TAPHONOMY FOR TAXONOMISTS: IMPLICATIONS OF PREDATION IN SMALL MAMMAL STUDIES.

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ABSTRACT. Predation is one of the most recurrent sources of bone accumulations. The influence of predation is widely studied for large mammal sites where humans, acting as predators, produce bone accumulations similar to carnivore accumulations. Similarly, small mammal fossil sites are mainly occupation levels of predators (nests or dens). In both cases, investigations of past events can be compared with present day equivalents or proxies. Chewing marks are sometimes present on large mammal predator accumulations, but digestion traits are the most direct indication of predation, and evidence for this is always present in small mammal (prey) fossil assemblages. Digestion grades and frequency indicates predator type and this is well established since the publication of Andrews (1990). The identification of the predator provides invaluable information for accurate interpretation of the palaeoenvironment. Traditionally, palaeoenvironmental interpretations are obtained from the taxonomic species identified in the site, but rather than providing direct interpretations of the surrounding palaeoenvironment, this procedure actually describes the dietary preferences of the predators and the type of occupation (nests, marking territory, dens, etc). This paper reviews the identification of traits produced by predators on arvicolins, murins and soricids using a method that may be used equally by taxonomists and taphonomists. It aims to provide the "tools" for taxonomists to identify the predator based on their methodology, which is examining the occlusal surfaces of teeth rather than their lateral aspects. This will greatly benefit both the work of taphonomists and taxonomists to recognize signs of predation and the improvement of subsequent palaeoecological interpretations of past organisms and sites by identifying both the prey and the predator.

KEY WORDS: predation, digestion, small mammals, taxonomy, taphonomy

1. INTRODUCTION

Small mammals (rodents, bats, shrews, hedgehogs, hares) represent around 80% of mammal species richness, and this gives them a special role in palaeoecology. Relative abundance of microfaunal skeletal elements is often greater than that of large mammal fossils, and species richness of small mammals may easily be double that of large mammals. In addition, fossil small mammals are good palaeoecological indicators because they are highly dependent on vegetation cover, they have a more limited territory than large mammals (they do not migrate on long distances) and their species richness correlates highly with vegetation species richness (Andrews & O'Brien, 2000, 2010).

Predation is the main factor accumulating small mammal assemblages both in modern and in fossil sites (Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Sanchez et al., 1997; Mondini, 2002; Gómez, 2005, 2007; Verzi et al., 2008; Stoetzel et al., 2010; Lloveras et al., 2013; Matthews et al., 2005, 2006). Predation of small mammals may be recognized by the presence of digestion on their teeth and skeleton, shown by the pioneering studies of Mellet (1974), Mayhew (1977) and Andrews (1990), together with recent studies (Fernández-Jalvo, 1995; Fernández-Jalvo et al., 1998; Sanchez et al., 1997; Stoetzel et al., 2011; Montalvo et al., 2007, 2011; Lloveras et al., 2008c; 2014). Tooth marks are rare on micromammal bone, for damage inflicted by mammalian predators during ingestion (unless the size of the prey is large, e.g. rabbit), and subsequent digestion of the ingested bones are often so extensive as to obliterate evidence of tooth marks (Andrews, 1990).

Mikkola (1983) published an extensive description of the diets of European owls. In addition, species of raptors and small carnivores were being investigated to extend

palaeontological implications due to predation by Dodson & Wexlar (1979), Korth (1979) Andrews & Evans (1983), Andrews, (1990). These authors demonstrated that predator digestion produces different grades and intensities of preservation (e.g. anatomical element survival, breakage, digestion, postcranial vs. cranial element preservation) of their prey assemblages. They also show how predation affects interpretations of palaeoecological and palaeolandscape interpretations (Fernández-Jalvo et al., 1998; Scott et al., 1996; Stoetzel et al., 2011), highlighting the great range of predators which are the main producers of small mammal assemblages.

Predation is a complex ecological process occurring at the level of ecosystem and is based on predator-prey relationships. Two factors are important here, first 'density dependence' (Allee, 1931; Begon et al., 1990; Sidorovich et al., 2011) of prey according to population fluctuations, and second, the trophic preferences of the predator. The size ratio of the predator/prey relationship, diurnal or nocturnal hunting behaviour, and hunting strategy and territory size are all factors that may vary from one predator to another (summary in Andrews, 1990). The species composition of prey remains may or may not be an indicator of predator species, and in any case it cannot be relied on. Breakage may be influenced by post-depositional factors and anatomical element survival patterns, both of which may obscure breakage resulting from predation.

The distinction and identification of the predator(s) helps to better identify the nature and origin of the assemblage, the source of the fossil specimens and potential spatial-time mixtures during the initial stages of site formation. Palaeoecological studies based on small mammals need to take these factors into account when comparing fossil species (prey assemblages selected by predator's preferences and deposited in the predator's habitats) with their modern equivalents (ecological studies of living

specimens in their own habitat), both with individual species comparisons and at the community level, for example through multivariate statistical analysis, indices focused on frequency percentages, taxonomic weighting of the fauna relative to their living relatives, or ratios of frequencies of key-taxa. On the other hand, past biomes may represent habitats with no modern counterpart (Fernández-Jalvo et al., 1998, 2011).

Differences in habitat due to predator-prey behaviours have to be taken into account during habitat reconstruction. For example, the small mammal, amphibian and squamate faunas recovered from Pleistocene deposits at Azokh cave (Southern Caucasus) are mostly species or genera found today in semi-arid environments, but the evidence from the local flora and large mammals preserved in the cave indicates that the local environment was deciduous woodland. Such apparent contradiction based on taxonomic identifications is due to different sources of predation. Large mammals were mainly preyed by humans in the surroundings (Marin-Monfort et al., 2016) and local flora was the most available woods collected from the nearby habitats in the mountain slope (Allué, 2016). Taphonomic analysis of the small mammals showed that small mammals were the prey assemblage of *Bubo bubo* (Andrews et al., 2016). Amphibians and squamates showed signs of digestion (Blain, 2016) indicating the source could also be these eagle owls. The inference was that *Bubo bubo* was roosting close to or inside the cave, which was in a wooded valley, but it was hunting several kilometres away in the adjoining open country, as modern eagle owls do, in this case the lowland arid zone (Andrews et al., 2016).

In other example, the combination of taxonomic, taphonomic and palaeocological studies at the open air site of Olduvai Bed I (Fernández-Jalvo et al. 1998) differentiated taphonomic effects on the fauna from real environmental and ecological changes. A change in the taxonomic richness and composition of the faunas at the base of Bed I site

75 FLKNN (richer in murins) and those from upper Bed I site FLKN (richer in gerbillins)
76 was previously proposed by Jaeger (1976) to be indication of a drastic climatic change
77 which could actually be linked to the first appearance of representatives of the genus
78 *Homo* (*Homo habilis*). Fernández-Jalvo et al. (1998) showed that the FLKNN faunas
79 were accumulated by predators with light categories of digestion (with FLKNN2 most
80 possibly be *Tyto alba*). The small mammal faunas following the sequence of Bed I
81 (FLKN6-4) were probably the prey of mammalian carnivores, and these are better
82 adapted to detect and hunt burrowers, such as *Gerbillus* and *Gerbilliscus* (*Tatera*).
83 These rodents are usually found in arid environments or in environments with sandy and
84 soft soils, but their abundance in upper Bed I may be an artefact of predation rather than
85 indicating these environments. Unit FLKN4, apart from mammalian carnivores, showed
86 also the influence of a nocturnal raptor (likely *Bubo lacteus*), and different rodent
87 species could be distinguished to have been hunted by each predator on the basis of the
88 category of digestion. The change from murin-dominated faunas at FLKNN to more
89 gerbillin-dominated faunas at FLKN6 to 4 was attributed to change in predator instead
90 of a climatic change. On the other hand, the faunas from the top of upper Bed I, sites
91 FLKN3 to 1, which showed the highest Gerbillinae/Murinae ratios, but low species
92 richness, were accumulated by two nocturnal owls that normally have prey assemblages
93 with high species richness, *Bubo lacteus* and *B. africanus* respectively, and the low
94 species richness in these levels is anomalous and inconsistent with these owl's
95 behaviour. This indicates that the low species richness at FLKN 3-1 is due to the
96 predator and not a postdepositional artefact (i.e. reworking or time-averaging), and
97 together with the high Gerbillinae/Murinae ratio shows that the palaeoecological trend
98 towards aridity at the top of Bed I could be generated by climate change, with a marked
99 shift from woodland vegetation (FLKNN and FLKN6-4) to a more open woodland or

wooded grassland. Identical indications were obtained from large mammals, based on taxon-free analysis of bovid postcrania (Plummer & Bishop, 1994).

The aims of this article are firstly to provide a simplified method adapted from original taphonomic protocols in order to enable taxonomists to recognize signs of predation and, therefore, the influence of predation in a fossil assemblage; and secondly to obtain a better approach of the predator's diagnosis, which bone remains may not be fossilized at the site. Digestion patterns were described and illustrated in Andrews (1990) in most micromammal groups on dental lateral views, using SEM pictures. Each category of digestion in voles was sketched in Fernández-Jalvo & Andrews (1992) together with descriptions of digestion in murids and soricids. We focus now on the description and images of digestion and dental elements based on the views that are most frequently analyzed, stored and figured by taxonomists, here illustrated with images taken under the binocular light microscope. We aim to describe key features to facilitate the identification of the intensity and grades of digestion recorded on fossils which are diagnostic of predator action that, in some cases indicate the predator's identity at species level or, in some others, a general indication of the natural group's category. Some examples, from modern and fossil sites, are described here to show how predation increases the level of interpretation of past faunas, environments and ecosystems.

