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The evolution of Paleolithic hominin–carnivore interaction written in teeth: Stories from the Swabian Jura (Germany)

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ABSTRACT

The interaction between hominins and carnivores during the Paleolithic is highly dynamic, and the study of these relationships provides key insights into the evolution of human behavior. In this sense, the relations that hominins had with large carnivores can help us address topics that span from subsistence behavior to intra-site spatial organization. Usually, all these studies are developed by analyzing post-cranial faunal remains, including carnivore and non-carnivore anatomical elements. Teeth and activities related to teeth (e.g. bite marks) are additional elements that inform us about hominin–carnivore interactions. In the present paper, we analyze the changing forms of interaction between hominins and carnivores during the Paleolithic of the Swabian Jura (Germany) using carnivore tooth remains and carnivore bite marks. We observe that the relation between hominins and carnivores reflects a dynamic interaction from the Middle to the Upper Paleolithic that is documented through tooth remains and bones with tooth marks from carnivores. The present multidisciplinary contribution analyzes teeth and tooth marks to understand site formation process, carnivore hunting, tool use, human recycling behavior, the role of ornaments made from carnivore teeth, and domestication process.

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1. Introduction

The evolving interaction between hominins and carnivores during the Paleolithic is a dynamic issue and its study provides a better understanding of human behavior and its changes through time (Rosell et al., 2012). In this regard, the relationship between humans and large carnivores can provide valuable information on aspects ranging from subsistence strategies to ritual practices (e.g., Stiner, 2012; Conard, 2003). Hominin–carnivore interaction studies are commonly conducted by analyzing post-cranial faunal remains, including carnivore and non-carnivore skeletal elements. However, teeth and their signatures, such as bite marks, also provide key insight into the interaction between hominins and carnivores.

The study of tooth-related characteristics can provide interesting insight into the behavioral patterns of hominins (e.g., Rivals et al., 2009; Saladié et al., 2013; Bello et al., 2015). This potential is related to the application of new methods or the advancement of existing methods that have contributed to improved knowledge of human paleoecology (e.g., Bocherens et al., 2011), subsistence (e.g., Tornero et al., 2013) and social behavior (e.g., Álvarez-Fernández, 2010). Furthermore, teeth are one of

the most well-preserved faunal remains at archeopaleontological sites (Hillson, 2005), and are involved in a wide range of the activities performed by hominin groups (Reitz and Wing, 2008).

In this paper, we analyze the changing interaction between hominins and carnivores during the Paleolithic in the Swabian Jura (Germany) from a transdisciplinary perspective, using carnivore tooth remains and tooth-related signatures. The aim is to provide a general overview of the relationship between hominins and carnivores and its evolution during the Middle and Upper Paleolithic (approx. 50–27 kyrs uncal BP) in this geographical area.

We address aspects such as the alternating use of space by hominins and carnivores, direct interaction, and the use of carnivores as a raw material or as prey. Furthermore, we look at factors related to the cultural significance of carnivores and even wolf domestication, one of the latest forms of hominin–carnivore interaction, using only tooth-related studies.

The Swabian Jura has preserved outstanding evidence for the study of how hominins interacted with carnivores (e.g., Münzel et al., 2011; Kitagawa et al., 2012), and tooth-related studies are crucial to approaching the evolution of such interactions in relation to hominin behavioral changes. Archeological evidence points to a complex relationship in this singular area, and hominin–carnivore interaction is analyzed in order to establish its importance in relation to the cultural

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fluorescence that occurred at the beginning of the Upper Paleolithic (Conard, 2003), as it seems this interaction had a substantial effect on modern behavior.

2. Materials and methods

We used different tooth-related materials to analyze the interaction between hominins and carnivores during the Paleolithic in the Swabian Jura (approx. 50–27 kyrs uncal BP). The materials analyzed do not consist solely of tooth remains, but also include bone remains bearing tooth marks on their surfaces. The bone remains studied are from herbivorous animals, but also from large carnivores and hominins.

