



General palaeontology, systematics and evolution (Invertebrate palaeontology)

Leporids as a potential resource for predators (hominins, mammalian carnivores, raptors): An example of mixed contribution from level III of Teixoneres Cave (MIS 3, Barcelona, Spain)



Les léporidés, une ressource potentielle pour les prédateurs (hominidés, mammifères carnivores, rapaces) : un exemple de contribution mixte dans le niveau III de la grotte de Teixoneres (MIS 3, Barcelone, Espagne)

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ABSTRACT

Apart from humans, other predators can take part in creating bone accumulations by generating waste materials that may have been mixed with those produced by hominids and leading to the formation of palimpsests. This is discussed here in the case of Middle Paleolithic leporid assemblages, to which carnivores have frequently contributed. Level III of Teixoneres Cave (MIS 3) is a sample that can be used to address the origin of leporid assemblages in archaeological contexts. Applying an archaeozoological and taphonomical methodology has made it possible to state that the assemblage of leporids in the site has been generated by a mix of contributions, in which small mammal carnivores and nocturnal raptors seem to play an important role, together with occasional hominid inputs. The aim of this paper is to present new data about Neanderthal activities at this site and support the hypothesis related to short-term human occupations in the cave.

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R É S U M É

En plus des hominidés, d'autres prédateurs peuvent prendre part à la formation d'accumulations en générant des déchets qui se mélangent à ceux produits par les hominidés, conduisant à la formation de palimpsestes. Ceci est fréquemment discuté dans le cas d'assemblages de léporidés du Paléolithique moyen, auxquels les carnivores ont

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souvent contribué. Le niveau III de la grotte de Teixoneres (MIS 3) constitue un exemple qui peut être utilisé pour comprendre l'origine des assemblages de léporidés dans des contextes archéologiques. L'application d'une méthodologie archéozoologique et taphonomique a permis d'affirmer que l'assemblage de léporidés dans le site a été généré par différents agents, parmi lesquels les petits mammifères carnivores et les rapaces nocturnes semblent jouer un rôle important, ainsi que quelques visites occasionnelles de groupes humains. Le but de cet article est de présenter de nouvelles données sur les activités des Néandertaliens dans ce site et de contribuer à l'hypothèse relative à des occupations humaines de courte durée dans la grotte.

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1. Introduction

Taphonomic evidence shows that caves were used both by hominins and carnivores during the Pleistocene, and, in some cases, human and carnivore occupations alternated (e.g., Binford, 1981; Blasco Sancho, 1995; Brugal and Fosse, 2004; Domínguez Rodrigo et al., 2007; Rosell and Blasco, 2009; Stiner, 1994; Yravedra, 2011). This phenomenon produces overlapped assemblages that, when associated with low sedimentation rates, generate palimpsests that are difficult to tackle archaeologically.

In the case of small mammals, such as rabbits, this phenomenon is especially critical. The presence of these animals in a cave can be related to multiple factors, such as natural accumulations and inputs from hominins or carnivores (mammals and raptors).

The anthropic origin elucidates human strategies for acquiring, processing and consuming animals. By contrast, a non-anthropoc origin might be associated with carnivore predation or mortality in a generic sense (Callou, 2003; Sanchis, 2010). The other contribution, less common and with a lower impact, could occur without any predator activity. Rabbits, because of their fossorial behaviour and reduced mobility, tend to create colonies and dig burrows (tunnel systems) in sandy archaeological sediments. In these environments, they may become trapped and die, facilitating the preservation of anatomically connected skeletal remains (Stahl, 1996). Predator activity is, however, the most significant cause of death in rabbits (e.g. Delibes and Hiraldo, 1981). Because of their high reproductive rates and their fast adaptation, rabbits have been abundantly present in different biotopes found on the Iberian Peninsula. This has led to their importance in the food chain of a wide variety of predators – several diurnal and nocturnal raptors as well as mammal carnivore species. This is why some studies have focused on distinguishing the agent generating leporid accumulations, such as nocturnal raptors (e.g., Cochard, 2004a, 2004b; Guillem and Martínez Valle, 1991; Lloveras et al., 2009a, 2012a; Martínez Valle, 1996; Sanchis, 1999, 2000, 2001; Yravedra, 2004, 2006), diurnal raptors (Hockett, 1993, 1995, 1996; Lloveras et al., 2008a), wolves and dogs (Payne and Munson, 1985; Schmitt and Juell, 1994), the Iberian lynx (Lloveras et al., 2008b; Rodríguez-Hidalgo et al., 2013), foxes (e.g. Cochard, 2004a, 2004c; Hockett, 1999; Hockett and Haws, 2002; Krajcarz and Krajcarz, 2012; Lloveras et al., 2012b; Mondini, 2000; Sanchis, 1999, 2000, 2010; Sanchis and Pascual, 2011) and hominins (e.g., Blasco and Fernández

Peris, 2012a, 2012b; Blasco et al., 2013; Cochard et al., 2012; Hawkes et al., 2001; Landt, 2004, 2007; Lloveras et al., 2009b; Lupo and Schmitt, 2002; Pérez Ripoll, 1991, 1993, 2001, 2002, 2004; Sanchis, 2010; Sanchis and Fernández Peris, 2008; Steadman et al., 2002). Although most of these studies focused on ingested remains, the recent interest in non-ingested carnivore waste tends to fill the gap in that respect.