1.1. Different views, identical purpose.

Taxonomic identifications are frequently based on lower M1 among arvicolins, upper and lower M1 for murids, P3-M3 among soricids, also including skull fragments, mandibles and maxillae. Most of the species-diagnostic characters are found on occlusal surfaces of molars and depend upon cusp morphology that characterises the taxonomic

groups. On skulls, which are rarely preserved complete in fossil sites, the main characters rely upon foramina, bone size and shape. Mandibles are generally better preserved than skulls, and mandibular characters rely on crests and apophyses disposition of the ascending ramus as well as on the relative proportions of molars when are preserved *in situ*. Other skeletal elements like post-crania and incisors rarely have taxonomic diagnostic characters and are generally disregarded by taxonomists. In contrast, taphonomists study many aspects of the postcranial, cranial and dental elements, observe modifications of tissues like dentine vs. enamel vs. bone, and preferentially study the labial or lingual sides of the molars rather than the occlusal surfaces. Incisor and postcranial modifications, both on articular and shaft surfaces, are also important taphonomically. These differences in practice may explain why these observations are rarely made by the same person. Also, because small vertebrates are generally very abundant in fossil sites, observations of the whole skeletal assemblage may sometimes be impractical.

Most taxonomists, as well as taphonomists intend to obtain palaeoecological information. The former base their conclusions from the small mammal species represented at the site, the latter also consider modifications recorded on the small mammal fossils that indicate the taphonomic agent or the predator that hunted them. This combination of palaeoenvironmental indications obtained from the prey and the predator together provides a more precise palaeoecological scenario. As seen in nature today, most of the small mammal accumulations from fossil sites are prey assemblages (i.e. they bear signs of digestion, even for only 1% or lower of the fossil remains). A consequence of this is that small mammals are transported from their living habitat to the locations of the nests, dens or roosting/marketing territory areas of predators, i.e. the fossil site today.

Taphonomy was created by Efremov in 1940 who proposed Taphonomy, a New Branch of Paleontology, due to the great difficulties to obtain reliable palaeontological reconstructions, "*phylogenetic theories and laws formed on the basis of data obtained on fossils as if these latter presented a true and complete image of animal life during past geological eras*". Most especially "*methods of palaeoecological analysis become hardly possible when a fauna is found in casual groups, tanatoceonoses (thanatocoenosis), and not at the place where it existed when living*" (Efremov, 1940 page 81-82).

Despite the time span since the discipline was created and the improvements of new analytical techniques and methodologies in palaeoecological interpretations, if fundamental taphonomic aspects, such as thanatocoenosis, preservation modes of the fossil assemblages, time-averaging or reworking are not considered, palaeontological interpretations may not be accurate enough and susceptible of misinterpretation. We, therefore, consider the need to extend invaluable collaboration between taxonomists and taphonomists to join efforts and obtain a better approach to the past.

1.2 Predators and digestion

Digestion is the most direct indication of predation. The effects of digestion are the result of a combination of hydrochloric acid and enzymes from the gastric acids. The acid component causes corrosion and etching of the osseous tissues, affecting first and most intensively the enamel, the most mineralized tissue component (Andrews, 1990) with a prismatic ultrastructure that may also facilitate penetration of gastric juices (Dauphin et al., 2015). Dentine, root and bone tissues are less affected as they are richer in collagen and organic content with a more homogeneous ultrastructure than enamel .

Breakage before/during ingestion increases the effects of digestion as gastric juice fluids penetrate into the bone and tooth (Racynski & Ruprecht, 1974; Mayhew, 1977; Andrews, 1990).

Three natural groups of predators may be distinguished: nocturnal raptors, diurnal birds of prey and mammalian carnivores. Nocturnal owls have relatively low levels of gastric acidity, and since they often swallow their prey complete they may produce lower levels and less frequent digestion and breakage. Diurnal raptors frequently tear the prey with beak and claws to facilitate the ingestion. Diurnal birds of prey have stronger acidity and may digest their food for longer periods than nocturnal avian predators. Avian raptors, both nocturnal and diurnal, have an incomplete digestion restricted to the stomach (proventriculus or glandular stomach and the gizzard or muscular stomach). Non-digestible remains (e.g. bones, claws, hair, feathers, insect chitin exoskeleton) are regurgitated forming a pellet. In contrast, mammalian carnivores have a complete digestion along the gastro-intestinal digestive tract and high levels of acidity of gastric juices (higher than most diurnal raptors), and they have teeth and chew their prey before ingestion. Breakage before digestion is usual, with thin edges and rounding by digestion on broken edges of both bones and teeth. Indigestible prey remains are ejected in the scats.

Differences in digestion may be influenced by several factors in addition to that of predator differences. One is the degree of hunger of the predator, such that food is retained in the stomach for longer in a very hungry predator and all prey remains may be heavily or fully digested (Raczynski & Ruprecht, 1974). Related to this are variations in prey availability. In glut years prey may be so abundant that even predators normally producing heavy digestion may regurgitate prey before it is fully digested (Andrews, 1990); when prey is rare, for example, during the winter (or dry seasons in tropical

environments) it may be more digested than individuals eaten in summer. Another factor is the age of the predator; juvenile barn owls, for example, may produce moderate or even heavy digestion on bones and teeth while adults produce little or no digestion (Andrews, 1990; Williams, 2001). Taking account of these variations requires extensive sampling from different times and places of all predators of small mammals.

Figure 1 double column width

2. RESULTS.

Both taxonomic and taphonomic observations are based upon examination by binocular microscope at relatively low magnification (x6 to x50). Four stages are currently recognized for both molars and incisors: undigested, light digestion, moderate digestion and heavy digestion. Extreme digestion is encountered for some predators (mammalian carnivores, including humans, and avian raptors), and the most relevant feature is that teeth at this stage of digestion may not be taxonomically identifiable. We encourage taxonomists to separate even the most digested teeth during sorting and to mount them, because extremely digested teeth are important to identify the predator even though they may be difficult to be taxonomically identified.

Early work on the teeth of small mammals from the same pellet or scat observed that the shape and enamel thickness cause different responses to the effects of digestion (Andrews, 1990) with faster loss of enamel in arvicolin molars than in murids, cricetids and soricomorpha. Demirel et al. (2011) attempted a comparison of the effects of digestion between arvicolins and murids and glirids, but without quantifying the results, and similarly, Andrews & Fernández-Jalvo (2012) attempted the same thing, with the addition of soricids. Stoetzel (2009) figured teeth of Gerbillinae, rodents and shrews from light to extreme digestion degrees in similar ways as arvicolins by Fernández-

Jalvo & Andrews (1992). This was a good attempt to show the different traces of digestion in the different types of molars, but the comparative sequence of digestion in teeth of different prey from the same pellet or scat was not shown. We are here going to display images of the molars and incisors of arvicolins, murins and soricids according to traits and degrees of intensity of digestive effects produced by the same predator (Fig. 1).

Figure 2 full page

2.1. Molars - digestion evidence

Molars are the most diagnostic element for taxonomic purposes, the shape and dimensions of which are characteristic at species level of classification. However, different small mammal groups have different molar structures and enamel thickness, making it necessary to adapt both the taphonomic and taxonomic methodology for different species.

Digestion in arvicolin molars is the easiest to distinguish, because these hypsodont or semi-hypsodont rodents have molars with a prismatic shape and occlusal surfaces with dentine exposed. Digestion is traditionally analyzed in arvicolins at the lateral view near the occlusal end of molars (Fig. 2). The opposite end of the occlusal surface has frequently the appearance of a higher degree of digestion than the rest of the tooth. Therefore, these ends, equivalent to root tips, are usually not analyzed for digestion. Bunodont molars like those of murids (Murinae and Gerbillinae) have lower crowns with smooth cusps, thicker enamel and closed roots, all of which provide resistance to digestion (Figs. 3 and 4). Similarly, soricid teeth display different structures, enamel thickness and prominent cuspids (Fig. 5). The loss of enamel cannot be mistaken for

tooth-wear, because the reduction by digestion extends along the lateral sides, whilst tooth wear reduces enamel mainly at the occlusal plane (see Fig. 3 top left).

