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Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: Faunal study of Mousterian levels (MIS 3)

Activités de Néandertaliens et carnivores dans la grotte de Llonin, Asturies, Nord de la péninsule Ibérique : étude de la faune des niveaux moustériens (MIS 3)

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ABSTRACT

This paper presents a study of the macromammalian fauna recovered from Mousterian levels of Llonin Cave. The sample is highly heterogeneous and comprises six species of ungulates, including *Rupicapra pyrenaica*, *Capra pyrenaica*, and *Cervus elaphus*, and seven species of carnivores, predominantly *Ursus spelaeus*, *Crocuta spelaea*, *Canis/Cuon* and *Panthera pardus*. The archaeozoological and taphonomic study of the remains shows preferential use of basal levels of the cave as a den for hyenas and leopards. Neanderthals were also present during this phase and they would have acted mainly on deer and some caprines, while the action of hyenas would mainly have been linked to scavenging of elements left by humans and the introduction of bear remains. Leopards would have transported caprines in order to consume them. The study of several coprolites confirms that hyenas and leopards were

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Middle Palaeolithic
Hyenas
Leopards

the main occupants of the cave. The information from the animals processed by humans together with other archaeological evidence and the intervention of various carnivores in these basal levels enables us to characterise a palimpsest of occupations that would have been short and sporadic in the case of humans.

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R É S U M É

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Nous présentons ici les résultats de l'étude de la faune de macro-mammifères récupérée dans les niveaux moustériens de la grotte de Llonin. Très hétérogène, l'échantillonnage est constitué de six espèces d'ongulés, parmi lesquelles *Rupicapra pyrenaica*, *Capra pyrenaica* et *Cervus elaphus*, et de sept espèces de carnivores, où prédominent *Ursus spelaeus*, *Crocuta spelaea*, *Canis/Cuon* et *Panthera pardus*. L'étude archéozoologique et taphonomique des restes détermine une utilisation préférentielle de la cavité dans les niveaux de base comme tanière de hyènes et de léopards. Les Néandertaliens sont également présents au cours de cette phase et agissent principalement sur le cerf et quelques caprins, alors que l'action de l'hyène est essentiellement liée à la consommation de charognes abandonnées par les humains et à l'introduction des restes d'ours. Le léopard transporte les caprins pour les consommer. L'étude de plusieurs coprolithes confirme que l'hyène et le léopard étaient les principaux occupants de la cavité. Grâce aux informations issues de la faune transformée par les humains, à d'autres preuves archéologiques et à l'intervention de plusieurs carnivores dans ces niveaux de base, on peut caractériser un palimpseste d'occupations qui, dans le cas des humains, seraient brèves et sporadiques.

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1. Introduction

Over time, caves can act as large containers of animal bones. In caves that are considered archaeological sites due to the presence of lithic records or other human evidence, the faunal remains may be from a variety of origins. In addition to humans, different cave-dwelling carnivorous mammals or birds of prey would have frequented these enclaves in search of shelter, a breeding area or a place to transport and consume prey (Andrews, 1990; Bourdillat, 2014; Brugal, 2010; Brugal and Fosse, 2004; Fosse, 1995). The eco-ethological characteristics of the various actors are fundamental when assessing the ability to accumulate and modify bone remains (Binford, 1981; Brugal and Fosse, 2004; Domínguez-Rodrigo, 1993). Sometimes, in addition to the prey they brought in, the skeletons of the carnivores themselves can also be found in the caves, as they would have been places of life and death. This may be the case of the basal levels of Llonin Cave, where the bone accumulations are due to different occupation events and the activities carried out by humans and carnivores. All of this suggests a complex taphonomic history at the beginning of the sequence. It is a model that has already been described for other sites in the Iberian Peninsula and specifically for the upper Pleistocene in Cantabrian region, such as A Valiña (Fernández Rodríguez, 2010), El Esquilleu (Yravedra, 2013) and Amalda (Altuna, 1990; Yravedra, 2006a, 2013), among others.

In this paper, we present the results of the archaeological and taphonomic study of macromammalian fauna from levels VIII (*Cono Posterior*) and VI (*Galería*) of Llonin. On the one hand, the main objective has been to determine the role of humans in their formation,

define the occupation pattern of the cave and obtain information about the animal-based subsistence model of Neanderthals in this Cantabrian region. On the other hand, in the case of carnivores, the intention has been to verify their importance in this phase and the reason for their presence in the cave and to determine their impact on the accumulation and modification of the bone assemblages.

2. Llonin Cave

Llonin Cave is located on the eastern edge of Asturias in the municipality of Peñamellera Alta, in the basin of the rivers Cares and Deva, surrounded by a mountainous landscape. Along the axis created by the aforementioned rivers there are another thirteen caves and shelters with rock art. The entrance lies 112 masl, 23 m above the stream of La Molinuca, its nearest drainage point, and 18 km from the Cantabrian Sea. Its orientation is ENE. After a small vestibule, the cave forks into two parts: the right-hand one leads to a narrow gallery ending above the principal panel and the left-hand one enters a large, fairly high chamber with an enormous debris cone (Fig. 1). This entrance was almost completely blocked by archaeological and calcite deposits until it was opened up in 1957.

The research carried out has made it possible to exhume a significant archaeological and parietal and portable art record (Fortea, 2001; Fortea et al., 1992, 1995, 1999, 2007; González Pumariega, 2007; Rasilla, 2014; Rasilla and Santamaría, 2011–2012; Rasilla et al., 2014, 2016; Ríos González et al., 2007). The archaeological sequence contains Mousterian, Gravettian, Upper Solutrean,

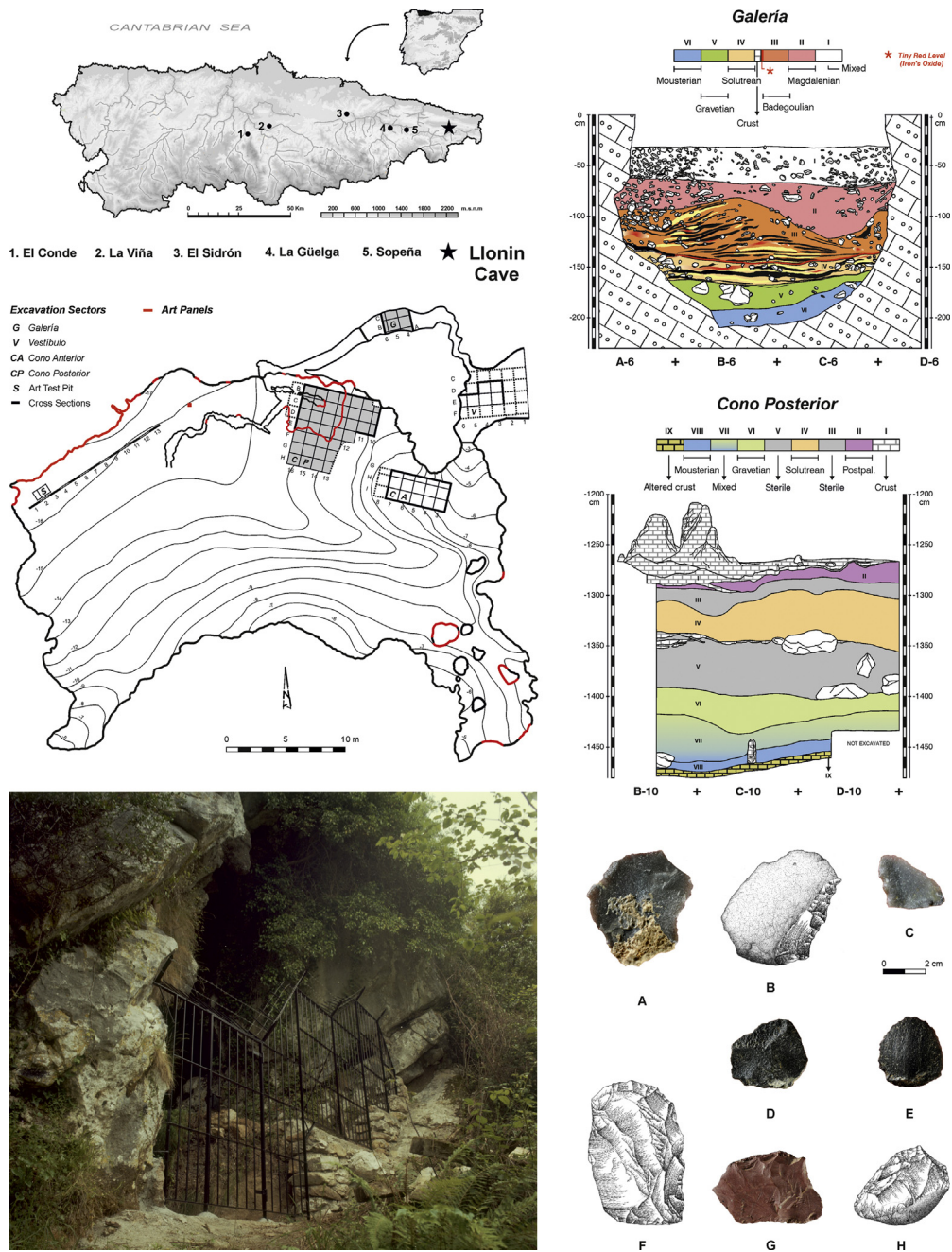


Fig. 1. Top left: situation of the cave and the main Mousterian sites in Asturias. Middle left: plan and location of the excavation and parietal art sectors (study areas shown in grey). Bottom left: view from the entrance and vestibule. Photo: J. Fortea. Top right: stratigraphic cross-section of the *Galería* (G). Middle right: stratigraphic cross-section of the *Cono Posterior* (CP). Bottom right: Llonin Mousterian lithics. Level VIII (CP): A. Subradial flake with concretion; B. Sidescraper-denticulate; C. Fragment of convergent sidescraper. All in quartzite. Level VI (Galería): D. Subradial flake; E. Retouched flake (Kombewa type); F. Endscraper and sidescraper-denticulate; G. Splintered piece; H. Sidescraper. All in quartzite except G, which is radiolarite flynt. Drawings: E. Duarte. Photos: A, D and E, Elsa Duarte; C and G, Marco de la Rasilla.

Fig. 1. En haut à gauche : situation de la grotte et des principaux sites moustériens des Asturies. Au milieu à gauche : plan et emplacement des secteurs de fouilles et d'art pariétal (zones d'étude en gris). En bas à gauche : vue de l'entrée et du vestibule. Photographie : J. Fortea. En haut à droite : coupe stratigraphique de la galerie (G). Au milieu à droite : coupe stratigraphique du cône postérieur (CP). En bas à droite : pièces lithiques moustériennes de Llonin. Niveau VIII (CP) : A. Éclat subradial concrétionné ; B. Racloir-denticulé ; C. Fragment de racloir convergent. Toutes les pièces sont en quartzite. Niveau VI (galerie) : D. Éclat subradial ; E. Éclat retouché (type Kombewa). F. Grattoir et racloir-denticulé. G. Pièce esquillée ; H. Racloir. Toutes les pièces sont en quartzite, sauf G en radiolarite. Dessins : E. Duarte. Photographies : A, D et E, Elsa Duarte ; C et G, Marco de la Rasilla.

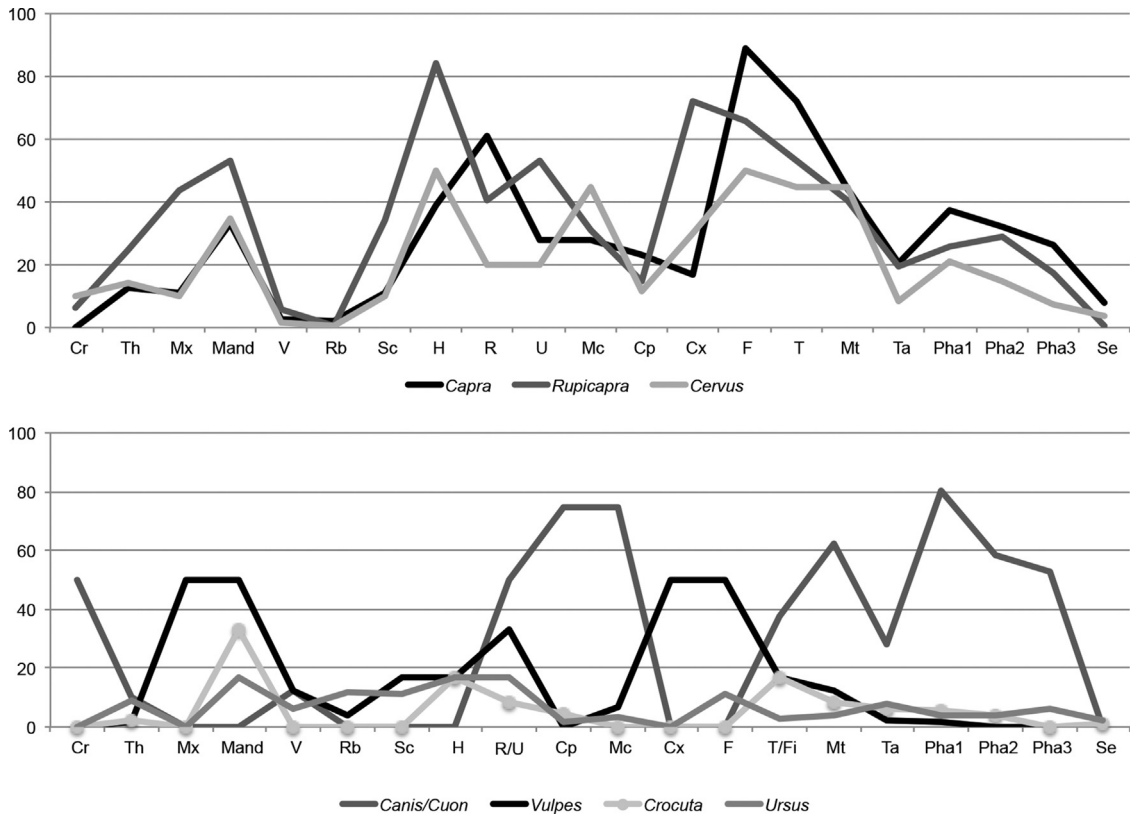


Fig. 2. Anatomical representation (% Surv) of the main species of ungulate and carnivore from level VIII (CP).
Fig. 2. Représentation anatomique (% Surv) des principales espèces d'ongulés et de carnivores du niveau VIII (CP).

Badegoulian, Middle and Upper Magdalenian, Azilian and Bronze Age remains, distributed throughout the *Galería* (G), the *Vestíbulo* (V) and the *Cono Anterior* (CA) and *Cono Posterior* (CP) (Fig. 1).