This growing body of actualistically-based research into small carnivores as taphonomic agents is indirectly related to the two main schools of thought that emerged after the debate about the capabilities of pre-Modern Humans that took place during the 1990s: one holds that these hominids were versatile enough to adapt to their environment (e.g., Blasco and Fernández Peris, 2012a, 2012b; Blasco et al., 2013; Cochard et al., 2012; Finlayson et al., 2012; Hardy et al., 2013; Henry et al., 2011; Morin and Laroulandie, 2012; Peresani et al., 2011; Salazar-García et al., 2013); the other maintains that they were not efficient enough to face new conditions (e.g. Brown et al., 2011; Fa et al., 2013; Wynn and Coolidge, 2004). This is closely related to the general belief that Neanderthals specialized in big game, at least in some areas (e.g., Balter and Simon, 2006; Bocherens and Drucker, 2006; Gaudzinski-Windheuser and Roebroeks, 2011; O'Connell, 2006; Richards and Trinkaus, 2009). Some studies carried out during recent decades counter this argument with evidence of the use and consumption of small animals in the Mediterranean region that goes back to the Middle and early Late Pleistocene (e.g., Blasco, 2011; Blasco and Fernández Peris, 2012a, 2012b; Blasco et al., 2013; Brown et al., 2011; Cochard et al., 2012; Finlayson et al., 2012; Hardy and Moncel, 2011; Klein and Scott, 1986; Peresani et al., 2011; Stiner, 2001, 2005), and even as far as the Early Pleistocene of Sima del Elefante (Atapuerca, Spain), with two cut-marks on the mid-shaft of one leporid radius at TE12a (Blasco et al., 2011; Huguet, 2007; Huguet et al., 2013). In the Iberian Peninsula, apart from Bolomor Cave (MIS 9–5e) and Gibraltar sites (MIS 3) (Blasco, 2008, 2011; Blasco and Fernández Peris, 2012a, 2012b; Brown et al., 2011; Finlayson et al., 2012), there are other Middle Paleolithic archaeological localities with evidence of human consumption of small animals, although this evidence is scarce and the authors argue that these localities do not present systematic consumption. This is the case with Cova Negra (MIS 5e–3) (Martínez Valle, 1996; Pérez Ripoll, 1977; Sanchis, 2010), Cova Beneito (MIS 3) (Martínez Valle, 1996) and El Salt (MIS 3) (Galván and Hernández, 2013), among others.

Teixoneres Cave is presented as a new example of a Middle Paleolithic site where the presence of leporids continues along the sequence. Human and carnivore activity on larger fauna have been confirmed at the site (Rosell et al., 2008, 2010a, 2010b). It is suggested that something similar is true for leporid remains, but this has not yet been established. Level III (MIS 3) is particularly relevant because human activity seems to be more intensive, as is the presence of leporid bones. For this reason, various different objectives have been proposed, with the aim of knowing what happened to leporids from this specific archaeological level. The main goal is to figure out which accumulator agents were consuming the leporid remains. In the case of human activity, it is also important to corroborate human consumption of this prey at the site and, as far as possible, infer from this Neanderthal diet and subsistence strategies in the Middle Paleolithic.

2. Materials and methods

2.1. Teixoneres Cave

Teixoneres cave (Moià, Barcelona) is an archaeological site located in the Northeast of the Iberian Peninsula, at 785 m above sea level (Fig. 1), within a karstic system drained by the Torrent del Mal. It is composed of three chambers (X, Y and Z), forming a “U” shape made up of 30 m diameter circles. The main access is through chamber X, and there is a second small entrance in chamber Z. It was discovered to be an archaeological site in the 1940s and was excavated by several different teams, until an interdisciplinary research team from IPHES was put in charge of the excavation, applying extension method of fieldwork that concerns the whole surface of the site.

The site is composed of ten archaeo-paleontological levels (Fig. 1), which are simultaneously divided into 15 sublevels. They include two speleothems that compose levels I and IV, respectively. The upper levels (from I to IV) have been dated by uranium-thorium techniques to a range from ca. 14–16 Kyr (for level I) to ca. 100 Kyr (for level IV) (Tissoux et al., 2006). This was also confirmed by biostratigraphy (López-García et al., 2012). In turn, these archaeological levels are divided into five formation phases (Rosell et al., 2010a). The second phase is where level III is located. Level III is composed of two different sublevels (IIIa and IIIb) basically distinguished by:

- IIIb contains a higher proportion of reddish clays, while IIIa contains more light brown silts;
- falling of limestone blocks in the whole site surface at IIIa base, especially on the main entrance;
- archaeological record density increases at IIIb, where anthropic activity is enhanced.

The sediment comes from allochthonous colluvial clays and silts, introduced in the cave through at least two ways: the main entrance and a chimney located at the northeast side of the cave. Those sediments imbricate at the centre of the main gallery. An autochthonous component is formed by limestone blocks falling from the walls and the roof of the cave. In addition to this, no rounded-angle gravel

accumulations indicating the presence of low-flow water streams and/or channels were detected. Palaeoecological studies of the site confirm that climate conditions for level III were propitious, with warm temperatures and high humidity, typical of semi-open landscapes with patches of forest (López-García et al., 2012).

A wide diversity of taxa has been identified at this site. These include carnivores such as *Ursus spelaeus*, *Crocuta crocuta*, *Canis lupus*, *Vulpes vulpes*, *Lynx spelaea* and *Meles meles*; but also a vast range of herbivores, such as *Stephanorhinus hemitoechus*, *Equus ferus*, *Equus hydruntinus*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius* and caprids. Small animals (*Erinaceidae*, tortoises, birds and leporids – *Oryctolagus cuniculus* and *Lepus* sp.) are also present in the site. Although *Lynx spelaea* is recovered at the Formation Phase 2 (levels II–III), up to now, this taxon was only found at level II and no lynx remains were recovered from level III. On the other hand, human activity has been confirmed by the presence of cut-marks and fresh fractures on macro-faunal remains (especially ungulates), burned bones and Mousterian lithic tools, together to the presence of hearths, mainly located at the entrance of the cave. In spite of this evidence, the regular use of the cave by carnivores (mainly hyenas and cave bears, as well as other small carnivores) seems to have been the main dynamic; nevertheless, it seems to be occasionally broken by short-term Neanderthal occupations (Rosell et al., 2010a, 2010b).