Figure 3 double column width, Figure 4 single column

Light digestion on **arvicolin** molars at the occlusal surface, in the lingual and buccal sides of the tooth, is observed as gaps or interruptions of enamel at the corners of the salient angles of the tooth prisms, leaving dentine exposed which acquires a rounded aspect (Figs. 2A1 and 2A3). Figure 2 shows light digestion on occlusal views (A1, the view used by taxonomists), and below the same picture outlined to indicate areas where enamel is lost. Broken lines (black arrow) show the edge of dentine at the horizontal plane emerging on the salient angle on the occlusal surface. These broken lines at a light degree of digestion outline a narrow convex shape (Fig. 2A1, black arrow). Figure 2A3 shows the enamel reduction of the same molar in lateral view (the view used by taphonomists), showing enamel reduction concentrated on the tips of the columns, at the occlusal area. **Murid** molars from the same pellet as arvicolins digested at **light** stages are described by Andrews (1990) and Fernández-Jalvo & Andrews (1992) as having “...a smoother (and matt=loss of shiny) enamel and more rounded shape so that digestion is harder to identify” (Fernández-Jalvo & Andrews, 1992 page 412). Figure 3 shows the occlusal and lateral views of murin first upper molar. Figures 3A1 and 3A2 show a smoother-matt enamel and more rounded shape of the cusp edges (one of them pointed by a black arrow) than non-digested and unworn murid molars (on top left of the Fig. 3) in contrast to flattened cusps by tooth wear (on top left of the Fig. 3). The matt surface of the enamel can be seen by moving the tooth back and forth to detect changes in brightness. Loss of shiny surface is noticed when analyzing the entire assemblage, distinguishing between that and matt surfaces. No damage is visible on **soricid** molars that are present in pellets with lightly digested arvicolins (Fig.1).

Moderate digestion on **arvicolin** molars at the occlusal view shows bigger gaps of enamel at the salient corners or vertices and dentine is exposed with a more rounded and wider outline (Fig. 2B1) than in light digestion. The slightly inclined view of the tooth in Fig. 2B2 shows that the enamel has been removed from the vertex along half of the column height (Fig. 2B3 black arrow), although, sometimes, the enamel is superficially removed along the entire height of the columns of the crown, leaving the dentine slightly exposed. Figure 2 shows occlusal views on top (2B1 and 2B2) and lateral views at the bottom (B3). Broken lines delineate a more flattened (wider) convex shape than in light digestion. **Murid** molars accompanying arvicolins digested at **moderate** stages have been described by Andrews (1990) to “*show a pitted enamel surface*”. The murid molars acquire an irregular pitted enamel that can be easily observed on lateral views (Fig. 3B2 grey arrow, and Fig. 4), but also on occlusal view. There is no loss of enamel at this stage, at least when the tooth is observed under the binocular microscope. On lateral view, the tooth shows an incipient enamel reduction at the edge of the crown-root junction (Figs 3B2 and 4, black arrows). **Soricid** molars accompanying moderately digested arvicolin teeth show slightly matt enamel. The matt surface of the enamel can be seen by moving the tooth back and forth to detect changes in brightness (Figs. 5A1-5A4). Again, matt surface is noticed when analyzing the entire assemblage, detecting some specimens are matt and some others are shiny.

Figure 5 double column width

Heavy digestion on **arvicolin** molars shows extensive removal of enamel along the height of the salient angles and the dentine is flattened and heavily wavy (Figs. 2C1-C3); heavily pitted enamel is partly removed along the edges of wear facets. The dentine is locally removed on the occlusal areas, causing the edges of some salient angles to have a concave shape in occlusal views (broken lines in figures 2C1 and 2C2,

295 pointed by arrows) also seen in lateral views (Fig. 2C3, black arrows). **Murid** molars
 296 accompanying **heavily** digested arvicolins (i.e. from the same pellet or scat) are
 297 described by Andrews (1990) noting that “...*the surface is heavily pitted (sometimes*
 298 *losing the colour) the enamel partially removed on the cuspids and along the edge of*
 299 *the wear facets....the dentine is not affected*” (Fernández-Jalvo & Andrews, 1992, page
 300 412). Figures 3C1 and 3C2 show incipient removal of enamel, and Figures 3D1 and
 301 3D2 display a more advanced grade of digestion with a greater loss of enamel along the
 302 height of the crown (black arrow), but dentine is not altered. The enamel is partially
 303 removed at the alveolar junction, where crown contacts the roots (Fig. 3C2 black
 304 arrow), except when the tooth is protected by the jaw. **Soricid** molars accompanying
 305 heavily digested arvicolins (Fig. 5B1-5B4) also show pitting and loss of enamel at the
 306 alveolar junction, where the crown contacts the roots, as seen in Figure 5B3 (outlined),
 307 with dentine unaltered and, sometimes, roots exposed (black arrow).

308 As digestion continues reaching **extreme** stages, the occlusal and root alveolar ends of
 309 **arvicolin** teeth become dissolved away and rounded, whilst the dentine collapses
 310 inwards and the broken lines in occlusal view are now concave for all columns (see
 311 Figs. 2D1 and D2). In lateral view, digestion has deeply penetrated the salient angles to
 312 the extent that the enamel remains along the sides of the original columns leaving
 313 dentine extensively exposed and collapsed (gaps in the dentine marked in Figure 2D3 as
 314 brown strips). **Murid** molars accompanying arvicolins digested at **extreme** stages (i.e.
 315 from the same pellet or scat) “*show extreme digestion, with more of the enamel*
 316 *removed*” (as shown in Figures 3E1 -E2). **The same pattern is observed in soricid**
 317 **molars** (Figs. 5C1-5C4) where ... “*enamel may be largely removed, leaving islands of*
 318 *cracked and scored enamel, or it may be entirely missing and the dentine hollowed out*
 319 *and etched so that only the bare outlines of the teeth remains*” (Andrews 1990;

Fernández-Jalvo & Andrews, 1992: page 412). Even though these extremely digested teeth have difficulties for taxonomic identification, the number of elements with extreme traits of digestion is already important information to characterize the predator that produced the assemblage.

The extent of digestion along the height of the molar crown depends to some extent on the length of time the molar remains in its alveoli. Teeth remaining in place in jaws are partly protected from the effects of digestion, the root end showing no evidence of digestion when the exposed end is digested. This is the case of the tooth pictured in Figure 3D2 that was removed from a maxilla and the contact between the crown and the roots is not damaged (pointed here by an empty arrow). The teeth selected here show similar degrees of digestion on both buccal-lingual sides of the tooth. However, sometimes the tooth shows less digestion on one side compared to the other side. In such cases the tooth should be classified as the highest degree of digestion observed. Table 1 summarizes traits of digestion and key features to distinguish between grades of digestion for these three groups of small mammals.

Table 1 about here

2.2. Incisors - digestion evidence

Incisors are the most homogenous skeletal element among all rodents and the easiest element on which to identify digestion. Rodents have one side of the incisor covered by enamel and the other half with the dentine exposed. In spite of the usual lack of taxonomic diagnostic traits in incisors, those preserved in jaws together with diagnostic molars may be analyzed to confirm digestion and provide evidence of the origin of the small mammal bone assemblage. The distal end of the incisor (the root tip) is not analyzed because the continuously growing incisors of rodents are highly mineralized

and digestion appears at a higher degree of digestion than actually affecting the rest of the tooth. Therefore, incisors recently broken that do not preserve the occlusal tip are discarded for digestion analyses. This does not apply to incisors broken before digestion as shown in Figure 6 (B2 and D2 on the tip). In contrast to rodent incisors, the incisors of soricids have the enamel completely covering the dentine. In principle, incisors preserved in jaws are enough to confirm the identification of the predator obtained from molars. However, most incisors occur as isolated teeth, separated from their jaws, and digestion is easily distinguished on these as the enamel appears retracted from the dentine. This trait can only be produced by digestion as abrasion equally affects both the enamel and the dentine, and soil corrosion affects the tooth at random spots along the incisor surface (Fernández-Jalvo et al., 2014). In order to distinguish digestion on the incisors, the mandible has to be turned laterally to be able to see the lateral side of the teeth and, especially, the enamel-dentine junction.

Figure 6 double column width

Digestion first affects the enamel of rodent incisors as a pitted surface at the tip of the incisor (i.e. matt surface = lack of brightness) indicating a very light digestion established by Williams (2001) in several *Tyto alba* assemblages. Very light digestion is described by Williams as a "*form of digestion that could not be seen with the naked eye, and appeared as a very slight dulling of the enamel surface, often at the tips. Although no actual enamel loss could be seen, the shiny coating of the enamel was no longer visible*" (page 132). Very light digestion can be seen by moving the tooth back and forth to detect changes in brightness.

Light digestion on rodent incisors affects the enamel surface showing pitting and matt surface, or thinning and removing the enamel only from the tips of the incisor as seen in

Figure 6 (A1 upper incisor, A2 lower incisor black arrow). In some cases of light digestion, enamel is totally removed from the tips of the incisors and the dentine partially thinned, indicating the incisors were still retained in the jaws while digested (see the small box on top left of Fig. 6A1,). **Moderate** digestion on rodent incisors is marked by the dentine surface becoming wavy (Fig. 6B1 black arrow), and as the enamel is more intensively digested it becomes retracted back down the incisor i.e. toward the root (Fig. 6B1 and 6B2). **Heavy** digestion removes so much of the enamel that it remains only as islands remnants (Figs. 6C1 and 6C2 black arrow) and the dentine is broadly wavy and may appear cracked. Digestion on soricid incisors is not evident until heavy degrees of digestion in rodents, where it forms dispersed islands along the crown (Fig. 5B4 black arrows).