The primary faunal collection analyzed was that from Hohle Fels (HF), although other sites were involved in the search for specific scenarios of hominin–carnivore interaction, such as Geißenklösterle (GK), Vogelherd (VH) and Hohlenstein Stadel (HS). All of the sites are located in the Swabian Jura, the largest karst system in southwestern Germany, in both main valleys, the Ach and the Lone (Fig. 1). All of the sites considered have been the subject of previous works and they are well dated and chronologically ascribed (Conard and Bolus, 2003, 2008). Table 1 summarizes the most relevant archeological characteristics of the sites analyzed and main bibliographical references in relation to hominin–carnivore interaction.

All of the materials analyzed were approached from a taphonomic perspective, and both anthropic and non-anthropic marks were studied through the generation of high-resolution silicon casts. The aim was to better observe all of the marks on the surface by illuminating the cast from underneath (Fig. 2). This method is a useful and economical alternative in the taphonomic study of bone surfaces, and it has been used in previous studies of tooth microwear (e.g., Semperebon et al., 2004).

The benefits of this method have been previously described for the study of tooth microwear in ungulates and carnivores (e.g., Rivals, 2015) and primates (Solounias and Semperebon, 2002). Nevertheless, this is the first time that this method has been applied to the study of bone surfaces and tooth taphonomy beyond paleoecological approaches, although it has been described in detail (Camarós et al., submitted for publication).

3. Results

3.1. Direct interaction

The Swabian Jura is not an area with abundant fossil hominin bones, although some evidence has been recovered from Hohlenstein Stadel,

Vogelherd, Sirgenstein, Geißenklösterle and Hohle Fels (see Conard and Bolus, 2003). The cave of Hohlenstein Stadel is the only site at which not only Neanderthal hominin remains have been recovered (Orschiedt, 1999; Street et al., 2006) (Fig. 3.1), but also anatomically modern human (AMH) remains dating from the Upper Paleolithic, Mesolithic and Neolithic (Orschiedt, 1998; Orschiedt, 1999, Rigaud et al., 2014) (Figs. 3.2 and 3.3).

One of the noteworthy features of some of the specimens recovered from Hohlenstein Stadel is the fact that they exhibit carnivore tooth marks on the bone surface. This evidence reveals a direct interaction between hominins and carnivores. Taphonomic studies have not been able to reveal the nature of this direct interaction and therefore give rise to several different scenarios.

The Neanderthal remain exhibiting carnivore damage consists of an adult male diaphysis of a right femur, unearthed in the archeological horizon of the *Schwarzes Moustérien* (Völzing, 1938; Kunter and Wahl, 1992). This Neanderthal bone, the only one recovered in the Swabian Jura (Street et al., 2006), presents the typical morphology of a diaphyseal cylinder shaped by intense carnivore chewing (Fig. 3.1). Both epiphyses have been consumed and the entire bone surface is covered with pits of a considerable size, according to Domínguez-Rodrigo and Piqueras (2003) and Andrés et al. (2012). All these features are related to the activity of a large carnivore such as a hyena or canid (Fosse et al., 2012; Binford, 1981). Both carnivore species have been identified in Middle Paleolithic layers at Hohlenstein Stadel (Kitagawa et al., 2012).

Anatomically modern human remains from the Neolithic *Knochenrümmerstätte* also exhibit carnivore damage on the surface of some of the specimens (Orschiedt, 1998, 1999) (Figs. 3.2 and 3.3). The damage is mainly associated with furrowing and small to medium-size carnivores (Orschiedt, 1998, 1999).

Although the presence of carnivore activity on the surface of hominin bones clearly testifies the direct interaction, it is quite difficult to infer the type of scenario that originated the damage. It is obvious that carnivores modified the bones postmortem, but it is difficult to determine whether the hominins were eaten after death and/or burial or, on the contrary, whether they were eaten after a carnivore attack. Both scenarios are highly interesting and have important implications with regard to behavioral interpretations. In the case of the Neanderthal specimen, it is impossible to prove whether the corpse was just scavenged, or whether the individual was hunted by a large carnivore, as has been suggested in other cases with other Neanderthal fossils (Camarós et al., 2015). On the other hand, the Neolithic AMHs were probably modified post-mortem by a small carnivore after having



Fig. 1. Archeological sites from the Swabian Jura (Germany) considered and cited in the study (Map: Landesmuseum Baden-Württemberg).

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