2.2. Methodology

Despite a distinction among different sublevels for level III, the sample presented here was analysed and processed as a single unit, because part of the leporid assemblage came from some areas of the cave where the sublevel differentiation is not clear. It is expected to deepen research on archaeo-stratigraphy by getting further results on that field.

Leporid remains were recovered from the excavation field work using the 3-D location system and, in addition, sediment was water-screened on a superimposed mesh from 5 to 0.5 mm, to avoid possible biases of smaller remains. The remains were identified both anatomically and taxonomically in order to distinguish the different leporid taxa (Callou, 1997; De Marfà, 2009).

The age profile was deduced by considering the degree of ossification and of fusion of the epiphyses of long bones. Three categories were established (Cochard, 2004a; Jones, 2006; Sanchis, 2010): infantile (<3 months), juvenile (3/5–9 months) and adults (>9 months). To reach an approximation to the sex-ratio in the assemblage, a scatter plot was used, taking into account the distal and trochlear breadth of the humerus (Jones, 2006).

All the remains were quantified in order to calculate the Number of Identified Specimens (NISP), the Minimum Number of Elements (MNE), the Minimum Number of Individuals (MNI) and Minimal Anatomical Unit (MAU) and their frequencies (Brain, 1981; Lyman, 1994). For the MNE, the age profile and the portion and face of each bone (Schmidt, 1972), epiphysis and diaphysis included, were taken into consideration (Rosell, 2001). Laterality of the bones was also used for the MNI. The survival rate was

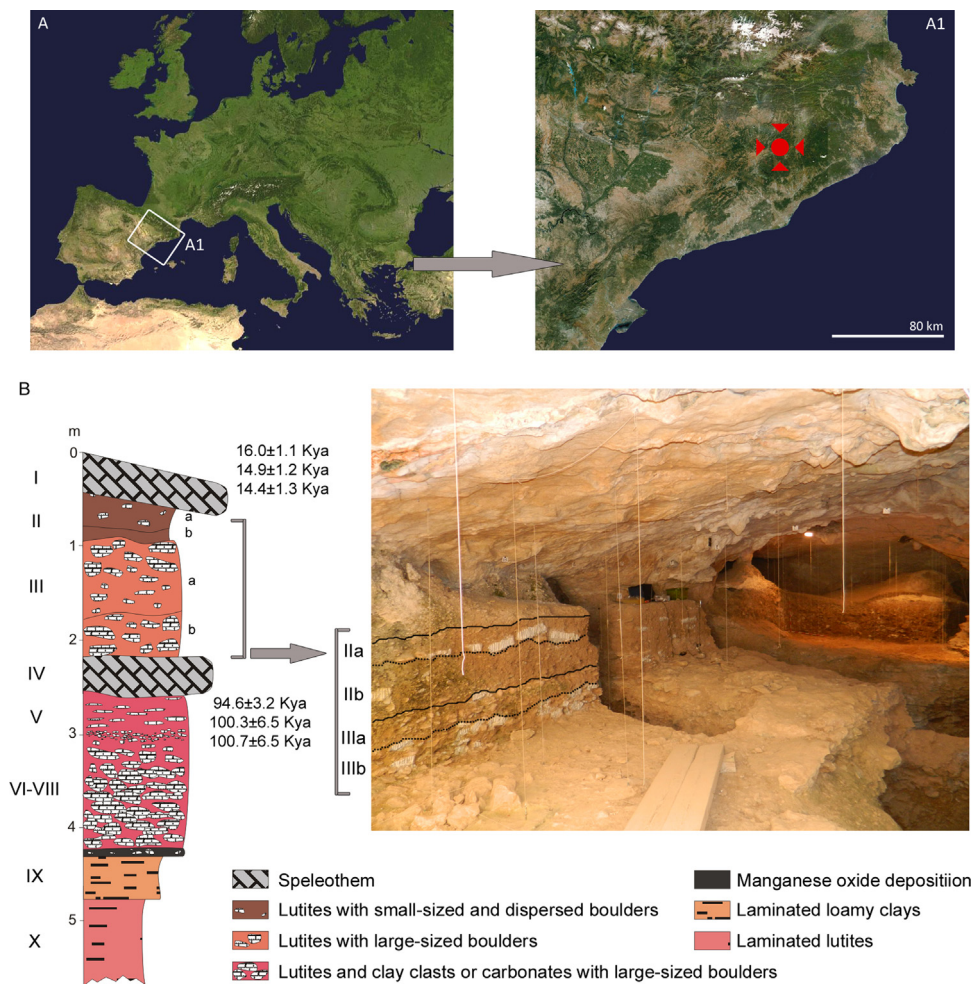


Fig. 1. Situation of Teixoneres Cave (A, A1) and the image of the cave with its stratigraphical profile (B).

Fig. 1. Position géographique de la grotte de Teixoneres (A, A1) et photographie de la grotte avec sa coupe stratigraphique (B).

gauged from the ratio of elements recovered to elements expected.

Differential conservation in relation to bone density was evaluated by using the bivariate *Pearson's r* correlation, taking into account the data provided by [Pavao and Stahl \(1999\)](#) for *Oryctolagus cuniculus*. *Lepus* sp. was excluded from this calculation, due to its limited representation.

An Olympus SZ11 Stereo Microscope with zoom up to 110 was used for analyzing modifications to the surfaces of bones. Fragmentation was evaluated to compare it with that produced by different agents. Green and dry bone fractures were established by following the criteria given by [Sanchis \(2010\)](#) and [Cochard et al. \(2012\)](#). Green fractures have curved and/or spiral form with oblique angles and smooth edges, while dry fractures present transverse forms with straight rough edges.

