Coprolites in natural traps: direct evidence of bone eating carnivorans from the Late Miocene site of Batallones-3 (Madrid, Spain)

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We describe two carnivoran coprolites found in the pseudokarst natural carnivore trap of Batallones-3, from the Late Miocene of Spain. The larger one, comprising multiple indistinguishable fragments of broken and corroded bones, indicates that the producer of the dropping might have been highly capable of crushing the softer parts of large bones. On the other hand, the smaller one shows several relatively larger and more complete bone fragments, thus exhibiting a greater capacity to break and swallow large portions of bone. The external morphology of the large coprolite is similar to that of extant bears, whereas the smaller one more closely resembles that of the living insectivorous hyaenid *Proteles* in morphology, on one hand, and that of the viverrid *Genetta* in size, on the other. We hypothesize that the amphicyonid *Magerycion anceps* was the producer of the large coprolite and the jackal-sized basal hyaenid *Protictitherium crassum* excreted the smaller one. Thus, we present the first direct evidence of a bone durophagous diet in the carnivorans of Batallones.

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Keywords: Iberian Peninsula, Late Miocene, Pseudokarst, fossil faeces, Carnivora

Introduction

Locality and age. The Cerro de los Batallones (late Miocene [MN10]) is a pseudokarst complex of 9 fossil sites located 30 km south of Madrid (Figure 1). It represents one of the richest and best-preserved Neogene mammalian assemblages on the Iberian Peninsula (Morales *et al*. 2004, 2008). The fossiliferous deposits are embedded in marls deposited in hourglass-shaped cavities with upper openings (Pozo *et al*. 2004; Calvo *et al*. 2013) in which two types of assemblages can be found: (1) carnivoran-dominated assemblages in the lower part of the hourglass structure (e.g., Batallones-1 and BAT-3), interpreted as carnivore traps (Domingo *et al*. 2011, 2013a, 2013b) and (2) herbivore-dominated assemblages in the upper parts (e.g., Batallones-4 and Batallones-10), interpreted as herbivore traps (Calvo *et al*. 2013). The coprolites studied in the present paper were found in one of these lower, carnivoran-dominated assemblages (BAT-3). Furthermore, these upper and lower deposits have been found to contain several discrete fossiliferous levels (Martín-Perea *et al*. 2020).

The fauna of the Cerro de los Batallones localities has yielded a rich and diverse assemblage of vertebrate fossils including freshwater fish, amphibians and sauropsids (testudines, squamata) and predatory birds (Morales *et al*. 2008; Pérez-García & Murelaga 2013; Pérez-García & Vlachos 2014; Morales 2017; Villa *et al*. 2018), micromammals (López-Antoñanzas *et al*. 2010, 2014; Álvarez-Sierra *et al*. 2017; Medina-Chavarrías *et al*. 2019), equids, bovids, mosquids, giraffes, rhinoceroses, proboscidians, suids (Morales et al. 2008; Sánchez et al. 2009, 2011; Pickford 2015; Ríos *et al*. 2017; Romano *et al*. 2017; Sanisidro 2017; Morales 2017; Domingo *et al*. 2018; Ríos & Morales 2019), and carnivorans, which include the most diverse sample. The last group comprises a large amount of skulls, mandibles and almost complete skeletons of two species of sabre-tooth cats, a hyaenid, two species of derived

amphicyonids, an ailuropod ursid, a large ailurid, mephitids and mustelids (e.g., Abella *et al*. 2013, 2015; Antón *et al*. 2004, 2020; Peigné *et al*. 2005, 2008; Salesa *et al*. 2006, 2008, 2010, 2012, 2019; Domingo *et al*. 2013a, 2016; Monescillo *et al*. 2014; Siliceo *et al*. 2014, 2015, 2017, 2020; Fabre *et al*. 2015; Valenciano *et al*. 2015, 2020; Fraile 2016, 2017; Abella & Valenciano 2017; Morales *et al*. 2017; Valenciano 2017a, 2017b). This fauna, alongside the micromammal remains, enabled all the sites to be assigned to the late Miocene (Vallesian, c. 9.6-9.3 Ma) (Peláez Campomanes *et al*. 2017). However, there are minor differences in both micro- and macromammal taxonomic composition among the different localities that have been attributed to slight temporal differences. Indications are that BAT-10 is older than BAT-1, and that BAT-1 is older than BAT-3 (López-Antoñanzas *et al*. 2010; Siliceo *et al*. 2014)), whereas the difference in age between Batallones-2, 3 and 5 remains unknown (Valenciano *et al*. 2020).

Furthermore, the carnivoran guild of BAT-3 is the most diverse of the whole complex. It includes two machairodont felids *Machairodus aphanistus* (Kaup, 1832) and *Promegantereon ogygia* (Kaup, 1832) (Monescillo *et al*. 2014; Siliceo *et al*. 2014), as well as the small feline *Leptofelis vallesiensis* (Salesa, Antón, Morales & Peigné, 2012), the plesiomorphic hyaenid *Protictitherium crassum* (Filhol, 1883) (Fraile 2016, 2017), the ailuropod ursid *Indarctos arctoides* (Depéret, 1895) (Abella 2011; Abella *et al*. 2012, 2013, 2015; Abella & Valenciano 2017a), two amphicyonids *Magericyon anceps* Peigné, Salesa, Antón, Morales, 2008 (Siliceo *et al*. 2017) and the thaumastocyonine *Ammitocyon kainos* Morales, Abella, Sanisidro, Valenciano (Morales *et al*. in press), the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Valenciano *et al*. 2015; Valenciano 2017a, 2017b), the small size hypercarnivorous mustelid *Circamustela peignei* Valenciano, Pérez-Ramos, Abella & Morales, 2020 (Valenciano 2020a), the

badger *Adroverictis* sp., and two mephitids *Promephitis* sp., nov., and Mephitidae gen. nov and sp. nov (Valenciano 2017b).

Coprolite generalities. Coprolites are among the most important ichnofossils from the fossil record (Hunt & Lucas 2020) and can be found in a diversity of taphonomical, ecological, and geological contexts (Qvarnström *et al*. 2016). As trace fossils, coprolites represent specific moments in time, providing individual windows into the evolution of ecological interactions such as predation, herbivory, and parasitism, and can contain palaeoecological proxies spanning from thousands to millions of years in the past (Dentzien-Dias *et al*. 2013; Qvarnström *et al*. 2017; Barrios-de Pedro *et al*. 2018; Riley 2018). And although they might not give the general diet reconstruction of a species, they can provide direct information about the last food income and feeding behaviours of ancient vertebrates (e.g., Mellett 1974; Meng & Wyss 1997; Chin *et al*. 1998, 2003; Prasad *et al*. 2005; Chin 2007; Backwell *et al*. 2009), serving as ichnological proxies for the presence of animals in palaeoecosystems (Edwards & Yatkola 1974; Farlow *et al*. 2010; Hunt & Lucas 2007, 2010).