Mousterian archaeological evidence is scant, in both G and CP, which indicates sporadic presence in the cave. However, while G was accessed via the main entrance, CP was accessed via a separate entrance, which is now impassable, situated several metres below the current entrance (Fortea et al., 1992, 1995, 1999; Rasilla and Santamaría, 2011–2012). This is also confirmed, even for the Gravettian archaeological record, by the fact that the parietal art of that cone and of the intermediate panels followed the slope of the debris cone as the archaeological levels built up (Fortea et al., 2004). The basal levels (VIII of CP and VI of G) present a scant lithic collection that is characteristic of the Mousterian Period (Fig. 1). Unfortunately, in CP there is also one level (VII) that is mixed with materials typical of the Mousterian (VIII) and Upper Palaeolithic/Gravettian (VI), which we did not analyse so as not to distort the results (Rasilla and Santamaría, 2011–2012: 34–38). We also have some problematic radiocarbon dating (Rasilla and Santamaría, 2011–2012: 38). However, we have a new dating of CP level VIII (deer ulna with cut marks) carried out by ultrafiltration at the Australian National University’s Research School of Earth Sciences. The result of the dating (43.539 ± 2419 BP) confirms that the level belongs to the Mousterian (MIS 3).

The environmental characterisation of the sequence is currently in progress. Micromammal, bird and anthracology studies provide preliminary information about the context. With regard to micromammals, there are data on a sample of 353 molars. In both sectors (VIII CP, VI G) the *Microtus agrestis–arvalis* group is particularly notable. Other well-represented species include *Sorex araneus–coronatus*, *Microtus lusitanicus*, *Pliomys lenki*, *Arvicola sapidus*, *Arvicola terrestris*, *Talpa europaea*, and *Apodemus flavicolis*, and to a lesser extent *Microtus oeconomicus*, *Chionomys nivalis*, *Eliomys quercinus*, *Galemys pyrenaicus*, and *Sorex minutus*. Most of these species frequent low-density forests with abundant undergrowth and open areas such as meadows, grasslands and rushes. They require humid environments, in terms of both soil and atmosphere, inhabiting mild Atlantic or Central European climates. The appearance of semiaquatic or riparian species such as *Galemys pyrenaicus* and *Arvicola sapidus* is linked to permanently wet areas. This association has been established for some levels of other upper Pleistocene Cantabrian sites, such as Askondo Cave (García-Ibaibarriaga et al., 2015), Cobrante Cave (Sesé, 2009), Castillo Cave (Sesé, 2017), and Coimbre Cave (Iriarte-Chiapusso et al., 2017).

The collection of birds found in level VIII (CP) consists of 405 remains, predominantly corvids (58% of the NISP), and in particular choughs (36%), of which

Pyrrhocorax pyrrhocorax is the main taxon. The composition is similar to that of other contemporary Cantabrian sites (Elorza, 1990; Moreno-García, 2017; Núñez-Lahuerta et al., 2018). The species identified still inhabit this area today, with exception of *Lagopus lagopus*, which is now confined to northern Europe (Lagerholm et al., 2017). Although its presence in Llonin may suggest there would have been a colder climate, it is a taxon that would have been almost cosmopolitan throughout the Upper Pleistocene (Tyrberg, 2007) and is poorly represented at the site. The remainder of the collection is typical of the upper Pleistocene in northern parts of the Iberian Peninsula, with a predominance of *Pyrrhocorax* (Núñez-Lahuerta et al., 2018). No anthropogenic modifications have been observed, although some remains show signs of other predators. The presence of ribs, vertebrae and skull fragments suggest a natural accumulation, although it is necessary to complete the taphonomic study in order to determine the origin of these accumulations. The assemblage from level VI (G), consisting of 37 remains, confirms the importance of corvids, especially *Pyrrhocorax*.

The picture provided by micromammals and birds is consistent with the initial results from the anthracological analysis, which has so far focused on level VI (G). The *Cono Posterior* has not yielded any charcoal remains, despite the sampling efforts carried out, which is probably due to the different formation of the deposits. The woody flora identified in level VI (G) shows the predominance of Rosaceae such as *Sorbus*, accompanied by Scots pines (*Pinus* sp. *sylvestris*), birch (*Betula* sp.) and a layer of Fabaceae shrubs. This assemblage involves the existence of open forests, with heliophilous and pioneer vegetation, consistent with other anthracological studies in the region (Rasilla et al., in press; Uzquiano, 2005). The sporadic presence of mesophilic taxa (*Alnus-Corylus*, deciduous *Quercus* sp. and *Salix* sp.) may be associated with more protected areas in the bottom of the valley. The predominance of open formations with heliophilous and frugal species (some of which prefer a cold climate, as is the case of Scots pines (*Pinus* sp. *sylvestris*) whose current optimum environment is montane and subalpine zones, with dry summers and a markedly continental climate) suggests that the conditions in the surroundings of Llonin would have been cooler and more arid during the Mousterian period.

3. Methods

Two sieves were used to recover the archaeological material from Llonin, with a mesh size of 2.38 mm and 1.41 mm, respectively. The taxonomic identification of the macromammal remains was carried out using the collections of the Museu de Prehistòria de València (Gabinet de Fauna Quaternària Innocenci Sarrión), Instituto Pirenaico de Ecología, Museo Anatómico de la Universidad de Valladolid and Estación Biológica de Doñana. The bears found at Llonin belong to the species *Ursus spelaeus*, as shown by the robustness of their metacarpal I, compared with the gracile nature of these elements in *U. arctos* (Torres, 1988: 122–123). Indeterminate remains were assigned to different weight categories (very small, small, medium and large). They were quantified in terms of number of

identified specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI). The MNE has been calculated based on the number of epiphysis and diaphysis, as well as the laterality and the fusion pattern of the articulations. The skeletal survival rate (%Surv) was calculated in accordance with Brain (1981). To determine the role of differential preservation in the formation of the assemblage, a Pearson correlation coefficient was applied for deer (Kreutzer, 1992) and caprines (Lyman, 1994). The ages at death were established from the state of tooth eruption and wear or joint fusion. For the hyena the study by Fourvel (2012) was used, which compiles the data from several authors regarding tooth eruption and wear in current and fossil hyena populations. For the bear, owing to the lack of molars and the abundance of incisors, four age classes were considered (Fourvel et al., 2014): juveniles (deciduous or emerging permanent teeth), subadults (unworn permanent teeth), adults (partially worn permanent teeth) and seniles (advanced wear of permanent teeth). For the leopard the age was inferred from the state of the teeth (Stander, 1997). For the fox the analysis was based on the tooth eruption and wear sequence compiled by Hillson (1986) and the information about joint fusion compiled by Harris (1978). For the wolf/dhole the pattern of tooth wear used was by Gipson et al. (2000). For the chamois age was estimated based on tooth eruption and wear (Pérez Barbería, 1994; Pérez Barbería and Mutuberría, 1996). For the Iberian ibex age was established by tooth eruption and wear (Payne, 1987; Pérez Ripoll, 1988) and joint fusion (Serrano et al., 2004). In the case of caprines, according to information from current Pyrenean populations, four age groups were considered: very young or kid aged 0–1 years, young or primal aged 1–2 years, subadult aged 2–4 years, adult aged > 4 years (Ricardo García, personal communication). For the deer Mariezkurrena (1983) and Azorit et al. (2002) were followed for tooth eruption and wear, and Mariezkurrena (1983) for joint fusion. It was not possible to determine the sex in caprines and deer according to the proposed methods (for example, Altuna, 1978; Arceredillo et al., 2011; Mariezkurrena and Altuna, 1983) due to the low number of bones with measurable sexual dimorphism. In order to ascertain the relative abundance of carnivores, the rate of carnivorism was estimated according to MNI (Klein and Cruz-Urbe, 1984). Different types of modifications caused by the dental action of carnivores were considered: notch, score, pit, puncture, crushing, furrowing, crenulated edges and bone loss, according to the definitions proposed by Binford (1981), Brain (1981), Haynes (1980, 1983), Sala (2012) and Sala and Arsuaga (2018). The effect of digestion on the bones was also considered (Esteban-Nadal et al., 2010; Fosse et al., 2012; Horwitz, 1990; Sutcliffe, 1970). In order to estimate the size of the carnivore responsible for the bite marks the pits/punctures on cortical and cancellous bone tissue were measured (length and width) and the measurements were compared with the data published by Andrés et al. (2012), Delaney-Rivera et al. (2009), Domínguez-Rodrigo and Piqueras (2003), Saladié et al. (2013), and Selvaggio and Wilder (2001). The measurements were taken using digital callipers and are expressed in millimetres. The work of Villa and Mahieu (1991) was used to identify the origin

of the fractures. The degree of fracturing was measured by estimating the circumference preserved (C1: 1–25%; C2: 26–50%; C3: 51–75%; C4: 76–100%) of the remains with and without the joint. The degree of fragmentation was established according to Bunn (1983). The distinction between accumulations created by different carnivores and those of human origin was established according to the criteria proposed by Cruz-Urbe (1991), Domínguez-Rodrigo (1994a, b), Domínguez-Rodrigo and Pickering (2010), Domínguez-Rodrigo et al. (2012), Fosse (1997), Fosse et al. (2012), Fourvel (2012), Fourvel et al. (2014), Kuhn et al. (2010), Pickering (2002), Ruiter and Berger (2000), Sala (2012), Sauqué and Sanchis (2017), Sauqué et al. (2014, 2017a), and Yravedra (2006a). With regard to anthropic modifications, cut marks and percussion impacts were identified (Binford, 1981; Capaldo and Blumenschine, 1994; Shipman and Rose, 1984).

We undertook macroscopic analyses of sixteen coprolites recovered from level VIII following the methods described in Sanz et al. (2016). Every specimen was measured for classes of preservation, volume, shape of the extremities, texture, hardness and maximum length and width or diameter. Micromorphological analyses of thin sections were performed on the four tubular-shaped coprolites from level VIII. The coprolites (samples named TC1, TC2, TC3, and TC4) were embedded in epoxy resin, cut with an IsoMet low speed saw, mounted on glass slides, cut to a thickness of 1 mm, and then polished to 30 μm . After preparation, the slides were scanned on a flatbed scanner at a high resolution (1200 dpi) in reflected light to allow detailed observations at mesoscopic level (Arpin et al., 2002). Microscopic analysis was then performed using a polarising microscope (Nikon AZ100) at $\times 20$, $\times 100$, $\times 200$ and $\times 400$ magnifications under plane polarised light (PPL) and cross polarised light (XPL) for the observation of isotropic and anisotropic materials. Microphotographs were taken using a Nikon DS Fi2 camera. Micromorphological descriptions were carried out following the guidelines by Bullock et al. (1985) and Stoops (2003), whereas the interpretative concepts were taken from Courty et al. (1989) and Stoops et al. (2010).

4. Archaeozoological and taphonomic study

4.1. Species and age structure

Level VIII (CP) yielded 6122 remains, of which 2503 (40.9%) have been identified (Table 1). The remaining 59.1% are elements assigned to size groups, with a predominance of medium-sized elements. About ungulates, according to %NISP, the most numerous are chamois (21.9%), Iberian ibex (10.8%) and deer (8.6%). The presence of equids, bovines and roe deer is scant. The carnivore group is even more heterogeneous, comprising wolf/dhole (6.2%), bear (5.6%), leopard (4.4%), fox (2.1%), hyena (0.9%) and wild cat (<0.1%), as well as a collection of coprolites (11.1%). The presence of birds (16.2%) and other small animals (0.6%) has also been recorded. The MNI confirms chamois (27.4%) as the predominant taxon, while deer (16.1%) exceeds Iberian ibex, which shares third position with bear (14.5%).

Table 1

Species represented according to NISP and %NISP.

Tableau 1

Espèces représentées selon le NISP et le % de NISP.

Taxa	VIII Cono Posterior	VI Galería		
Equidae	2	0.1		
<i>Bos/Bison</i>	3	0.1	1	0.4
<i>Capra pyrenaica</i>	270	10.8	14	5.7
<i>Rupicapra pyrenaica</i>	548	21.9	100	40.5
Caprinae	216	8.6	40	16.2
<i>Cervus elaphus</i>	216	8.6	13	5.3
<i>Capreolus capreolus</i>	7	0.3		
Cervidae	15	0.6	7	2.8
Total ungulates	1277	51.1	175	70.9
<i>Ursus spelaeus</i>	141	5.6	1	0.4
<i>Crocota spelaea</i>	22	0.9		
<i>Panthera pardus</i>	110	4.4	4	1.6
<i>Felis silvestris</i>	1	0.0		
<i>Canis lupus</i>	21	0.8	5	2.0
<i>Cuon alpinus</i>	2	0.1		
<i>Canis/Cuon</i>	133	5.3	7	2.8
<i>Vulpes vulpes</i>	54	2.1	7	2.8
Carnivora	44	1.7	7	2.8
Coprolites	277	11.1	4	1.6
Total carnivores	805	32.2	35	14.2
<i>Erinaceus europaeus</i>	4	0.1		
Leporidae	1	0.0		
<i>Castor fiber</i>	4	0.1		
<i>Marmota marmota</i>	6	0.2		
Testudines	1	0.0		
Aves	405	16.2	37	15.0
Total small prey	421	16.8	37	
Very small size	1			
Small size	16		1	
Middle-small size	4			
Middle size	3226		82	
Large size	36		3	
Indeterminates	340		371	
Total Indet.	3619		461	
Total	6122		708	

The assemblage from level VI (G) is smaller, with 708 remains, of which 247 (34.9%) have been identified (Table 1). The remaining 65.1% are unidentified elements with a predominance of medium-sized elements. About ungulates, according to %NISP, the most numerous are chamois (40.5%), caprine (16.2%), Iberian ibex (5.7%) and deer (5.3%). The carnivore group is less abundant and comprises wolf/dhole (4.8%), fox (2.8%), leopard (1.6%) and bear (0.4%), in addition to four coprolites (1.6%). Birds are well-represented (15%).

In level VIII chamois is the species with the highest MNI (Table 2), eight immature specimens with deciduous teeth and nine with worn permanent teeth. In the case of Iberian ibex, seven individuals were identified, predominantly animals with permanent teeth, in addition to a very young specimen and another young one. In the case of deer, the teeth show six animals, predominantly very young and young; however, the repetition of certain bones indicates the presence of another five large individuals (adults/subadults). There are one young individual and one adult each of roe deer, bovine and equid show. In level VIII there are three hyena individuals (immature, adult-old and senile). Nine bear individuals were identified, two very young, one subadult, two adult, and four senile. This age structure coincides with the dominance of fused

Table 2

Mortality profiles of ungulates and carnivores from level VIII (CP) and of ungulates from level VI (G). m (months), y (years).

