



Carnivore activity in the Sima de los Huesos (Atapuerca, Spain) hominin sample



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ARTICLE INFO

Article history:

Received 10 March 2014

Received in revised form

8 May 2014

Accepted 9 May 2014

Available online

Keywords:

Taphonomy

Tooth marks

Middle Pleistocene

Homo heidelbergensis

ABSTRACT

The Sima de los Huesos (SH) site is the largest accumulation of human remains from the Middle Pleistocene known to date. Studies in the last two decades have proposed different hypotheses to explain carnivore activity in the SH human sample. This study provides new data in order to test these different interpretations, and therefore to understand the role of the carnivores in site formation at SH. Carnivores are usually not the origin of large accumulations of hominin fossils in the Eurasian record. The results show that marks of carnivore activity in the SH sample appear very infrequently, which we interpret as indicating that carnivore activity was very sporadic at the site. This is in stark contrast with previous studies. The comparison of bone modification patterns at SH to actualistic carnivore data allows us to suggest that bears were likely to have been the carnivore responsible for the modification observed on both human and bear fossils.

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1. Introduction

The study of carnivore activity on bones is crucial to understanding the carnivores' role in the site formation since some carnivores are able to accumulate bones in cave dens. Most carnivores produce a distinct pattern of bone modification and have different accumulation behaviours. For this reason, the characterization of these two parameters is important to facilitate understanding of the role played by carnivores in paleontological and archaeological sites.

Carnivores are not the main culprits responsible for the origin of most large accumulations of human fossils in Eurasia. Generally, the large human fossil accumulations in the Eurasian Pleistocene record are interpreted as: i) cannibalism, e.g. *Homo antecessor* from Gran Dolina (Fernández-Jalvo et al., 1996) or *Homo neanderthalensis* from El Sidrón cave (Rosas et al., 2006) and Moula-Guercy (Defleur et al., 1999); ii) intentional or natural burial, e.g. *H. neanderthalensis* from Sima de las Palomas (Walker et al., 2011), La Ferrassie (Bouyssonie, 1954; Heim, 1976; Maureille and Peer, 1998), Krapina (Trinkaus, 1985; Bocquet-Appel and Arsuaga, 1999), La Chapelle-aux-Saints (Rendu et al., 2014), Amud and Kebara (Tillier et al.,

1991; Gargett, 1999) or early *Homo sapiens* from Predmostí (Svoboda, 2008), Skhul (Grün et al., 2005) or Qafzeh (Vandermeersch, 1981; Gargett, 1999). On the other hand, the *Homo erectus* accumulation in Locality 1 of Zhoukoudian has been interpreted as a human assemblage collected by *Pachycrocuta brevirostris* (Boaz et al., 2004). Nevertheless, some human fossils from the European record display carnivore tooth marks associated with carnivores' scavenging or are found in carnivore accumulation contexts, e.g. Baigara (Kuzmin et al., 2009), Kalamakia (Harvati et al., 2013), Cova Negra (Arsuaga et al., 2007), Cueva del Camino (Arsuaga et al., 2012), Valdegoba (Quam et al., 2001), Jarama VI (Lorenzo et al., 2012). None of the latter constitutes significant human accumulation, since they are typically isolated human remains.

The Sima de los Huesos (SH) site (Atapuerca, Burgos, Spain) is the largest accumulation of human remains from the Middle Pleistocene discovered to date. With respect to carnivore modification in the SH human sample, a previous study suggested that carnivores can be excluded as major agents involved in the accumulation of human remains due to the absence of both tooth marks and herbivore remains (Arsuaga et al., 1990).

A later taphonomic study (Andrews and Fernández-Jalvo, 1997) maintained that carnivore tooth marks are very common in the SH sample, since they are present on over half of the SH human assemblage. The same authors argue that at least two sizes of

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carnivores had access to the human bodies, a lion-sized carnivore first and a fox-sized canid, which scavenged the remains left by the former (Andrews and Fernández-Jalvo, 1997). Furthermore, the same paper argued that tooth marks made by cave bears were observed only on bear bones.

In other work, Arsuaga et al. (1997) argued that the tooth marks documented by Andrews and Fernández-Jalvo (1997) could have been produced by carnivores who became trapped in the caves, including bears. Therefore, there has never been a consensus regarding the influence of carnivore activity on the human remains from SH.

The present study concerning the taphonomy of the SH sample aims to provide new data in order to evaluate the different interpretations proposed. Furthermore, the objective of the present work is to describe and to quantify the carnivore modification observed in the SH sample, to understand the role of carnivores in the site formation. In order to establish coherent interpretations, we have approached this study through actualistic research with living carnivores.

2. Materials and methods

2.1. The Sima de los Huesos site

The Sima de los Huesos (SH) is well-known for yielding the largest collection of Middle Pleistocene hominin fossils ever found at a single site. This site has yielded a large collection composed of thousands human fossils (Martínez et al., 2013) belonging to at least 28 individuals (Bermúdez de Castro et al., 2004). The skeletal remains were described by their discoverers as belonging to the Neandertal lineage (Arsuaga et al., 1993; Martínez and Arsuaga, 1997) and classified as *Homo heidelbergensis* in a broad sense, which includes incipient Neandertal fossils. To Stringer (2012), this taxon should be restricted to fossils not exhibiting any Neandertal apomorphy and thus the SH hominins should be excluded. However, a recent study shows that the mitochondrial DNA of a Sima de los Huesos hominin shares a common ancestor with Denisovan mtDNA rather than with “classic” Neandertal mtDNA (Meyer et al., 2014), which could be interpreted as the result of gene exchanges between the Neandertal lineage and the *H. heidelbergensis* (in the restricted sense) populations. Together with the human bones, more than 176 individuals of *Ursus deningeri* (García and Arsuaga, 2011) and other carnivores have been recovered, including: *Vulpes vulpes*, *Canis* sp., *Panthera leo* cf. *fossilis*, *Panthera* sp. (jaguar size), *Felis silvestris*, *Lynx pardinus spelaeus*; *Martes* sp., *Mustela nivalis*, *Mustela putorius* and *Meles meles* (García et al., 1997; García, 2003; García and Arsuaga, 2011) as well as microfaunal remains (Cuenca-Bescós et al., 1997). As yet, no ungulate remains have been found at the site.