The maximum degree of digestion (**extreme**) on rodent incisors is characterized by the loss of shape of the incisor (often confused with ribs or long bone shafts), with the enamel remnants present as very small islands or completely absent and/or the dentine collapsing in on itself along the incisor (marked in Figure 6D1 as brown spots). **Soricid** incisors lose the enamel and the dentine appears highly rounded (Fig. 5C4). The extent and degree of progressive enamel loss along the length of the incisor is to a large extent dependent on the time the incisor remains in its alveoli: if it falls out quickly, the digestion spreads along the exposed parts of the incisor, but if it remains *in situ*, digestion may penetrate and affect the rest of the incisor less intensively. For this reason it is, therefore, important to differentiate between isolated incisors and those still present in the mandible or premaxilla. Nonetheless, as described below, jaws are also corroded by digestion dissolving the inferior border of mandibles and the maxillary bone, allowing digestion to corrode the tooth.

The numbers of digested molars and incisors from predators-accumulated assemblages are shown in table 2. Together with maximum degrees of digestion, these may indicate the digestion category of the predator (Andrews, 1990). Identification of the predator at the species level is possible following Andrews (1990) methodologies, but this includes postcranial digestion, skeletal element survival and breakage analyses. An easy approach to rates of breakage may be obtained from upper and lower jaws.

Table 2 around here
Figure 7, 1.5 columns width

2.3. Mandibles and maxilla.

Both mandibles and maxillae, when molars are in their alveoli or even when teeth are absent, may be kept for taxonomic analyses. The number of jaws where teeth remain *in situ* (in their alveoli) and breakage of jaws is already an important source of information to identify the predator. Breakage in mandibles and maxillae (Fig. 7) may be indicative of the predator: from minimum most frequently among nocturnal owls, which swallow their prey complete to mammalian carnivores that produce maximum breakage as they chew their prey, with diurnal raptors in between that tear apart the prey before ingestion. Breakage before digestion (i.e. during ingestion), on the other hand, facilitates penetration of the gastric juices and increases the effects of digestion. In addition, the number of teeth (both molars and incisors) remaining in place in the upper and lower jaws are less digested than isolated teeth, as they are protected to some extent by soft tissues and by the jaw bone. Mandibular teeth are usually less digested than teeth in maxillae as the bone from the latter has higher porosity that facilitates the penetration of gastric juices into the interior of the maxillae. Therefore, discrimination between teeth remaining in place in the jaws and those found isolated helps to identify

the predator. We have, however, to keep in mind that the final breakage rate of jaws observed in fossil assemblages may be increased by subsequent taphonomic processes, such as trampling, weathering, fall of rocks or compaction of sediments as described below in fossil sites (heading 3.2). Furthermore, arvicolin molars have a cylindrical shape and they are very easily detached from their alveoli during sampling, sieving or sorting, especially those species with unrooted teeth.

2.4. Digestion and predator categories

Table 2 reviews the main differences between the frequencies of digestion for 33 predators. It is important to notice here that some predators belong to one category for incisor digestion and to another for molars (Table 3), and both need to be considered in order to build up a composite analysis of predator identification. When available, sample sizes for molars and incisors should each exceed 100 specimens in order to obtain reliable measures of degree and proportion of digestion.

Table 3 around here
Figure 8, double column width

There is a general difference in digestion frequency between mammalian carnivores and diurnal raptors on the one hand and nocturnal predators on the other. Diurnal raptors and mammalian carnivores sometimes display 100% of digestion of molars and incisors elements (Table 3, Fig. 8). The exception for the owls is *Athene noctua* (little owl) which has 100% of in situ incisors digested, and *Otocyon megalotis* (bat eared fox) for the carnivores, where digestion is less intense. Based on field observations of their behaviours and taphonomic studies of their food remains (Andrews, 1990), in the latter case, the bat eared fox is primarily insectivorous and may not have a normal canid digestive system, producing lower degrees and frequencies of digestion, and in the former case, the little owl is not able to ingest whole animals and may act more like a

diurnal raptor, tearing open its prey before eating it. Breakage would expose the bones of its prey more strongly and quickly to digestive action. Viverrids and mustelids show a relatively low percentage of digested teeth (<35% in incisors and ~20% in molars), but heavy-extreme grades of digestion.

Slight differences can be observed between Table 3 shown here and similar tables in Andrews (1990, Table 3.14) and Table 3 in Demirel et al. (2011). Table 3 here is more precise and adapted to both authors. We have slightly changed percentages based on descriptions and tables by Andrews (1990) and non-published notes of sample analyses of *in situ* and isolated teeth (molars and incisors) by this author. Digestion traits and grades described in detail by Andrews (1990) have been applied to both arvicolins and murids (as well as soricids) recovered from the same pellet or scat produced by the same predator, also considering results and descriptions by Demirel et al. (2011).

3. DISCUSSION.

3.1. Predator hunting habits from modern analogues

Different predators occupying the same area can produce differing prey assemblages if they have differing hunting profiles. Sometimes these different profiles can appear to indicate different habitats, and it is only by knowing about the predator habits that the significance of these differences can be recognized. Three pellet collections were made in 1987 at Neuadd, Wales; three predators were identified visually, *Tyto alba* (barn owl), *Strix aluco* (tawny owl) and *Falco tinnunculus* (kestrel), all roosting in different parts of the same barn over a single period of a few weeks. This example is important, because it obviates the well known seasonal change of preys by predators, but it shows an exceptional case of three raptors predating simultaneously the same area and collecting different prey species (Fig. 9). *Falco tinnunculus* and *Tyto alba*, have similar

faunal profiles, both with assemblages dominated by arvicolins, and a more equable assemblage accumulated by *Strix aluco*, with equal numbers of arvicolins and birds and other prey species also well represented. This degree of difference in faunal distribution could easily be interpreted as representing differences in habitat in a fossil assemblage of subsequent sedimentary units and predator shift, but we know by direct observation that they represent the same habitat and the difference in prey distribution is the result of different predator hunting habits and preferences.

Figure 9, 1.5 columns width

Diurnal and nocturnal birds of prey and small carnivores all contribute to the accumulation of small mammals in their pellets or scats. Table 4 summarizes the size, nesting and hunting environment of the most common predators responsible for fossil assemblages of small mammals (and small amphibians and squamates). Data on ecology and prey species richness are extracted from Mikkola (1983), Andrews (1990), Denys et al. (2004), Denys (1997) and some specialized studies about predators' diet. The data show that nesting or roosting sites frequently occur in environments different from the hunting areas; for example it is commonly seen that predators roost/nest in woodland habitats while hunting prey in more open habitats.

Table 4 around here

Each predator may, therefore, have its own specificity in terms of diet preferences. Some generalists like *Tyto alba* in Europe can sample a good diversity of rodent and shrews of their territory while Denys (1997) showed that *Tyto alba* in different regions of Africa may collect between 4 and 15 rodent species and from 5 to 19 small vertebrates species. For example, *T.alba* accumulations from Highveld in Transvaal (South Africa) reach the highest species richness, while barn owl accumulations from

more arid environments (SW Africa, Sudano-Sudanian savannas) the lowest (Table 3 in Denys, 1997).

Some other less well known predators also sample high diversities of small vertebrates. For instance, Denys (1997) showed that *Bubo africanus* can accumulate from 4 to 9 rodent species and from 6 to 23 small vertebrate species. On the contrary *B. lacteus* prey accumulations have low species richness. Distinguishing between *B. lacteus* or *B. africanus* origin in a fossil assemblage may help to recognize that some species absences result from predation bias and not from stratigraphic gaps.

Typical examples of predation bias are the eagle owls *Bubo bubo* and *Bubo africanus*. Both roost and nest in closed woodland or rocky areas in woodland while habitually hunting in open habitats, often near water. Fernández-Jalvo et al. (1996), Scott et al. (1996) have already shown the importance of landscape and hunting territory as well as the importance of nests analysis and pollen analyses between sites. These authors studied modern pollen spectra of regurgitation pellets of *Bubo africanus* at Clarens (Ouwerv and Kloof Valley, South Africa) compared with a nest situated on a mountain wooded slope close to the hunting territory of the owl in open habitats. Pollen from the pellets yielded predominance of open grassland, whilst pollen from the nest was a mixture of pollen from both the grassland and the woody vegetation of the mountain slope. The most abundant small mammal species at both sites (nest and pellets, Table 5) is *Otomys irroratus* and *Rhabdomys pumilio* that inhabit open grasslands or mountain savannas, as indicated by pollen (Fernández-Jalvo et al., 1996; Scott et al., 1996). The respective species richness is 7 for both sites (assuming that *Otomys* sp. indet. corresponds to one of the three *Otomys* species identified in this assemblage). Species that are not found in common like *Otomys slogetti*, *O. angoniensis*, *Aethomys chrysophilus*, *Dendromus* sp. and *Crocidura* sp. are either open grassland (*O. slogetti*),

bush (*A.chrysophilus*), swamps or water proximity (*Dendromus* some *Crocidura*) and indicate the richness of hunting territories of the predator. Despite the fact that nest and the hunting territory are in different environments (as indicated by the pollen spectra), the prey assemblages were the same. Percentage and abundance of digestion are slightly greater in the nest by juveniles than by adults in the pellets (Table 6), confirming descriptions by Andrews (1990) and Bruderer & Denys (1999). This present-day example shows that, if the predator is not identified, the environmental implications provided by pollen and small mammals separately may give a different scenario... *Combination of environmental indications from these inferred predators, the micromammal remains and the pollen spectra* (both influenced by predation) *may provide, therefore, a more detailed record of contemporary local landscape.* (Fernández-Jalvo et al., 1996, page: 265).