Mechanical modifications by carnivores on bone surfaces were observed, such as tooth-marks (pits, punctures and scores). The distribution, orientation and dimensions of these modifications were recorded. Other damages produced during consumption (notches, crenulated edges or

pitting) were also taken into consideration. Digested bones were documented as chemical alterations, and five degrees of corrosion were distinguished, from 0 to 4 ([Andrews, 1990](#)): (0) no-corrosion; (1) light corrosion with small holes and slightly rounded edges; (2) moderate corrosion where pitting effect increases and bone destruction begins with fissures and rounded edges; (3) strong corrosion affecting the whole bone with important destruction of tissues; (4) extreme corrosion affecting the bone structure that hinders its identification. Tooth-marks were also compared with those generated by humans mentioned by [Landt \(2007\)](#), [Pérez Ripoll \(2004\)](#), [Sanchis \(2010\)](#) and [Sanchis et al. \(2011\)](#). Those modifications are typically shallow in cross-section and ovoid/irregular in plain view (pits); or elongated with rounded cross-section that occasionally shows internal crushing (scores), often associated with other damages ([Landt, 2007](#)).

Cut-marks ([Shipman, 1981](#); [Shipman and Rose, 1983](#)), bone breakage ([Cochard et al., 2012](#); [Sanchis, 2010](#)) and burned bones were listed as anthropic modifications to bone surfaces. The distribution, orientation and

dimensions of cut-marks were taken into consideration. Five degrees of coloration (0 to 5) were used for classifying burned bones (Stiner et al., 1995), where 0 is no burnt (no coloration) and 5 calcined (white).

3. Results

Level III of Teixoneres Cave provided 3964 leporid remains. The MNE is 1512, and the majority of elements are well represented. Of these, radii (78), humeri (77), femora (73) and calcanea (70) are best represented. A MNI of 49 were morphologically attributed to the species *Oryctolagus cuniculus*, considering radius, calcaneus and tibia; and just one from the genus *Lepus*, established by a tibia. Although the sample includes both genera, rabbits seem to be the highly represented taxon. In spite of this, we prefer to use the term leporid or lagomorph from here, as more caution is needed when classifying diaphyseal long bone fragments (without ends).

Adults seem to predominate in the assemblage (76%), while the percentages of identified juveniles (6%) and infants (18%) are lower. Following Jones' (2006) criteria for distinguishing sex-ratio profiles in the assemblage, the data presented in a scatter plot seem to be dispersed homogeneously and it is not possible to distinguish two clear groups, implying that neither sex predominates (Fig. 2).

The % MAU was calculated, to evaluate the anatomical representation of the assemblage. This shows which elements were absent as a percentage of what one would have expected to find. According to this, the skeletal representation is biased. The best-represented elements are those from the proximal appendicular skeleton, of which the radius (79.59%) and humerus (78.57%) have the highest values. The femur and calcaneus are also well represented (74.49% and 71.43%, respectively), whereas carpal/tarsal bones and vertebrae are under-represented. Despite that, there are no significant differences in representation between the anterior and posterior limbs, while the bones of the axial and cranial skeleton are under-represented. According to Pavao and Stahl's (1999) criteria, a differential conservation index shows that the biases away from some parts of the anatomy are not due to bones being lost because of their low density (Pearson $r=0.22$). The biases should therefore be caused by other biological agents unrelated to bone density (Table 1).

A high degree of fragmentation is observed; only 13.75% of the remains were recovered complete. For the long bones (stylopodials and zeugopodials) the fragmentation is even more obvious, with less than 4% of bones complete for each category. Of the fragmented bones, shaft fragments predominate for long bones (>53% of representation in each category). Only the humeri present different tendencies, with a higher presence of distal epiphysis (51.91% of humeri fragments).

Taking the assemblage as a whole, 1974 bone fracture planes were analysed. Most of them (97.11%) were attributed to fresh breakage, presenting curved shaped fractures, oblique angles and smooth edges (Sanchis, 2010). Ten long bone shaft cylinders were also identified in the assemblage (0.3% of the assemblage), including femur (NISP=5), tibia (NISP=2), radius (NISP=2) and an

Table 1

NISP, MNE, MNI and % MAU of Teixoneres level III assemblage.

Tableau 1

NSPI, NME, NMI et %UMA de l'assemblage du niveau III de la grotte de Teixoneres.

MNI = 49	NISP	MNE	% MAUO. <i>cuniculus</i>
Cranium	110	20	–
Mandible	132	50	51.02
Incisive	164	149	–
Molar/premolar	270	243	–
Vertebra	156	109	5.3
Rib	177	132	11.2
Scapula	109	38	38.78
Pelvis	120	53	54.08
Humerus	130	77	78.57
Femur	190	73	74.49
Radius	113	78	79.59
Ulna	131	66	67.35
Tibia	286	67	68.37
Metacarpus	149	127	32.40
Metatarsus	250	213	54.34
Astragalus	25	24	24.49
Calcaneus	81	70	71.43
Tarsal	2	2	2.04
Phalanx	315	307	12.05
Long bones	971	–	–
Flat bones	64	–	–
Irregular bones	7	–	–
Indet.	6	–	–

NISP: Number of Identified Specimens; MNE: Minimum Number of Elements; MNI: Minimum Number of Individuals; MAU: Minimal Anatomical Unit. Six remains (NISP and MNE) have been excluded because they have been morphologically attributed to *Lepus* sp. Isolated teeth has been excluded from the total MNE counting.