Coprolites may also provide information on the diagenetic history of the fossil remains themselves (Chin 2007). Over time, following burial, they undergo taphonomic processes, becoming permineralized or lithified and forming a cast or mould of the original faecal matter (Bajdek *et al*. 2017; Mychajliw *et al*. 2020). In general, coprolites from sites protected by geologic features such as caves and rock shelters exhibit the highest level of preservation. In contrast, coprolites from open sites can become severely degraded by these taphonomic processes (Reinhard *et al*. 2019).

Coprolites of herbivorous animals are generally scarcer in the fossil record than those of carnivores, because the phosphate content of the latter from the soft tissue and bones of

prey animals predisposes them to mineralization (Thulborn 1991; Chin 2002; Hunt & Lucas 2019). On the other hand, coprolites of bone-crushing hyenas are disproportionately represented in the fossil record, not only because of their chemical composition, but also due to: (1) their social and denning behaviour, resulting in large accumulations; (2) their inhabiting caves, which enhances the potential for preservation; and (3) the fact that hyena coprolites are resistant, and can undergo taphonomic resedimentation (Hunt & Lucas 2019). Bones as a supplementary food source necessarily constitute a net gain if the cost of processing them (both ingestion and digestion) can be managed. The average compact bone consists of approximately 30% organic matrix (Eastoe & Eastoe 1954; Guyton & Hall 2006), mostly collagen fibres. The organic component (nutritional value) is even greater if the marrow in the cancellous bone is also considered. Living spotted hyenas (*Crocuta crocuta* Erxleben 1777) in Africa possess morphological and physiological adaptations enabling efficient consumption of bones; accordingly, they are known to consume the entire carcass (freshly killed or scavenged), leaving no bones behind (Kruuk 1972).

Carnivoran bone cracker adaptations. Living hyenas are known to crush the bones of their prey to extract the nutritious marrow within. This feeding ability is rare today, and both African and Asian hyenas, particularly the spotted hyena, are the only true 'bone-crackers' in our modern ecosystems. Bone-crackers (modern and extinct) play an important ecological role as apex predators and providers of free organic material needed for decomposition, essential with regard to maintaining a healthy ecosystem (Wang *et al*. 2018).

In general, hyaenids present the most advanced dentition for crushing bones, whilst retaining the basic feliform dental plan, which involves highly reduced grinding

151 components (in M1, m1 talonid and m2), which allows room for enlargement of the
152 premolars (Wang *et al*. 2018). The composition of hyena droppings is quite distinctive,
153 enabling them to be differentiated from those of most other carnivorans, a consequence
154 of their high bone content diet (Larkin et al. 2000). The gastrointestinal system of
155 hyenas has apparently evolved to process large quantities of bones. Hyaenid faeces,
156 particularly those of the spotted hyena, are known to contain well-digested calcium
157 phosphates in the form of white powders and bone residues (Estes 1991). To a lesser
158 extent, the scat of striped hyenas *Hyaena hyaena* (Linnaeus 1758) is also white or light
159 grey (Macdonald 1978; Hulsman *et al*. 2010). These white powders consist of calcium
160 and phosphate salts, $Ca_3(PO_4)_2$ $1.5Ca(OH)_2$, similar to hydroxyapatite, the main
161 inorganic component in bones (Kruuk 1972; Wang *et al*. 2018). Supposing that the
162 common ancestor of *Crocuta* Kaup 1828 and *Hyaena* Brisson 1762 already possessed
163 this bone-dissolving gastrointestinal system, then this must have occurred over 8.6 Ma
164 (Koepfli *et al*. 2006; Wang *et al*. 2018).
165 Although the vast majority of Miocene coprolites have either been described as being
166 excreted by bone-cracking large Hyaenidae or by the Borophaginae canids (e.g
167 Pesquero *et al*. 2011; Wang *et al*. 2018 and references therein), other fossil coprolites
168 have been described as belonging to other vertebrates, including crocodilians,
169 notoungulates, sirenians, rodents, as well as undetermined carnivorans (Dentzien-Dias
170 *et al*. 2018); some of them even reveal shark bite marks (Godfrey & Smith 2010).
171 Batallones-3 does not present any typically large durophagous bone-cracker species;
172 hence, study of these coprolites constitutes a very interesting approach to bone
173 consumption in other dietary groups of carnivorans. The main aim of the present
174 research paper involves analysing the morphology and bone content of the only two
175 coprolites unearthed in the whole Cerro de los Batallones site complex in order to

obtain information on the possible producer of the scat and to more clearly elucidate their dietary ecology.

Materials and methods

Abbreviations. BAT: Batallones fossil site from Cerro de los Batallones fossil site complex.

MNCN- Museo Nacional de Ciencias Naturales, Madrid, Spain.

Studied material. The fossil sample of coprolites of BAT-3 comprises the following two specimens: BAT-3'9.178 and BAT-3'10.153.

Methodology. We followed the method proposed by Diedrich (2012) and modified by Wang *et al*. (2018) to characterise the external morphology of hyaenid coprolite aggregate pellets (Figure 2).

3-D models. Coprolites BAT-3'9.178 and BAT-3'10.153 were CT-scanned at the "Servicio de Técnicas No Destructivas: Microscopía Electrónica y Confocal y Espectroscopía" of the MNCN-CSIC in Madrid, Spain. The scanned data were imported into FIJI 1.52 (National Institutes of Health, USA) for artefact removal and contrast enhancement. The data were finally segmented, rendered and analysed in Avizo 7.1.0 (VSG, Burlington, MA, USA) in order to generate 3D models and to perform metrical and morphological analyses. We measured the trend and plunge of elongated bone fragments with a clearly longer axis, using the coprolites' long axis as the pole (0º trend, 90º plunge) and its corresponding plane (0º trend, 0º plunge) with a theoretical fixed north bearing to measure the trend. Trend and plunge data were plotted on an equal area

Schmidt stereographic projection with inverse area smoothing.