The site is a small subterranean gallery deep inside the Cueva Mayor Karst system, far from the present day entrance. The site has an inclined area (Ramp), where three stratigraphic sections (SRA, SRM and SRB) have been excavated, and a pseudo-horizontal area called Sima de los Huesos (SH) *sensu stricto*. Within the SH site, the pseudo-horizontal area has been excavated in extension, whereas the excavation of the ramp has been carried out with pits. Inside this chamber, there are twelve lithostratigraphic units (LU), but only two of them (LU-6 and LU-7) are fossiliferous stratigraphic levels (Fig. 1) (Aranburu et al., submitted). The lower fossiliferous level (LU-6) is referred to as “Red Clay”, and is rich in human and carnivore fossils. The red clay is pure, devoid of extraclasts, and indicates low energy accumulation (decantation), which is compelling evidence that the fossils were not subjected to long-distance transport and likely accumulated in situ at SH (Aranburu et al., submitted). Above the Red Clay level there is a carnivore-

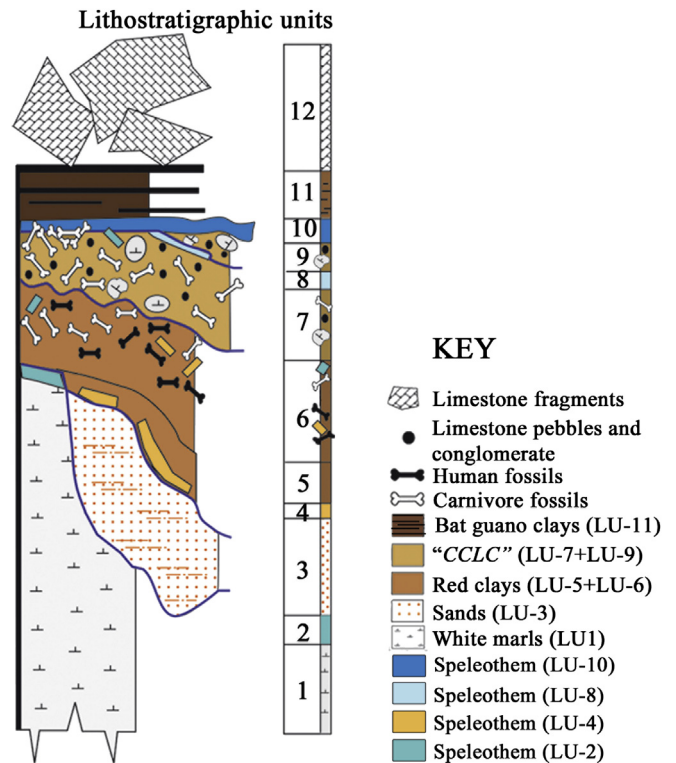


Fig. 1. Composite stratigraphic section of Sima de los Huesos site. Note that the colours correspond to the Munsell tables in wet sediment.

bearing level (LU-7) (Aranburu et al., submitted). It can be said that there is only one hominin fossil deposit in SH (i.e., a single geological event: LU-6) because some hominin cranial fragments and teeth from SRA, SRM and SRB fit together perfectly with LU-6 remains found at SH *sensu stricto* (Arsuaga et al., 1997; Bischoff et al., 2007). Thus, human bones are present only in the red clay level (LU-6) in SH, but carnivores (especially bears) are present in both stratigraphic levels (LU-6 and LU-7).

The biostratigraphic evidence place the site in the Middle Pleistocene (Bischoff et al., 2007; Cuenca-Bescós and García, 2007). Using a suite of independent geochronological methods the new age for the Sima de los Huesos hominin accumulation is estimated in 430 ka (Arnold et al., 2014).

2.2. The SH fossil samples

The human sample from SH is a large collection composed of thousands of bone fragments of all skeletal portions. Some of the remains fit together to form complete bones. For the purposes of this study, we have investigated the bones that provide relevant information regarding carnivore modification, e.g. long and flat bones (innominate, cranial, costal and vertebral remains). We analysed a total of 2401 human fossils from SH (see SI). These fossils correspond to skeletal elements found in all anatomical regions of the human sample. Dental remains and bone fragments smaller than 1 cm were excluded.

For the taphonomic study of the bear remains we analysed all non-dental bear remains recovered between the 2005 and 2011 campaigns. The specimens come from both LU-6 and LU-7. In order to analyse the ‘non-bear’ carnivore remains, we studied the entire non-dental sample in the collection. In sum, a total of 1200 carnivore skeletal remains from the site including *U. deningeri* (NISP = 464), *V. vulpes* (NISP = 634), *P. leo* cf. *fossilis* (NISP = 54),

Panthera sp. (NISP = 1) and *L. pardinus spelaeus* (NISP = 46) were studied.

2.3. The modern comparative samples

In order to establish coherent hypotheses we have approached this study through actualistic research with living carnivores. Taking into account the large-size carnivore species present in the SH chamber, that are potentially the responsible of the bone modifications, we have performed actualistic experiments on ursids, canids, and large felids (Sala, 2012; Sala and Arsuaga, 2013; Sala et al., 2014). The field work with ursids (Number of Identified Specimens (NISP) = 261) was carried out in the wild (Sala and Arsuaga, 2013); for the study on live canids, the experiments were conducted using both wild and captive specimens (NISP = 687) (Sala et al., 2014); in the case of large felids, several taxa have been analysed (lions, jaguars, etc.) using captive animals (NISP = 660) (Sala, 2012). In all these cases, we compared our results with those conducted by different authors (Haynes, 1983; Domínguez-Rodrigo, 1999; Domínguez-Rodrigo and Piqueras, 2003; Fosse et al., 2004; Yravedra et al., 2011; Andrés et al., 2012; Domínguez-Rodrigo et al., 2012; Fosse et al., 2012; Burke, 2013; Gidna et al., 2013; Saladié et al., 2013; Gidna et al., 2014).

2.4. Methodological procedure

In order to perform the study of the carnivore modification on the SH sample, we have analysed: i) the frequency, ii) the location and iii) the dimensions of the tooth marks. Tooth marks on bone surfaces were classified as pits, punctures, furrowing and scores (Haynes, 1980, 1983; Maguire et al., 1980; Binford, 1981). Pits and

punctures are marks generated by the pressure of a tooth on the cortical surface of a bone. Their difference lies in whether the mark crosses the cortical bone (puncture) or not (pit) (Fig. 2). Scores are elongated marks with a U-shaped cross-section and a flat bottom that are produced by tooth cusps' movement over the bone surface (Fig. 2). Furrowing is the result of carnivore gnawing and involves the extraction or absence of portions of the cancellous bone tissue. Furrowing can be light, moderate or heavy depending on the portion of cancellous tissue removed (Haynes, 1982). In the SH sample, the absence of cancellous tissue does not necessarily point to carnivore activity, since the red clay is extremely humid, plastic and sticky. It is a sediment that, when adhered to the bone, sometimes causes spongy tissue loss, even during the excavation process. Therefore, the carnivore activity is only taken into consideration when the absence of cancellous tissue is accompanied by conspicuous tooth marks. All observations were made with a Nikon SMZ800 Stereoscopic zoom microscope.

Bone damage frequency was documented by quantifying the presence of tooth-marked bone fragments (NISP) taking the bone type and region into account.