Six restes (NR et NME) ont été écartés pour leur attribution morphologique à *Lepus* sp. Les dents isolées n'ont pas été considérées pour recompter le NME total.

undetermined long bone. None of them exceed 50% of total bone length, being two femora, one tibia and one undetermined bone less than 25% of the total shaft length. All the shaft cylinders measure less than 40 mm long, and three of them have alterations caused by digestion.

A total of 640 leporid remains present modifications produced by carnivores (16.15%). Most of them (51.92% of the modified remains and 9.21% of the total remains) were caused by digestion. Of the digested bones, there is a predominance of those that have been slightly digested (85.21% of digested bones) with rounded edges, showing early stages of tissue loss. Water effect was ruled out on these bones because no homogeneous polish/rounded surfaces and micro-striations were detected (Bromage, 1984). Grade 3–4 corrosion is also present and, even at low proportions, it especially affects calcanea.

Mechanical modifications are present on 8.53% of all the remains in the assemblage. Of these, tooth-marks predominate: 3.15% are pits/punctures and 1.61% scores (Fig. 3). Notches or crenulated edges are also represented in lower proportions. Of the mechanical alterations, 37.01% are located on the diaphyses of long bones. Flat bones have also been affected, containing 31.64% of the tooth-marks in the assemblage. In this respect, the mandibles and pelvis were most affected, with around 23% of each type of bone showing mechanical modifications.

Anthropic damage is present on 2.14% of the assemblage (Tables 2 and 3). It was mainly detected by the

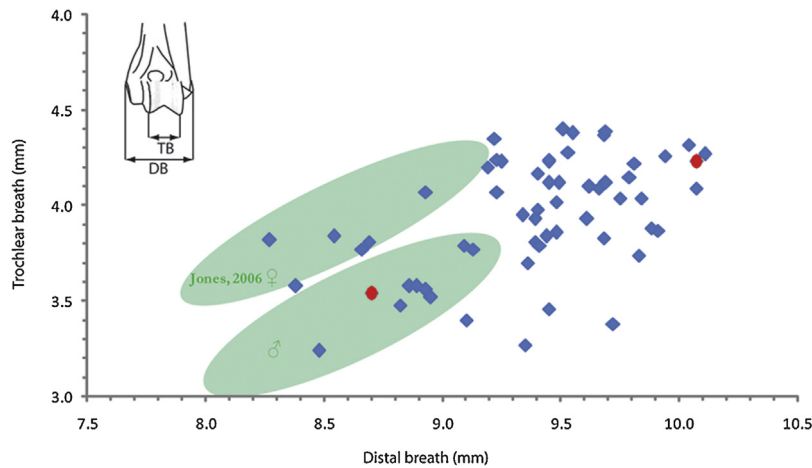


Fig. 2. Scatter plot showing the sex-ratio of rabbits at level III of Teixoneres Cave, considering the total breadth and the trochlear measurements of distal humeri. Jones' data (2006) was considered as a reference. Rounded points refer to remains with direct evidence of human processing. TB: trochlear breadth; DB: distal breadth.

Fig. 2. Diagramme de dispersion indiquant le *sex-ratio* des lapins du niveau III de la grotte de Teixoneres, consid rant le diam tre transversal total et le diam tre de la trochl e de la partie distale de l'hum rus. Les donn es de Jones (2006) sont utilis es comme r f rence. Les ronds se r f rent aux restes osseux avec une  vidence directe d'activit  humaine. TB : diam tre transversal de la trochl e ; DB : diam tre transversal total.

presence of cut-marks (0.76%), and thermo-alterations on bones (0.91%); nevertheless, other modifications, such as tooth-marks and breakage (0.48%) might be also attributed to human action because of its shallow and irregular morphology and its association with flexion fractures and crenulated edges (Landt, 2007; Sanchis, 2010; Sanchis et al., 2011).

Cut-marks have been identified on tibia (NISP= 7) and metatarsus (NISP=8), which together represent 50% of the remains having this type of modification (Fig. 4). Other unidentified long bones also have cut-marks on

them (NISP= 2), as do the pelvis (NISP= 2), femur (NISP= 3) and scapula (NISP=3), among others. Incisions seem to predominate, associated with skinning, disarticulation and defleshing. Skinning and defleshing are better represented (Table 2). Human breakage produced on bones by bending or tooth pressure was detected associated with notches and human tooth-marks (Landt, 2007).

With respect to burned bones (Fig. 5), these represent a significant part of those remains showing direct evidence of processing by hominins. They are in small fragments which are less than 2 cm long. Most of them (NISP= 22) are

Table 2
Leporid bones with cut-marks at level III of Teixoneres Cave.

Tableau 2
Ossements de l porid s avec des marques de d coupe dans le niveau III de la grotte de Teixoneres.

Activity	Skeletal element	No. remains	No. striations by group	Type	Location	Orientation
Skinning	Nasal	1	1	Incisions	Dorsal	obl.
	Metacarpal IV	1	1	Incisions	Diaphysis	tr
	Metatarsal II	4	1–30	Incisions-scrapes	Proximal end	obl.
	Metatarsal III	3	1–7	Incisions-scrapes	Diaphysis	obl.-tr.
Disarticulation	Metatarsal V	1	4	Incisions	Proximal end	obl.
	Pelvis	1	3	Incisions	Diaphysis	obl.
	Ulna	1	3	Incisions	Acetabulum	obl.
	Pelvis	1	34	Incisions	Proximal end	tr
Defleshing					Ischium/pubis	obl.-long.-tr.
	Scapula	3	1–4	Incisions	Diaphysis	obl.-tr.
	Femur	3	1–2	Incisions	Proximal end	tr.
					Diaphysis	obl.-tr.
	Humerus	1	1	Incisions	Distal end	obl.
	Radius	1	1–4	Incisions	Diaphysis	obl.
	Tibia	7	1–5	Incisions	Proximal end	obl.
					Distal end	
					Diaphysis	
	Long bones, indet.	2	1	Incisions	Diaphysis	obl.

obl.: oblique; long.: longitudinal; tr.: transversal.

