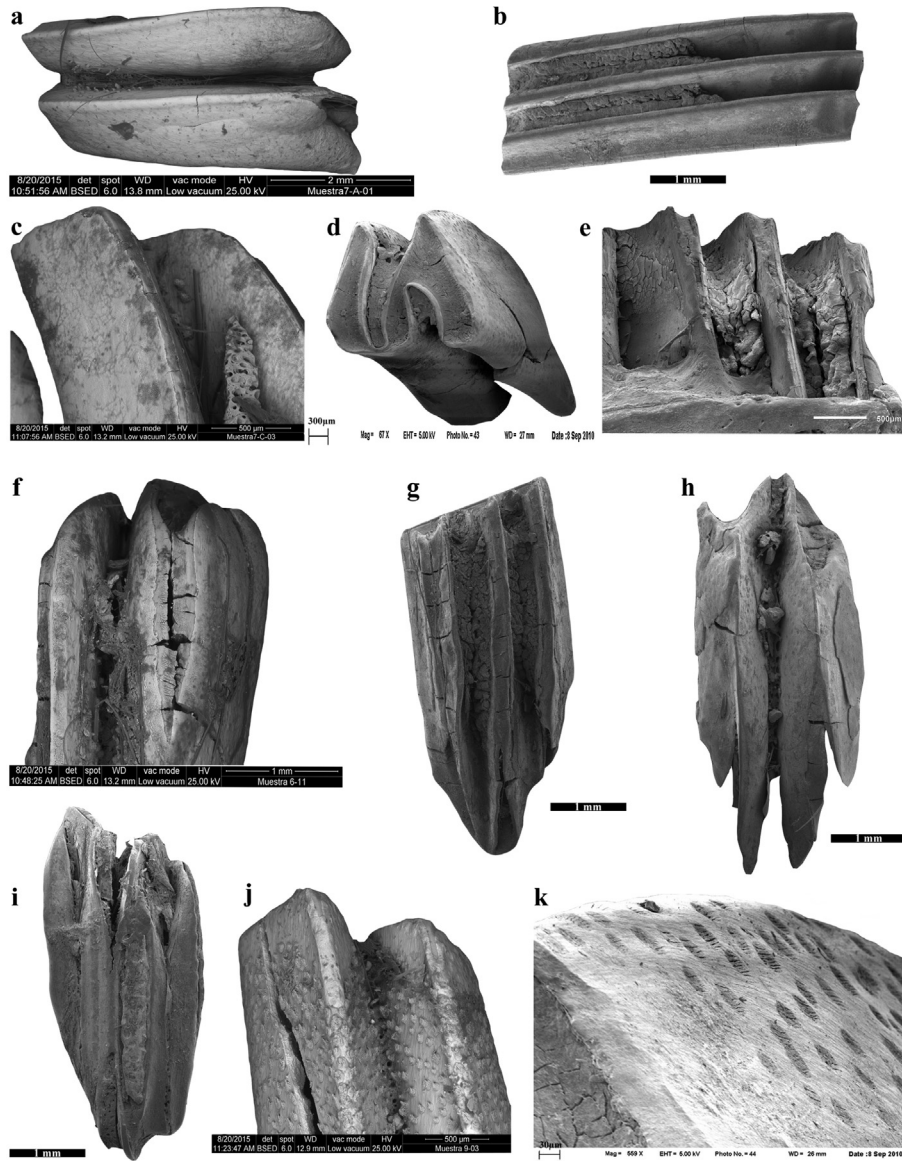
Fig. 3. Examples of digested molars of caviomorph rodents from South America. a: light corrosion in Caviinae molar (sample 7); b: light corrosion in Abrocomidae molar (sample 2); c: light corrosion in Caviinae molar (sample 7); d: light corrosion in Caviinae molar (sample 14); e: moderate corrosion in Abrocomidae molar (sample 13); f: moderate corrosion in Caviinae molar (sample 11); g: heavy corrosion in Abrocomidae molar (sample 8); h: heavy corrosion in Caviinae molar (sample 8); i: extreme corrosion in Caviinae molar (sample 13); j: saliences of cementum and light corrosion in Caviinae molar (sample 6); k: striated depressions in Caviinae molar (sample 14).