Tables 5 and 6 around here

3.2. Predator hunting habits in palaeontological studies:

Several examples of taphonomic studies applied to improve ecological interpretations have been published. One of them is the Middle Pleistocene cave at Westbury-sub-Mendip (~500kyr, Grün & Stringer, 1999; Schreve et al., 1999) firstly described by Bishop (1974) and summarized subsequent excavations by Andrews et al. (1999). Table 7 shows the species richness from 8 units, the identification of the predator responsible for accumulating the small mammal assemblages and how these faunas were affected by the predator's preferences. *Bubo bubo* and *Tyto alba* are both opportunistic owls, adapting to different prey in different habitats, and selective, hunting over open country and selecting the most abundant prey species. So the high/low species richness in these units may not be always the result of the predator's hunting bias but respond to

ecological requirements and vice versa. The general principle here is that when the levels of species richness of the fauna are consistent with the accumulating agent, the ecological signal is low, but when the species richness is inconsistent with the accumulating agent, the ecological signal is high. Following this principle, it was possible to discriminate between warm and cold phases during the accumulation of the small mammal assemblages. These indications were supported by palaeoecological tests applied to the small mammal faunas (Andrews, 1990)

Table 7 around here

Another example, recently published (Fernández-Jalvo & Avery, 2015), showed the interest of applying small mammal taphonomic studies to a variety of objectives. That taphonomic study was an attempt to apply the methodology here described to microfaunal assemblages taxonomically studied by Avery (2007). The site, Wonderwerk cave in the Kuruman Hills in South Africa, has an age ranging from about 2 My at the bottom to Holocene at the top (Matmon et al., 2012; Chazan et al., 2008). In addition to the identification of the agent that produced the small mammal assemblages and obtain palaeoecological information, the study also intended to investigate the incidence of fire already described in the site (Chazan et al., 2012; Berna et al., 2012). The taphonomic analysis was focused on the bottom of the sequence (Strata 12 and 11). Applying this analysis to taxonomic elements, i.e. molars and jaws, the predator inferred could only be a category 1 (following Andrews, 1990 categories), most probably *Tyto alba*. When the taphonomic analysis was extended to isolated incisors and postcranial remains, results obtained from the skeletal representation, breakage traits and the light digestion grade confirmed this identification (Fernández-Jalvo & Avery, 2015).

Figure 10, 1.5 columns width

The taxonomic identifications and the Taxonomic Habitat Index (THI, Andrews et al., 1979; Evans et al., 1981; Matthews et al., 2005) indicates both that the faunas from the two strata are dominated by open savanna and arid environments at Wonderwerk cave. The influence of the predator's hunting preferences in open habitats increased the high abundance savanna grassland in the environments indicated by the THI (Fig.10). However, since the same predator was the agent of accumulation at all levels, the light differences in THI environment between strata appear not to be caused by the predator, but by an environmental/climatic shift from more aridity in St12 to moister (fynbos) environments in St11. The environmental/climatic shift is also recorded by phytoliths (Chazan et al., 2012) and isotopes (Horwitz et al., 2016), supporting the change through the sequence, less accused by the microfauna taxa.

3.2.1. PRERESA: the application of the simplified method validated by a taxonomist.

PRERESA takes the name from the enterprise that extracted sands and gravels from one of the lowest terraces of Manzanares river, SE Madrid (Spain). Both large and small mammals have been recovered from this open air site which is late Pleistocene in age, dated by OSL in 84 ± 5.6 ka BP, end of MIS 5 (Sesé et al., 2011). The site covers 255 m², and it also has lithic tools typical of the middle Palaeolithic together with remains of microvertebrates (Table 8).

Table 8 around here

The taphonomic study of macromammals by Yravedra et al. (2012) and Yravedra (2014) has found indications that the site was formed at different times. In one unit, a large bovid skeleton has its elements almost in anatomical connection, together with

remains of a cervid, and both of them are preserved almost intact with some carnivore tooth marks (1%). In another unit, remains of a proboscidean have cut and percussion marks on the bone surfaces, and broken diaphysis fragments, both indicating the access of humans (i.e. Neanderthals) to butcher the carcass of this large mammal to obtain meat and marrow. The site has been artificially divided into units, but all of them could be considered as a single one, given the extensive time averaging observed in these fossil associations.

Most small mammal fossils are extracted from excavations together with the sediment and processed by wet sieving. Some bone accumulations of microfauna have been uncovered, dug separately and registered as single fossils, initially considered to be a raptor pellet. These concentrations or pellets are more frequent from cave environments that have a higher environmental relative humidity that favours the preservation of these accumulations. Therefore, these pellet-like accumulations are unusual in open air sites, probably favoured in PRERESA for the terrace environment that has higher soil moisture rates than non-fluvial open-air environments. There is a high abundance of rabbit, followed by *Microtus cabreræ*, *M. duodecimcostatus*, *Arvicola* together with murids and cricetids (Sesé et al., 2011). Digestion is relatively high, both in percentages and grades. The methodology here described has been applied on the arvicolin collections of this site, on already mounted molars that were placed in occlusal view for taxonomic identifications.

Table 9 around here

Results from the observations taken by the taphonomist (YFJ) in occlusal view and confirmed subsequently by inspection are shown in Table 9, together with observations by the taxonomist (CS) following the indications of Figures 2 to 6 and descriptions in

this paper. Most molars recovered from the site are arvicolins. From this inspection, we may confirm that the method proposed here to identify digestion and grades from occlusal views is perfectly valuable coinciding in a high percentage (almost 100%). Murin and possibly soricid molars with matt surfaces (light and moderate respectively) may cause some difficulties to taxonomists given the need of moving the tooth back and forth under the light to detect changes in brightness. Murin molar moderately digested (pitted and irregular surface), heavily digested (enamel partially removed) and extreme (collapse of the dentine) were classified without difficulty. Two soricid molars with loss of enamel were identified as heavy grades of digestion. One rodent incisor preserved *in situ* showing light digestion was distinguished by the taxonomist according to indications and figures displayed here.

Initially, the taxonomist could not always identify digestion when the arvicolin molars were affected in light degrees (Table 9, highlighted in grey). A second inspection showed the presence of small gaps in the enamel outline on the occlusal view, and this was agreed. Loss of enamel could then be observed from the occlusal edges of the salient angles as shown in Figure 2A. On five occasions, the taxonomist identified heavy digestion when the anteroconid (valuable for taxonomic identification) appeared almost eaten away (Fig. 11A1, black arrow). In these cases, however, enamel was only removed from half of the column length of the molar, which is characteristic of moderate digestion (Fig. 11A3). Three more molars were also referred by the taxonomist as been heavily digested, and this time the gap in the vertex of the salient angle was as wide as in Figure 2C, but again digestion only reached half the length of the tooth. In such case, it would be preferable for the taxonomist to incline the tooth to observe if the enamel has been removed along the whole length of the tooth, as described for heavy digestion, or only the half, as characteristic of moderate digestion.

Figure 11 double column width

The percentage of digested teeth in PRERESA affects 78% for small mammal molars. Extreme cases of digestion have been recorded in 7 arvicolin molars and 2 murins (Table 9, Fig. 12B). Murids are scarce (5 of them heavily worn out), but they may reach moderate and heavy degrees. Only 3 molars of soricid are present in this sample. The final percentages of light (52%), moderate (34%), heavy (8%) and extreme (6%) grades of digestion are the same identified by the taphonomists and the taxonomist as shown in Table 9. There are several examples of teeth broken before digestion, mainly affecting the biggest sized prey, i.e. *Arvicola* and *Oryctolagus* (Fig. 11C black arrows). These indications together with the high grades of digestion, reached sometimes, indicate that the small mammal assemblage may have been produced by mammalian carnivores as result of regurgitations and scats. A quick look at the postcranial skeleton shows abundant breakage and tooth marking before digestion, which in postcranial bones is a relatively high degree of digestion. The complete taphonomic analysis of PRERESA microfauna fossil assemblage is currently under progress.

The fossil remains at PRERESA (Fig. 11D) are also affected by weathering (cracking due to exposure to weathering agents (sun, humidity and temperature changes, Fig. 11D white arrow) Advanced stages of weathering cause the collapse of the dentine, as shown by Andrews (1990), characteristic of most molars in PRERESA that show dentine subsidence on the occlusal surface (see Figs 11A1 and 11D, grey arrows). Dentine collapse at the interior of the cusps is not linked to reduction of the enamel on the salient angles due to digestion (the edge of the dentine does not outline a concave shape). Plant-root corrosion (known as root-marks) are also present in these fossils (Fig. 11E grey arrow) affecting the enamel and the dentine randomly on the surface (i.e. not concentrated on the tips or salient angles of the teeth). Loss of shiny surfaces may

appear locally on the enamel when affected by biochemical alteration (i.e. root-mark or soil corrosion), but it is not all over the surface as produced by digestion. Both weathering and root-marks are frequent taphonomic modifications indicating long time exposure and an active soil, characteristic of open air sites.