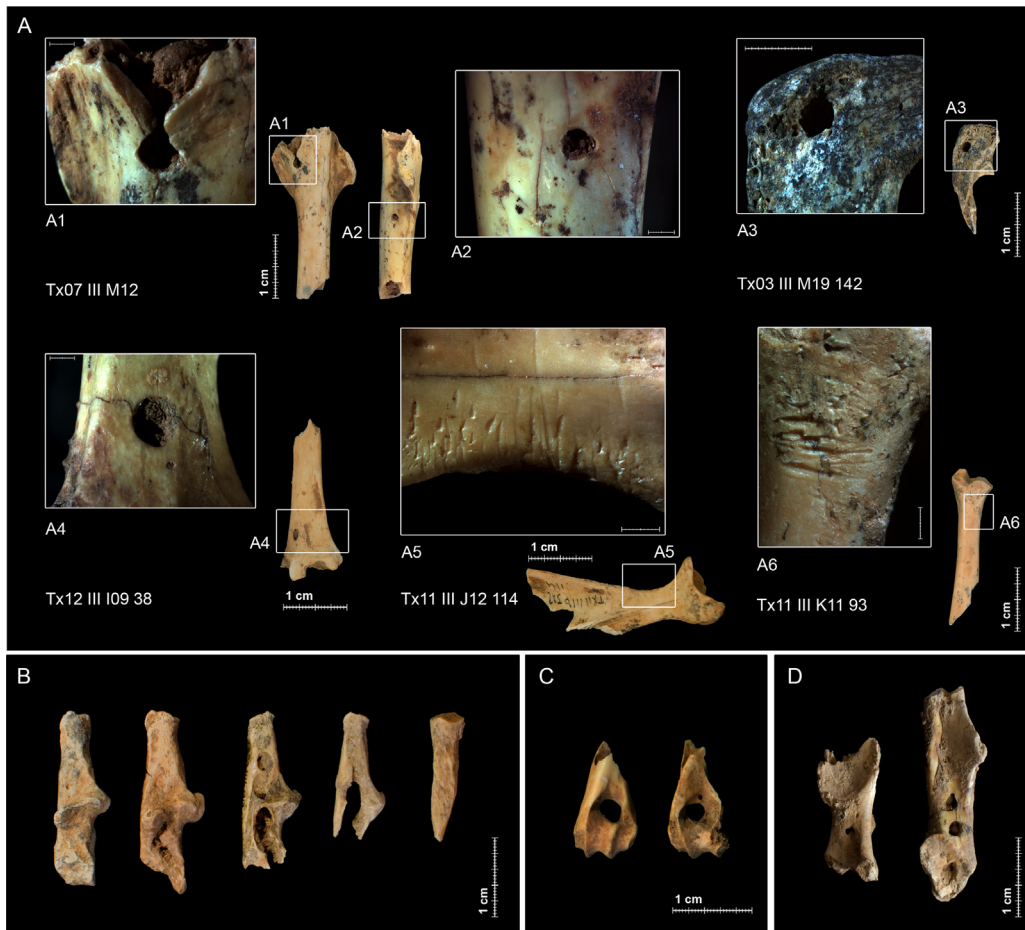


Fig. 3. Carnivore modifications observed at Teixoneres level III. Punctures (A1, A2, A3, A4, D) and scores (A5, A6) are shown in the images, considering their disposition on bones surface. Corrosion produced by digestion is also present in different grades (B, C). A1 & A2: left femur; A3: right ulna; A4: right tibia; A5: left scapula; A6: right radius; B: calcanea; C: humeri; D: pelvis.

Fig. 3. Modifications réalisées par les carnivores sur l'assemblage du niveau III de la grotte de Teixoneres. Perforations (A1, A2, A3, A4, D) et rainures (A5, A6) sont indiquées en relation avec leur position sur l'os. La corrosion liée à la digestion de l'os est représentée par différents degrés (B, C). A1 & A2: fémur gauche; A3: ulna droite; A4: tibia droit; A5: scapula gauche; A6: radius droit; B: calcanéum; C: humérus; D: coxaux.

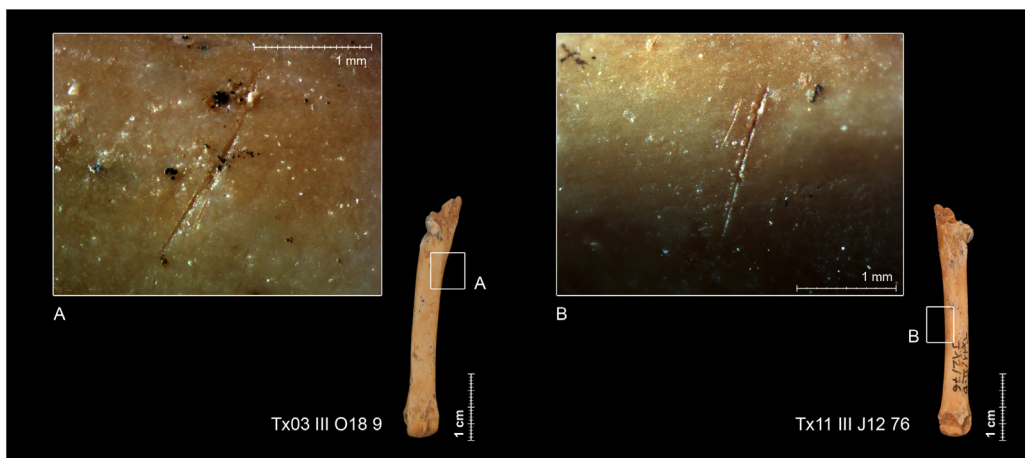


Fig. 4. Anthropic cut-marks on metatarsal remains from Teixoneres level III (A, B) and their situation on bones surface.