Following Esteban-Nadal *et al*. (2010), all the fragments were measured in length and volume (Supplementary material 1). However, only the ones exhibiting a more complete morphology are presented in the present paper (TABLE 1). The label number was given in the order of segmentation and has no specific meaning whatsoever.

Results

Bone fragments inside the coprolites showed preferential orientations very similar to that of their major axis (0/360º trend, 90º plunge). This is particularly so in the large one, with a mean trend and plunge closely resembling the coprolite's major axis (308.0º trend, 87.7º plunge; Figure 3), whereas in the small one, bones present a smaller, albeit still steep (93.9º trend, 64.4º plunge) mean plunge compared to that of the coprolite's major axis (Figure 3).

Description and interpretation.

BAT-3'9.178: Consists of a large fragment of an almost cylindrical coprolite 116.3 mm in length, 52.5 mm in width, 34.7 mm in height and a volume of 83.5738 cm^3 (Figure 4). It shows no apparent torsion and consists of one massive portion of scat, with no internal or external divisions. The total number of bone fragments presenting a volume greater than 4.21 mm^3 is 134, although most of them are exclusively small fragments of trabecular bone. In consequence, few fragments are of sufficient size or have sufficiently intact surfaces to be considered for description. Hence, we mainly focused upon fragments with some preserved portion of cortical bone, and on others displaying any outstanding morphological trait.

The main bones found in the coprolite are (3D images as supplementary files, each one with its label number):

9: Two associated fragments of bone (21.13 mm), one of these constituting a large piece of cancellous bone and the other a relatively flat fragment of triangular cortical bone. The latter presents a rounded depression that might represent a partial tooth mark.

29: A relatively large and flat portion of cancellous bone (24.19 mm). Although its shape is not recognizable, its size and morphology are worth highlighting.

104: A thick portion of cortical and cancellous bone (14.28 mm) possibly belonging to the surface of a bone epiphysis or vertebra.

107: A large portion of cancellous bone attached to a thick portion of curved cortical bone (27.61 mm). Possibly also from the side of a bone epiphysis or vertebra.

108: A large and robust portion of cortical bone (19.38 mm). It has a marked crest along the centre, this constitutes one of the only distinctive structures recovered in this sample.

116: Fragment of curved bone surface (18.92 mm), which may represent the largest and most distinct portion of bone surface in the whole sample. However, its overall size and shape are insufficient for a precise anatomical determination.

BAT-3'10.153: It is much smaller in size than the other coprolite, measuring 51.6 mm in length, 22.3 mm in width and 21.8 mm in height (Figure 4). It consists of three clumped fragments, which show a slight torsion-like morphology. It is relatively thick and although it is thinner at both ends it does not present an elongated tip.

The main bones found in the coprolite are (3D images as supplementary files #2):

15: An elongated fragment (8 mm) of cortical bone, which shows a foramen half-way along its length. It could be part of a larger bone.

16: A relatively large fragment of an undetermined bone (21.02 mm). It represents a portion of the curved shaft of a long bone, with cancellous bone in its inner part.

17: A relatively long and flat bone fragment (17.83 mm) with several longitudinal crests dividing the surface into several flat-to-concave areas. It could be part of the epiphysis of a long bone or a fragment of the spine of a scapula.

21: An elongated and triangular bone fragment (20.97 mm). This bone is one of the most complete remains; it appears to be almost complete, only missing the two epiphyses. It also presents a foramen towards the central part of the shaft.

22: A large and almost semi-circular bone fragment (17.60 mm). It might be one half of a proximal epiphysis, likely belonging to a femur. There is a small cavity interpreted herein as the *fovea capitis*, which serves for the attachment area for the *ligamentum teres*. It also presents a rounded puncture and a cutting chip that could be interpreted as a tooth mark.

26: An elongated and curved bone fragment (4.98 mm). There are two rounded structures in the middle of the bone, one larger than the other, forming a line running parallel to both sides of the bone. This could represent a mandibular or maxillary fragment with tentatively two teeth.

27, 29 and 30: These three elongated bone fragments (3.03 mm, 5.24 mm and 8.37 mm, respectively) could belong to one single larger fragment which, due to its morphology, could be interpreted as a small vertebrate mandible. It has some sulci and foramina similar to those found in reptile bones, but this is difficult to assert due to the corrosion and general state of preservation of the specimen.

33: A compact small cylindrical fragment of bone (2.68 mm) with a foramen on one of its sides. It could be identified as a fragment of a large long bone, but its broken nature hinders a more specific determination.

43: A robust bone structure (19.96 mm) that appears to be part of a larger, more complex structure, due to its morphology and overall inner structure. Although it cannot be completely proven due to its state of preservation, this structure might well represent a partial skull of a small undetermined vertebrate.

Discussion

Following Diedrich (2012), **BAT-3'9.178** is a long oval portion of scat similar in shape to those of *Ursus arctos* (Chame 2003) (Figure 5). The large amount of broken bone material in the coprolite appears to indicate a high consumption rate of bone matter;

however, this is still far from that found in modern hyaenas (Estes 1991). Although some of the remains still possess some cortical bone, most of the fragments consist mainly of cancellous bone. This leads to the interpretation that only parts of the epiphysis of long bones or vertebrae were gnawed and consumed by the producer of the coprolite, similar to what is mostly consumed by modern canidae (Mech 1970; Munthe, 1989; Sillero-Zubiri 2009).

The size of this coprolite fragment means it can only have been produced by one of the four large-sized carnivorans present in BAT-3 (TABLE 2): the sabre-tooth cat *Machairodus aphanistus*, the amphicyonids *Ammitocyon kainos* and *Magericyon anceps* or the bear *Indarctos arctoides*. The first two are large hypercarnivorous carnivorans, [*Machairodus aphanistus* 117-285 kg following Domingo *et al*. (2013a) and *Ammitocyon kainos* 231 kg according to Morales et al. (in press)] with an extreme specialized dentition for cutting meat which would have prevented them from eating all but the most easily accessible portions of flesh on a carcass, leaving large quantities of food (including bones) for other carnivorans and scavengers (Ewer 1954, 1998; Turner 1992; Pesquero *et al*. 2011).