4. FINAL REMARKS.

1. We provide here a taphonomic methodology based on the dental elements and views studied by taxonomists, in order to facilitate the identification of modifications by predation to taxonomists.
2. Taxonomists illustrate and mainly focus their analyses on occlusal views of molars to identify species, and they also consider mandibles and maxillae with molars preserved in their alveoli, which may also preserve incisors *in situ*.
3. Taphonomists study the lateral sides of molars, where the effects of digestion are greatest, together with isolated incisors and postcranial skeleton. Some taxa, such as murins and soricids, may cause difficulties to taxonomists in identifying light and moderate degrees of digestion on the occlusal surfaces of molars and these should be inclined to observe the lateral view.
4. Digestion is a progressive process that produces a continuous modification on the different types of bony tissues. This effect makes digestion distinctive so that it cannot be mistaken for any other taphonomic modifications such as soil corrosion, plant root marks or abrasion.
5. Abrasion results from physical friction of sediment and water against bone and teeth, and it affects all tissues equally, producing even rounding of all tissues (Fernández-Jalvo et al., 2014).

- 685 6. Chemical corrosion by soil acidity or root marking also affects all parts of the
686 tooth or bone, leaving randomly dispersed spots of chemical corrosion on
687 enamel, dentine or bone surfaces. Corrosion does not initiate on the tips and
688 salient angles of the teeth as digestion does, but can start anywhere on the tooth
689 surface (Fig. 11E).
- 690 7. Digestion starts at the salient angles or tips of cusps. The action of digestion on
691 isolated ever-growing arvicolin teeth is greatest at the alveolar ends. This makes
692 it advisable to avoid roots when classifying digestion and only use tips of
693 incisors and occlusal ends in molars.
- 694 8. Light degree produces a 'melted' appearance on the tips and salient angles, with
695 the dentine appearing rounded; on occlusal surfaces of arvicolins this may be
696 seen as slight rounding of the corners of molars and loss of enamel from the tips
697 of rodent incisors and salient angles. Murins have matt enamel surface and
698 rounding on the occlusal edges of the molars. Soricid teeth are not damaged at
699 this stage of light digestion observed in arvicolins and murins. Rodent incisors
700 lightly digested show pitting and loss of shiny of the whole enamel surface or
701 enamel removal from the tips of the incisors.
- 702 9. Moderate digestion on arvicolins show loss of enamel along the salient columns
703 reaching half of the length of the enamel on the lateral view of the molar. This is
704 readily seen on the occlusal surfaces by rounding of the tops of the salient
705 angles. For murins, moderate digestion is restricted to heavy pitting of enamel
706 and incipient enamel reduction at the edge of the crown-root junction in lateral
707 view. Light pitting (matt=loss of shiny surfaces) appears on soricid molars
708 accompanying arvicolins and murids moderately digested. Rodent incisors

moderately digested impart a wavy texture to the dentine and enamel removed from almost the half of the tooth. Soricid incisors show enamel matt surface.

10. Heavy digestion in arvicolin molars produces extensive removal of enamel along the entire lengths of the salient angles, and some of these salient angles have collapse of the dentine providing a concave outline in occlusal view. In murins there is loss of enamel from the cusp tips or towards the height of the crown, as well as from the alveolar junction between the crowns and the tooth roots. Soricid molars also show pitting and loss of enamel at the alveolar junction, where the crown contacts the roots. Rodent incisors heavily digested show most of the enamel removed, which forms small islands dispersed on the dentine of rodent and soricid incisors.

11. Extreme grades of digestion for both incisors and all molars (arvicolins, murins and soricids) totally removes most enamel, and the dentine becomes so weak that it starts to collapse.

12. Degrees of completeness of skulls, jaws and limb bones are greatest for prey of nocturnal birds of prey, with more intense breakage accompanied by heavy to extreme grades of digestion among diurnal raptors and mammalian predators. Inferior borders of mandibles are not broken by abrasion, but breakage is frequent in digested mandibles. Maxillae are more fragile and may also break during recovery. Nonetheless complete cranial elements may indicate predators that produce little damage to the bones of their prey (e.g. *Tyto alba*).

13. We have documented here the taphonomic modifications for incisors and molars of arvicolins, murins and soricids. Further studies of other rodent groups, particularly glirids, and cavid, need further comparative analyses. We also need to extend studies to different geographic areas, to additional samples of

these and other predators, and to other prey groups (amphibians, squamates, birds, fishes) in order to refine the data and provide better identification criteria.

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1040

1041 **Figure captions.**

- 1042 Figure 1. Light, moderate, heavy and extreme digestion in arvicolin, murid and soricid
1043 molars from the same predator's pellet or scat (after Stoetzel, 2009 modified). The shape
1044 and enamel thickness of the tooth produce different responses to the effects of digestion.
1045 For instance, enamel removal appears in arvicolins already at the earliest stage of light
1046 digestion, whilst in murins and soricids, only at heavy grades of digestion. Lightly
1047 digested murin molars have a smoother, matt enamel surface and more rounded shape

than non-digested teeth, but sorcid molars accompanying arvicolins or murins lightly digested (from pellets of category 1 predators) show no digestion signs.

Figure 2. Signs of digestion in arvicolin lower 1st molars (molar shown in D, uncertain). A: light digestion, B: moderate digestion, C: heavy digestion, D: extreme digestion. 1 occlusal views, 2 occlusal slightly inclined views, 3 lateral views. The bracket at the bottom of occlusal views (1 and 2) indicates the side shown in lateral view (3). Black lines indicate the loss of enamel and broken lines delineate the edge of the dentine exposed by digestion with a convex shape in light and moderate degrees. Dentine collapse (shown in D as brown strips and pointed in C by arrows) makes the occlusal dentine outline (broken lines) to acquire a concave shape. Arrows points to key features to distinguish grades of digestion. (Scale bars= 500 microns, except for A3 and B3 = 1 mm). Figure 3. Signs of digestion in murid upper 1st molars. Top left square: occlusal views of non-digested teeth: tooth wear showing the edge of the cusps flattened and non-digested unworn tooth showing sharp cusp edges. A: light digestion, B: moderate digestion, C: heavy (low level) digestion, D: Heavy (high level) digestion, E: extreme digestion. 1 occlusal views, 2 lateral views (except for E: extreme grade of digestion that 1 shows the *in situ* teeth in maxillae to show it is an upper 1st molar, and 2 is occlusal view, showing enamel reduction (black line) and dentine exposed (broken lines) with collapse of the dentine. The tooth shown in figure D was removed from the maxilla, which protected the crown-root junction and enamel reduction (empty arrow) is not here evident. Arrows points to key features to distinguish grades of digestion. (Scale bars = 500 microns, except for C, D and E1 = 1 mm).

Figure 4. Scanning electron micrographs of a murid molar showing moderate digestion. Top image is at secondary electron mode to show the topography of the tooth heavily pitted and the reduction of enamel at the crown-root junction (black arrow) that also characterizes this grade of digestion. Bottom image is at backscattered electron mode to show no reduction of enamel on the cusps rounded by digestion and partially flattened by microwear.

Figure 5. Signs of digestion in sorcid P3-M3 dental series. Pellets containing sorcid teeth accompanying arvicolin and/or murid teeth at light grades of digestion do not show any digestion feature. Digestion traits in sorcids start to be shown when arvicolin and murid molars show moderate grades of digestion (A1-A4) as matt surfaces

observed when analysing the whole assemblage and moving the tooth back and forth, with some teeth appearing matt (moderately digested) and others shiny. B1-B4 are soricid teeth affected by heavy digestion when the crown-root junction shows loss of enamel or remnants of enamel islands on the incisor. C1-C4 shows soricid teeth at an extreme degree of digestion with almost no enamel and dentine is hollowed. Arrows points to key features to distinguish grades of digestion. (Scale bars = 1mm, except for A3 = 200 microns, and B3, B4 and C3 =500 microns. A1, B1 and C1 have identical magnification).

Figure 6. Signs of digestion in rodent incisors: 1 upper incisor, 2 lower incisor. A: light digestion (enamel pitted all over the incisor and/or reduction of enamel on the tip of the incisor; the top left square shows digestion concentrated on the tip). B: moderate digestion (dentine starts to have a wavy texture, black arrows, and enamel is retracted back down the incisor i.e. toward the root). C: heavy digestion (enamel reduced to small islands –black arrows- and dentine heavily wavy texture). D: extreme digestion (dentine collapses, shown here as brown strips) enamel absent or reduced to small islands. Black lines delineate the enamel and broken lines point to the dentine exposed by digestion. (Scale bars = 1 mm).

Figure 7. Breakage in mandibles (top) and maxillae (bottom) from low breakage (A and B) to the highest level of breakage indicated by E (after Andrews, 1990).

Figure 8. Percentage of digestion of incisors and molars per predator species. Three natural groups can be distinguished: nocturnal raptors, diurnal birds of prey and mammalian carnivores. *Athene noctua* and *Otocyon* are separated by broken lines from the rest of natural group to which they belong as the former shows heavier rates of digestion amongst owls and the latest, much lower traits of digestion than other mammalian carnivores. Also note the low percentages of digestion in viverrids and mustelids prey remains, although digestion reaches extreme degrees.

Figure 9. Prey assemblages of three predators (*Strix aluco*, *Tyto alba* and *Falco tinnunculus*) roosting in the same spot area, a barn in Wales (Neuadd, UK), which pellets were collected over a period of few weeks. The diagram shows the distributions of seven prey items for each of the three predators.