Fig. 4. Marques de découpe anthropiques sur des métatarses du niveau III de la grotte de Teixoneres (A, B) et leur position sur la surface de l'os.

Table 3

Values (and percentages) of the modifications produced by both hominids and carnivores by anatomical elements.

Tableau 3

Valeurs (et pourcentages) des modifications produites par les hominidés et les carnivores par élément anatomique.

Skeletal element	Anthropogenic modifications										Carnivore modifications								
	Cut-marks (%)	Thermo-alterations								Human tooth-marks (%)	Pits/punctures (%)	Scores (%)	Digested bones						
		G1	G2	G3	G4	G5	G 2-3	G 2/3	G 3-4				Total (%)	G1	G2	G3	G4	Total (%)	
Cranium	1 (0.9)											1 (0.9)		5			1		6 (5.5)
Mandible												4 (3.0)	4 (3.0)	12	1				13 (9.8)
Teeth														22	3				25 (5.8)
Vertebra												4 (2.6)	2 (1.3)	14	1				15 (9.6)
Rib							2			2 (1.2)		2 (1.1)	2 (1.1)	11					11 (6.2)
Scapula	3 (2.8)			1						1 (0.9)		5 (4.6)	2 (1.8)	13	2	1			16 (14.7)
Pelvis	2 (1.7)						1			1 (0.8)		9 (7.3)	2 (1.7)	18	3				21 (17.4)
Humerus	1 (0.8)										1 (0.8)	16 (12.2)	5 (3.8)	24	2				26 (19.8)
Femur	3 (1.6)				1					1 (0.5)		6 (3.1)	4 (2.1)	20	2	1			23 (12.0)
Radius	1 (0.9)			1				1		2 (1.8)	1 (0.9)	2 (1.8)	7 (6.2)	8		1			9 (8.0)
Ulna	1 (0.8)	1				1				2 (1.5)		10 (7.6)	4 (3.1)	31	7	1			39 (20.8)
Tibia	7 (2.4)			1	1		1			3 (1.0)		8 (2.8)	7 (2.4)	18	2				20 (7.0)
Metacarpus	1 (0.7)											5 (3.4)	3 (2.0)	5					5 (3.4)
Metatarsus	8 (3.2)										1 (0.4)	15 (6.0)	11 (4.4)	14	1				15 (6.0)
Astragalus														2			1		3 (12.0)
Calcaneus												11 (13.6)	1 (1.2)	21	6	9	1		37 (45.7)
Phalanx						1				1 (0.3)	2 (0.6)	24 (7.6)	2 (0.6)	22					22 (7.0)
Long bones	2 (0.2)		12	4	2	1	2		1	22 (2.3)	2 (0.2)	3 (0.3)	8 (0.8)	44	5	1			50 (5.1)
Flat bones							1			1 (1.3)				5	2				7 (10.9)
Irregular bones														2					2 (28.6)
Total specimens	30 (0.76)	1	12	7	4	3	7	1	1	36 (0.9)	7 (0.18) ^a	125 (3.15)	64 (1.61)	311	37	15	1		365 (9.2)

^aThe values referred to human tooth-marks only consider pits and scores. Notches and anthropogenic breakage are not represented. "G" refers to different thermo-alteration grades for anthropic modifications (Stiner et al., 1995), and digestive grades for carnivore modifications (Andrews, 1990).

Les valeurs qui concernent les traces des dents seulement prennent en considération les enfoncements et les sillons. Les encoches et la fracturation d'origine anthropique ne sont pas représentées. « G » se réfère à différents grades de crémation pour les modifications anthropiques (Stiner et al., 1995) et de corrosion digestive pour les modifications produites par des carnivores (Andrews, 1990).



Fig. 5. Burning damage at Teixoneres level III (A). Some examples of different grades of coloration are shown (B) taking into account [Stiner et al. \(1995\)](#). Double colorations are also present in the site (C).

Fig. 5. Traces de combustion sur les os du niveau III de la grotte de Teixoneres (A). Quelques exemples de différents degrés de coloration (B) selon [Stiner et al. \(1995\)](#). Les colorations doubles sont aussi présentes dans l'assemblage (C).

parts of long bones that could not be identified because the fragments are too small ([Table 3](#)). No burnt ends have been found in the assemblage. Grade 2 and double colorations predominate on the burned bones, being found in high proportions (on 33.33% and 25% of the burned bones, respectively). The differential burning grade is significant enough to determine anthropic consumption.

4. Discussion

The leporid remains from level III of Teixoneres Cave seem to agree with the interpretation suggested in previous works ([Rosell et al., 2010a, 2010b](#)), where it was interpreted as a carnivores' den where hominins were occasionally active. The data presented here support the main hypothesis that both human and carnivores consumed leporid remains, forming a palimpsest. This seems to be confirmed by the presence of modifications to bone surfaces made by both of them. The possibility that leporids entered the site naturally is rejected due to the low proportion of complete bones, and also because no bones were found in anatomical connection. Additionally, no burrows were identified during the fieldwork.

To get accurate interpretations, taphonomical data obtained from level III were compared with other studies

of accumulations produced by various known predators. Although previous studies proved the presence of hyena in the site, it is highly unlikely that this carnivore intervened on leporid remains. Even if it were the case, its powerful mandibles should destroy the bones and digestive corruptions must be more severe than the ones detected. *M. meles* was also excluded despite it being present in the site since (a) no studies exist about leporid accumulations exclusively produced by badger. Only one study is published ([Maylle et al., 2008](#)), but fox also intervened on the remains and there is no clear distinction of who produce each modification. And, (b) badgers tend to produce scores similar to gnawing and clearly distinctive, with wide grooves of variable length, flat bottoms and parallel between. On this basis, we used different criteria to distinguish between other potential predators ([Table 4](#)):

- anatomical representation;
- fragmentation;
- digestive alterations;
- mechanical modifications produced by carnivores or hominins.