At the other end of the diet spectrum is the hypocarnivorous *Indarctos arctoides*, a member of the Ursidae family related to modern giant pandas. Its estimated body mass ranges from 137 to 266 kg (Abella 2011; Abella *et al*. 2013; Domingo *et al*. 2016). It has been suggested that this bear might have had a more omnivorous diet than that of giant pandas (Abella *et al*. 2012; Abella *et al*. 2011; Abella *et al*. 2014), but also that their diet would have included abundant plant material (Abella *et al*. 2011; Monescillo *et al*. 2014; Domingo *et al*. 2016). Consequently, as frequently occurs with other bear scats (Hewitt & Robbins 1996), this would have hindered the fossilization process. However, the dentition of *I. arctoides* shows a certain capacity for durophagy, similar to

325 that of smaller species of related bears (de Bonis *et al*. 2017). This would have allowed
326 this species to shift from eating tough plant material to gnawing bone with some degree
327 of success, especially in individuals challenged with finding their favourite food
328 sources, e.g. the young. For this reason, this species cannot be completely ruled out as
329 the producer of this particular coprolite.
330 Finally, *Magericyon anceps* was a large amphicyonid (Peigné *et al*. 2008) present in
331 two of the Batallones fossil traps (BAT-1 and BAT-3; Siliceo *et al*. 2015, 2017, 2020),
332 with an estimated body mass of 175-195 Kg (Domingo *et al*. 2013a; Siliceo *et al*. 2015).
333 The described dentition is similar to other larger Amphicyonidae, but slightly more
334 trenchant, thus indicating a dentition less capable of crushing (Peigné *et al*. 2008).
335 However, the wear pattern observed in the carnassial teeth of *M. anceps* is quite similar
336 to that of other large amphicyonines, implying a similar occlusal mechanism, which
337 probably helped this animal to gnaw on the epiphysis (much softer than the diaphysis)
338 of long bones, using its P4-M2 and m1-m2 teeth in the same way as extant canidae.
339 Moreover, although in BAT-3 there are not abundant remains of this species, the same
340 mortality rate as in BAT-1 is to be expected, because the majority of the individuals are
341 young adults and juveniles (Peigné *et al*. 2008). As previously mentioned, this age
342 group might well have consumed a slightly different diet than their more adult
343 counterparts. We therefore hypothesize that this species represents the most likely
344 producer of this coprolite.
345 In this specific case we do not coincide with Lofgren *et al*. (2017), who consider that
346 the coprolite was likely produced by the more abundant of the two species, since the
347 reconstructed diet of *M. anceps* more closely resembles the crushed bone fragments
348 found inside the coprolite.
349

BAT-3´10.153 constitutes an irregular portion of scat following Diedrich (2012). It is similar in shape to the scats of the living aardwolf *Proteles cristatus* (Sparrman 1783) (Stuart & Stuart 1994) or the common genet *Genetta genetta* (Linnaeus 1758), and similar in size to the latter (Chame 2003) (Figure 5). Isolated bones account for 35.79% of the total volume of the coprolite (approximately 26.13% were individualised), but a large amount thereof could consist of digested bone matter or powder as described in Estes (1991). Most of the bone fragments are amorphous and unidentifiable, and just a few of them can be partly identified anatomically, but not taxonomically. In other published articles, the percentage of unidentifiable (both anatomically and taxonomically) bone fragments from fossil coprolites and extant scats from canids ranges from 80% to 95% (Fosse *et al*. 2012; Wang *et al*. 2018)

The three individual sections of the coprolite can be characterised by containing bone fragments presenting different sizes and morphologies, especially on comparing the ones located at both ends. The assemblage in one of these sections could represent the remains of a small vertebrate (perhaps a reptile), due to the abundance of small, dense individual bones (around 15), together with a large mass of broken cancellous bone matter. On the other hand, the other outer section mainly consists of relatively large cortical bones or fragments of long bones arranged subparallel to the long axis of the coprolite (see figure 4). Indeed, the relative size of these fragments is noteworthy in relation to the size of the coprolite, even more so when compared with the larger one (Figure 6). The size and morphology of this coprolite appear to indicate that several carnivorans that could have produced it. The first and most probable carnivoran is *Protictitherium crassum*, a small-medium sized carnivoran situated at the base of the Hyaenidae (Fraile 2016, 2017; Morales *et al*. 2019). This coprolite morphology is

375 similar to that of small hyenas such as *Proteles cristatus* (Stuart & Stuart 1994) and its
376 size fits well with the ones produced by medium-to-large viverrids (Chame 2003).
377 Furthermore, the fact that the coprolite has relatively large broken cortical bone
378 fragments might suggest that this individual was already performing "bone-cracking"
379 feeding, but did not have the enzymatic adaptation of extant hyenas to almost
380 completely dissolve bones, reducing them to powder during digestion (Estes 1991).
381 This fits well with an early member of the hyaenid family, such as *P. crassum*, which
382 has slightly enlarged premolars but does not yet present reduced postcarnasssial molars
383 like the more derived hyaenids, thus distributing the crushing dental apparatus between
384 the premolars and the molars (Fraile 2016, 2017).
385 Another species that could have produced this coprolite is the medium-sized feline
386 *Pristifelis* Salesa, Siliceo, Antón, Peigné, Morales 2012. However, this species is not
387 described in BAT-3, and as occurred with the larger coprolite, these felids are
388 interpreted as hypercarnivorous animals, and might not have been able to break bones to
389 feed upon them. Furthermore, the shape of the coprolite does not fit well with those of
390 this group, since felid scats are more elongated (Chame 2003). Gilmour & Skinner
391 (2011), however, on studying the scats of small felids, concluded that they have
392 disproportionately large bone fragments in their scat compared with canids, whose scats
393 contain relatively more abundant and smaller bone fragments. Furthermore, a broad
394 musteloid sample is present in BAT-3, comprising relatives of the living martens,
395 badgers, skunks, and honey badgers, of which the badger-sized *Adrovericti*s sp.
396 Ginsburg & Morales, 1996 and the giant sized Eomellivorini *Eomellivora piveteaui*
397 (Valenciano *et al*. 2015; Valenciano & Govender 2020b) might have been the producers
398 of the coprolite. *Eomellivora* may have had a clearly durophagous diet, based on dental
399 morphology. However, its large size rules out its assignment to this coprolite. Although