Tableau 2

Profil de mortalité des ongulés et des carnivores du niveau VIII (CP) et des ongulés du niveau VI (G) ; m (mois) et y (années).

Taxa	MNI	Age	Element
<i>VIII Cono Posterior</i>			
<i>Cervus</i> (11)	2	2–3 m	mandible (d3, d4) unworn
	1	5–12 m	M1 unworn
	1	14–15 m	m1 slightly worn, m2 unworn
	1	>25–26 m	maxilla (P2, P3, P4) worn
	1	senile	p2 + p4 highly worn
<i>Capra</i> (7)	5	adult	ossify long bones
	1	6–12 m	mandible (deciduals, m1, m2)
	1	>25 m	p3
	1	1–2 y	m2
	1	2–3 y	mandible (p2–m3)
	1	3–4 y	mandible (p2–m3)
	1	6–8 y	mandible (p2–m3)
<i>Rupicapra</i> (17)	1	4–8 y	m3
	1	2–3 m	maxilla (deciduals, m1)
	3	12–18 m	mandibles with deciduals
	1	22 m	mandible (d4, m1, m2, m3)
	1	22–25 m	mandible (d2, d3, d4, m1, m2, m3)
	1	<25 m	d4
	1	25 m	mandible (d3, d4)
	1	3 y	mandible (p4, m1, m2, m3)
	2	5 y	mandible (p3, p4, m1)
	1	6 y	mandible (p2, p3, p4, m1)
	2	7 y	mandible (p3, p4)
	2	9–12 y	mandible (p3, p4)
	1	>12 y	mandible (p4, m1, m2, m3)
<i>Crocuta</i> (3)	1	young	phalange/metapodia no ossify
	1	6–10 y (class 4)	mandible (premolars worn)
	1	>10–15 y (class 5)	premolars + m1 highly worn
<i>Ursus</i> (9)	2	very young	decidual teeth unworn
	1	subadult	permanent incisives unworn
	2	adult	permanent incisives worn, ossify long bones
	4	senile	I3 and i3 highly worn
<i>Canis</i> (2)	1	ca. 6 y	P4, ossify postcraneal
	1	senile	m2 highly worn
<i>Cuon</i> (1)	1	subadult	permanent teeth unworn
<i>Canis/Cuon</i> (2)	2	adult	ossify postcraneal
<i>Panthera</i> (1)	1	adult	permanent teeth slighworn, ossify long bones
<i>Vulpes</i> (3)	3	8–10 m (phase 1)	P4 unworn, ossify postcraneal
<i>VI Galería</i>			
<i>Cervus</i> (2)	1	5–25 m	D2 worn, M1 not emerged
	1	>32 m	m3 worn
<i>Capra</i> (3)	2	1–2 y	mandible (de3, d4, m1 worn); m1 worn
	1	>2 y	P4 worn
<i>Rupicapra</i> (7)	1	9–18 m	mandible (d2–m1) worn
	2	25–29 m	p2 unworn
	2	>25–29 m	p2 worn
	1	2–3 y	mandible (p2–m3) worn
1	8 y	mandible (p2–m3) highly worn	

bones, except for a distal radius from one immature individual. Their graphic representation shows an attritional profile, where the youngest and most senile are overrepresented in relation to the live population. About other carnivores, a 2.5-year-old leopard, two wolves (adult and senile), one subadult dhole and three adult foxes were identified (Table 2).

Seven chamois were distinguished in level VI, predominantly individuals with functional permanent teeth and one very young individual. The three Iberian ibexes correspond to two subadults and one adult. Deer are represented by two individuals, one young and one adult (Table 2). The scant carnivore remains from level VI yielded one adult

individual of *Canis*, *Canis/Cuon*, *Vulpes*, and *Ursus*, and one young *Panthera*.

4.2. Anatomical representation

According to %Surv, in terms of the main ungulates in level VIII, chamois, Iberian ibex and deer (Fig. 2; Tab. A1), all the anatomical elements are present, though with a bias towards skull, axial skeleton and small bones. On the other hand, we have determined isolated teeth, sternum or sesamoid bones in Caprinae (Tab. A1) and ribs and vertebrae in medium-sized indeterminate animals. In caprines, the limbs are better represented than in deer, especially the

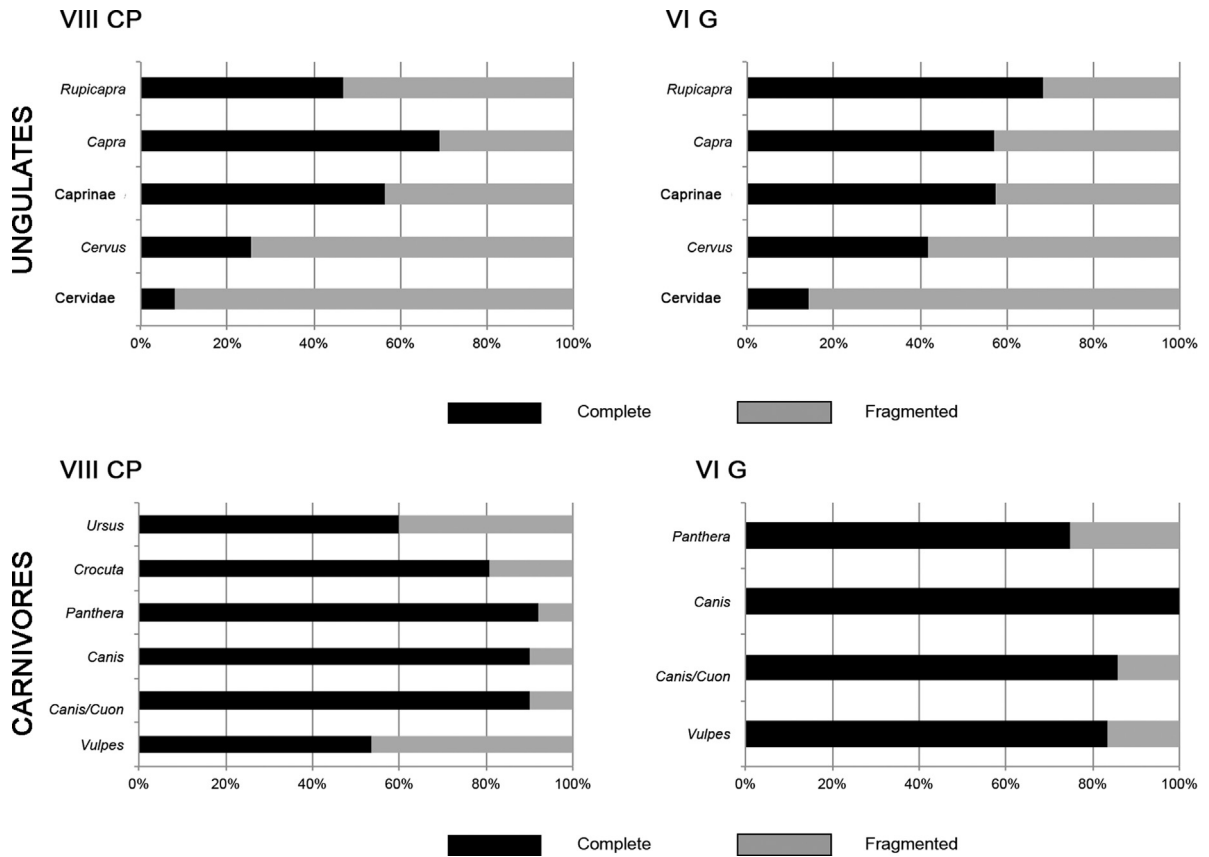


Fig. 3. Level of fragmentation of ungulate and carnivore bones from levels VIII (CP) and VI (G).
Fig. 3. Niveau de fragmentation des os d'ongulés et de carnivores des niveaux VIII (CP) et VI (G).

stylopodium and zeugopodium. In the case of carnivores from level VIII (Fig. 2; Tab. A2), there is considerable bias in all the anatomical groups, except for the leopard, of which there is a semi-complete specimen. The taxonomically and anatomically indeterminate fragments mostly correspond to long bones.

About the elements from level VI, it is difficult to assess their representation due to the small size of the assemblage (Tab. A3, A4). All the anatomical groups are present in the chamois, particularly the skull, based on the abundance of isolated teeth, radius, femur and pelvis; there are few axial elements, as is the case in *Capra* and *Caprinae*. This situation is the same for carnivores.

4.3. Fragmentation and origin of the fractures

There is a clear dichotomy in the levels of fragmentation of caprines (30–50%) and deer (>70%) from level VIII. In both cases, the values of fresh fractures are far higher than fractures on dry bone. In the ungulates from level VI, the above-described pattern for deer and caprines is repeated. The carnivores from level VIII present very few fragmented bones (10–20%), with higher values for bears (40%) and foxes (50%). The fractures in carnivores are mostly post-depositional, except in the case of bears, where

the fractures mostly occurred on fresh bone. The carnivore remains from level VI are quite complete (Fig. 3; Table 3).

Fracture morphotypes are described for long bones in the main ungulates and bear from level VIII (Figs. 4 and 5). Diaphyseal fragments with and without complete circumference, distal fragments with complete circumference, and proximal fragments with complete and incomplete circumference are represented for caprines. For deer, however, a greater proportion of diaphyses with incomplete circumference is observed and there are no cylinders. The bear remains show diaphyses and articular areas with the complete circumference. In general, a pattern of greater fragmentation is observed in ungulates and bears whereas greater preservation is noted in other carnivores.

4.4. Surface modifications

In level VIII 403 remains were identified, with 603 modifications (Table 4), mostly on ungulates (192 remains/320 modifications) and indeterminate species (173/218), primarily medium-sized fragments, and to a lesser extent on carnivores (38/65). Modifications due to the action of carnivores are the most abundant (480), followed by anthropogenic (92) and indeterminate (31) modifications. The latter correspond mainly to notches, which may have been produced by humans or other predators.

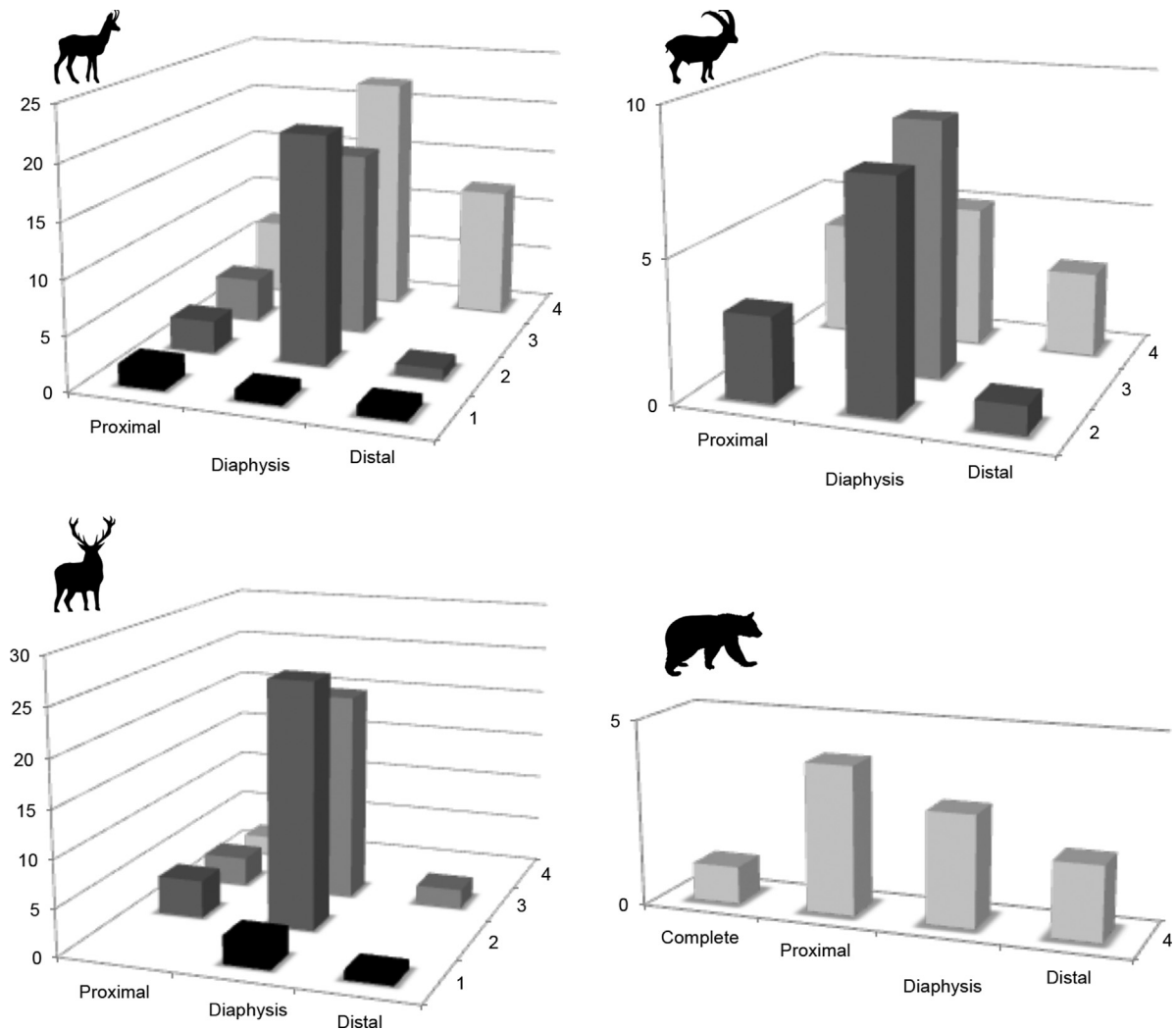


Fig. 4. Fracture morphotypes on the long bones of *Rupicapra*, *Capra*, *Cervus*, and *Ursus* from level VIII (CP).
Fig. 4. Morphotypes de fractures sur les os longs de *Rupicapra*, *Capra*, *Cervus* et *Ursus* du niveau VIII (CP).