Different authors use different approaches to measuring tooth marks. Some prefer size ranges as (Andrews and Fernández-Jalvo, 1997; Pinto et al., 2005; Rabal-Garcés et al., 2012), others prefer a mean plus 1 Standard Deviation (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Saladié et al., 2013), and some prefer 95% confidence intervals since this represents the variation of the majority of each sample (Andrés et al., 2012; Sala et al., 2014). Methodologies in measuring tooth marks have been honed in recent decades due to new and larger experimental collections. Also, the new studies point out that when using samples of marks and not isolated marks,

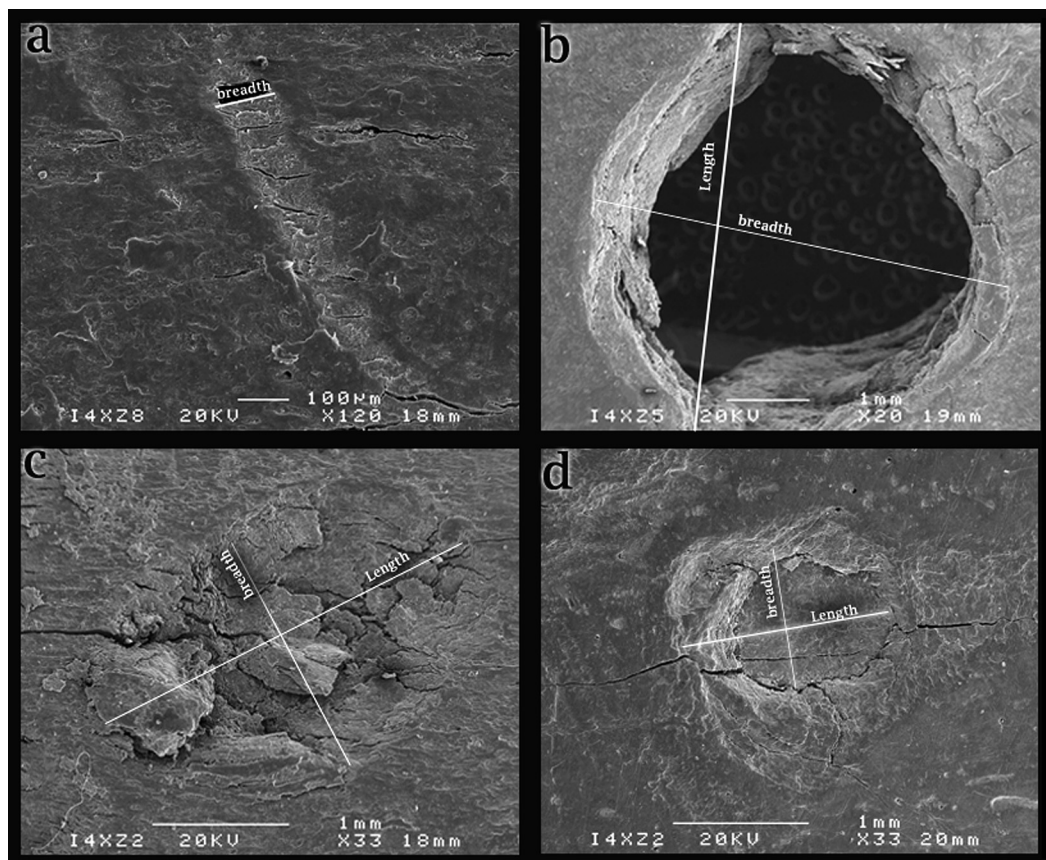


Fig. 2. Examples of SEM images of tooth marks (a: scores; b: punctures and c: pits) showing the measurements considered in this study.

large and small carnivores can be best differentiated using the tooth pit mean rather than size ranges (Andrés et al., 2012). Moreover, since tooth marks could vary in size depending on element type (e.g. anatomical region, bone density, soft tissue associated with each bone portion, etc.), we think that using size ranges can lead to confusion in their interpretation. With these factors in mind, we have focused on the following methodology in this work. Tooth marks were measured in length and breadth (Fig. 2), targeting three areas to account for the various bone densities based on their resistance to tooth penetration: spongy or cancellous, thinning cortical, and cortical bone (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009). The length and breadth of marks were measured using standard digital calipers (Sylvac) with an error of 0.01 mm. The SH dimensional data were compared to experimental data obtained from living carnivores (*P. leo*, *Canis lupus*, and *Ursus arctos*), taking into account the 95% confidence interval (Sala, 2012). For the univariate analysis, we performed a Kruskal–Wallis test to compare the tooth marks found on the bear and human fossils with those produced by living carnivores. When a significant difference

($p < 0.05$) was found, we performed a Mann Whitney test (Mann and Whitney, 1947) between all possible pairs of samples (fossils and different kinds of carnivores) to determine which differed significantly. Recent studies (Andrés et al., 2012; Sala, 2012; Sala et al., 2012, 2014) show that the tooth pit length on shafts is the best indicator of the carnivore taxa responsible for the marks. For this reason, we will focus particularly on this feature when comparing the samples.

In order to compare the taphonomic histories of the different stratigraphic levels, we analysed bear remains from the two fossiliferous layers (LU-6 and LU-7).

3. Results

3.1. Tooth mark frequencies in the human sample

After a detailed analysis of the sample of 2401 human fossils from SH, it is estimated that only 86 (3.65%) show tooth marks. With respect to the long bones (Tables 1 and 2), tooth marks are present, especially in the epiphysis, but pits and scores are also

Table 1
Tooth mark frequencies in the human bone assemblage by bone type and location of tooth marks.