400 the size could fit well with a mustelid the size of *Adroverictis*, the reconstructed diet
401 (which was likely more omnivorous) together with the morphology of the scat also
402 brings us to rule out this species with a certain degree of certainty.
403 As previously mentioned, the carnivoran guild of BAT-3 is the most complex of all the
404 Batallones fossil sites, presenting many different body sizes and dietary groups.
405 Moreover, the Batallones carnivoran assemblage is unique compared to sites of similar
406 age on the Iberian Peninsula due to the complete absence of large or medium hyenas.
407 The lack of these forms, present both before and after this period in this region (Fraile *et*
408 *al*. 1997; Morales *et al*. 2015), is difficult to assess without conducting a detailed
409 analysis comparing the ecomorphologies of the carnivoran guilds of the Vallesian, in
410 order to provide a broader view of how the ecological roles of these niches evolved
411 throughout this time period; similar to those already performed by Morlo *et al*. (2020)
412 across the Middle/Late Miocene boundary in Germany.
413 Finally, a taphonomical issue is raised by the presence of these coprolites in BAT-3. As
414 previously mentioned, the lower carnivoran-dominated assemblages, such as BAT-3
415 and BAT-1 have been interpreted as natural traps (Domingo *et al*. 2013a, 2013b;
416 Domingo *et al*. 2016; Domingo *et al*. 2011). In BAT-1 for example, none of the large
417 bones within the trap were found to be eaten or gnawed (Domingo *et al*. 2013), although
418 some Moschidae remains present corrosion surfaces that could be interpreted as
419 resulting from digestion (Sánchez *et al*. 2011). Future taphonomical analyses for
420 Batallones-3 should address whether or not the presence of coprolites suggest the site
421 acted as a den rather than a natural trap, since the latter is likely to present fewer
422 coprolites.
423
424 **Conclusions**

Two coprolites were discovered in one of the nine sites of the Batallones complex. Although these fossils are rarely preserved, the particular genesis of these carnivoran natural traps in cavities would theoretically have helped to conserve them.

The larger coprolite could be described as a "long oval" portion of a scat. It mainly presents broken parts possibly involving an epiphysis of a long bone or a vertebra. This fact would indicate that the producer would have been able to gnaw on a bone, *Magericyon anceps* being the most likely species or, to a lesser extent, *Indarctos arctoides*.

The small coprolite could be defined as an almost terminal "irregular portion" of a scat with the size and morphology of those produced by large viverrids and small hyaenas. It presents two differentiated parts: one that appears to result from eating a complete and unidentified small vertebrate, and the second produced by swallowing the remains of a relatively large broken bone. The species that produced this coprolite could have been possibly either *Protictitherium crassum* or, less likely, *Adroverictis* sp.

Finally, study of these coprolites provides direct evidence of bone consumption amongst carnivorans in the trophic network of the feeding complex of the Batallones palaeocommunity. In the case of *Magericyon*, this bone consumption appears to confirm that large Amphicyonidae display adaptations related to generalist feeding; nonetheless, one of the members of the group, *Magericyon anceps* seems to have developed a tendency towards hypercarnivorism.

Acknowledgements

This study was supported by the Spanish Research Projects CGL 2015-68333-P, CGL2016-76431-P and PGC2018-094122-B100 (AEI/ FEDER, UE), the BSCH-

UCM910607 of the Universidad Complutense de Madrid, the Research Groups CSIC 64 1538 and CAM-UCM 910607 and PVC-GIUV, and the Generalitat de Catalunya (CERCA Programme, and Beatriu de Pinós contract 2017 BP 00223 from AGAUR to JA). We thank Alejandro Serrano for his work on the CT-images as an ICP technician and Alejandro Pérez-Ramos for his help dealing with the files. The "Juan de la Cierva Formación" program (FJC2018-036669-I), from the Spanish Ministry of Science, Innovation, and Universities funded also AV. DMMP was funded by a FPI Predoctoral grant BES-2016-079460. We thank Cormac De Brun for the thorough language review. The editor B. Britt and the reviewers Dr. de Bonis and Dr. Morlo are also acknowledged for valuable comments that helped to improve the final version of this manuscript.

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927 **Figure caption**

928

929 Figure 1

930 A, Map of the Iberian Peninsula showing the location of Madrid and Valdemoro. B,

931 Location of Batallones-1 and Batallones-3 sites, west of Valdemoro.

932

933 Figure 2

934 Nomenclature of individual pellets in a complete assemblage of faeces from a single

935 dropping event by the extant spotted hyena, *Crocuta crocuta*. Horizontal axis indicates

936 the orientation of the dropping. After Diedrich (2012): Figure 4 and Wang *et al*. (2018):

937 Figure 1.

938

939 Figure 3

940 Stereographic projections of the elongated axis of bone fragments in the coprolites.

941 Mean trend and plunge represented by plus sign. A, BAT-3'9.178 coprolite. B, BAT-

942 3'10.153 coprolite.

943

944 Figure 4

945 View of the disposition of the bone fragments present in A, Transparent outline of the

946 coprolite BAT-3-'10.153 with the fragments in colours. B, Inner view of coprolite

947 BAT-3-'10.153 with amorphous bone matter in grey and fragments in colours. C, Inner

948 view of coprolite BAT-3-'10.153 only showing fragments in colours.

949 D, Transparent outline of the coprolite BAT-3'9.178 with the fragments in colours. E,
950 Inner view of coprolite BAT-3'9.178 only showing fragments in colours. Scale bar 1
951 cm.
952
953 Figure 5
954 Figure comparing extant dropping outline morphology from Chame (2003) to the
955 coprolites BAT-3'9.178 and BAT-3-'10.153
956
957 Figure 6
958 View of the disposition of the bone fragments present at the coprolites. A, BAT-3'9.178
959 and B, BAT-3-'10.153. Same size, not to scale.
960
961 **Table captions**
962 Table 1
963 Measurements of the Maximum length and second maximum length (in mm) and the
964 volume (in mm^3) of the described bone fragments found inside the coprolites BAT-
965 3'9.178 and BAT-3'10.153 from BAT-3, Spain.
966
967 Table 2
968 Estimated body mass (in Kg) of the BAT-3 carnivorans discussed in this work and both
969 the average body mass (in Kg) and the coprolite length (in cm) of the extant carnivorans
970 used for comparison. References: 1.- Domingo *et al*. 2013a, 2016; 2.- Fraile 2016; 3.-
971 Garshelis 2009; 4.- Holekamp and Kolowski 2009; 5.- Larivière S. & Calzada, J. 2001;
972 6.-Lariviére & Jennings 2009; 7.- Nowak 2005; 8.- Sillero -Zubiri 2009; 9.- Sunquist &