molars of some tribes of Sigmodontinae (e.g., Akodontini, Abrothrichini), with high degree of wear in senile individuals, exhibit thin radial enamel and inner exposed dentine. Therefore, the enamel can be quickly removed and separated from dentine by the effects of digestion, even considering predators with moderate modifications (Fig. 4g). It is interesting to note that the SEM examination of teeth samples using backscattered detectors allowed us to distinguish between the dentine and enamel (Fig. 4a), in those cases that these dental tissues were difficult to differentiate using stereomicroscope (Fig. 4b).

The particular and simplified configuration of the molars of Ctenomyidae has promoted a new description of the categories of digestive corrosion (Table 4). Its thick radial enamel gradually exhibits evidence of corrosion; from light and moderate pitting (Fig. 5 a–d) to thinning or loss of enamel walls (continuously or in patches, see Fig. 5e). In addition, the dentine can be depressed, cracked and collapsed in the center of the tooth like the effects of

weathering. This unusual type of character should be treated with caution because of some pellets or scats could have been exposed to weathering agents, affecting their bones and teeth. Although the enamel wall of the molars of Ctenomyidae is thick, the dentine is widely exposed on the occlusal surface and the dentine tracts can promote rapidly modifications by digestion since acids mainly attack from the occlusal surface and from the edges of the tooth (Fig. 5c, d and f). In this sense, molars of Ctenomyidae are more affected than those of Sigmodontines. However, a delay in the categories of digestion of Ctenomyidae was observed compared with those of Caviidae and Abrocomidae, which are more intensively affected by digestive action (Table 5).

A general scheme of digested molars per group of taxa is shown in Fig. 6. The enamel of digested Caviinae and Abrocomidae molars is removed at the earliest stage of light category of digestion, and Ctenomyidae and Sigmodontinae, accompanying the former small mammal groups, show digestion traits only at moderate category
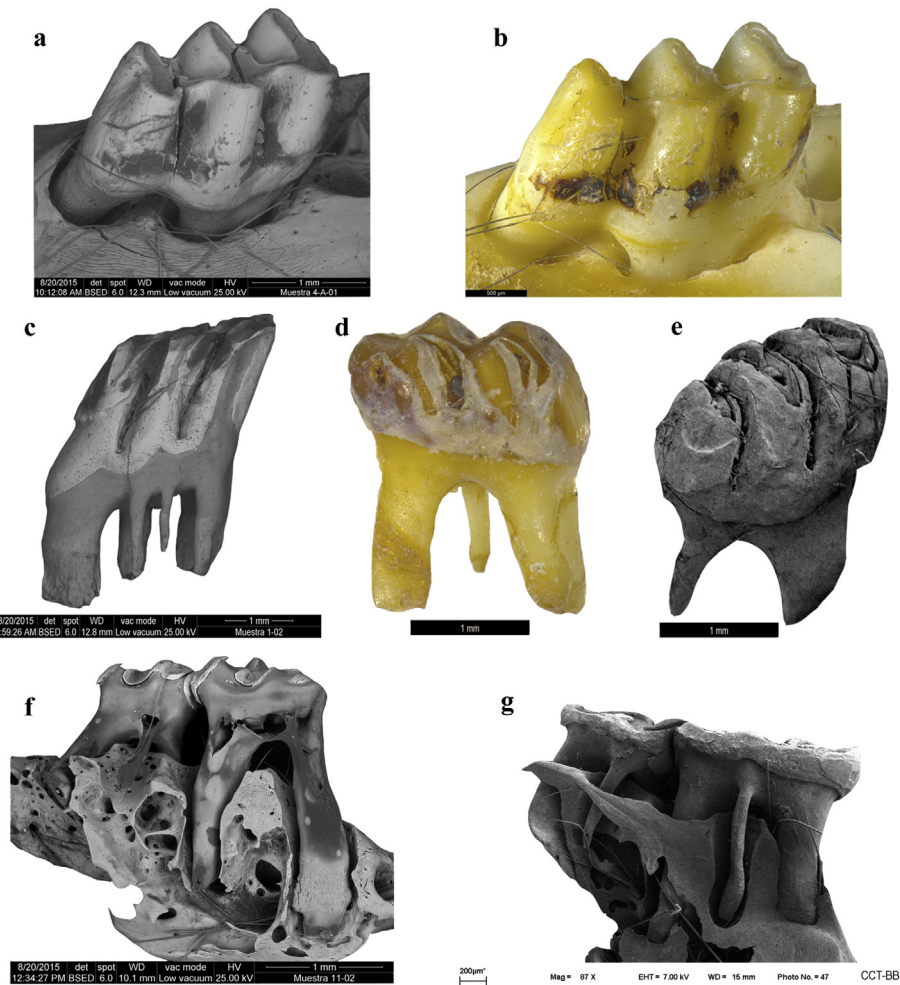
Fig. 4. Examples of digested molars of Sigmodontinae from South America. a: light corrosion (sample 12); b: light corrosion (same molar of the previous picture); c: moderate corrosion (sample 7); d: heavy corrosion (sample 12); e: heavy corrosion (sample 9); f: extreme corrosion (sample 7); g: heavy corrosion (sample 7; Photo taken from Montalvo et al., 2014, Fig. 5 d). a, c, f and g pictures taken by SEM using backscattered detectors. b and d pictures taken by stereomicroscopy.