Bone type	Location	Pitting	Scores	Punctures	Furrowing	% Of NISP with tooth marks
Femur (N = 79)	Proximal epiphysis	1 (1.27%)	1 (1.27%)	3 (3.80%)	4 (5.06%)	15 (18.99%)
	Diaphysis	8 (10.13%)	4 (5.06%)	1 (1.27%)	1 (1.27%)	
	Distal epiphysis	0.00	2 (2.53%)	2 (2.53%)	3 (3.80%)	
Tibia (N = 33)	Proximal epiphysis	0.00	0.00	0.00	0.00	1 (3.03%)
	Diaphysis	0.00	0.00	0.00	0.00	
	Distal epiphysis	0.00	0.00	0.00	1 (3.03%)	
Humerus (N = 89)	Proximal epiphysis	0.00	4 (4.49%)	1 (1.12%)	4 (4.49%)	9 (10.11%)
	Diaphysis	0.00	0.00	1 (1.12%)	0.00	
	Distal epiphysis	0.00	1 (1.12%)	0.00	1 (1.12%)	
Radius (N = 63)	Proximal epiphysis	0.00	1 (1.59%)	1 (1.59%)	0.00	1 (1.59%)
	Diaphysis	0.00	0.00	0.00	0.00	
	Distal epiphysis	0.00	0.00	0.00	0.00	
Ulna (N = 59)	Proximal epiphysis	0.00	0.00	0.00	1 (1.69%)	1 (1.69%)
	Diaphysis	0.00	1 (1.69%)	0.00	0.00	
Metacarpal (N = 89)	Diaphysis	0.00	0.00	1 (1.12%)	0.00	1 (1.12%)
	Distal epiphysis	0.00	0.00	0.00	0.00	
Metatarsal (N = 120)	Diaphysis	0.00	0.00	0.00	0.00	0.00
	Distal epiphysis	0.00	0.00	0.00	0.00	
Clavicle (N = 42)	Diaphysis	0.00	0.00	0.00	0.00	0.00
	Articular surface	0.00	0.00	0.00	0.00	
Skull (N = 370)		1 (1.29%)	2 (0.59%)	0.00	1 (1.29%)	4 (1.10%)
Mandible (N = 100)	Body	0.00	0.00	0.00	0.00	0.00
	Ramus	0.00	0.00	0.00	0.00	
Innominate (N = 169)	Ilium	0.00	4 (2.37%)	5 (2.96%)	4 (2.37%)	14 (8.28%)
	Isquium	1 (0.59%)	0.00	1 (0.59%)	1 (0.59%)	
	Pubis	0.00	0.00	0.00	0.00	
	Sacrum	0.00	0.00	0.00	0.00	
	Acetabulum	1 (0.59%)	0.00	0.00	0.00	
Vertebrae (N = 208)	Vertebral body	0.00	1 (0.48%)	1 (0.48%)	2 (0.96%)	2 (0.96%)
Scapula (N = 68)	Body	0.00	0.00	0.00	0.00	1 (1.47%)
	Glen. Art.	0.00	0.00	0.00	0.00	
	Spine/acromion	0.00	1 (1.47%)	1 (1.47%)	0.00	
Ribs (N = 197)	Diaphysis	0.00	0.00	1 (0.51%)	0.00	1 (0.51%)
	Articular surface	0.00	0.00	0.00	0.00	
Foot bones	Talus (N = 25)	0.00	1 (4.00%)	0.00	1 (4.00%)	2 (8.00%)
	Calcaneus (N = 26)	0.00	1 (3.85%)	0.00	2 (7.69%)	2 (7.69%)
	Navicular (N = 25)	0.00	0.00	0.00	0.00	0.00
	Medial Cuneiform (N = 14)	0.00	0.00	0.00	0.00	0.00
	Intermediate Cuneiform (N = 15)	0.00	0.00	0.00	0.00	0.00
	Lateral cuneiform (N = 12)	0.00	0.00	1 (8.33%)	0.00	1 (8.33%)
	Cuboid (N = 21)	0.00	0.00	0.00	0.00	0.00
	Prox. Phalange (N = 111)	0.00	0.00	0.00	0.00	0.00
	Interm. Phalange (N = 69)	0.00	0.00	0.00	0.00	0.00
	Dist. Phalange (N = 81)	0.00	0.00	1 (1.23%)	0.00	1 (1.23%)
	Carpal (N = 6)	0.00	0.00	0.00	0.00	0.00
	Prox. Phalange (N = 113)	1 (0.88%)	1 (0.88%)	0.00	0.00	2 (1.77%)
	Interm. Phalange (N = 79)	0.00	0.00	0.00	0.00	0.00
	Dist. Phalange (N = 77)	0.00	0.00	0.00	0.00	0.00

Table 2

Tooth mark frequencies in the hominin and bear bone assemblages by bone type and location of tooth marks.

	Hominin sample “Red clay” level (LU-6)					
	Long bones (N = 532)			Flat bones (N = 1025)		Articular bones (N = 651)
	Proximal Ep	Diaph	Distal Ep	Cortical	Cancellous	Compact bone
Pits	1 (0.19%)	8 (1.50%)	0.00	2 (0.17%)	1 (0.09%)	1 (0.15%)
Scores	6 (1.13%)	5 (0.94%)	3 (0.56%)	4 (0.35%)	4 (0.35%)	3 (0.46%)
Punctures	5 (0.94%)	3 (0.56%)	2 (0.38%)	3 (0.26%)	6 (0.52%)	2 (0.31%)
Furrowing	9 (1.69%)	1 (0.19%)	5 (0.94%)	2 (0.17%)	6 (0.52%)	3 (0.46%)
	<i>U. deningeri</i> “Red clay” level (LU-6)					
	Long bones (N = 70)			Flat bones (N = 85)		Articular bones (N = 74)
	Proximal Ep	Diaph	Distal Ep	Cortical	Cancellous	Compact bone
Pits	0.00	0.00	0.00	2 (2.35%)	0.00	2 (2.70%)
Scores	3 (4.29%)	0.00	1 (1.43%)	1 (1.18%)	2 (2.35%)	1 (1.35%)
Punctures	3 (4.29%)	2 (2.86%)	1 (1.43%)	1 (1.18%)	1 (1.18%)	2 (2.70%)
Furrowing	1 (1.43%)	2 (2.86%)	0.00	2 (2.35%)	3 (3.53%)	1 (1.35%)
	<i>U. deningeri</i> “Café con leche” level (LU-7)					
	Long bones (N = 76)			Flat bones (N = 79)		Articular bones (N = 60)
	Proximal Ep	Diaph	Distal Ep	Cortical	Cancellous	Compact bone
Pits	2 (2.63%)	4 (5.26%)	1 (1.32%)	5 (6.33%)	3 (3.80%)	0.00
Scores	2 (2.63%)	2 (2.63%)	2 (2.63%)	1 (1.27%)	1 (1.27%)	0.00
Punctures	4 (5.26%)	0.00	1 (1.32%)	1 (1.27%)	1 (1.27%)	1 (1.67%)
Furrowing	2 (2.63%)	0.00	1 (1.32%)	2 (2.53%)	1 (1.27%)	0.00

present in the diaphysis of long bones. The furrowing of trabecular tissue is light in all cases except in the AT-1802 femur that is moderate to high (Fig. 3). In general terms, the femur is the anatomical region that shows the highest incidence of tooth marks, although the marks frequency is less than 20%. After the femur, the humerus is the second most affected anatomical element, and tooth marks are most common on the proximal epiphysis. Three percent of the tibiae also show tooth marks that are concentrated on the distal epiphysis. Radii and ulnae show tooth mark frequencies of 1.59 and 1.69%, respectively, predominately furrowing and scores. The percentage of carnivore-modified metacarpals is very low, and modification of metatarsals is absent. None of the clavicles studied show evidence of modification by carnivores.

As in the case of long bones, the most common modification found after analysing flat bones (Tables 1 and 2) is light furrowing (except the highly furrowed AT-835 innominate bone that appears in Fig. 3) in cancellous bone accompanied by conspicuous marks in both cortical and cancellous tissues. The analysis of flat bones shows that only 8.28% of innominate bones show activity attributed to carnivores and this activity is concentrated on the ilium. This is a very low frequency rate given the fact that this is one of the elements that is most vulnerable to modification by carnivores. The remaining flat bones show tooth mark frequencies that are even lower than in the case of the innominate. After the pelvis, the scapula is the flat bone that shows the highest incidence of carnivore activity, manifested most commonly as marks on the glenoid and spine/acromion. Crania, jaws, vertebrae and ribs show low tooth mark frequencies, affecting between 0 and 1.10% of the remains analysed.