973 Sunquist 2009; 10.-Valenciano 2017; 11.- Wade-Smith & Verts 1982; 12.- This study,
974 approximated based on similar-sized living relatives.
975
976 **Supplementary data captions**
977
978 Supplementary material 1
979 Measurements of the Maximum length and second maximum length (in mm) and the
980 volume (in mm^3) of all the bone fragments found inside the coprolites BAT-3'9.178 and
981 BAT-3'10.153 from BAT-3, Spain. The numbers only reflect the order in which the
982 images were segmented from the original CTscan files.
983
984 Other supplementary material
985 Supplementary 3D files of the described bone fragments found inside the coprolites
986 BAT-3'9.178 and BAT-3'10.153 from BAT-3, Spain.
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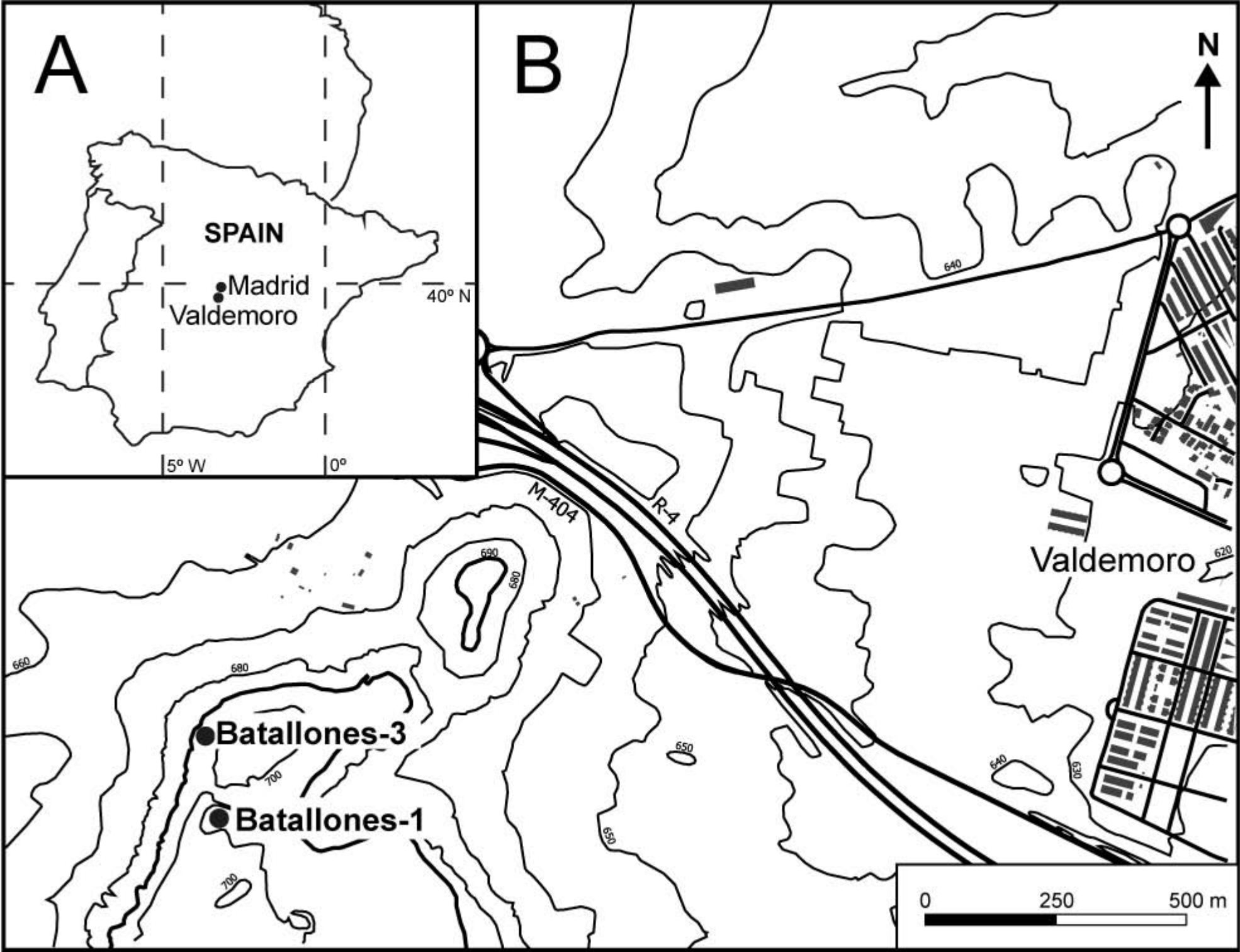
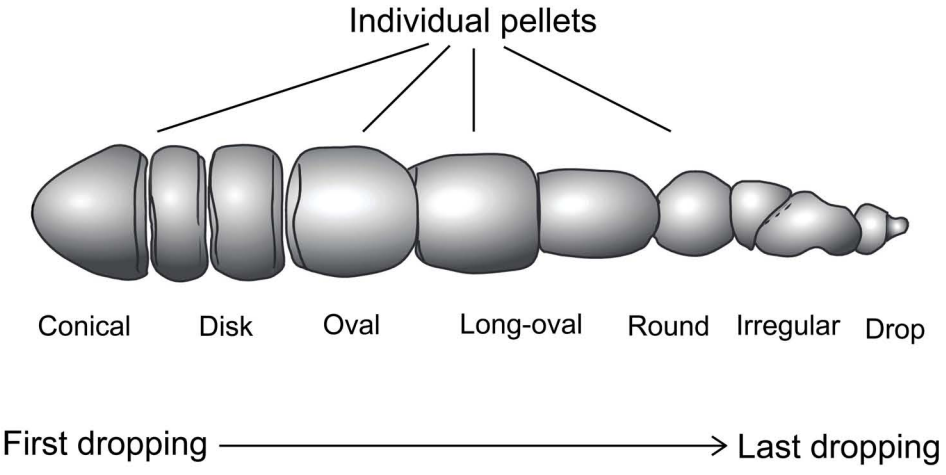
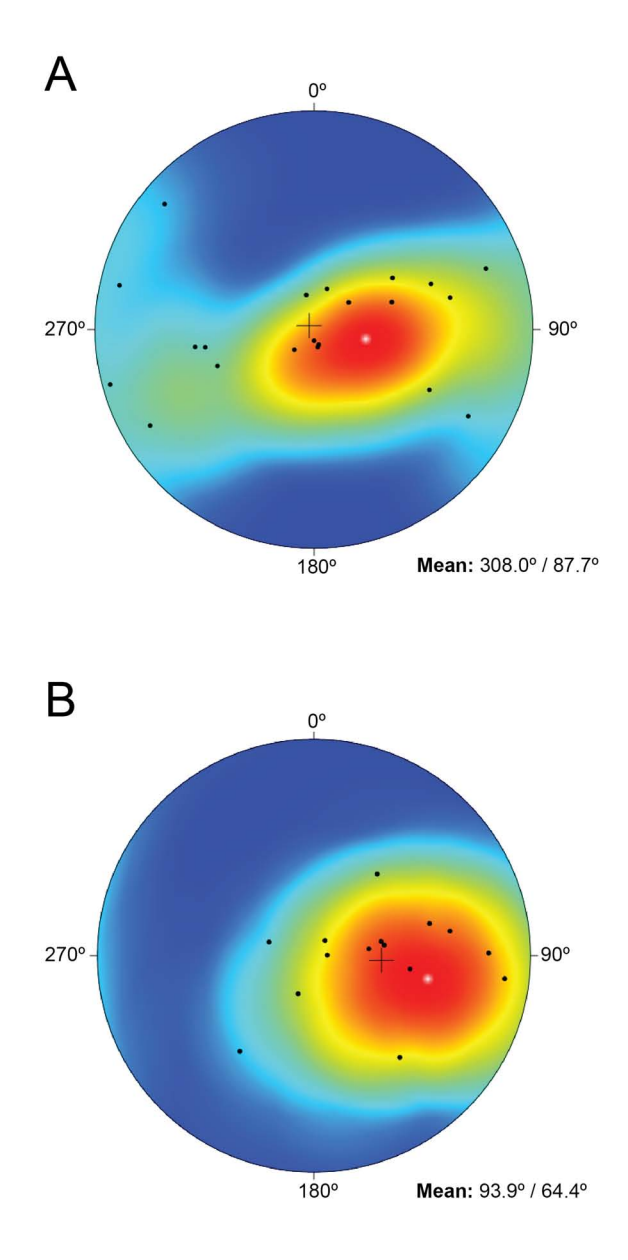
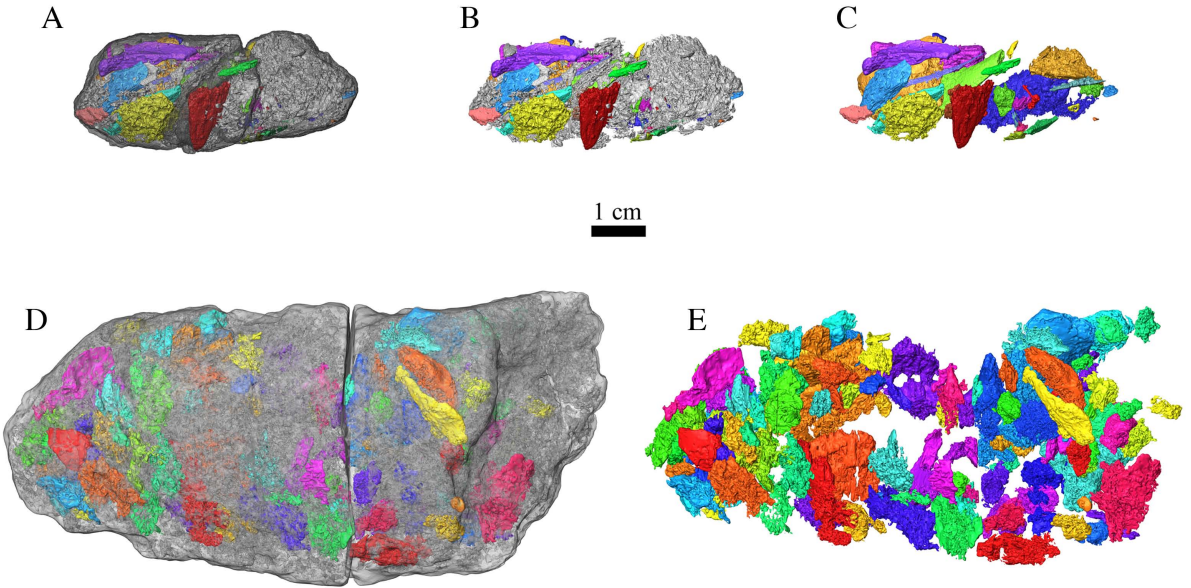