whilst Monodelphini start showing signs of digestion when Caviinae and Abrocomidae are already affected at heavy grades of digestion. In other words, a category 1 predator's pellets may contain Caviinae and Abrocomidae molars affected in a light degree with enamel removal from the salient angles of prisms (similar to Arvicolinae), Ctenomyidae molars showing a light pitting in the occlusal surface, Sigmodontinae molars with a matt enamel surface and more rounded cups (like Muridae), and Monodelphini molars showing no digestion signs (similar to Soricidae) according to descriptions in Fernández-Jalvo et al. (2016).

Previous studies and our results agreed with these descriptions and demonstrated that diurnal and nocturnal birds of prey and carnivorous mammals yield differences among small mammal assemblages because they have distinctive hunting methods and produce different degrees of modification during ingestion and digestion of their prey, even in the same taxa (e.g., Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Iglesias, 2009; Fernández, 2012a; Gómez, 2005, 2007; Gómez and Kaufmann, 2007; Montalvo et al., 2007, 2008a,b, 2012b, 2014, 2015b, 2015c; Montalvo and Tallade, 2009, 2010; Montalvo and Tejerina, 2009; Quintana, 2015; Rudzik et al., 2015; Fernández-Jalvo et al., 2016). For any predator there is variation in degrees and proportions of digestion. These arise depending on the state of hunger of the predator and in some cases to its age (juvenile or adult). Where

prey is very abundant, prey may be regurgitated only half digested and with little evidence of digestion; where prey is rare, a few individuals may be heavily digested even by category 1 predators (Andrews, 1990). In fact, diurnal raptors such as *E. leucurus* and *G. polyosoma* are very destructive, but we found Caviinae (Fig. 3a and c) and Ctenomyidae (Fig. 5b) molars were only digested at a light degree of digestion. Likewise, incisors of Sigmodontinae and Ctenomyidae with light corrosion were obtained from carnivorous scats such as *L. longicaudis* (Fig. 1a), *L. geoffroyi* (Fig. 1b) and *P. concolor* (Fig. 1g). However, the average of samples of each predator has shown a distinctive degree of digestive corrosion and a particular range of proportions (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 2016).