Carnivore marks mostly appear on ungulate bones (52.9%) (Fig. 6), although also on those of carnivores (13.3%) and indeterminate remains (33.8%), mainly medium-sized. Marks of this type are related to dental action (76.7%) and digestion (23.3%). Chamois bones are the most affected by carnivore bite marks, particularly elements of the stylopodium and girdles, where the largest muscle bundles are found: humerus (18.1%), femur (12.7%), scapula (11.4%) and pelvis (12%); lower values for vertebrae (6.6% cervical, 1.2% thoracic and 2.4% sacrum), tibia (6.6%), ulna (6%), metapodial (4.8%), talus (3%), mandible (1.8%), radius, calcaneus and third phalanges (all three with 0.6%) (Table 5). As regards chamois bones, the most notable modifications are pits, punctures, scores and crenulated edges, which account for 72.9% (Table 4). On a total of 66 chamois remains, most of them show one (36.4%) or two (27.3%) modifications per bone; 16.7% present three, 12.1% four, 4.5% five and 3% between 6 and 8 modifications. The action

of carnivores also appears on other ungulates, although on a lower number (*Caprinae*, *Capra*, *Cervus*, and *Capreolus*). In Iberian ibex bite marks are particularly found on the stylopodium, zygopodium, mandibles and cervical vertebrae; on 15 bones, most show one (40%) or two (53.3%) modifications, and only 6.7% show three on the same remains. On a total of 11 deer bones with bite marks, most have one modification (72.7%), 18.2% have two and 9.1% have three. There are few bite marks on deer and they appear particularly on the vertebrae (40% on thoracic and 13.3% on cervical vertebrae).

The bear is the carnivore with the greatest number of modifications (Fig. 7). Particularly notable modifications are pits and crenulated edges associated in some cases with furrowing and with the disappearance of articular areas (scooping out), as well as scores, but there are no digested remains (Table 4). The most bitten bones are ribs (40.7%) with 35.2% of the marks, femur and ulna with

Table 3
Origin of fractures of ungulate and carnivore bones from levels VIII (CP) and VI (G).

Tableau 3
Origine des fractures des os d'ongulés et de carnivores du niveau VIII (CP) et VI (G).

Taxa	NISP	Complete	Fragmented			
			Recent	Fresh	Dry	Indet.
<i>VIII Cono Posterior</i>						
<i>Rupicapra</i>	548	233	55	110	18	132
<i>Capra</i>	270	173	19	41	8	29
Caprinae	216	107	26	20	5	58
<i>Cervus</i>	216	53	8	94	1	60
<i>Capreolus</i>	7	2		4		1
Cervidae	14	1	1	9		3
<i>Bos/Bison</i>	3	2				1
Equidae	2					2
Total	1276	571	109	278	32	286
<i>Ursus</i>	141	75	16	20	2	28
<i>Crocuta</i>	21	17		2		2
<i>Panthera</i>	95	80	8	1	4	2
<i>Canis</i>	21	18	1	1		1
<i>Cuon</i>	2	2				
<i>Canis/Cuon</i>	133	110	11	2	5	5
<i>Vulpes</i>	54	22	13	5	7	7
<i>Felis</i>	1					1
Carnivora	43	36	5		1	1
Total	541	360	54	31	19	47
<i>VI Galería</i>						
<i>Rupicapra</i>	100	67	2	13	1	17
<i>Capra</i>	14	8	0		1	5
Caprinae	40	19	7	3	2	9
<i>Cervus</i>	13	5	1	2	1	4
Cervidae	7	1	0			6
Total	174	100	10	18	5	41
<i>Panthera</i>	4	3		1		
<i>Canis</i>	5	5				
<i>Canis/Cuon</i>	7	6		1		
<i>Vulpes</i>	7	5	1	1		
Carnivora	5	2	1	1		1
Total	28	21	2	4	0	1

11.1% of the marks and thoracic vertebrae and humeri with 9.3%. The other elements present lower values: scapula, second phalanx and sacrum (3.7% each), calcaneus, sternum, first phalanx, fourth metatarsal, patella, cervical and lumbar vertebrae (1.9% each) (Table 5). In this regard, the bite marks appear to be concentrated on the axial area and at the top of the limbs. Of a total of 30 bones with bite marks, most present one (50%), two (30%) and three (13.3%) modifications per element, and few show four (3.3%) and six (3.3%) modifications.

Several deer, caprine, medium-sized animal and large bovid bones were identified with signs of digestion in the form of polishing, porosity and bone loss (Table 4). In the medium-sized group there is a predominance of long and cancellous bone fragments, in addition to elements of the axial region. Compact and small bones, such as phalanges and tarsal bones, are the most affected in deer. Among caprines, though, a greater diversity of digested remains is observed, from long bone fragments to skull fragments or smaller elements, such as patellae and phalanges (Table 6). Based on the length of the digested remains, in deer we observed mostly fragments measuring 31–40 mm (46.1%) and >40 mm (38.5%), with fewer measuring 21–30 mm

(15.4%) and none measuring <20 mm; in chamois, mostly fragments measuring 21–30 mm (50%) and 11–20 mm (40%), with just one element >40 mm (10%) and none measuring <20 mm; in the medium-sized remains, predominantly fragments measuring 21–30 mm (40.3%) and 11–20 mm (38.7%), lower values for those measuring 31–40 mm (12.9%) and >40 mm (8.1%), and again, none measuring <20 mm. The intensity of digestion is stronger in deer, with considerable bone loss, than that observed in caprines (Figs. 6 and 8).

Marks of anthropic origin, especially cut marks and some percussion notches, appear on ungulate and indeterminate medium-sized remains, and on one carnivore bone (Fig. 9; Table 7). Additionally, 24 long bone fragments were identified whose morphotype corresponds to percussion flaking. The ratio between anthropogenic modifications and those caused by carnivores shows different values for deer (49.2), Iberian ibex (9.1) and chamois (7.3) and suggests greater human intervention on deer and a more significant role of carnivores in the accumulation of caprine bones. Anthropic marks on deer are especially notable on the stylopodium (16.1% of marks on humerus and femur), zygopodium (12.9% on tibia and 6.5% on radius/ulna), second phalanges (12.9%) and metacarpal (6.5%), with values



Fig. 5. Fractured remains of the main species from level VIII (CP). Deer (*Cervus elaphus*): tibia (A), radius (B), metacarpal (C) and first phalanges (D–E) with fresh fractures. Chamois (*Rupicapra pyrenaica*): long bone cylinders with fresh fractures (F–J), humerus with fresh fracture (K) and metatarsus with dry fracture (L). Wolf (*Canis lupus*): radius (M) with fresh fracture. Cave bear (*Ursus spelaeus*): femur (N) and humerus (O) with fresh fractures. Cave hyena (*Crocuta spelaea*): humerus with fresh fracture (P).

Fig. 5. Restes fracturés des principales espèces du niveau VIII (CP). Cerf (*Cervus elaphus*) : tibia (A), radius (B), métacarpe (C) et premières phalanges (D–E) avec des fractures fraîches. Isard (*Rupicapra pyrenaica*) : cylindre d'os longs avec des fractures fraîches (F–J), humérus avec fracture fraîche (K) et métatarse avec fracture sèche (L). Loup (*Canis lupus*) : radius (M) avec fracture fraîche. Ours des cavernes (*Ursus spelaeus*): fémur (N) et humérus (O) avec fractures fraîches. Hyène des cavernes (*Crocuta spelaea*): humérus avec fracture fraîche (P).

of around 3% for the other elements, except the axial skeleton, which shows a greater concentration of marks made by carnivores. Marks of human origin appear on the long bones of the hindlimb and mandibles in chamois. In the fragments of medium-sized animals the marks are predominantly on the axial skeleton.

In level VI, 53 marks were identified on 36 ungulate and indeterminate remains, mainly on chamois and medium-sized animal bones. There is very little evidence of anthropogenic modifications, and those caused by carnivores are mainly from digestion and pits (Table 4).

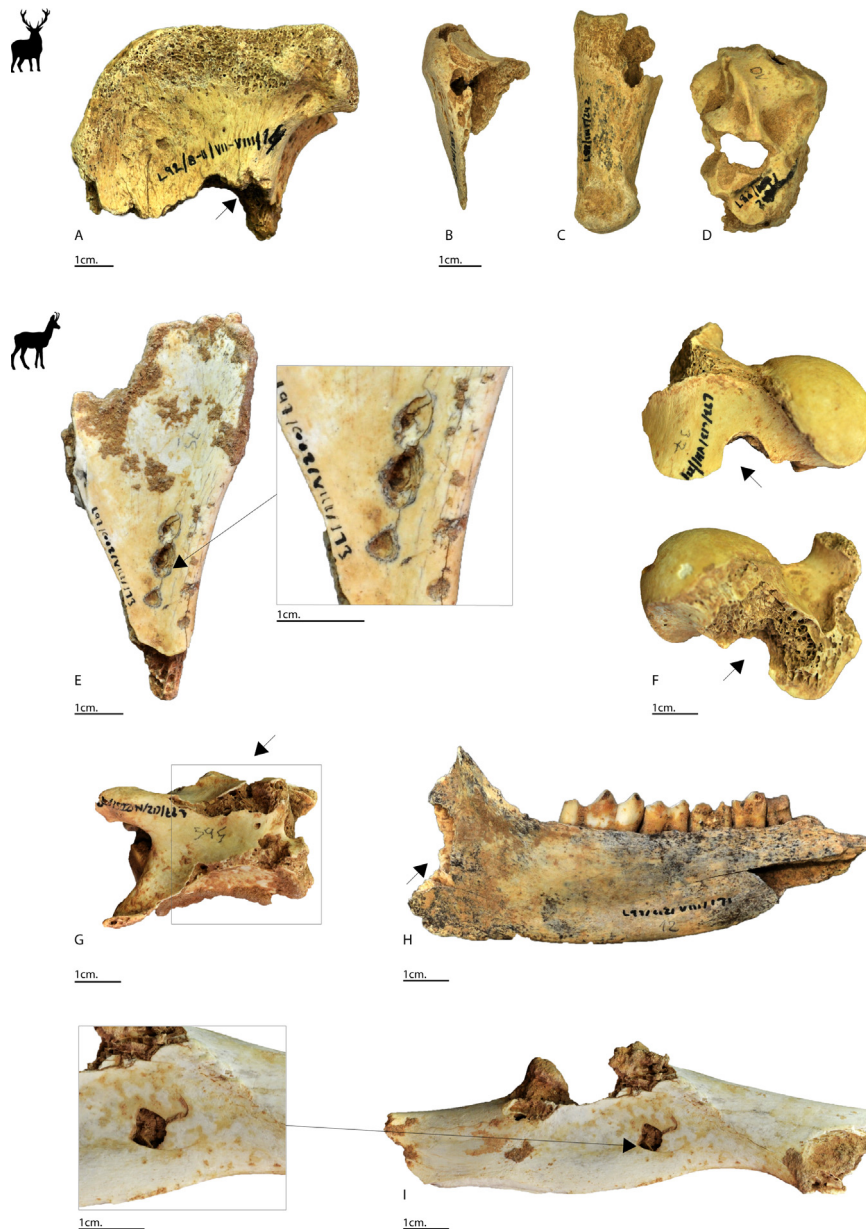


Fig. 6. Modifications produced by carnivores on ungulate bones from level VIII (CP). Deer (*Cervus elaphus*): tibia with crenulated edge (A); third phalanx (B), first phalanx (C) and radius (D) affected by digestion. Chamois (*Rupicapra pyrenaica*): scapula with three punctures (E); femur with notch (F); cervical vertebra (G) and mandible (H) with crenulated edge; pelvis with puncture (I).

Fig. 6. Modifications réalisées par des carnivores sur des os d'ongulés du niveau VIII (CP). Cerf (*Cervus elaphus*): tibia à bord crénelé (A); troisième phalange (B), première phalange (C) et radius affectés par la digestion. Isard (*Rupicapra pyrenaica*): omoplate avec perforations (E); fémur avec entaille (F); vertèbre cervicale (G) et mâchoire (H) à bord crénelé; bassin avec perforations (I).

4.5. Coprolites

4.5.1. Macroscopic analysis

Two basic types were identified (Fig. 10): 12 rounded (hyena type) and 4 tube-like coprolites. As diameter is the most significant measurement to discriminate between non-hyena carnivores and hyena (Chame, 2003), we obtained the following results:

- Rounded shape or hyena-like. Consisting of coprolites with a crumbly texture with phosphate particles compacted into thick aggregates with well-rounded extremities, very occasionally pointed, with a hard consistency. This is consistent with the defined hyena coprolite morphology (Brönnimann et al., 2017; Fernández Rodríguez et al., 1995; Horwitz and Goldberg, 1989).
- Cylindrical or tube shape. Consisting of cylindrical or tube-like coprolites with an internal structure of

Table 4
Elements with modifications caused by the action of humans and carnivores. *Two associated with furrowing and four with scooping out.

Tableau 4
Éléments comportant des modifications réalisées par l'action d'humains et de carnivores. * Deux liés à l'entaille et quatre à l'évidement.

Taxa	NISP with marks	N° marks	Anthropogenic		Carnivore							Indeterm.		
			cut marks	notch	notch	score	pit	puncture	crush	furrowing	crenulate		loss	peeling
<i>VIII CP</i>														
<i>Bos/Bison</i>	1	1												1
<i>Capra</i>	23	35	2	1	5	5	5	1		1	7		1	5
<i>Rupicapra</i>	96	191	13		9	22	57	24		8	4	18	12	12
<i>Caprinae</i>	17	23			3	3	5	3		1		1	1	6
<i>Cervus</i>	52	66	28	3	2	2	7	3			1			17
<i>Capreolus</i>	3	4		1	1	1								1
<i>Canis/Cuon</i>	2	3	1		1	1								
<i>Vulpes</i>	2	3					1				2			
<i>Crocuta</i>	2	2					1				1			
<i>Panthera</i>	1	1									1			
<i>Ursus</i>	30	54			1	11	19	3			1	19*		
<i>Carnivora</i>	1	2					2							
Middle size	166	208	43		7	22	40	4		1	6	3	3	66
Large size	1	1						1						
Indeterm.	6	9					2			1				5
Total	403	603	87	5	29	67	137	41		11	13	53	16	112
<i>VI G</i>														
<i>Capra</i>	1	1												1
<i>Rupicapra</i>	11	24			2	2	11	4			2		1	2
<i>Caprinae</i>	1	2				1	1							
Middle size	12	15	1				4							9
Large size	1	1		1										
Indeterm.	10	10												10
Total	36	53	1	1	2	3	16	4		0	0	2	1	22

Table 5
Elements affected by carnivore bite marks from level VIII (CP). MNE of each bone shown in brackets.

Tableau 5
Éléments affectés par des morsures de carnivores du niveau VIII (CP). Entre parenthèses le MNE de chaque os.