A
SPAIN
Madrid
Valdemoro
40º N
5º W
0º
B
N
M-404
R-4
Valdemoro
Batallones-3
Batallones-1
640
620
690
680
660
700
650
630
0
250
500 m


Individual pellets
Conical
Disk
Oval
Long-oval
Round
Irregular
Drop
First dropping
Last dropping


A
0º
270º
90º
180º
Mean: 308.0º / 87.7º
B
0º
270º
90º
180º
Mean: 93.9º / 64.4º


A
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C
1 cm
D
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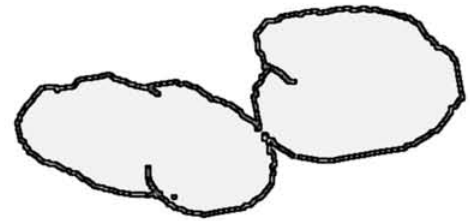
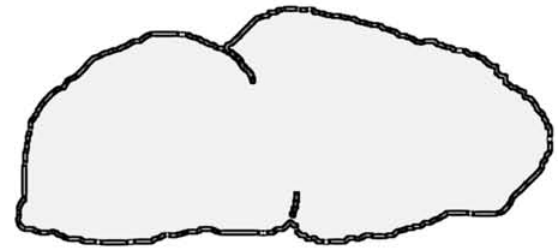
BAT-3´10.153