3.2. Implications in palaeontological and archaeological studies: the example of Cueva Huenul I *(CH1)*

According to the new methodology presented here, it is expected that taphonomic analysis of the small mammals from C1 and D1 showed great differences between the groups of prey listed above (Table 6). In fact, the Caviinae teeth were the most affected by digestion due to present hypsodont and prismatic molars with thin and no-continuous enamel, which favor the corrosion. On the contrary, the absence of evidence of digestion in Monodelphini
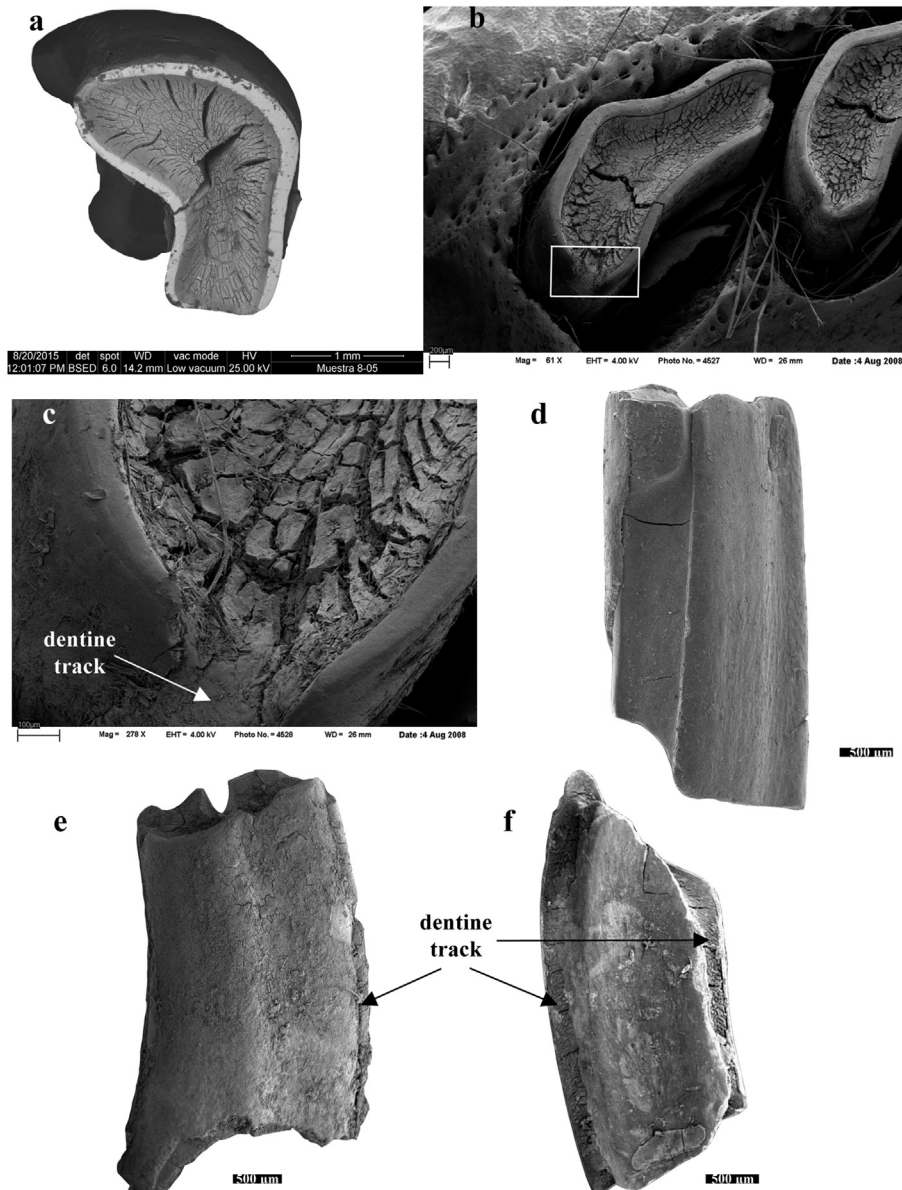
Fig. 5. Examples of digested molars of Ctenomyidae from South America. a: light corrosion (sample 3); b: light corrosion (sample 9); c: detail of the dentine track area of the previous picture; d: moderate corrosion (sample 13); e: heavy corrosion (sample 15); f: extreme corrosion (sample 11).

teeth is consistent with the presence of a thick and continuous layer of enamel, which provides resistance to corrosion. Finally, other coincidences with the taphonomic model presented here are the higher percentage of digestion in molars of Ctenomyidae respect to Sigmodontinae, and the lower proportion of digested incisors of Ctenomyidae respect to Sigmodontinae. As mentioned earlier the thicker enamel in the incisors of Ctenomyidae provides a delay in digestive corrosion, and the presence of both wide exposed surface of dentine and the dentine tracts in the molars of Ctenomyidae can yield a major corrosion. Finally, future studies that include modern pellet samples of *T. alba* with Caviinae, Ctenomyidae and Monodelphini are necessary to compare with the results of CH1.