	<i>Rupicapra</i>	<i>Capra</i>	<i>Caprinae</i>	Middle size	<i>Cervus</i>	<i>Ursus</i>
Cranium					1 (2)	
Mandible	2 (30)	4 (7)	1 (7)			
Cervical V.	4 (10)	3 (4)	1 (1)		1 (2)	1 (4)
Thoracic V.	1 (17)				3 (4)	3 (12)
Lumbar V.			1 (2)	1 (39)		1 (3)
Sacrum	1 (3)					1 (1)
Ribs		2 (6)		9 (481)		11 (27)
Sternum			1 (10)			1 (2)
Scapula	7 (13)	2 (3)	2 (6)			1 (2)
Humerus	12 (36)	1 (9)	1 (1)			2 (3)
Radius	1 (18)	3 (13)	2 (8)			
Ulna	4 (27)	2 (5)				2 (3)
Metacarpal	4 (14)				1 (11)	
Coxal	7 (27)				1 (9)	
Femur	10 (41)	6 (21)		1 (7)	1 (15)	2 (2)
Tibia	6 (27)	5 (17)		1 (5)		
Metatarsal	2 (15)				1 (14)	1 (3)
Patella		1 (2)				
Talus	3 (12)	1 (4)				
Calcaneus	1 (10)					1 (1)
Metapodial				1 (5)	1 (6)	
1st phalanx		1 (27)			1 (19)	1 (6)
2nd phalanx						1 (6)
3rd phalanx	1 (22)					
Diaphysis				31 (1472)		
Plate				2 (590)		
Cancellous				6 (259)		

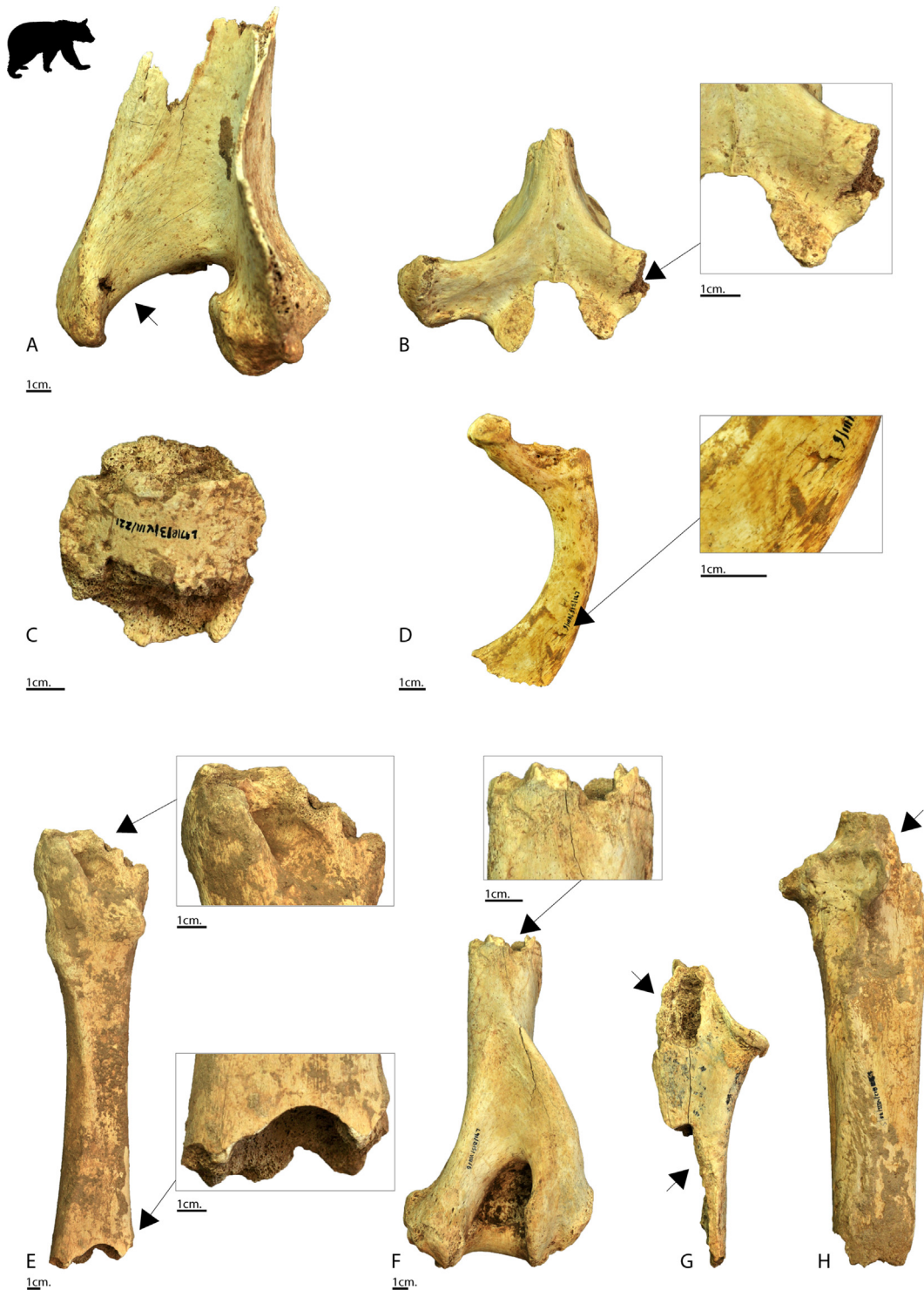


Fig. 7. Modifications produced by carnivores on bear bones from level VIII (CP). Cave bear (*Ursus spelaeus*): scapula with puncture (A); thoracic vertebra with furrowing (B); patella with furrowing (C); rib with pit (D); femur with furrowing on the proximal end and crenulated edge associated with scooping out on the distal end (E); humerus with crenulated edge, scores and pits associated with scooping out (F); ulnae with furrowing on the proximal articulation and crenulated edges, scores and pits associated with scooping out on the diaphysis (G–H).

Fig. 7. Modifications réalisées par des carnivores sur des os d'ours du niveau VIII (CP). Ours des cavernes (*Ursus spelaeus*) : omoplate avec perforations (A) ; vertèbre thoracique avec entaille (B) ; patella avec entaille (C) ; côte avec trou (D) ; fémur avec entaille sur l'extrémité proximale et à bord crénelé lié à un évidement sur le distal (E) ; humérus à bord crénelé, rayures et trous liés à un évidement (F) ; ulnas avec entaille sur l'articulation proximale et à bord crénelé, rainures et cavités liés un évidement sur la diaphyse (G–H).

Table 6
Digested elements from level VIII (CP).
Tableau 6
Éléments digérés du niveau VIII (CP).

	<i>Rupicapra</i>	<i>Capra</i>	Caprinae	Middle size	<i>Cervus</i>	<i>Bos/Bison</i>
Antler/Cc	1					
Teeth	1					
Cervical V.				3		
Thoracic V.	1		1	4		
Caudal V.				1		
Vertebrae				3		
Ribs				3		
Humerus	1				2	
Radius		1			1	
Ulna					1	
Metacarpal	1					
Carpal			1			1
Coxal	1		2			
Femur		1				
Tibia	1					
Metatarsal	1				1	
Patella	2	1				
Talus		1			1	
Calcaneus					2	
Tarsal			1			
Metapodial			1	1	1	
Metap. res.						
1st phalanx		1			5	
2nd phalanx					1	
3rd phalanx	2				2	
Diaphysis				15		
Plate				8		
Cancellous				28		

concentric layers with low compactness that conditions the preservation of the extremities and surfaces (only a few sharp-pointed extremities are observed). No aggregates were identified. The interior was spongier than in the spherical morphology. These features are consistent with non-hyena coprolites, as described by Brönnimann et al. (2017), Brugal (2010), Chame (2003) and Sanz et al. (2016). The diameter of the spherical samples is between 26 and 42 mm, whereas in the cylindrical coprolites it is between 20 and 32 mm.

4.5.2. Microscopic analysis

Micromorphology analysis was performed on the cylindrical or tube shape samples (TC1, TC2, TC3 and TC4) to more closely identify the producer. The internal

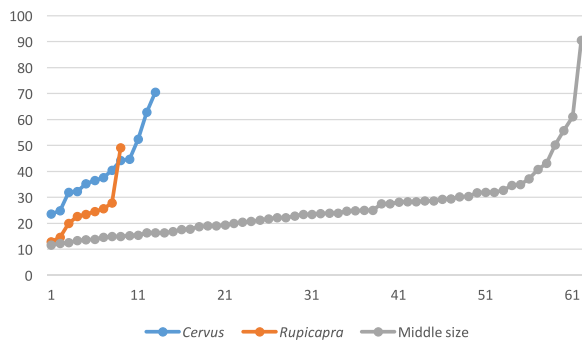


Fig. 8. Dimensions of digested remains.
Fig. 8. Dimensions des restes digérés.

microfeatures of the tube shape share the following common characteristics: The results provide a heterogeneous dotted phosphatised matrix with a yellowish to pale grey appearance under PPL, isotropic under XPL and highly autofluorescent under UVF/BLF light (Fig. 10). It has an external brownish cortex related to the intestinal mucus, of 0.001 mm, smaller than the hyena type and in the range

Table 7
Elements with anthropogenic modifications from level VIII (CP). MNE of each bone shown in brackets.

Tableau 7
Éléments comportant des modifications anthropogéniques du niveau VIII (CP). Entre parenthèses, le MNE de chaque os.

	<i>Rupicapra</i>	<i>Capra</i>	<i>Cervus</i>	Middle size	<i>Canis/Cuon</i>
Cranium			1 (2)	1 (53)	
Mandible	2 (30)	1 (7)			
Vertebrae				1 (57)	
Thoracic V.				4 (46)	
Lumbar V.				1 (39)	
Ribs				17 (503)	
Scapula			1 (2)		
Humerus			4 (19)		
Radius	1 (36)		2 (6)		1 (2)
Ulna			1 (7)		
Metacarpal			2 (11)		
Coxal		2 (4)	1 (9)		
Femur	1 (41)		4 (15)		
Tibia	2 (27)		4 (13)		
Metatarsal	3 (15)		1 (14)		
Calcaneus	1 (10)		1 (4)		
Metapodial			1 (6)		
1st phalanx	1 (33)		1 (19)		
2nd phalanx			3 (14)		
Diaphysis				14 (1472)	

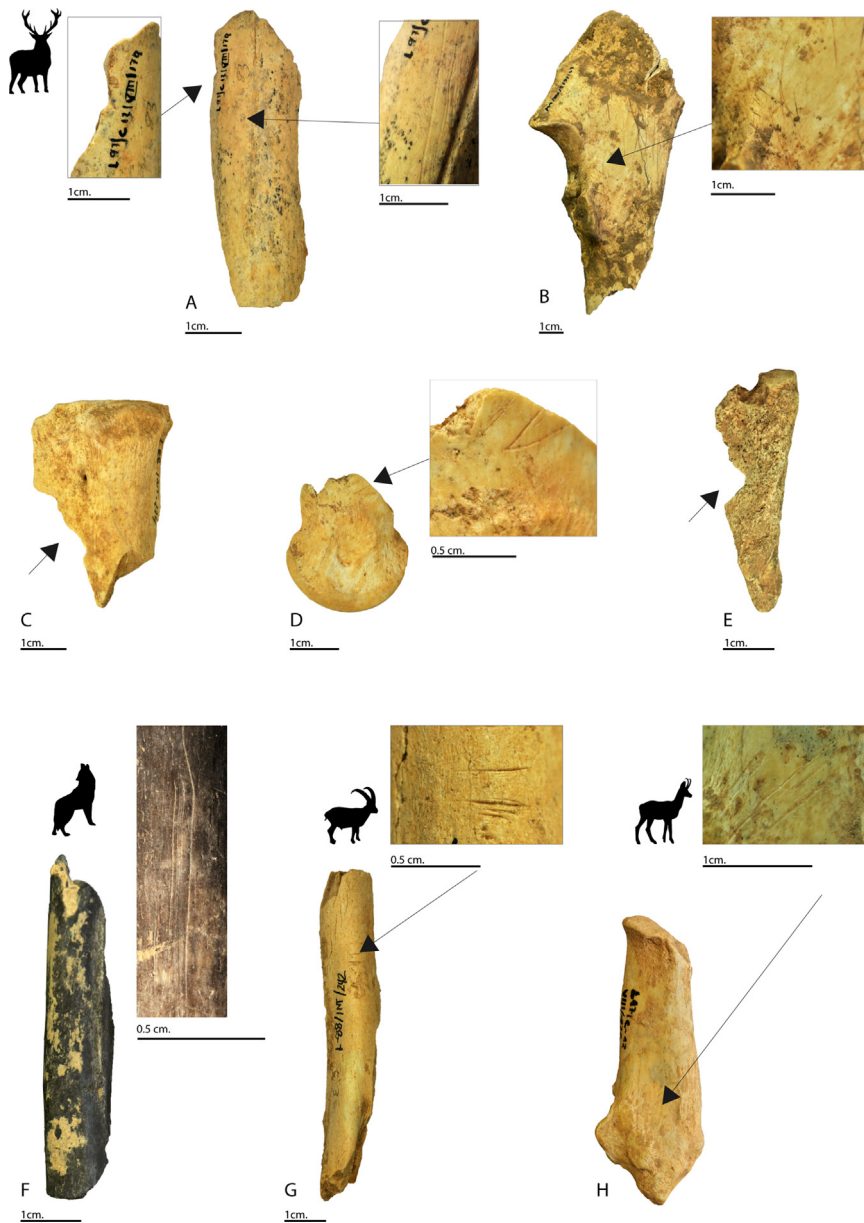


Fig. 9. Evidence of anthropogenic processing on ungulate and carnivore bones from level VIII (CP). Deer (*Cervus elaphus*): percussion impacts and/or cut marks on metacarpal (A), ulna (B), metacarpal (C), second phalanx (D) and first phalanx (E). Wolf/Dhole (*Canis/Cuon*): radius with cut marks (F). Iberian ibex (*Capra pyrenaica*): pelvis with cut marks (G). Chamois (*Rupicapra pyrenaica*): calcaneus with cut marks (H).
Fig. 9. Preuves de la transformation anthropogénique sur des os d'ongulés et de carnivores du niveau VIII (CP). Cerf (*Cervus elaphus*): impacts de percussion et/ou cut marks sur métacarpe (A), ulna (B), métacarpe (C), deuxième phalange (D) et première phalange (E). Loup/cuon (*Canis/Cuon*): radius avec cut marks (F). Bouquetin ibérique (*Capra pyrenaica*): bassin avec cut marks (G). Isard (*Rupicapra pyrenaica*): calcaneus avec cut marks (H).

observed for *Panthera* and *Lynx* sp. (Sanz et al., 2016). It contains common feldspar mineral compounds. The size of organic embedded components such as subrounded bone fragments (related to a high degree of digestion) and amorphous organic matter is within the millimetre range (Fig. 10). Rare hair pseudomorphs were identified, which matches the described *Panthera* and *Puma* sp. samples better than the *Lynx* samples (Brönnimann et al., 2017). The presence of some pseudomorph calcitic grass stems was recorded, which in modern samples is usually

related to incompletely digested bowel content from their prey (medium-sized herbivores) but also to grass-eating behaviour to induce regurgitation of undigested matter (zoopharmacognosy), such as fur or an unguis (from prey or self-grooming) (Sanz et al., 2016). In addition, abundant pseudomorph rounded voids related to digestion gases and elongated pores associated with degraded plant tissue were observable along with some Fe-Mn impregnations (Fig. 10). No faecal spherulites or phytoliths were observed.