Figure 10. Taxonomic Habitat Index (THI) based on small mammals from Stratum 11 and Stratum 12 of Wonderwerk cave (South Africa).

Figure 11. Fossils from PRERESA site (Madrid, Spain). A: moderately digested M1 of *Microtus cabrerae*. The occlusal view (A1) shows a reduced anteroconid by digestion (black arrow) that may indicate to taxonomists a heavier digestion than actually affecting the tooth. The lateral view, A2, shows enamel reduction at a light grade of digestion in contrast to moderate digestion in A3 (affecting the half of the height of the tooth). In case of discrepancies between one side and the other of the tooth, digestion should be classified as the highest degree observed, i.e. moderate in this case. B lateral view of an extremely digested *Microtus* sp. molar, the arrow indicates a strong reduction of the enamel and collapse of the dentine. C. Lagomorph teeth broken before digestion. Breakage is pointed by black arrows and the edge of breakage is heavily rounded by digestion as the rest of the tooth. D Scanning electron micrograph of a *Microtus* cf. *cabrerae* molar at backscattered electron mode showing strong cracking of the dentine (white arrow) and collapse of the dentine at the interior of the cusp (grey arrow as in A1) due to weathering. E. Lateral view of a rodent incisor showing the effects of root-mark corrosion (grey arrow). Note enamel corrosion is located at the middle anterior part of the incisor (roots may corrode the tooth at any part of its surface), in contrast to enamel reduction at the tip of the incisor typical of digestion (as shown in Fig.6).

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Highlights: (3 to 5 bullet points, maximum 85 characters with spaces/highlight)

- The most common source of microfauna assemblages is predation by raptors or mammals=85
- Prey composition reflects predator's preferences, not necessarily the environment=83
- Digestion on the prey remains is the most direct evidence of predation=72
- Digestion key traits for arvicolins, murids and soricids are reviewed here=76
- A method suitable for taxonomists and taphonomists to identify digestion and predator=87

Table 1 Summary and keys to distinguish categories of digestion, both in molars and incisors, in Arvicolines, Murids and Soricids.

	Digestion	Arvicolines		Murids		Soricids
		Occlusal	Lateral	Occlusal	Lateral	
Molars	Light	Enamel gaps on salient angles, dentine emerges outlining a narrow convex shape.	Small enamel reduction (less than a third of the height of the tooth). Dentine exposed and rounded.	Rounded cusps, smoother than non-worn teeth	Matt (=loss of shiny) enamel.	No digestion can be seen: enamel is shiny, no rounding, no damage.
	Moderate	Wider enamel gaps and more flattened dentine exposed on salient, dentine retracted inwards outlining a wider convex shape than in light digestion	Enamel removed along the half height of the tooth (some columns may have superficial reduction of enamel along the entire height of the column).	Pitted enamel surface, all over the tooth enamel.	Incipient enamel reduction at the crown-root junction.	Matt surface (=loss of shiny) enamel.
	Heavy	Dentine, locally removed in some salient angles outlining a concave shape on occlusal view.	Extensive removal of enamel along the entire height of the salient angles. Dentine flattened and broadly wavy.	Enamel removed from the cups and heavily pitted. Dentine is exposed and not affected or rounded.	Enamel removed towards the height of the tooth and at the crown-root junction. Dentine/roots are not affected or rounded.	Enamel heavily pitted and partially removed, dentine exposed at the edge contact between the crown and the roots. Dentine is not affected or rounded.
	Extreme	Dentine collapsed inwards, providing a concave outline in all or most salient angles.	Dentine collapsed inwards. Enamel along the sides of the original columns.	Enamel forming small islands or completely removed, with or without dentine hollowed out and etched.		Enamel forming small islands or completely removed, with or without dentine hollowed out and etched.
Incisors		Rodents				Soricids
	Light	Enamel shows pitting and matt surface (=loss of shiny) all over the tooth, or retraction on the tip leaving the dentine exposed and rounded. Sometimes, enamel is totally removed from the tip and dentine is retracted and producing an uneven outline.				No digestion can be seen: enamel is shiny, no rounding, no damage.
	Moderate	Dentine becomes wavy. Enamel removed from almost the half of the tooth.				Matt surface (=loss of shiny) enamel.
	Heavy	Enamel forms islands. Dentine broadly wavy and/or cracked.				Enamel forms islands.
	Extreme	Enamel completely removed or forming small islands. Dentine collapses in on itself along the incisor.				Small islands of enamel or completely removed, dentine highly rounded and wavy.

Table 2: summary of literature data about percentages of incisors and molars digested when available. **Percentages are combined with grades of digestion to identify the predators.** Percentages of *in situ* incisors do not discriminate between jaws with or without teeth; isolated incisors are in general unidentified; percentages of molars is here based on all molars, the %value being given by number of digested molars divided by total number of molars, but the same percentage would be obtained if only first molars were examined if the percentage of first molars digested is divided by the total number of first molars.

Predator	% incisors digested <i>in situ</i> on mandible	% isolated incisors digested	% molars digested	References
<i>Tyto alba</i>	3.6-18	5-27.6	1	Andrews, 1990; Bruderer & Denys, 1999; Matthews, 2006
<i>Bubo virginianus</i>	14.3	32.5	47.9	Gómez, 2005
<i>Bubo bubo</i>	41.8	48	11	Andrews, 1990; Sanchiz Serra, 2000; Cochard, 2004; Lloveras et al. 2008c
<i>Bubo spp</i>	12	14.9	0	Dauphin et al., 2003
<i>Bubo lacteus</i>	14.5	25	0	Andrews, 1990
<i>Bubo africanus</i>	58.3	57	4	Andrews, 1990
<i>Strix nebulosa</i>	8	30	4	Andrews, 1990
<i>Strix aluco</i>	53.8	66	22	Andrews, 1990
<i>Athene noctua</i>	100	73	51	Andrews, 1990
<i>Asio flammeus</i>	7.9	13	2	Andrews, 1990
<i>Asio otus</i>	17.6	27	1	Andrews, 1990
<i>Nyctea scandiaca</i>	16.6	8	5	Andrews, 1990
<i>Falco tinnunculus</i>	60.8	60	53	Andrews, 1990
<i>Caracara plancus</i>		100	100	Montalvo & Tallade, 2009
<i>Elanus caeruleus</i>	36.76	51.3	77.5	Souttou et al., 2012
<i>Elanus leucurus</i>	100	100	100	Montalvo et al., 2014
<i>Aquila adalberti</i>		91	100	Lloveras et al 2008a
<i>Circus cyaneus</i>	100	100	46	Andrews, 1990
<i>Circus aeruginosus</i>		100	70	Denys et al., 2007
<i>Genetta genetta</i>	35.2	35	15	Andrews, 1990
<i>Felis serval</i>	100	100		Matthews, 2002, 2006
<i>Felis caracal</i>		100		Matthews, 2002, 2006
<i>Felis catus</i>		100		Andrews, 1990
<i>Puma concolor</i>	100	100	100	Montalvo et al., 2007
<i>Canis mesomelas</i>		100		Matthews, 2002, 2006
<i>Ichneumia albicauda</i>		40		Andrews, 1990
<i>Otocyon megalotis</i>	14.3	20	10	Andrews, 1990
<i>Lynx pardinus</i>		98.6	97.2	Lloveras et al., 2008b
<i>Vulpes vulpes</i>	100	100	70	Andrews, 1990; Sanchiz Serra, 200; Mallye et al., 2008
<i>Alopex lagopus</i>	100	100		Andrews, 1990
<i>Pseudalopex griseus</i>	100	100	100	Mondini 2000; Gomez & Kaufman, 2007
<i>Martes martes</i>	33.3	28	24	Andrews, 1990
<i>Conepatus chinga</i>		100	97.3	Montalvo et al., 2008

Table 3. Summary of digestion category on molars (1st molar and *in situ* molars in jaws) and incisors (both isolated and preserved in jaws) of small mammals content in avian predator 's pellets (modified from Andrews, 1990 and Demirel et al., 2011).

* mammalian carnivores (including humans) can be, in general terms, be included in category 5 of extreme digestion (>50%). Some exceptions, however, such as viverrids and mustelids have extreme grades of digestion, but low percentages of digestion (~20%), or some canids that show lower than extreme grades of digestion. Felids are clear representatives of category 5.