Both the hand and foot bones (excluding metatarsals and metacarpals, which were included with long bones) show low frequencies of tooth marks, or none at all in some cases (Table 1). Carnivore tooth marks are rare in the sample of tali, and they are probable in only two remains (AT-1700 and AT-1a322) (Pablos et al., 2013). In the calcanei sample there are also two cases with light furrowing (AT-1740 and AT-2741) and scores (AT-2741) (Pablos et al., in press). The third cuneiform (AT-492) and the distal foot phalanx (AT-674) show punctures. With regard to hand bones, there are only tooth marks on proximal phalanges, occurring in very low proportions.

These data show that evidence for carnivore activity in the human sample from SH is very rare and is concentrated mostly on the epiphyses of long bones (femora, tibiae and humeri). In the other skeletal elements, carnivore modification rates do not exceed 8%.

3.2. Tooth mark frequencies in the carnivore sample

After a thorough analysis of 1200 carnivore fossils from SH, we find that 4.41% of the remains show evidence of carnivore activity. Considering the different carnivore taxa separately, none of the 54 remains assigned to *Panthera leo* cf. *fossilis* show tooth marks. The single *Panthera* sp. fossil did not show evidence of carnivore modification. The tooth mark frequencies for small carnivores like *Vulpes vulpes* and *Lynx pardina spelaea* are also very low. In the case of the fox (*V. vulpes*) only 0.32% of the 634 analysed remains have pits and punctures. These marks are found on only two remains: a scapula and a mandible (Fig. 4). For lynx, 4.35% of specimens show carnivore tooth marks, specifically pitting, scores and punctures. Furrowing is not documented among the small carnivores analysed.

For *Ursus deningeri* the results show that 6.25% of the remains display some sort of modification attributed to carnivore activity (Fig. 5). Table 2 shows the percentages of each type of carnivore mark registered among the *U. deningeri* remains analysed from the two fossiliferous layers of SH. This demonstrates that ratios of modified to unmodified bones are generally low in both levels, and always less than 4%. In the same way, we can observe that there are no substantial differences in carnivore modification, even when compared with the hominin sample (Table 2). The tibia, scapula, humerus, femur and radius present the highest proportions of tooth marks in the *U. deningeri* sample in both stratigraphical levels. As in the case of the hominin sample, furrowing is light to moderate (Fig. 5) in the bear sample.

3.3. Metric data on tooth marks

Table 3 provides summary statistics for metric characteristics of the tooth marks in the human, ursid, and small carnivore (fox and lynx) fossil samples, respectively. As shown in Table 3, the



Fig. 3. Examples of tooth marks in the human sample studied. A) Scores in Cranium 3 (AT-444), Cranium 4 (AT-600) and a scapula (AT-1873). B) Pits and punctures on a rib (AT-2289), innominate (AT-1796), vertebra (AT-2289) and humerus (AT-4175). C) Furrowing on an innominate bone (AT-835), femora (AT-1802, AT-612 and AT-1030) and an ulna (AT-1270). Scale bar 1 cm.

measurements of tooth marks on fox and lynx bones are considerably smaller than those on *Ursus deningeri* remains.

Comparisons of the metric data from tooth marks on the SH human sample with those produced by living carnivores such as canids, ursids, lions and jaguars (Domínguez-Rodrigo and Piqueras, 2003; Sala, 2012; Saladié et al., 2013; Sala and Arsuaga, 2013; Sala et al., 2014), all of which are present in the SH site, are presented in Fig. 6 and Table 4. As is shown in Fig. 6, the tooth mark dimensions from the SH sample are comparable with large carnivores, especially bears. Smaller carnivores, such as wolves or foxes, can be ruled out due to these tooth marks dimensions. Significant differences are found in at least one metric characteristic between tooth marks in the SH sample and those produced by all modern carnivores except ursids (Table 4). Similarly, the dimensions of tooth marks on the *Ursus deningeri* fossils from SH differ significantly from those produced by modern wolves and lions, but not bears (Table 4).

As shown in Table 4, no statistical differences were found existing between the tooth marks on human and ursid samples. In a graphical comparison of the maximum and minimum measurements of pits and punctures between human and ursid fossils from

SH (Fig. 7), similar dimensions are observed in these two species. Mann–Whitney *U* tests confirm that there are no significant differences between the human and bear fossils with regard to the dimensions of the ratio between maximum and minimum tooth marks (pits and punctures) on the bones (Fig. 7).

4. Discussion

No carnivore represented in SH performed, a priori, systematic accumulations of skeletal remains, as was the case for hyenas. However, for ursids, cannibalistic behaviour is well documented in hibernation dens (Stiner, 1998, 1999; Pinto and Andrews, 2002; Rabal-Garcés et al., 2012). Actualistic studies regarding lions and bears demonstrate that these carnivores do not systematically transport carcasses (Schaller, 1972; Domínguez-Rodrigo, 1994; Sala and Arsuaga, 2013). Canids are able – but in very rare cases – to collect and accumulate bones in breeding season. However, in any case, this behaviour never involves large bone accumulations, and if so, they are never monospecific, much less exclusive to humans or other carnivore's accumulation (Joslin, 1967; Mech, 1970; Fox, 1971; Binford, 1981; Domínguez-Rodrigo, 1994; Yravedra et al., 2011;

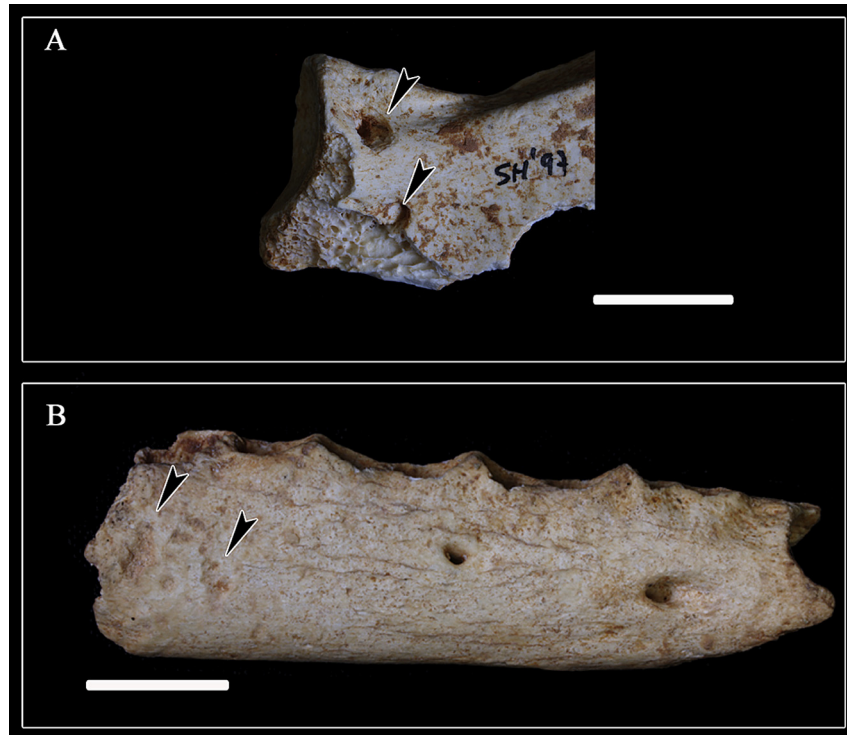


Fig. 4. Images of tooth marked *V. vulpes* remains from SH. A) Scapula with two adjacent punctures. B) Mandible with pitting on the mandibular body. Scale bar 1 cm.

