Palaeogeography, Palaeoclimatology, Palaeoecology 443 (2016) 249–262

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Not only hyenids: A multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula)

Montserrat Sanz [a,*], Joan Daura [a], Natalia Égüez [b], Jean-Philip Brugal [c]

[a] Centro de Arqueologia (UNIARQ), Universidade de Lisboa, Faculdade de Letras, Alameda da Universidade, 1600-214 Lisboa, Portugal
[b] Graduate School Human Development in Landscapes, Institute for Prehistoric and Protohistoric Archaeology, Christian-Albrechts-University, 24118 Kiel, Germany
[c] Aix-Marseille Université, CNRS, UMR 7269, Maison Méditerranéenne des Sciences de l'Homme, BP 647, 5 rue du Château de l'Horloge, 13094 Aix-en-Provence, France

ARTICLE INFO

Article history:
Received 24 May 2015
Received in revised form 19 November 2015
Accepted 29 November 2015
Available online 7 December 2015

Keywords:
Cova del Coll Verdaguer
Coprolite
Upper Pleistocene
Micromorphology
Carnivore
Hyenid

ABSTRACT

Three morphotypes of fossil fecal material (coprolites) have been identified from the Upper Pleistocene site of Cova del Coll Verdaguer (NE Iberian Peninsula). Coprolites are commonly found in Pleistocene records and also in places in which human and carnivore activities co-occurred. However, coprolite identification is typically limited to hyenids, the most readily recognizable fossilized feces, owing to their distinctive shape and good preservation, although non-hyena carnivore coprolites are also likely to be present in these assemblages. Several criteria for a multi-scale integrative analysis are proposed here for discriminating different morphotypes. Hence, this analysis provides an opportunity to assess the involvement of several carnivores in bone accumulations, to identify carnivores not specifically represented by skeletal remains and to evaluate interactions between humans and the carnivore guild, especially medium and small carnivores.

1. Introduction

Human and carnivore interaction during the Pleistocene has become one of the main concerns in the study of ancient hominid behavior, with a primary focus on animal carcass acquisition by early humans, i.e., the scavenging versus hunting debate (Huguet et al., 2013, and literature cited therein). Carnivores and humans form part of the same guild, that of meat-eaters, and they share trophic niches (Stiner, 1994). Given this context, vertical shafts, caves, lakesides, and riparian settings have been used by humans and carnivores as kill sites, scavenging areas, and shelters and, as such, are potential places of encounter (Brugal and Fosse, 2004, and literature cited therein).

Caves are used by several carnivores as maternity dens, shelters, or places for hibernation (Fosse, 1997; Brugal and Fosse, 2004; Diedrich and Žák, 2006). Among the carnivores, the hyenids are a well-known group of cave dwellers, represented primarily by the cave hyena *Crocuta spelaea* in the Middle to Upper Pleistocene European record. Hominins also used caves for short-term occupations, which would have given rise to the co-occurrence of human and predator activities. This co-occurrence is recorded in a variety of ways and at different intensities, including human–carnivore succession or alternation (the so-called "mixed" occupations); anthropogenic accumulations with scarce carnivore activity; and finally, carnivore dens and lairs with low human presence, some of them simply indicative of a fortuitous association (Villa et al., 2010).

One method for identifying hominid–carnivore interactions in the archaeological record is based on taphonomic analyses of anthropogenic and gnaw marks, bone breakage and fragmentation, and prey type and selection; however, establishing diagnostic criteria to determine which carnivore interact with humans is far from straightforward. In the Pleistocene fossil record, hyenids are regularly associated with faunal assemblages (Diedrich and Žák, 2006; Daura et al., 2013; Fourvel et al., 2014). Indeed, the intensity of the bone damage attributed to the hyenas is especially high, the most significant being their consumption of the spongy epiphyses of limb bones, resulting in shafts in the case of large ungulates and splinters in that of small/medium ungulates. However, few juvenile bones from small-sized prey are expected in the assemblage (Cruz-Uribe, 1991; Brugal et al., 1997; Pickering, 2002).