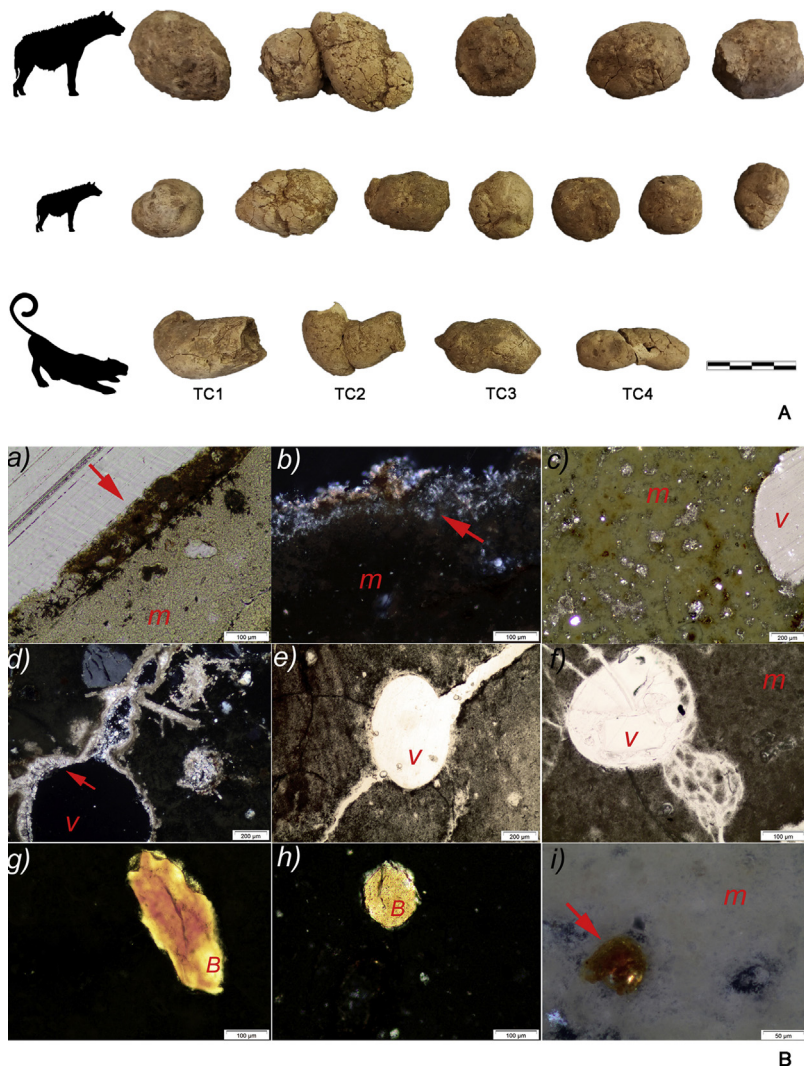


Fig. 10. A. Macrophotographie qui montre les deux types de morphologies détectées. Première et deuxième rangées pour le type globulaire, lié au genre *Crocuta* et troisième rangée (en bas) pour le détail des coprolithes tubulaires analysés (TC1, TC2, TC3 et TC4), liés au genre *Panthera*. À noter la deuxième rangée de taille globulaire : ces coprolithes sont probablement issus de jeunes animaux. L'échelle est de 4 cm. B. Microphotographies de morphotypes tubulaires qui montrent (a) détail de l'écorce externe marron sur l'échantillon TC1 (indiquée au moyen d'une flèche rouge) avec la matrice adjacente (m), image en PPL ; (b) même chose que (a), mais pour l'échantillon TC2, image en XPL ; (c) détail de la matrice pointillée phosphatée (m), dont l'aspect va du jaunâtre au gris pâle, image en PPL ; (d) vue des vides pseudomorphiques arrondis liés aux gaz de digestion (v) et pores allongés liés au tissu végétal dégradé sur l'échantillon TC1. À noter la précipitation calcitique qui recouvre le vide en raison de processus diagenétiques (indiqués au moyen d'une flèche rouge), image en XPL ; (e) creux arrondis pseudomorphiques liés aux gaz de digestion (v) sur l'échantillon TC3, image en PPL ; (f) vides pseudomorphiques arrondis liés aux gaz de digestion (v) sur l'échantillon TC4, image en PPL ; (g) détail des fragments osseux digérés subarrondis (B) sur l'échantillon TC2, image en PPL ; (h) détail des fragments osseux digérés subarrondis (B) sur l'échantillon TC4, image en PPL ; (i) détail de nodule de Fe, ce type de nodules étant disséminés dans la matrice de tous les échantillons, ici échantillon TC4, image en PPL.

Fig. 10. A. Macrophotographie qui montre les deux types de morphologies détectées. Première et deuxième rangées pour le type globulaire, lié au genre *Crocuta* et troisième rangée (en bas) pour le détail des coprolithes tubulaires analysés (TC1, TC2, TC3 et TC4), liés au genre *Panthera*. À noter la deuxième rangée de taille globulaire : ces coprolithes sont probablement issus de jeunes animaux. L'échelle est de 4 cm. B. Microphotographies de morphotypes tubulaires qui montrent (a) détail de l'écorce externe marron sur l'échantillon TC1 (indiquée au moyen d'une flèche rouge) avec la matrice adjacente (m), image en PPL ; (b) même chose que (a), mais pour l'échantillon TC2, image en XPL ; (c) détail de la matrice pointillée phosphatée (m), dont l'aspect va du jaunâtre au gris pâle, image en PPL ; (d) vue des vides pseudomorphiques arrondis liés aux gaz de digestion (v) et pores allongés liés au tissu végétal dégradé sur l'échantillon TC1. À noter la précipitation calcitique qui recouvre le vide en raison de processus diagenétiques (indiqués au moyen d'une flèche rouge), image en XPL ; (e) creux arrondis pseudomorphiques liés aux gaz de digestion (v) sur l'échantillon TC3, image en PPL ; (f) vides pseudomorphiques arrondis liés aux gaz de digestion (v) sur l'échantillon TC4, image en PPL ; (g) détail des fragments osseux digérés subarrondis (B) sur l'échantillon TC2, image en PPL ; (h) détail des fragments osseux digérés subarrondis (B) sur l'échantillon TC4, image en PPL ; (i) détail de nodule de Fe, ce type de nodules étant disséminés dans la matrice de tous les échantillons, ici échantillon TC4, image en PPL.

4.6. Preservation of the faunal deposit

The relationship between %Surv and the density of each skeletal element was significant for deer ($r=0.7687$; $P=0.000074895$), but not for caprines. In this regard, the differential destruction of less dense elements in deer may be related to hyenas scavenging on their remains.

The main diagenetic alterations observed are calcareous concretions, which represent 42.7% (VIII) and 27.9% (VI). There are also manganese stains of varying importance: 12.2% (VIII) and 15.1% (VI). Pending the sedimentological results, both processes could be related to phases of high humidity and even of flooded areas inside the cave, which are not favourable for human habitation.

5. Discussion

5.1. Accumulations by humans or carnivores?

Humans and carnivores were involved in the accumulation and alteration of bone remains in the basal levels of Llonin, but they acted differently on each taxon. We will therefore describe the principal modifications caused by the three main agents: Neanderthals, hyenas and leopards.

Anthropogenic modifications appear mainly on deer remains. This, together with the high degree of fragmentation and the morphotypes of long bone fractures, mainly with incomplete circumferences, points to the predominantly human accumulations of these ungulates. On the other hand, the location of the cut marks, their orientation and features inform us about the butchering of these cervids: oblique and longitudinal incisions and scrapes on the diaphyses of the stylopodium, zygopodium and metapodium are related to flesh removal and/or cleaning of the periosteum; oblique incisions on the proximal ulna are due to disarticulation processes, while those observed on the phalanges, calcaneus and skull resulted from skinning. These marks suggest the complete processing of deer that ended with fracturing the bone and accessing the marrow, as shown by the percussion impacts. This evidence appears on adult and immature deer remains, so they would not have been selected by age. According to this and the skeletal pattern observed, Neanderthals hunted deer and transported the entire animal to the cave for processing and consumption, which has also been established at other Middle Palaeolithic Cantabrian sites (Yravedra, 2013; Yravedra et al., 2016). The palaeoenvironmental studies carried out on basal levels of Llonin and analyses of plant macroremains available for the region corroborate the existence of open forests with the presence of species that thrived in mild Atlantic or central European climates and montane or even subalpine zones during the Mousterian (Costa et al., 1997), an ideal habitat for deer (Carranza, 2011).

Human evidence on caprines is scarcer, as we consider the leopard to be the main agent responsible for the accumulation of these herbivores and we believe they would have also been transported to the cave whole. The abundance of chamois and Iberian ibex reflects the rocky,

mountainous terrain in the immediate surroundings of the cave (Granados et al., 2001; Pérez-Barbería et al., 2010).

Carnivore bones modified by humans appear more frequently during the Upper Palaeolithic, mainly on small animals, but there is increasing evidence of confrontational processes between Neanderthals and carnivores. At Llonin we have documented flesh removal marks on a wolf/dhole radius. There are already some known references in the Iberian Peninsula regarding anthropic processing of canids during the Middle Palaeolithic (Blasco and Fernández, 2012; Díez, 2006; Gómez-Olivencia et al., 2018; Morales et al., 2012; Pérez Ripoll et al., 2010; Rodríguez-Hidalgo et al., 2015), or other carnivores such as the hyena (Rodríguez-Hidalgo, 2010), lion (Blasco and Fernández, 2012; Blasco et al., 2010), leopard (Arribas, 1997; Sanchis et al., 2015; Walker et al., 2012), lynx (Caparrós et al., 2012; Gómez-Olivencia et al., 2018; Sala et al., 2012), wild cat (Gabucio et al., 2014), brown bear (Caparrós et al., 2012) or cave bear (Yravedra, personal comment). The question is whether Neanderthals hunted carnivores or made use of the remains of dead animals. In any case, there would have been a great deal of competition between them (Brugal and Fosse, 2004).

The rate of carnivorism according to the MNI is 34.5% in level VIII and 23.5% in level VI. The great diversity of species of both herbivores and carnivores is typical of carnivore dens (Binford, 1981; Klein and Cruz-Urbe, 1984), and hyenas in particular can feed on almost all available resources (Kruuk, 1972; Kuhn et al., 2010; Sutcliffe, 1970). In this regard, the dimensions of digested deer remains and in some cases their extreme alteration seem to suggest the involvement of the hyena, possibly as a carrion-eating agent that would have fed on the remains left by humans (Cruz-Urbe, 1991; Fosse, 1997; Fosse et al., 2012; Haynes, 1983; Horwitz, 1990; Sutcliffe, 1970), and they differ from the characteristics of wolf coprocenoses (Esteban-Nadal et al., 2010). In theory, this scavenging activity should provide a bone record with a high number of modifications (Domínguez-Rodrigo and Pickering, 2010), but that is not the case. This could be the result of the intensity of processing and human consumption of the prey, which would leave few consumable remains for scavengers, or due to lower intensity of their consumption by hyenas.

Hyenas could also be responsible for the modifications found on bear remains. No evidence has been found of human intervention on them, but there are carnivore bite marks associated with an extreme modification pattern consisting of destruction of articular areas, fracture morphotypes with a predominance of complete circumferences and an attritional mortality profile (Diedrich and Žák, 2006; Fosse, 1997). Likewise, the pits and punctures found on bear bones are large, in the range of those made by present-day hyenas (Fig. 11). No digested bear bones have been found, but this appears to be a variable criterion (Domínguez-Rodrigo and Pickering, 2010), although these remains could be contained in the coprolites recovered or could have been destroyed or deposited in other places. It is likely that hyenas would have been attracted by the carcasses of bears that died during hibernation, leading to two possible scenarios:

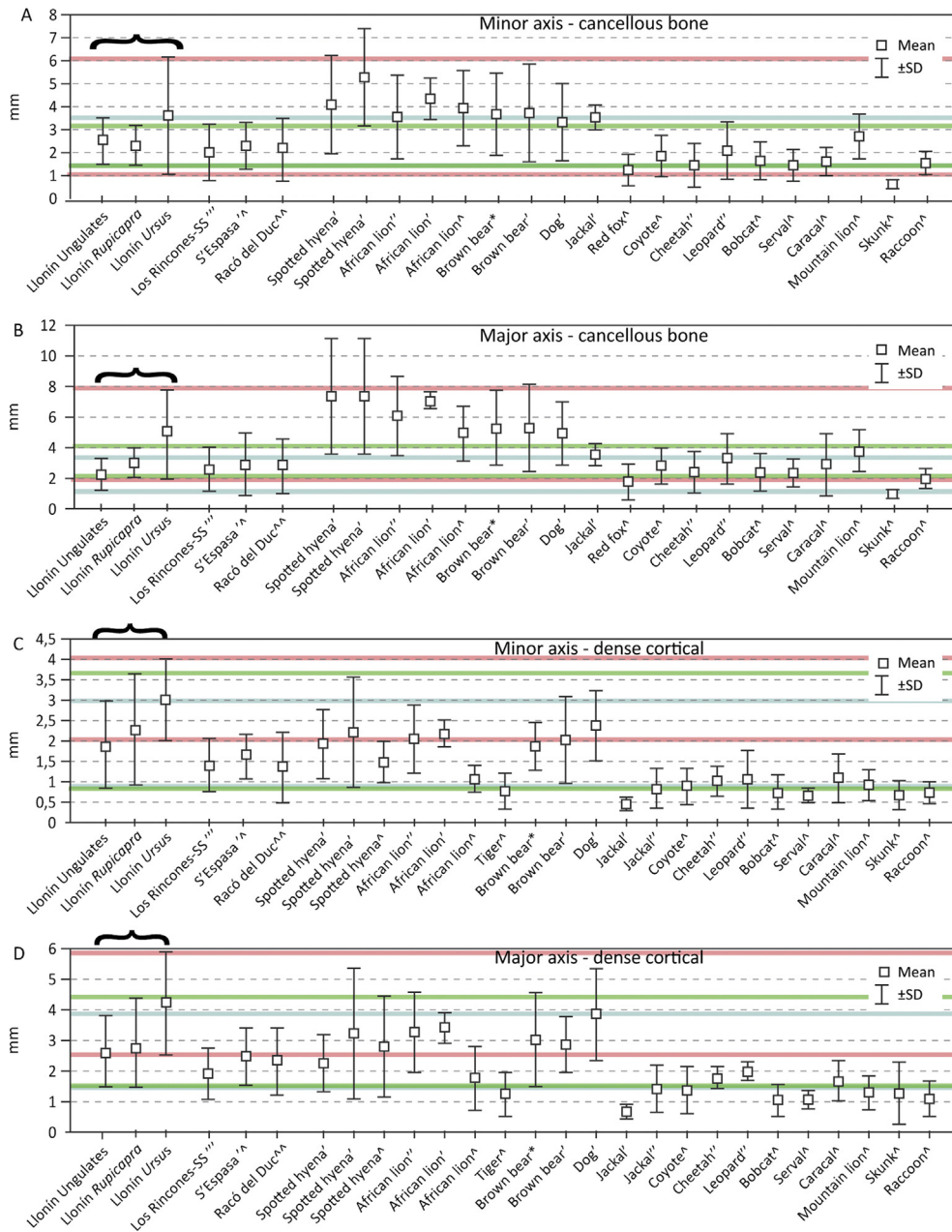


Fig. 11. Dimensions of the pits/punctures on ungulate (*Capra*, *Rupicapra*, Caprinae and *Cervus*), chamois and bear bones from level VIII (CP) and their comparison with those present in archaeological assemblages of caprine bones interpreted as bone accumulations by leopards (Los Rincones, S'Espasa and Racó del Duc) and with those of different present-day carnivores. Key to the data: *Selvaggio and Wilder, 2001; ~Domínguez-Rodrigo and Piqueras, 2003; ~Delaney-Rivera et al., 2009; *Saladié, 2009; ~Sauqué et al., 2014; ~Sauqué et al., 2017a; ~Sauqué and Sanchis, 2017.

Fig. 11. Dimensions des trous/cavités sur des os d'ongulés (*Capra*, *Rupicapra*, Caprinae et *Cervus*), d'isard et d'ours du niveau VIII du cône postérieur et comparaison avec celles d'os dans les ensembles archéologiques de caprins, interprétés comme provenant d'accumulations par des léopards (Los Rincones, S'Espasa et Racó del Duc) et avec ceux de plusieurs carnivores actuels. Clé des données : *Selvaggio et Wilder, 2001 ; ~Domínguez-Rodrigo et Piqueras, 2003 ; ~Delaney-Rivera et al., 2009 ; *Saladié, 2009 ; ~Sauqué et al., 2014 ; ~Sauqué et al., 2017a ; ~Sauqué et Sanchis, 2017.

- the bears occupied Llonin, or
- the bears were located in other galleries or caves and their remains were transported to Llonin by hyenas.

Bearing in mind how small the NISP is compared with the MNI (141/9) and the considerable anatomical bias, the

second hypothesis seems more likely, which means differential transport (Fourvel et al., 2014). Likewise, there is no other evidence at Llonin of the use of the cave by bears (beds, trampling or scratch marks on the walls) resulting from these animals moving around during hibernation (Diedrich, 2011; Sauqué et al., 2015). Scavenging activity

by these bears on dead individuals has been identified at monospecific *Ursus spelaeus* sites, but the remains present larger marks than those made by hyenas and many complete elements are preserved (Pinto-Llona and Andrews, 2004; Pinto Llona et al., 2005; Rabal-Garcés et al., 2011). Therefore, the accumulation of bears at Llonin is more likely linked to scavenging activity by hyenas, which entails significant alteration of the remains (Diedrich, 2013, 2018; Fourvel et al., 2014). Both bears and deer exceed the weight range of the prey hunted by hyenas (Hayward, 2006) and the bite marks on these animals are located mainly on the axial skeleton, which is more consistent with scavenging. In level VIII there are also some *Canis/Cuon*, *Vulpes*, *Crocuta* and *Panthera* bones with bite marks, which could have been scavenged by hyenas and other carnivores.

Regarding the leopard, we believe that it is the main agent responsible for the accumulation of caprine bones. Unlike the bear and deer remains scavenged by hyenas, the bite marks on chamois bones are mostly located on the stylopodium and girdles. Moreover, the destruction pattern is not as strong as the one found on bear remains, the dimensions of the tooth marks are smaller than those made by hyenas and similar to those caused by smaller carnivores such as leopards (Fig. 11). In this regard, the capacity of these felines to accumulate and modify caprine bone remains has been established at different sites in the Iberian Peninsula, such as Boquete de Zafarraya (Barroso et al., 2006; Caparrós et al., 2012; Geraads, 1997), Amalda VII (Yravedra, 2006a), Los Rincones (Sauqué et al., 2014, 2016), Racó del Duc (Sauqué and Sanchis, 2017) and S'Espasa (Sauqué et al., 2017a). In all cases they are caves situated in steep areas close to the habitat of rock-dwelling species such as Iberian ibex and chamois. In southern and inland Mediterranean sites, the Iberian ibex is the predominant ungulate, while in the Cantabrian region, as observed at Amalda VII and at Llonin, it is the chamois (Sauqué and Sanchis, 2017). Current studies on leopard behaviour conclude that its range of prey is 20–80 kg, although the optimum size would be 23 kg (Hayward et al., 2006; Mills and Harvey, 2001), which perfectly matches the chamois and, to a lesser extent, the robust Cantabrian Iberian ibex. In sites of the Iberian Peninsula that have been interpreted as leopard dens, caprines have been found together with remains of the leopards themselves, although this is not always the case (Ruiter and Berger, 2000). The caprine bones found there show a small number of modifications caused by biting, between 5 and 20% (Sauqué et al., 2017a). In the case of Llonin, in level VIII carnivore-modified bones account for 15% (chamois) and 7.4% (Iberian ibex); in level VI, 11% (chamois) and 7.1% (Iberian ibex). This modification pattern with predominantly one or two marks per bone is consistent with that observed in the sites described as leopard dens and is less similar to the actions of hyenas (e.g., Sauqué et al., 2015, 2017a, b). Likewise, the degree of fragmentation is not very significant, e.g., at S'Espasa it is 64.7% and at Racó del Duc 52%, and at Llonin VIII it is 53.4% for chamois and 31.1% for Iberian ibex. The modification pattern of long bones from caprines in leopard dens is moderate and there are many complete bones (Sauqué and Sanchis, 2017). However, the long bones found at Llonin show a very high level of fragmentation and practically

no complete bones are preserved. This may be the consequence of a more complex taphonomic history where, in addition to human accumulation and processing, the scavenger activity of hyenas and perhaps canids may have contributed to a greater degree of destruction of these elements (Domínguez-Rodrigo et al., 2012). In any case, the dimensions of digested chamois bones and fragments of medium-sized animals at Llonin (Fig. 9) are greater than those found in actualistic studies on *Canis lupus* (Esteban-Nadal et al., 2010; Fosse et al., 2012). In this regard, some digested caprine bones are quite long (12–15 cm), which we relate to the regurgitation of these elements by hyenas (Fosse et al., 2012).

Two medium-sized remains show both anthropogenic and carnivore modifications, but they do not overlap. They consist of a rib with incisions and bites on the articular region and a digested vertebra with incisions. It has only been possible to define the primary access of humans in the case of the vertebra, which would be later scavenged by carnivores.

Regarding the coprolites found in level VIII, most of them are related to hyenas. The hyena-like globular fossil coprolites clearly match the modern *Crocuta* scat range (Larkin et al., 2000) and the tube-like ones are clearly differentiated from those of the hyena because of their smaller diameter. Based on the macroscopic characteristics of these coprolites, they are closer to those of large felids, such as leopards (*Panthera pardus*), mountain lions (*Puma concolor*) and jaguars (*Panthera onca*). The four samples analysed under the microscope show similar features to those of modern jaguars (*Panthera onca*) and leopards (*Panthera pardus*) (Campmas et al., 2018; Sanz et al., 2016). It is well known that fossils of extinct *Panthera* species, such as the European jaguar (*Panthera gombaszoegensis*) and the American lion (*Panthera atrox*), show characteristics of both the modern lion and jaguar (Janczewski et al., 1995). Therefore, following the macro- and micromorphological analyses we suggest that the origin of the tube-like coprolites is the *Panthera* sp. Moreover, the leopard record in the studied levels and their possible responsibility for caprine accumulations, together with the appearance of their coprolites, provide proof of their occupation of the cave and consumption of prey, representing the first coprogenic evidence of this species in a European archaeo-palaeontological context. Feline coprolites have been found at Cova del Coll Verdager but they are more compatible with the lynx (Sanz et al., 2016).

To confirm the hypotheses proposed here regarding the origin of the accumulations, especially in the case of the leopard/caprine binomial, it would be interesting to carry out a carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) isotope study based on bone collagen in the future to learn about ancient trophic networks and, in particular, the relationship between predators and prey (Bocherens and Drucker, 2003; Bocherens et al., 2011). It would also be interesting to apply new techniques (Aramendi et al., 2017; Arriaza et al., 2017; Yravedra et al., 2017, 2018) to analyse and compare carnivore bites on caprine set bones from different sites as Llonin, Racó del Duc or Los Rincones, where the leopard seems to be the main modification agent.

5.2. Cave occupation models

The bone remains studied appear to be a cumulative palimpsest resulting from low rates of sedimentation. Initially, the cave served as a place of life and death and was alternately occupied by humans and carnivores (Fig. 12), a pattern observed at other Pleistocene sites of the Iberian Peninsula (e.g., Altuna, 1990; Blasco, 1995; Fernández Rodríguez, 2010; Martínez Valle, 1996; Rosell et al., 2010b; Yravedra, 2006a, 2010a, 2010b, 2013; Zilhão et al., 2010). Llonin was occupied by hyenas, leopards and various species of canids, as well as by humans. The other species represented correspond to exogenous accumulations and are related to the predation and/or scavenging activities of hyenas.

Neanderthals inhabited Llonin at certain times, as shown by the described anthropic evidence found on some of the faunal remains and the lithic assemblage found here. Regarding the morphology of the cave, the concretions and manganese stains on some remains reveal the existence of high levels of humidity inside the cave, which would have made it unsuitable for human habitation but would have been ideal for cave-dwelling carnivores. This seems to be in line with a model of sporadic human occupations without the presence of hearths. As discussed in section 2, access to the cave by humans and carnivores would have been via a different entrance to the current one, which is now sealed off and at a lower level. Likewise, it is possible that human occupations were located in the outer part of the cave near the entrance, which would explain the lack of hearths inside it. The gallery would have been accessed via the current entrance; the lack of space in this area could also have influenced the nature of the occupations. We have been unable to obtain information regarding the seasonality of human occupations due to the high fragmentation of the assemblage and the lack of information on the age at death and sex of ungulates.

The presence of hyenas at Llonin is shown by both their remains and their action on herbivores and carnivores, especially deer and bears. The hyena assemblage from level VIII is scant and shows significant anatomical bias. In this regard, level VII (CP) presents stratigraphic problems but it has yielded many hyena remains, which could possibly complement those of the level VIII assemblage. Hyenas occupied the cave to feed, where they could transport parts of carcasses taken from other places or scavenge on the remains left by other agents. The appearance of coprolites at the base of the deposit confirms that hyenas occupied the inside of the cave to feed and they also defecated there (Diedrich and Žák, 2006; Fosse et al., 1998). Present-day hyenas defecate to mark their dens and coprolites are found together with the remains of their prey (Fosse, 1999; Fosse et al., 1998). The function as a breeding den cannot be confirmed due to the lack of young hyena remains, which are also normally associated with a large number of nibbling sticks that do not appear at Llonin (Diedrich and Žák, 2006), although some of the small, rounded coprolites may correspond to young hyenas. The hyenas may have used the old entrance as a breeding area, but we do not currently have access to that part. Cave occupation by cave hyenas as a

breeding den or as a temporary feeding place has been documented at numerous sites in the Iberian Peninsula from the middle Pleistocene and more intensely during the upper Pleistocene (e.g., Arrizabalaga and Altuna, 2000; Arsuaga et al., 2010; Blasco, 1995; Blasco and Montes, 1997; Davis et al., 2010; Fernández Rodríguez, 2010; Huguet et al., 2010; Riquelme and Carrión, 2010; Rodríguez-Hidalgo et al., 2010; Rosell et al., 2010a, b; Sala et al., 2012; Sauqué et al., 2017b; Zilhão et al., 2010). The maximum expansion of cave hyenas and their dens throughout Europe took place in the upper Pleistocene (Fosse et al., 1998).

Regarding the leopards and canids (wolves and foxes) found in level VIII, they occupied the cave to shelter and feed. In the case of leopards, this activity is evidenced by the appearance of their coprolites and the caprine accumulations, especially chamois. Some of these carnivores could have died in the cave, although the presence of a wolf/dhole bone with cut marks could be related to their acquisition by Neanderthals. In any case, it is difficult to establish the role played by canids at Llonin. With regard to wolves, their ability to accumulate remains in caves is limited and circumstantial, but a possible modification/scavenging action on remains (dispersing agent) accumulated by other agents cannot be ruled out and this could also be extended to foxes that occasionally can generate accumulations of ungulates (Domínguez-Rodrigo, 1994b; Krajcarz and Krajcarz, 2014; Yravedra et al., 2011, 2012, 2014).

Lastly, it should be mentioned that although the bear mortality profiles recorded at Llonin coincide with those of death during hibernation, the degree to which the bones are affected and the anatomical bias suggest an exogenous origin and they could have been carried into the cave by hyenas or other carnivores.