Domínguez-Rodrigo et al., 2012; Fosse et al., 2012; Sala et al., 2014). These data and the lack of herbivore remains rule out the carnivores as the culprits responsible for the SH human and carnivore bone accumulation. Consequently, we must take into consideration the fact that the carnivore modification in SH occurred post-accumulation of the human and carnivore corpses.

The low frequency of tooth marks in the SH sample obtained for the present study contrasts with previous studies; Arsuaga et al. (1990) maintained that the SH sample lacks evidence of carnivore activity, but Andrews and Fernández Jalvo (1997) maintained that carnivore modification is present on over half of the SH assemblage. The fact that there were inconsistencies between the present study and the study by Andrews and Fernández Jalvo (1997) could be explained by the sample size (we have examined a sample that is nearly two times their sample), methodological procedures, or both. Unfortunately, it is difficult to compare our data with published data because the previous study does not include a list of fossil specimens and one-by-one observations (similar to the one provided in the present study) and therefore it is impossible to find which fossils have discrepancies between both studies.

This low incidence – in both bear and human remains – indicates that i) the carnivores responsible did not produce high levels of bone modification, or ii) that carnivore access to the remains at the site was very sporadic at SH. Recent works demonstrate that the degree of bone damage depends on environmental circumstances, e.g. open-air versus closed contexts, geographical location and environments, prey availability, prey size, etc (Blumenschine, 1988; Gidna et al., 2013; Sala and Arsuaga, 2013; Sala et al., 2014). For this reason, the low frequency of tooth marked bones alone cannot provide us with sufficiently convincing information about the carnivore responsible for this bone modification. Nevertheless, the low frequency of tooth-marked bones is compatible, a priori, with bear activity (Sala and Arsuaga, 2013; Saladié et al., 2013). To test which is the best explanation for the

low frequencies of tooth-marked bones in the SH sample, it is necessary to compare the results with different known scenarios. A priori, the damage generated by trapped carnivores should be higher than that observed in actualistic studies in open-air contexts: around 20% in the case of bears following Sala and Arsuaga (2013), 71%–89% in the case of lions (Gidna et al., 2013), and between 60 and 90% for wild wolves (Sala et al., 2014), depending on bone type and prey size. Our observation in SH is that the percentage of the modified bones is much lower even if we compare it with actualistic data from open air contexts. If we compare the percentage and degree of bone damage of SH with monospecific cave bear sites – where an open entrance to caves allows bears a sporadic yet continuous access to carcasses – we can observe that the percentages are also higher than the SH sample, e.g. 35.86% in Coro Tracito (Rabal-Garcés et al., 2012), 20% in Sima de los Osos or 78% in Tito Bustillo (Pinto and Andrews, 2004; Pinto et al., 2005). Thus, the only explanation for the lower incidence of carnivore modification in SH is a very sporadic event. In other words, the survival of trapped carnivores inside the SH chamber was an unusual circumstance when the low incidence of tooth marks in the SH sample is taken into account.

To identify the carnivore or carnivores responsible for the bone changes in the SH sample, we compared the bone modification patterns with experimental data. Most bears do not usually gnaw heavily on bones after the soft tissue has been removed (Haynes, 1983). Bears are characterized by diversity of bone damage, but they generally inflict scarce fracturation and tooth-marked bones and light to moderate furrowing, particularly in cancellous portions (Saladié et al., 2013). The most common type of alteration produced by ursids is the furrowing of cancellous bone. Tooth marks are concentrated on long bone epiphyses (especially the proximal epiphyses of the femur and humerus) and on the axial skeleton (vertebrae, ribs, scapulae and innominate bones) (Sala and Arsuaga, 2013).

Felids are easily differentiated from other carnivores such as hyenids and canids because of their minor impact on long bone end



Fig. 5. Examples of tooth marks in the *U. deningeri* sample. A) Talus (F118) recovered at the interface between the café con leche and red clay levels in the 2005 campaign, B) Tibia (H049) from the red clay level excavated in the 2011 season. C) Tibia (F107) from the café con leche level recovered during the 2005 campaign. 1) Punctures, 2) Pits; 3) Scores, 4) Furrowing. Scale bar 1 cm.

modification and their more restricted variability in the way they modify bones (Domínguez-Rodrigo et al., 2012). Lions can modify significantly all skeletal elements but do not crush bones for marrow (Domínguez-Rodrigo, 1999; Sala, 2012; Gidna et al., 2013, 2014). This carnivore usually inflicts damage on the epiphyses on complete limb bones (Domínguez-Rodrigo, 1999; Gidna et al., 2014). The furrowing of epiphyses of long bones and cancellous

tissue of flat bones (Haynes, 1983; Domínguez-Rodrigo, 1999; Sala, 2012), and the presence of pits, isolated punctures and scores in both cortical and cancellous tissues (Sala, 2012) are typical. Isolated punctures in unbroken long bone diaphysis is a signature trait observed in large felid modifications, and is less common in experimental data collected regarding ursids and canids (Sala, 2012).

Table 3

Descriptive statistics for lengths and breadths of pits, punctures and scores in the human sample, *U. deningeri*, fox and lynx remains sample (n: number of cases; C.I.: Confidence Interval for mean and SD.: Standard Deviation).