Hyena ethology and cave-denning habits tend to overprint the signatures of other carnivores in bone assemblages that might present only a low intensity of bone modifications. To discriminate agencies other than hyenas, actualistic studies have focused on (i) prey size and patterns of bone damage (e.g., Sala and Arsuaga, 2013), (ii) dimensions of tooth marks (e.g., Delaney-Rivera et al., 2009 and literature cited therein) and, to a lesser degree, (iii) scats (coproscopy). This latter focus, however, might be useful in learning more about carnivore diets and their role in fossil assemblages. Various studies have analysed the bone content of current feces in order to determine the criteria

* Corresponding author.
E-mail addresses: msanzborras@campus.ul.pt (M. Sanz), jdauralujan@campus.ul.pt (J. Daura), neguez@gshdl.uni-kiel.de (N. Égüez), brugal@mmsh.univ-aix.fr (J.-P. Brugal).

http://dx.doi.org/10.1016/j.palaeo.2015.11.047
0031-0182/

(prey species, anatomical representation, damage inflicted by predators, and effects of digestion) that might be applied to the fossil register to identify carnivores. Such analyses have been conducted on hyenas (Horwitz, 1990; d'Errico and Villa, 1997; Pokines and Peterhans, 2007), on large felids (Domínguez-Rodrigo, 1999; Stiner et al., 2012), on small felids (Lloveras et al., 2008) and on canids (Schmitt and Juell, 1994; Esteban-Nadal et al., 2010; Lloveras et al., 2012).

Fossil feces can be dry or mineralized (i.e., coprolites, from the Greek *kopros*: feces and *lithos*: stone) and originate from marine and terrestrial invertebrates and vertebrates throughout the Phanerozoic. As such, they constitute a valuable source of data about past animals or plants (e.g., Khosla et al., 2015). Among land mammals, carnivores, and omnivores are the most likely to leave fossil scats because of their high calcium content due to bone ingestion (Kruuk, 1976). Most currently identified coprolites in the Pleistocene fossil record are from hyenids, thanks to their distinctive shape attributable to the peristaltic movement of their digestive tract. Hyaenidae coprolites present a spherical, globular, or slightly lengthened shape, with concave or flat ends, a dense cortical layer, and a clotted interior (Horwitz and Goldberg, 1989; Larkin et al., 2000), variation in both their shape and size (see Diedrich, 2012, Fig. 4) and a segmented nature.

A further morphology identified in coprolites is the tube-like shape (Brugal, 2010), referred to as either cylindrical or sausage shaped, with a tapered extremity in modern Carnivora feces, except for the scats of the hyena (Chame, 2003; Stuart and Stuart, 2013). This morphology is underestimated in the Pleistocene literature and previously barely reported, being referred to as non-hyenid coprolites, i.e., lynx, badger, fox, or wolf (Arribas, 1994; Brugal, 2010), the latter presenting an homogenous texture with no difference between the interior and the exterior and containing no bone fragments. A final coprolite morphology is that which is characterized by its tubercle-like shape and homogeneous texture, similar to hyena feces but larger and highly pinched, ascribed in the first instance to bear (Brugal, 2010).

Coprolites, scats, or dung can provide valuable data in relation the palaeoenvironment, palaeobiology, and palaeoeconomy since fossil feces trap pollen, beetles or parasites, and biomarkers (Carrión et al., 2001; Bon et al., 2012; Marinova et al., 2013; Taru and Backwell, 2013; Argant, 2014; Gil-Romera et al., 2014). However, to date, only hyenid coprolites have been analyzed macro and microscopically (Horwitz and Goldberg, 1989; Fernández Rodríguez et al., 1995; Larkin et al., 2000).

The main objective of this paper is to define several diagnostic criteria for the multi-scale integrated analysis of the coprolites of hyena and other carnivores. We undertake a study of coprolites from the Upper Pleistocene site of Cova del Coll Verdaguer where different morphotypes have been documented pointing to a variety of carnivore sources. The questions addressed by the present study are based principally on macroscopic analyses, morphometric comparisons with other fossil and modern scats and microscopic analyses.