5.3. Neanderthal subsistence in the Cantabrian region of the Iberian Peninsula

Most Asturian sites from the Middle Palaeolithic have MIS 3 sequences (Fig. 1) and generally offer limited data on the origin of faunal assemblages. In the *Galería del Osario* (Ossuary Gallery) of El Sidrón the faunal remains are scant and belong to different species of carnivores and ungulates, where some carnivore-marked remains have been identified (Rosas et al., 2014). At La Viña, erosive processes have led to the decomposition of organic matter, so hardly any faunal remains are conserved from the Mousterian level (Rasilla and Santamaría, 2011–2012; Santamaría, 2016). At La Güelga, some preliminary data have been published on the fauna from Mousterian levels. Eight thousand bones have been recovered in level 9 (D interior), of which deer and chamois account for 75%, with a smaller presence of roe deer and equids. The bone remains show anthropic signs in the form of cut marks, fractures and thermal alterations; moreover, this assemblage has been related to Mousterian lithic materials and combustion areas from a phase of intense anthropic occupation dating from 45 ky BP. The faunal assemblage from level 4b (D exterior) shows similar characteristics, with a predominance of deer (66%), chamois (21%) and the presence of other taxa such as the mammoth (Menéndez et al., 2009, 2014, 2017). At Sopena,

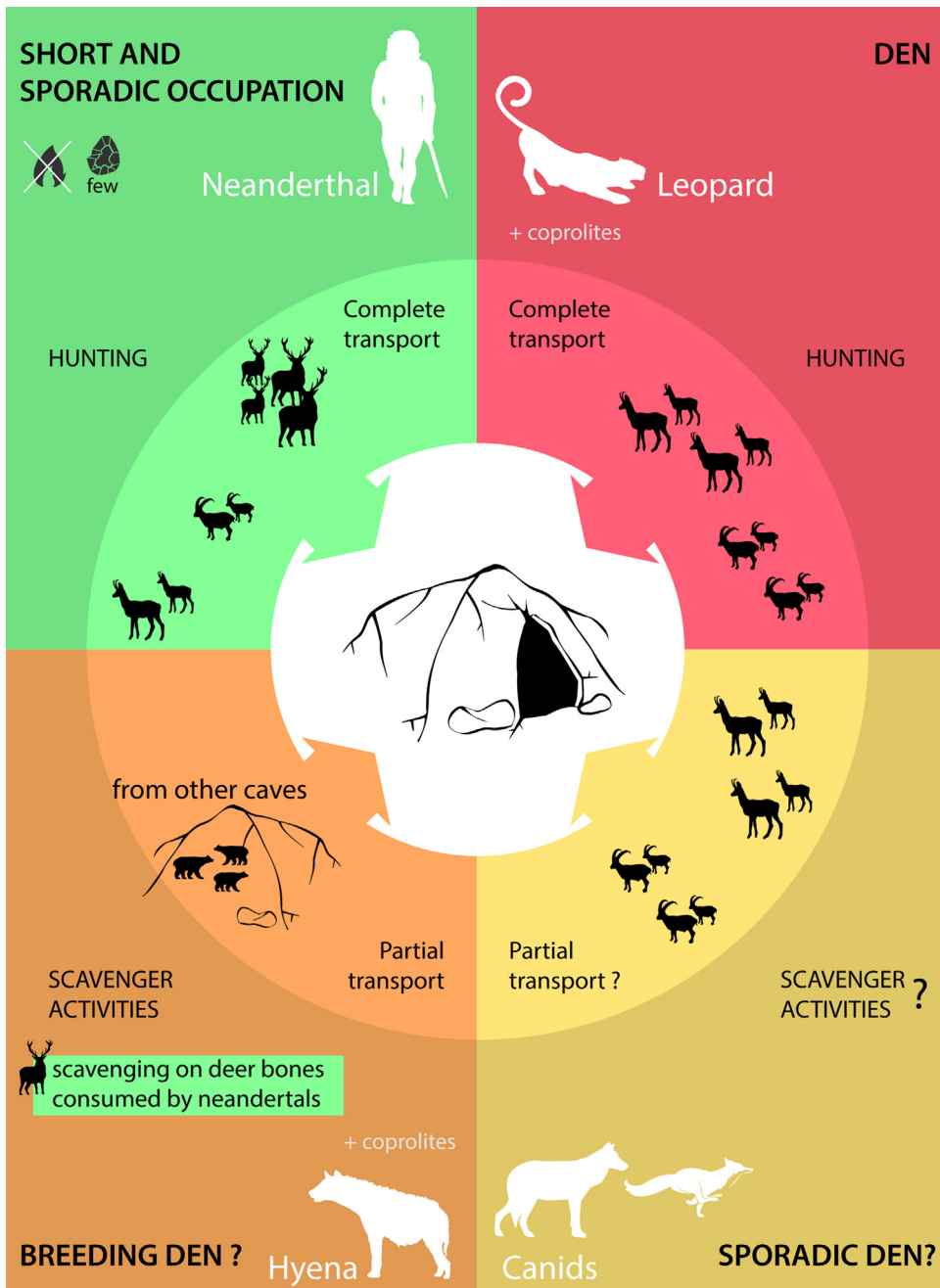


Fig. 12. Infographic on the occupation models from Llonin level VIII (CP).
Fig. 12. Infographie sur les modèles d'occupation du niveau VIII (CP) de Llonin.

the macrofauna found in Mousterian levels has been compiled into a list which includes several species of carnivores and ungulates (Pinto-Llona et al., 2012: 70), but the remains have not been the subject of a taphonomic study. Lastly, at El Conde only a list of species from the Mousterian level has been compiled, which was used to develop a palaeoenvironmental approximation, but again no taphonomic data are available (Arbizu et al., 2005).

Therefore, information on the human use of Mousterian fauna in Asturias is lacking. This is also the case in Galicia, where we have Mousterian levels 3 and 4 of Eirós Cave (Lombera-Hermida et al., 2014), but with no specific work about fauna. Consequently, to check the data obtained from the study of Llonin, we must look to Cantabria and the Basque Country. Even so, not all the sites in these areas provide specific data on fauna. On the

one hand, assemblages such as those of Lezetxiki V and Axlora offer taxonomic studies but with only partial taphonomic approximations (Altuna, 1972; Castaños, 2005). On the other hand, sites such as Hornos de la Peña (Yravedra, 2010b) and Otero (Yravedra and Gómez-Castanedo, 2010a) have Mousterian levels with faunal remains, but their results are not very representative due to some issues with the material collection. This is also the case with level VI of Lezetxiki, where the fact that 100% of the remains have been determined points to the selective collection of bone material (Martínez-Moreno, 2005). Despite this, in recent years sites such as El Esquilieu (Yravedra, 2006a, Yravedra, 2006b), El Ruso (Yravedra et al., 2010), Morín Cave (Yravedra and Gómez-Castanedo, 2010b), Covalejos (Castaños, 2005; Yravedra, 2013; Yravedra et al., 2016), El Castillo (Landry and Burke, 2006), Amalda (Yravedra, 2006a, 2007, 2010a) and Arlanpe (Arceredillo et al., 2013) have provided new data about Neanderthal subsistence models and the occupation of these caves by humans and carnivores. In all these assemblages with studies and updated reviews, notable similarities are observed. Firstly, occupations by Neanderthal groups appear to be short and seasonal, in cases where it has been possible to obtain data on seasonality, e.g., at El Ruso, El Esquilieu and El Castillo. The exception to this is level D of Arlanpe, where long occupations and intense processing of resources have been defined (Ríos-Garaizar et al., 2015). The model of short occupations is based on the accumulation of water in the caves, which would have rendered the space less habitable, and on alternating occupations by different carnivores, which lasted until the beginning of the Upper Palaeolithic (Yravedra, 2013). These two issues are present in the levels studied at Llonin. In most cases the caves hold palimpsests of occupations, where both carnivores and humans contributed to and altered the bone assemblages to a varying degree at different sites and levels. In the levels for which anthropic occupations and accumulations have been described, there is a preponderance of large (aurochs and horse) and medium-sized (deer) species. Access to these prey by Neanderthals is primary, and their transport is based on size: differential (large) or complete (medium). The documentation of cut and percussion marks shows complete and intense processing, including skinning, viscera removal, disarticulation, flesh removal and fracturing to access the marrow. Thermal alterations do not seem to be very significant though, except for El Esquilieu (Yravedra and Uzquiano, 2013; Yravedra et al., 2005), Covalejos (Yravedra et al., 2016) and Arlanpe (Arceredillo et al., 2013). However, their origin has only been established in the first case, linked to their use as fuel for fires.

Regarding small ungulates such as Iberian ibex, chamois and roe deer, they were accumulated by various different agents. At most sites Neanderthals do not play an important role in their procurement, although anthropic modifications have been identified on some remains at Amalda, El Ruso, Morín Cave and Covalejos. However, the number of human marks is small compared with the frequency of marks on deer or large ungulates. Nevertheless, this situation is slightly different at sites in mountainous locations such as El Esquilieu (Yravedra, 2006a, Yravedra, 2006b) and Valdegoba (Díez, 2006), where largely anthropic caprine

assemblages have been described (Yravedra and Cobo-Sánchez, 2015). In levels VI–XIII of El Esquilieu there is a considerable presence of cut marks and percussion fractures, and the action of carnivores is less frequent than in higher levels (III–IV). In other assemblages, this information is not clearly defined, as is the case at El Castillo, where anthropic modifications on ungulate remains have been recorded, but the data are presented grouping together Middle and Upper Palaeolithic levels (Landry and Burke, 2006). At Arlanpe, Iberian ibex and chamois represent most of the fauna, and although a larger number of anthropic modifications (7.7%) has been documented than those made by carnivores (4.2%), their location, especially regarding the indeterminate remains, makes it impossible to clearly separate their origin (Arceredillo et al., 2013). In the case of Llonin, as with most other sites, caprine remains are in the minority, so it seems that they were not significant prey in the Neanderthal diet. Both at Llonin and at many Cantabrian sites and other non-Cantabrian sites such as Boquete de Zafarraya or Moros de Gabasa carnivores are the main agents responsible for the accumulation of caprine bones. In most assemblages, based on the size of the pits, the fragmentation pattern and the fact that specimens were transported whole, the caprine accumulations are attributed to medium-sized carnivores, which would sometimes be felids such as the lynx or leopard or canids such as the fox (Yravedra, 2010a; Yravedra et al., 2010, 2015). At most of these Cantabrian sites the presence of carnivores has been inferred from their own bones and dental modifications on prey, but there are few digested bones, coprolites and elements from very young individuals, which would be related to the more intense use of the caves as breeding dens. This contrasts with Llonin, where these features are present. The alternating use of the space by carnivores and Neanderthals is confirmed not only by the primary accumulations of small ungulates, but also by the identification of scavenging activities on the remains left by humans. In this regard, there are records of taxa accumulated by humans, such as deer with dental modifications and even bones with overlapping lithic and dental marks, e.g., at Amalda, Covalejos and El Ruso. The difference with Llonin lies in the fact that the secondary modifications on deer remains are linked to the action of hyenas, a larger carnivore than those described in relation to the aforementioned assemblages. This mixture of anthropic and hyenid activities is observed in other assemblages such as those of Abrigo de Navalmaillo (Huguet et al., 2010), Furninha (Brugal, 2010), and Teixoneres (Rosell et al., 2010b).

In summary, the archaeozoological context of the Cantabrian area provides some data about the subsistence models of Neanderthal groups, although they are generally scarce. Since we are largely dealing with short occupations, the anthropic accumulations are not very abundant and repeatedly focus on large and medium-sized prey. The consumption of smaller ungulates such as caprines or roe deer has only been recorded in certain specific cases. Consumption is intense, but the use of fire as a culinary technique cannot be established in any of the cases. Llonin does not provide any further information on this matter, as no burnt remains have been identified yet. What is clear is the complexity of the formation and alteration of these

assemblages from the North of the Iberian Peninsula, where both Neanderthals and carnivores took prey to caves to feed on it, where different carnivores also scavenged on the remains left by humans and other carnivores. Sometimes it is therefore difficult to differentiate between occupations and the origin of the accumulations, although the fact that humans and carnivores chose different taxa at most sites, possibly as a result of interspecific competition for the available resources, could help us distinguish them.

This alternation between caprine predators seems to be common to other Middle Palaeolithic sites in the Mediterranean region of the Iberian Peninsula. In assemblages such as those of Cova Beneito and Cova Negra (Martínez Valle, 1996) or Abric del Pastor (Pérez Luis et al., 2017) we find similar mixed accumulations. However, there are also examples of the anthropic origin of these preys, e.g., in level IV of Abrigo de la Quebrada (Real et al., in press; Sanchis et al., 2013). It is interesting to reflect on why the anthropic caprine accumulations are not very significant in most Mousterian archaeological assemblages. In this regard, some authors (Yravedra, 2013; Yravedra and Cobo-Sánchez, 2015) have proposed and analysed different hypotheses. The first is related to the difficulty that Neanderthals had hunting this type of prey due to lack of tools or knowledge of techniques (Martínez-Moreno, 2005). But this idea has been disproved by the discovery of assemblages of entirely anthropic origin, such as El Esquilleu and Valdegoba. Secondly, it has been suggested that the location of the site may be important. Although sites with anthropic caprine accumulations tend to be in mountainous inland areas, there are exceptions that invalidate this theory, such as Amalda and Llonin, where caprines are not the taxon most frequently accumulated by Neanderthals. Lastly, it has been suggested that it may have been a matter of decisions made by Neanderthal populations and their preferences in terms of hunting and eating. But this idea is difficult to analyse and quantify at present. Llonin raises this issue again, as the cave is situated in a mountainous area where chamois and Iberian ibex would have been available, but there would also have been valleys and forests nearby where deer could be found. The Neanderthal groups that occupied Llonin chose to consume mostly deer, although they occasionally hunted caprines. This may be linked to the seasonality of the occupations, but we cannot offer reliable data in this regard. It could also reflect an eating preference or competition with other predators such as leopards, which prey primarily on caprines.

6. Conclusions

The study of the faunal remains from basal levels of Llonin once again reveals the great difficulty of characterising Palaeolithic archaeological assemblages in a cave. They consist of a mixture of materials resulting from the involvement of different agents throughout multiple events and they show modifications of biotic and abiotic origin. Despite this, our work has yielded three main conclusions:

- The origin of the bone accumulations is diverse: the deer remains are mainly related to Neanderthal activity, the

leopard was responsible for the caprine remains, and the action of hyenas was based on bringing bear bones into the cave and scavenging on the remains left mainly by humans.

- The cave served as a place of life and death and was occupied alternately by hyenas, leopards and other species of carnivores, as well as by Neanderthals for short, sporadic phases, which appears to be a common model during MIS 3.
- The cave is located in an area of transition between forest and steeper terrain. In this ecotone, the subsistence activities of Neanderthals revolved around the processing and consumption of deer and, to a lesser extent, caprines, which is consistent with the evidence found at other Middle Palaeolithic Cantabrian sites.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at: <https://doi.org/10.1016/j.crpv.2018.06.001>.

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