			<i>n</i>	Mean	CI-95%	CI + 95%	Minimum	Maximum	SD
<i>SH Hominin sample</i>									
Punctures	Length	Cancellous	25	5.52	4.85	6.18	3.05	9.58	1.61
		Thin cortical	9	6.01	4.36	7.66	2.96	10.36	2.15
		Cortical	8	4.57	3.41	5.74	2.75	6.78	1.39
	Breadth	Cancellous	20	4.28	3.65	4.91	1.88	7.06	1.34
		Thin cortical	6	4.36	3.06	5.66	2.59	6.29	1.24
		Cortical	7	3.74	2.82	4.67	2.58	5.29	1.00
Pits	Length	Cancellous	16	4.77	3.80	5.73	1.59	8.29	1.81
		Thin cortical	5	4.04	2.34	5.74	2.24	6.06	1.37
		Cortical	39	3.10	2.78	3.43	1.37	5.73	1.01
	Breadth	Cancellous	15	3.88	3.05	4.72	1.44	5.94	1.51
		Thin cortical	5	2.74	1.42	4.06	1.44	4.18	1.06
		Cortical	39	2.33	2.04	2.62	0.90	5.26	0.88
Scores	Breadth	Cancellous	28	3.65	3.02	4.28	1.07	5.95	1.63
		Thin cortical	36	2.24	1.87	2.61	0.50	6.02	1.10
		Cortical	11	2.94	2.25	3.63	1.63	4.67	1.03
<i>SH Ursus deningeri</i>									
Punctures	Length	Cancellous	16	6.82	5.93	7.71	3.91	9.56	1.67
		Thin cortical	6	6.46	4.19	8.72	3.91	9.39	2.16
		Cortical	3	7.22	4.14	10.30	5.81	8.13	1.24
	Breadth	Cancellous	13	5.37	4.50	6.25	3.23	8.97	1.45
		Thin cortical	4	5.85	2.03	9.68	3.23	8.97	2.40
		Cortical	3	5.59	2.16	9.03	4.27	7.03	1.38
Pits	Length	Cancellous	9	3.51	1.88	5.13	0.81	6.82	2.11
		Thin cortical	7	3.02	1.95	4.09	0.81	3.93	1.16
		Cortical	19	3.06	2.53	3.59	1.62	5.51	1.10
	Breadth	Cancellous	8	3.22	1.56	4.88	0.73	6.67	1.99
		Thin cortical	7	2.42	1.60	3.25	0.80	3.44	0.89
		Cortical	19	2.50	2.02	2.98	1.25	4.75	1.00
Scores	Breadth	Cancellous	15	3.82	2.96	4.68	1.57	7.30	1.55
		Thin cortical	13	2.06	1.13	3.00	0.64	6.52	1.55
		Cortical	8	3.37	2.22	4.51	1.57	6.22	1.37
<i>Lynx pardinus spelaeus</i>									
Punctures	Length	Cortical	1	0.95	—	—	—	—	—
	Breadth	Cortical	1	0.93	—	—	—	—	—
Pits	Length	Cortical	3	1.37	—	—	0.83	2.00	0.59
	Breadth	Cortical	3	0.81	—	—	0.65	1.12	0.27
Scores	Breadth	Cortical	1	0.11	—	—	—	—	—
<i>Vulpes vulpes</i>									
Punctures	Length	Cortical	2	2.40	—	—	2.06	2.74	0.48
	Breadth	Cortical	2	2.03	—	—	1.72	2.33	0.43
Pits	Length	Cortical	3	1.20	—	—	0.95	1.61	0.36
	Breadth	Cortical	3	1.05	—	—	0.82	1.43	0.33

Wolves modify carcasses in advanced stages that include fracturing the bones in order to consume the marrow (Binford, 1981; Haynes, 1982, 1983; Fosse et al., 2004, 2012; Sala et al., 2014). Generally, wolves tend to create numerous tooth marks when consuming prey, especially on the cortical areas of long and flat bones (Sala et al., 2014). The most common types of alteration produced by wolves are pits and scores, especially in the long bone diaphysis (Binford, 1981; Haynes, 1982; Fosse et al., 2004; Yravedra et al., 2011; Sala et al., 2014). However, furrowing with pitting and punctures are common on long bone epiphyses. In flat bones, tooth marks are generally most abundant in the cortical bone because the spongy bone is almost entirely consumed (Sala et al., 2014).

The Sima de los Huesos samples are characterized by the presence of light to moderate furrowing in long bones epiphysis and axial skeleton, but some scores, pits and punctures are also recorded. The location of teeth marks on certain elements is either a function of early access to largest muscle masses (femur, humerus), implying fresh-carcass access, or of later access to defleshed but still greasy skeletal parts. The epiphyses of femora, humeri, and other large elements retain grease longer than ribs. The presence of tooth marks is not usually associated with fracture edges, and the long bone ends are usually preserved. This fact allows us to rule out canids as wolves as the carnivore responsible for bone

modification. Isolated punctures in unbroken long bone diaphysis are not present in the SH sample. This fact leads us to suggest that bears could be a good candidate, but we cannot disregard lions as modification agents. These results contrast with the work of Andrews and Fernández-Jalvo (1997). As previously mentioned, bone damage depends on several environmental factors, so we will focus on the metric analysis to avoid possible misinterpretations.

Until now, it was thought that the hominin and bear sample of SH was modified by different carnivores (Andrews and Fernández-Jalvo, 1997: 215). For these authors, tooth marks in SH are interpreted as having been produced by two types of carnivores: a small canid (the size of a fox), which affected the extremities of the human fossils in particular, and lion, which had a particular impact on the axial skeleton of the human fossils. These authors also rule out the possibility that bears modified human bones at SH, but elsewhere they state that the size of the tooth mark on *Ursus deningeri* appears to remain consistent with the dentition of other bears (Andrews and Fernández-Jalvo, 1997). To test this initial hypothesis, we compared the tooth mark dimensions in human and bear samples. In order to carry out metrical comparisons, some authors group pits and punctures together since they correspond to the same mechanical effect (Pobiner, 2007; Sala and Arsuaga, 2013; Saladié et al., 2013). However, other authors consider only pits

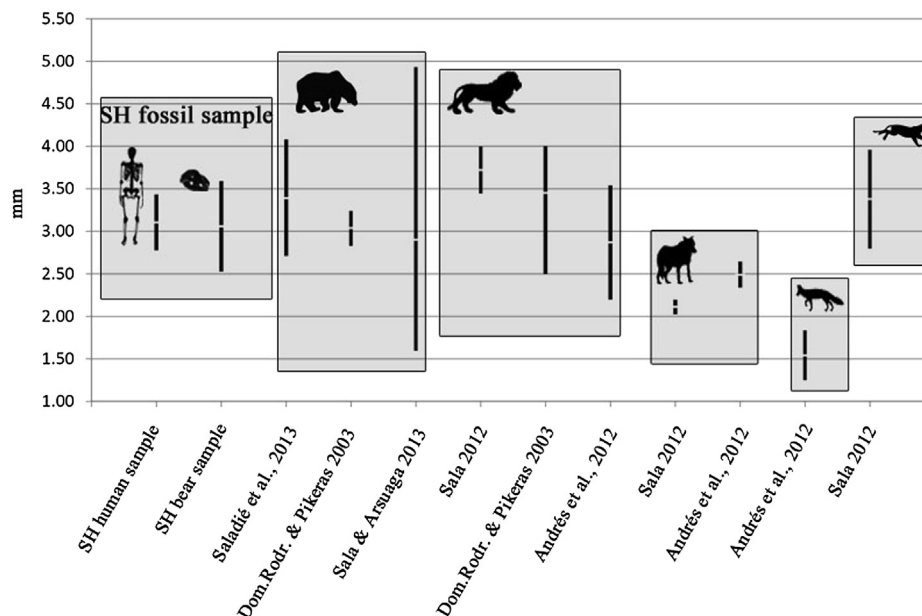


Fig. 6. Mean values and 95% confidence intervals of tooth pit length on dense shafts of SH sample (left) and other taxa (from left to right: bear, lion, wolf, fox and jaguar).

(Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés et al., 2012). In this work, we evaluate the two options in order to reduce the occurrence of possible methodological errors (Table 4). Moreover, we made the comparison using maximum and minimum measurements of pits and punctures between human and ursid fossils (Fig. 7). As shown in Table 4 and Fig. 7, no statistical differences were found between human and ursid samples when taking into consideration all the possible parameters and methodologies. Therefore, metric criteria do not suggest that different carnivores were responsible for the modifications observed on the human and bear fossils; thus, we have no reason to believe that the carnivores responsible for modifying the hominin and bear bones from SH belonged to different species. These results are in stark contrast with the work of Andrews and Fernandez-Jalvo (1997: 215) as was previously discussed.

In order to discriminate which carnivore (bear or lion) was mainly responsible for modifying the SH sample, metric characteristics of the tooth marks were analysed, and the results indicate that the carnivores are most likely to have been bears. Once again, we consider only pits (Fig. 6) and pits and punctures together (Table 4).

Significant differences are found in at least one metric characteristic between tooth marks in the SH sample and those produced by all the modern carnivores except ursids (Table 4). Similarly, the dimensions of tooth marks on the *U. deningeri* fossils from SH differ significantly from those produced by modern wolves and lions, but not bears (Table 4). Therefore, metric data combined with

observations of bone modification patterns allow us to suggest that bears are the main party responsible for the bone modification in both SH assemblages, bears and hominins. This is consistent with evidence that bears account for the most abundant carnivore remains at the site. Furthermore, there is evidence from claw marks documented on the cave wall that bears survived inside the chamber (Arsuaga et al., 1997). The results of the present analyses of both human and bear fossils indicates that carnivore modification of the SH assemblage seems to correspond to bear activity. In any case, neither lions nor bears transport bones or accumulate bones in their dens and, therefore, the accumulation of bones at SH would not be related to carnivore activity.

In the case of the small carnivores recovered from SH, the metric data indicate that tooth marks located on lynx and fox remains are much smaller than is the case for hominin and ursid remains. However, little more can be said about the tooth marks on these small carnivore remains given the scarcity of data available. Future findings will help to elucidate the origin of the carnivore marks found on the bones of these species.

How the human bodies arrived in this small chamber has been one of the most debated issues related to the formation of this site, and three different hypotheses have been proposed: i) a catastrophic event (Díez, 1990; Aguirre, 2000a,b); ii) the combined intervention of three agents: humans (collector agent), carnivores (transport agent) and mass transport as mud flow (reworking agent) (Andrews and Fernández-Jalvo, 1997; Fernández-Jalvo, 2003) and iii) the intentional accumulation of corpses inside the chamber (Arsuaga et al., 1990, 1997; Arsuaga and Martínez, 2004).

Table 4
Results of Mann Whitney *U*-tests for differences between the mean dimensions of tooth marks in the human and bear samples and those from experimental data from living carnivores. Bold indicates statistically significant differences at $p < 0.05$.

	U Mann–Whitney test						
	SH Homo – SH <i>U. deningeri</i>	SH Homo – <i>U. arctos</i>	SH Homo – <i>P. leo</i>	SH Homo – <i>C. lupus</i>	<i>U. deningeri</i> – <i>U. arctos</i>	<i>U. deningeri</i> – <i>P. leo</i>	<i>U. deningeri</i> – <i>C. lupus</i>
Pits and punctures length cortical	0.81	0.09	0.00	0.00	0.19	0.04	0.00
Pits and punctures length cancellous	0.32	0.22	0.02	0.00	0.10	0.52	0.00
Pits length cortical	0.85	0.23	0.00	0.00	0.33	0.06	0.02

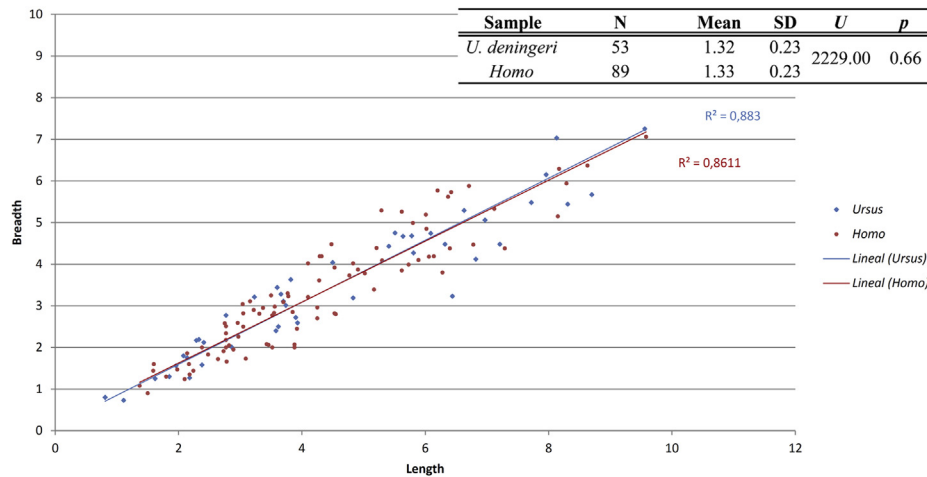


Fig. 7. Relationship between maximum and minimum size of tooth marks (pits and punctures) in the bear and human samples from SH.

With the present data, we can discard the second scenario. To achieve a more complete understanding of how the hominin fossils accumulated in the SH site, progress in other taphonomical aspects is necessary (e.g., spatial distribution of the fossils in the site, skeletal part representation, surface modifications and bone breakage), but so far, based on the bone modification we can rule out carnivores as the main agency for the hominin accumulation.

5. Conclusions

The results show that evidence of carnivore activity in the SH sample is of very low frequency indicating only sporadic carnivore activity at the site, in contrast with the results of previous studies. The comparison of bone modification patterns from SH with actualistic carnivore data suggests that the carnivore modification of both human and bear bones at SH most likely corresponds to bear activity. Due to the fact that bears do not transport carcasses into cave dens, the origin of the accumulation of human bodies must have a different explanation. Other possible origins of the accumulation of human corpses in SH will be analysed in forthcoming studies, but for now, we can rule out carnivores as taphonomical agents on the bone accumulation at SH.

Acknowledgements

This study was possible thanks to the Atapuerca excavation team, especially those involved in the excavations at the Sima de los Huesos site. The research was funded by the MINECO Project CGL2012-38434-C03-01 and by the Fundación Atapuerca (Post-doctoral grant to Nohemi Sala). We are indebted to many people that have allowed us access to important skeletal collections under their care and kindly provided their help, particularly Gary Haynes, Curtis Marean and Mary Stiner. Thanks to Lauren Ames, Mario Alcolea and Emma Pomeroy for the English revision of the manuscript. A. Gracia-Téllez has a Contract-Grant from the Ramón y Cajal Program, RYC-2010-06152. I. Martínez and A. Gracia are member of the “Human evolution and Quaternary Paleoenvironmental Reconstruction” UAH Research Team. Thanks also to the BBP group for their support and discussions.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2014.05.004>.

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