4. Final remarks

1. Predation is one of the most recurring causes of small mammal accumulations in palaeontological and archaeological sites, and digestive corrosion is the greatest evidence of this.

2. The taphonomic study of the rodents Sigmodontinae, Caviinae, Ctenomyidae and Abrocomidae, and the marsupials Monodelphini of central Argentina has allowed us to distinguish digestive corrosion patterns at each group.

3. SEM examination of teeth samples using backscattered detectors is useful to distinguish between the dentine and enamel, in those cases that these dental tissues were difficult to differentiate using stereomicroscope.

4. The morphology of the incisors of Caviinae, Abrocomidae, Sigmodontinae is similar than those rodent groups of North America, Europe and Africa (Arvicolinae and Muridae). However, for Ctenomyidae, because incisors have a wider labial surface and thicker enamel, and a delay in the appearance of digestion was observed when compared to other rodent incisors.
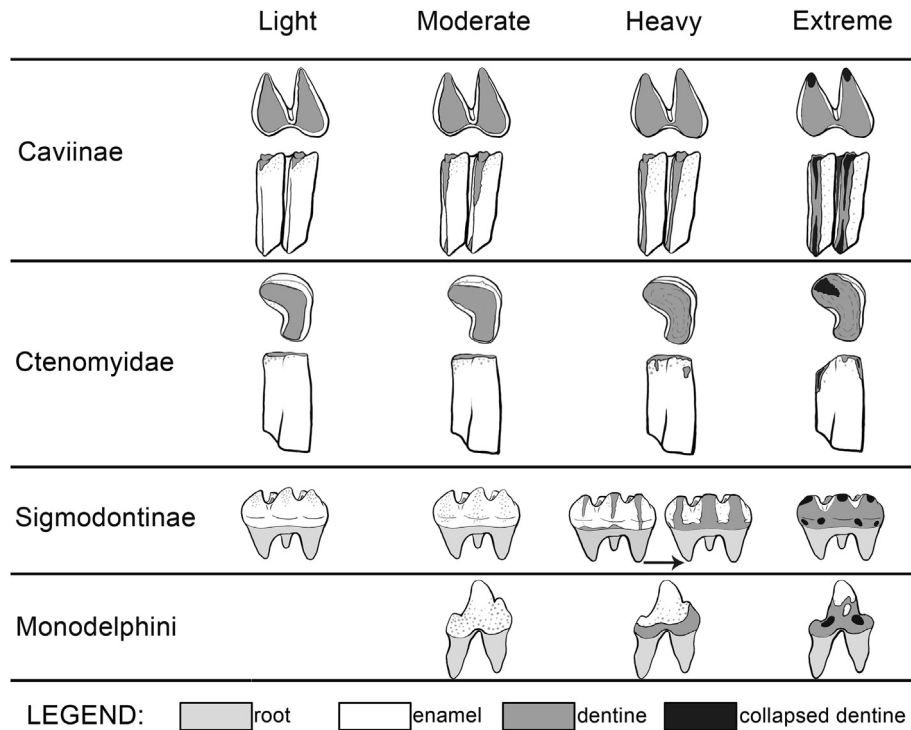
Fig. 6. Scheme of categories of digestion of molars for Caviidae, Ctenomyidae, Sigmodontinae and Monodelphini. The shape and enamel thickness of the tooth produce different responses to the effects of digestion. Design based on the original Stoetzel (2009, p. 150)'s scheme.

Table 6
Comparison of percentages of teeth digested for Cueva Huenul 1 between quadrat A1 (Fernández et al., 2012) and quadrats C1-D1. Abbreviations: L: light; M: moderate; H: heavy; E: Extreme; I: incisor; Mo: molar.