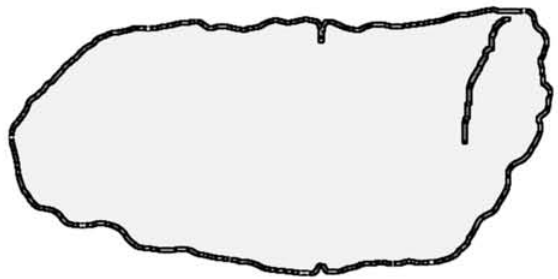
Genetta genetta



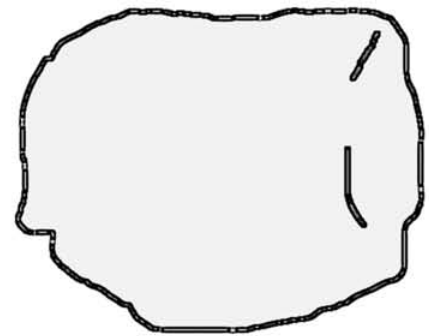
Proteles cristata



BAT-3´9.178



Ursus arctos



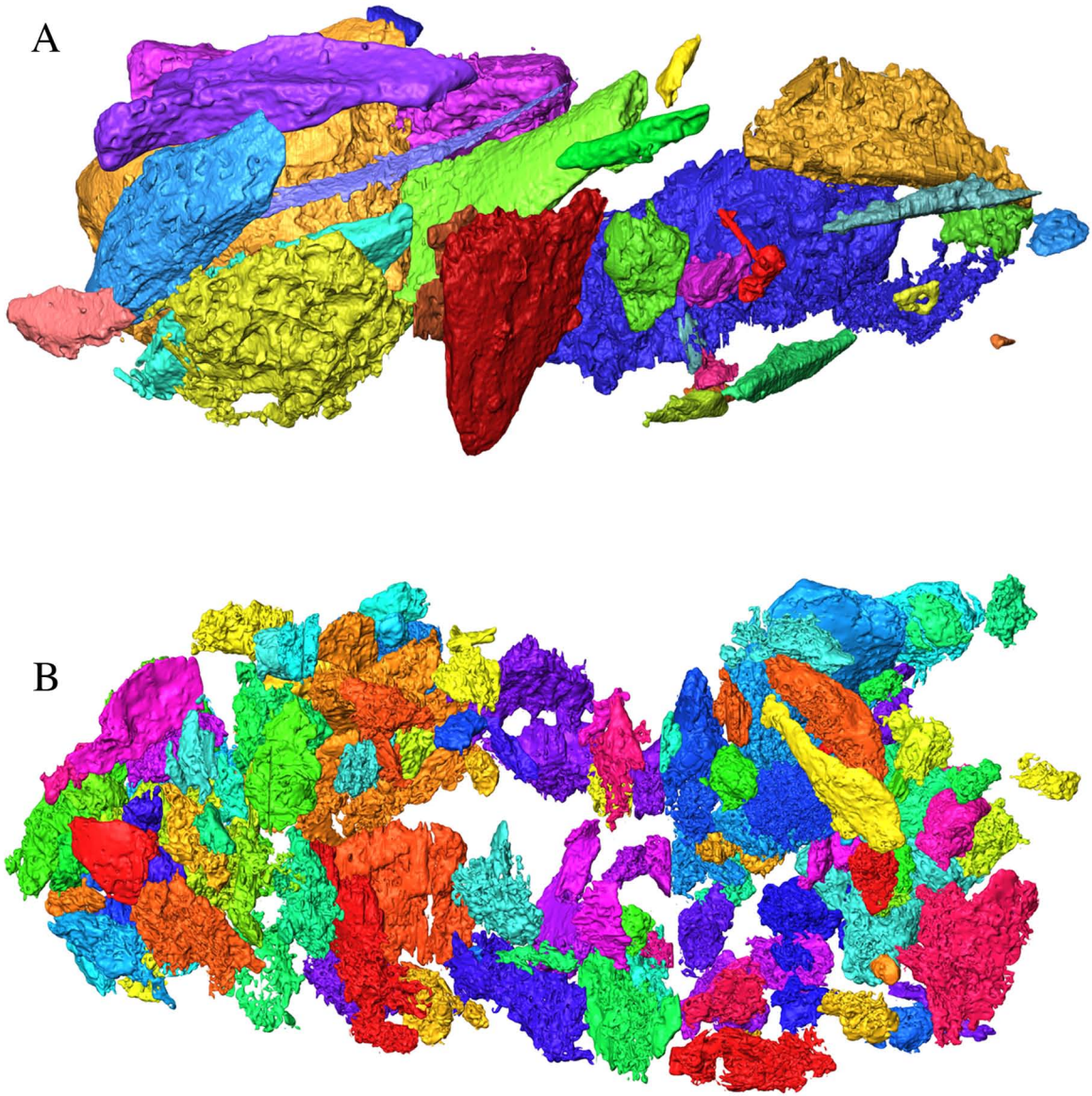

A
B

Table 1

Coprolite label	Number	Maximum length (mm)	Second maximum length (mm)	Volume (mm^3)
BAT-3'9.178	#9	21.13	16.53	507.07
	#29	24.19	22.05	577.15
	#104	15.27	9.63	193.45
	#107	27.61	19.33	1088.14
	#108	19.38	9.5	232.48
	#116	18.92	8.49	206.44
BAT-3'10.153	#15	8	1.99	9.841
	#16	21.02	12.4	645.641
	#17	17.83	5.07	107.562
	#21	20.97	8.91	270.119
	#22	17.6	16.19	902.955
	#26	4.98	0.77	2.036
	#27	3.03	1.46	1.763
	#29	5.25	1.56	3.871
	#30	8.37	2.15	12.228
	#33	2.68	1.89	3.911
	#43	19.96	8.83	355.843

Table 2

Fossil Species	Estimated body mass (Kg)	Ref.	Extant Species	Average body mass (Kg)	Ref.	Coprolite length (cm)
Machairodus aphanistus	117-285	1	*Panthera leo*	120-225	9	15
Magericyon anceps	175-195	1	*Ursus americanus*	40-225	3	8-11
Thaumastocyon sp.	170-321	1	*Canis lupus*	18- 80	8	16
Indarctos arctoides	137-266	1				
Promegantereon ogygia	28-97	1	*Panthera onca*	31- 121	9	2.6- 11.2
Eomellivora piveteaui	35.8-45.5	10	*Puma concolor*	34- 72	9	3.7- 6.1
Leptofelis vallesiensis	7–9	12	*Parahyaena brunnea*	28- 47.5	4	5
Protictitherium crassum	6- 7	2	*Gulo gulo*	6- 18	6	13
Circamustela peignei	3-5	12	*Mellivora capensis*	7- 13	7	6.8
*Adrovericti*s sp.	8-12	12	*Taxidea taxus*	6.3- 8.7	6	3.4- 4.9
Promephitis sp.	1-5	12	*Genetta genetta*	1- 3	5	5.5
Mephitidae Gen. nov and sp. nov	1-2.5	12	*Mephitis mephitis*	1.2-5.3	11	3-4.4