Predator category	Digestion category	1st molar digestion	In situ molar digestion	Incisor digestion	In situ incisor digestion
Category 1	Absent or minimal Molars <2% Incisors 5-13%	<i>Tyto alba</i> , <i>Asio flammeus</i> , <i>Asio otus</i> , <i>Bubo lacteus</i>	<i>Tyto alba</i> , <i>Asio flammeus</i> , <i>Asio otus</i> , <i>Bubo lacteus</i>	<i>Tyto alba</i> , <i>Asio flammeus</i>	<i>Tyto alba</i> , <i>Asio flammeus</i>
Category 2	Light digestion Molars 0-5% Incisors 10-30% (tips only)	<i>Nyctea scandiaca</i>	<i>Nyctea scandiaca</i>	<i>Asio otus</i> , <i>Nyctea scandiaca</i>	<i>Asio otus</i> , <i>Bubo lacteus</i> <i>Nyctea scandiaca</i>
	Moderate digestion Molars 4-6% Incisors 20-30%	<i>Bubo africanus</i> , <i>Strix nebulosa</i>	<i>Bubo africanus</i> , <i>Strix nebulosa</i>	<i>Strix nebulosa</i> , <i>Bubo lacteus</i>	<i>Strix nebulosa</i>
Category 3	Heavy (low level) digestion Molars 11-22% Incisors 50-70%	<i>Bubo bubo</i>	<i>Bubo bubo</i> , <i>Strix aluco</i>	<i>Strix aluco</i> , <i>Bubo africanus</i> , <i>Bubo bubo</i> , <i>Athene noctua</i>	<i>Bubo africanus</i> , <i>Bubo bubo</i> , <i>Strix aluco</i> , <i>Athene noctua</i>
Category 4	Heavy (high level) digestion Molars 50-70% Incisors 60-80%	<i>Strix aluco</i> , <i>Athene noctua</i> , <i>Circus cyaneus</i> , <i>Falco tinnunculus</i> , <i>F. peregrinus</i>	<i>Athene noctua</i> , <i>Circus cyaneus</i> , <i>Falco tinnunculus</i> , <i>F. peregrinus</i>	<i>Falco tinnunculus</i> , <i>F. peregrinus</i>	<i>Falco tinnunculus</i> , <i>F. peregrinus</i>
Category 5	Extreme digestion Molars 50-100% Incisors 100%	<i>Buteo buteo</i> , <i>Milvus milvus</i> Mammalian carnivores*	<i>Buteo buteo</i> , <i>Milvus milvus</i> , Mammalian carnivores*	<i>Buteo buteo</i> , <i>Circus cyaneus</i> , <i>Milvus milvus</i> , Mammalian carnivores*	<i>Buteo buteo</i> , <i>Circus cyaneus</i> , <i>Milvus milvus</i> , Mammalian carnivores*

Table 4: Summary of ecological data on various predators suggested as potential fossil small mammal predators

<i>Predator</i>	<i>Size</i>	<i>Environment of nesting</i>	<i>Environment of hunting</i>	<i>Rodent species diversity</i>	<i>References</i>
<i>T.alba</i>	small	Trees, houses, churches, Cliffs, caves	Open country around the nest or roost	5-19	Mikkola (1983) Denys (1997)
<i>Nyctea scandiaca</i>	large	Open ground	Open tundra	5-9	Mikkola (1983) Detienne et al. 2008
<i>Asio otus</i>	medium	Woods, hedges	Open environments	10 12	Mikkola (1983) Denys et al. 2004
<i>Bubo bubo</i>	large	Ground, crevices in cliffs, small caves	Wooded and open habitats near water	13-20	Mikkola (1983) Sandor & Ionescu 2009 Papageorgiou et al 1993
<i>Bubo africanus</i>	medium	Cliffs, rocks, woodlands, ground	Open habitats	6-23	Mikkola (1983) Denys (1997)
<i>Bubo lacteus</i>	large	trees	Open woodland or valleys with riverine vegetation	2-4	Mikkola (1983) Fernandez-Jalvo et al. 1996 Denys (1997)
<i>Strix aluco</i>	medium	Trees (80%), caves, human habitations, rabbit holes	Woodlands, rough grazing areas	8-16	Mikkola 1983 Zawadzka & Zawadzki 2007
<i>Athene noctua</i>	small	Trees (92%), habitations, cliffs,	Farmlands, open habitats	7	Denys et al. 2004
<i>Falco tinnunculus</i>	small	Trees, cliffs, ground	Open habitats	6-12	Mikkola 1983 Souttou et al. 2007 Geng et al. 2009
<i>Genetta genetta</i>	medium	Trees, woodland	? All habitats, preference for wooded habitats	5-9	Sanchez et al. 2008 LeJacques & Lodé 1994
<i>Vulpes vulpes</i>	medium	Burrows, caves, rocks	All habitats	7-9	Lanszki 2005

Table 5: Faunal lists of small mammals collected by *Bubo africanus* in a nest and in pellets at Clarens (Ouwerf) after Cacciani (2004). Note that species richness slightly different between pellets and the nest , but when the two samples are pooled together, the overall diversity is larger. *= Not counted, but present.

Species	Pellets (MNI=56)	Nest (MNI=64)	Total
<i>Otomys irroratus</i>	18	11	29
<i>Otomys slogetti</i>	2	0	2
<i>Otomys angoniensis</i>	0	4	4
<i>Otomys</i> sp.indet.	2	5	7
<i>Aethomys namaquensis</i>	1	3	4
<i>Aethomys chrysophilus</i>	0	1	1
<i>Rhabdomys pumilio</i>	6	5	11
<i>Mastomys natalensis</i>	2	3	5
<i>Dendromus</i> sp.	0	3	3
<i>Crocidura</i> spp.	4	0	4
<i>Pronolagus</i> sp. *	x	0	x
TOTAL	33	35	71
Species richness	7	7	10

Table 6 : Percentage of digested femurs and incisors from Clarens *B. africanus* nest and pellets (after Cacciani 2004).

Femurs	Pellets	Nest	Incisors	Pellets	Nest
Non-digested	44	25	Non-digested	23.5	9.1
light	56	67	light	45.1	31
moderate	0	8	moderate	21.6	39.3
heavy	0	0	heavy	9.8	19
extreme	0	0	extreme	0	1.6

Table 7 Comparison of the levels of species diversity in 8 units and subunits of the Westbury cave sequence. Levels of species richness are compared with the predator effects on these levels.

	NISP (numbers of specimens)	Species richness	Predator	Predator effect on levels of species richness	Ecological/taphonomic signal
Unit 11/1	1407	high	Category 1, vole specialist	low	Ecological signal/warm
Unit 11/4	16,200	high	<i>Bubo bubo</i> - generalist	high	Taphonomic signal
Unit 12	2892	high	<i>Asio otus</i> – arvicolid specialist	low	Ecological signal/warm
Unit 13-14	>2000 each	low	Unknown-arvicolid specialists	high	Taphonomic signal
Unit 15/4	1392	high	<i>Bubo bubo</i> - generalist	high	Taphonomic signal
Unit 15/5	693	high	<i>Buteo buteo</i> - specialist	low	Ecological signal/warm
Unit 15/8	45,751	low	<i>Tyto alba</i> - generalist	low	Ecological signal/cold
Unit 19/14	2356	high	<i>Tyto alba</i> -generalist	low	Ecological signal/warm

Table 8. Taxonomic identification of fossils from PRERESA by (1) Blain *et al.*, 2012; Blain & Sesé, 2014; (2) Sesé *et al.*, 2011); (3) Made & Mazo, 2014.

Anura (1)	Squamata (1)	Micromammals (2)	Macromammals (3)
<i>Bufo bufo</i> , <i>Epidalea calamita</i> , <i>Hyla</i> sp., <i>Pelobates cultripes</i> , <i>Pelodytes</i> sp., <i>Pelophylax perezi</i> ;	<i>Timon lepidus</i> , <i>Psammodromus algirus</i> , <i>Natrix maura</i> , <i>Coronella</i> sp., <i>Vipera latastei</i>	Erinaceomorpha : <i>Erinaceus europaeus</i> ; Soricomorpha: <i>Crocidura russula</i> ; Chiroptera: <i>Rhinolophus ferrumequinum</i> ; Rodentia: <i>Eliomys quercinus quercinus</i> , <i>Apodemus</i> sp., <i>Cricetulus (Allocricetus) bursae</i> , <i>Arvicola</i> aff. <i>sapidus</i> , <i>Microtus cabrerae</i> , <i>Microtus duodecimcostatus</i> ; Lagomorpha: <i>Oryctolagus cuniculus</i>	Carnivora: <i>Panthera leo</i> <i>Meles meles</i> ; Proboscidea: <i>Elephas/Mammuthus</i> sp.; Perissodactyla: <i>Equus ferus</i> ; Artiodactyla: <i>Capreolus</i> sp.; <i>Haploidoceros mediterraneus</i> , <i>Bos/Bison</i> sp.

Table 9. Results of digestion observed by taphonomist (TAPHO) and taxonomist (TAXO) in PRERESA site. The 1st observation done by the taxonomist showed discrepancies (highlighted in grey here) with taphonomic traits. The reason for such discrepancies are described in the text, agreed and amended after a second inspection.

		TAPHO	TAXO 1st inspection	TAXO 2nd inspection
Non.-digested	All	35	46	35
Light (52%)	Arvic.	81	76	81
	Murid	1	0	1
Moderate (34%)	Arvic.	46	38	46
	Murid	7	7	7
	Soricid	0		0
Heavy (8%)	Arvic.	8	16	8
	Murid	3	3	3
	Soricid	2	2	2
Extreme (6%)	Arvic.	7	7	7
	Murid	2	2	2
	Soricid	0	0	0
Recent breakage	Arvic.	4	4	4
Heavily worn out	Murid	5	5	5
TOTAL MOLARS (N=201)	TAPHONOMIST	TAXONOMIST		
Total Molars: Arvic.=181	142	78%	142	78%
Total Molars: Murid=17	13	76%	13	76%
Total Molars: Soricid=3	2	67%	2	67%
Total digested molars	157	78%	157	78%