2. Site description

Cova del Coll Verdaguer (41°23′35.08″N 1°54′39.81″E, ~450 m amsl) lies in the Garraf Massif, in the municipality of Cervelló (~20 km west of the city of Barcelona) (Fig. 1). The massif is a low-relief, intensely karstified, mountain range that rises to a height of less than 600 m. The cave formed in the Cretaceous dolostones and is currently accessible via an artificial entrance (ramp and shaft), the result of mining activities. The original entrance was closed by sediment collapse and reopened during archaeological fieldwork (Fig. 1.7–1.8). The cave consists of an artificial chamber (Sala Miners), excavated during sparry calcite mining and two original galleries (Sala Sal de Llop and Sala dels *Ursus*) filled with Upper Pleistocene sediments (Fig. 1.4). The site was discovered and first excavated during the sixties by amateurs from the Centre Excursionista de Vallirana (CEV), while current archaeological research was initiated in 2004 by the Grup de Recerca del Quaternari (GRQ), responsible for describing the sedimentological framework (Daura, 2008).

At least three deposit episodes have been recognized in the stratigraphic sequence (ca. 1.80 m thick) (Fig. 1.5) (Daura, 2008; Sanz, 2013). The episodes yield different layers and sub-layers according to unconformities, clast size, matrix abundance, and color. The top of the sequence is sealed by a flowstone dated by U-Th disequilibrium at 38.4 +2.3/−2.2 ka, which provides the minimum age of the deposit. The ages obtained by radiocarbon dating of charcoal (unit 1) and by stimulated luminescence (IRSL) dating of sediment (unit 2) are in good agreement and provide a range for the deposit between 33.4 ka and 55 ka (Upper Pleistocene). The presence of similar ecofactual (fauna, charcoal, coprolites) evidence throughout the sequence, including the sedimentological features and close dating, supports the study of the three deposit episodes as a whole.

3. Large mammal and taphonomical remarks

Table 1 records the fauna remains identified in Cova del Coll Verdaguer, which include ten species of macromammals. The sequence is dominated by the presence of red deer and brown bear, followed by ibex and horse. Other carnivores – including adult lynx, badger, fox, and wildcat – are present in much smaller numbers in the assemblage.

This large mammal assemblage can be attributed to a minimum of three biological agents. First and foremost, the site shows the intense presence of hyenid and their activities are clearly evident (Sanz, 2013) in the bone damage typical of that described in modern and fossil hyena assemblages (Pickering, 2002; Villa et al., 2010). Long bones are frequently transformed into cylinders and shaft fragments as a result of ravaging, while extremities are infrequent. Interestingly, no hyena bones are recorded in the faunal assemblage, despite the gnawing pattern documented on the bones (27.5%) and the presence of partly digested bones (6.5%) (Sanz, 2013). The most distinctive biochemical and physical alterations of these partly digested bones (NR = 51) are polishing (78% of digested bones), angularity with a knife-sharp appearance (66%), roundness (60%), and presence of cupules (58%) and slimming (52%). Other features are also present, including demineralization (49%) and circular holes (31%). These bones that show a high degree of gastric etching, together with bones (NR = 20) exceeding 40 mm in length, support hyena action (Esteban-Nadal, 2012).

Other carnivore taxa include several adult individuals (47% MNI of carnivore), especially lynx and fox, although it is not possible to specify their exact role in the prey accumulations. Breakage patterns and tooth marks are not sufficiently diagnostic, but we cannot dismiss their action, their activities probably having been obliterated by hyenid modifications.

A second agent can be identified by the abundant remains of brown bear, mainly documented by yearlings and neonate specimens (53% MNI of carnivore). The ethological observations of modern brown bear as well as the fossil record suggest a non carcass transport within the denning site (Sala and Arsuaga, 2013). The abundance of shed deciduous canines, replaced around the 14th month of life, and neonate remains point to maternal activity, indicating the hibernating behavior of females with cubs inside the cave (Andrews and Turner, 1991).

A third potential agent could be human occupations as indicated by the presence of a few stone tools ($N = 14$) and a charcoal concentration in Sala Sal de Llop. The lithic remains might correspond to artifacts cleaned inside the cave, while the charcoal could indicate an area restricted to human occupation. The presence of a few burned bones (0.9%) in the same area might also point to occasional marginal human activity; however, no cut-marks or any other anthropogenic damage have been observed in the bone assemblage.

4. Materials and methods

4.1. Macroscopic analysis

A total of 305 coprolite remains were studied, 277 of which were recovered during current work at the cave and are labeled as CV, and a further 28 that were recovered during previous excavations and are labeled