Taxa (N)	CH1 (A1)								CH1 (C1-D1)							
	% incisors digested				% molars digested				% incisors digested				% molars digested			
	L	M	H	E	L	M	H	E	L	M	H	E	L	M	H	E
Small mammals (I = 158/Mo = 370)	36.7	5.1	0.6	0	27.3	2.2	0	0	–	–	–	–	–	–	–	–
Sigmodontinae (I = 143/Mo = 256)	–	–	–	–	–	–	–	–	27.3	0	0	0	8.6	0	0	0
Caviinae (I = 10/Mo = 61)	–	–	–	–	–	–	–	–	70	0	0	0	88.5	0	0	0
Ctenomyidae (I = 80/Mo = 174)	–	–	–	–	–	–	–	–	18.7	0	0	0	16.7	0	0	0
Monodelphini (I = 21/Mo = 65)	–	–	–	–	–	–	–	–	0	0	0	0	0	0	0	0

5. The categories of digestive corrosion of Monodelphini teeth display similar characteristics than the insectivores Talpidae, Soricidae and Erinaceidae. In addition, a delay of evidence of digestion was recorded as it was observed in Soricidae molars, which is consistent with the presence of a thick and continuous layer of enamel, all of which provide resistance to corrosion.

6. The categories of digestive corrosion of Caviinae and Abrocomidae show similar features than Arvicolinae. However, the molars of Caviinae present abundant cementum protuberances placed on the enamel, and the digestive corrosion easily removes these protuberances, leaving numerous striated depressions.

7. The categories of digestive corrosion of Sigmodontinae molars present similar characteristics than Muridae. Nevertheless, the molars of some tribes of Sigmodontinae (e.g., Akodontini, Abrothrichini), with high degree of wear in senile individuals, exhibit thin radial enamel and inner exposed dentine. Therefore, the enamel can be quickly removed and separated from dentine by the effects of digestion.

8. The particular and simplified configuration of the molars of Ctenomyidae has promoted a new description of the categories of digestive corrosion. Its thick radial enamel gradually exhibits evidence of corrosion; from light and moderate pitting to thinning or loss of enamel walls (continuously or in patches). The dentine can be depressed, and collapsed in the center of the tooth like. Although the enamel wall of the molars of Ctenomyidae is thick, the dentine is widely exposed on the occlusal surface and the dentine tracts can promote rapidly modifications by digestion since acids mainly attack from the occlusal surface and from the edges of the tooth.

9. The enamel of digested Caviinae and Abrocomidae molars is removed at the earliest stage of light category of digestion, and Ctenomyidae and Sigmodontinae, accompanying the former small mammal groups, show digestion traits only at moderate category whilst Monodelphini start showing signs of digestion when Caviinae and Abrocomidae are already affected at heavy grades of digestion. In other words, a category 1 predator's pellets may contain Caviinae and Abrocomidae molars affected in a light degree with enamel

removal from the salient angles of prisms (similar to Arvicolinae), Ctenomyidae molars showing a light pitting in the occlusal surface, Sigmodontinae molars with a matt enamel surface and more rounded cups (like Murinae), and Monodelphini molars showing no digestion signs (similar to Soricidae).

10. Ctenomyidae is very important for the South American zooarchaeology because several of their fossils show indications of being part of the prehistoric human diets. This contribution may, therefore, be useful to know the origin of these faunas and the exact taphonomic agent that produced these assemblages.

11. Our results offer a new taphonomic methodology for the study of small mammal fossil of the palaeontological and archaeological sites from South America. In fact, the results obtained from CH1 are consistent with the taphonomic model presented here, showing great differences between the groups of prey.

12. In spite of the micromammalian samples only taken from central Argentina, the taxa considered in this paper (Ctenomyidae, Caviinae, Sigmodontinae and Monodelphini) are distributed in almost all South America, and, therefore, our results from modern samples can have a remarkable utility in the application of palaeontological and archaeological sites of this subcontinent, as shown in the analysis of small mammals from CH1.

Acknowledgments

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