The age of the prey has been dismissed as not being a reliable criterion for distinguishing predators, because

Table 4

Comparative table of assemblages produced by different carnivores and the assemblage observed at level III of Teixoneres Cave.

Tableau 4

Tableau comparatif des assemblages produits par différents carnivores et de l'assemblage du niveau III de la grotte de Teixoneres.

	<i>Bubo bubo</i>	<i>Tyto alba</i>	<i>Aquila chrysaetos/adaberti</i>	<i>Vulpes vulpes</i>	<i>Canis latrans/familiaris</i>	<i>Lynx pardinus</i>	<i>Homo</i>	Level III Teixoneres
<i>Age</i>	Variable	Immature	Variable	Variable	–	–	Variable/ < 85% adults	76% adults
<i>Anatomical representation</i>								
Girdles	Under-repr.	–	Coxal pred.	Coxal > 90%	–	50–60%	< 60%	Coxal > scapula
Appendicular	Post. > ant.	Ant. > post.	Post. (50–100%) > ant.	Ant. ≈ post. (40%)	Ant. ≈ post.	Ant. ≈ post. (50–60%)	Ant. ≈ post. (50%)	Ant. ≈ post. (> 70%)
Axial	Under-repr.	Present	Present	Under-repr.	Present	Under-repr.	Under-repr.	Under-repr.
Craneal	Under-repr.	–	Under-repr.	Under-repr.	–	Maxillar and mandible (> 64%)	Mandible (> 60%)	Under-repr.
<i>Fragmentation</i>								
Complete	45–75%	0.72%	c.65% non-ingested 27.9% ingested	Moderate (c.50%)	7%	20% ingested 70% non-ing	Low (< 20%)	13.75%
Shaft cylinders	< 1.5%	Scarce	< 1.5%	< 1.5%	Scarce	< 2.6%	> 5%	0.3%
Length	–	< 55 mm	–	–	< 10 mm	–	> 40 mm	< 40 mm
<i>Digestion</i>								
% digested	> 50%	–	< 1%	11–35%	100%	96.9%	–	9.21%
Light	> 38%	X	15–20%	< 10%		15%	–	85.21%
Moderate	15–20%	X	45–50%	20–30%		20–23%	–	10.14%
Strong	5–17%	–	25–30%	> 40%	X	40–50%	–	4.11%
Extreme	< 1%	–	< 6%	20–30%	X	18–22%	–	0.27%
<i>Mechanical modifications</i>	< 3%	0.8–1.4%	< 0.5%	1.7–32%	–	0.26–0.9%	–	8.45%

Bubo bubo: Cochard, 2004a, 2004b; Guennouni, 2000; Guillem and Martínez Valle, 1991; Lloveras et al., 2009, 2012a; Martínez Valle, 1996; Sanchis, 1999, 2000, 2001; Yravedra, 2004, 2006. *Tyto alba*: Hockett, 1991, 1995. *Aquila*: Cruz-Urbe and Klein, 1998; Hockett, 1993, 1995, 1996; Lloveras et al., 2008a; Martínez Valle, 1996; Schmitt, 1995. *Vulpes vulpes*: Cochard, 2004a, 2004c; Hockett, 1999; Hockett and Haws, 2002; Krajcarz and Krajcarz, 2012; Lloveras et al., 2012b; Mondini, 2000; Sanchis, 1999, 2000, 2010; Sanchis and Pascual, 2011. *Canis*: Payne and Munson, 1985; Schmitt and Juell, 1994. *Lynx pardinus*: Lloveras et al., 2008b; Rodríguez-Hidalgo et al., 2013. *Homo*: Blasco, 2011; Cochard, 2004a; Sanchis, 2010. Percentages reflect the representation of each item. Ant.: Anterior; Post.: posterior; Under-repr.: under-represented. Les pourcentages reflètent la représentation de chaque reste. Ant.: antérieur; Post.: postérieur; Under-repr.: sous-représenté.

various species do not show an exclusive behaviour pattern and there is wide intra-specific variability, conditioned by ecological circumstances (Cochard, 2004a; Sanchis, 2010).

With respect to the anatomical profile, the proportions presented for level III seem to be closer to accumulations produced by mammal carnivores (Table 4), such as fox (Cochard, 2004a, 2004b; Hockett, 1999; Hockett and Haws, 2002; Lloveras et al., 2012b; Mondini, 2000; Sanchis, 1999, 2000, 2010; Sanchis and Pascual, 2011) or lynx (Lloveras et al., 2008b). However, accumulations generated by hominins can also present similar proportions (Blasco, 2011; Blasco et al., 2013; Cochard, 2004a; Cochard et al., 2012) and for this reason, the skeletal representation cannot be used as the unique criterion for distinguishing predators in one assemblage.

The under-representation of cranium fragments might be explained as a result of bone density, but this is not an explanation for the bias found in vertebrae. This bias can be caused by mastication of these bones during human consumption, as Landt (2004) recorded using data from Bofi in Central Africa, but could also be due to the presence of mammal carnivores, such as foxes, who commonly eat bones while consuming prey and then defecate elsewhere (Cochard, 2004a; Sanchis, 2010). Other authors observed differences in skeletal profiles based on the functionality of the site (Charles and Jacobi, 1994; García-Argüelles et al., 2004). For example, in localities where the skinning of lagomorphs as a regular activity, the anatomical representation consists mainly of distal appendicular elements, such as patellas and caudal vertebrae. The limited presence of acropodials in level III of Teixoneres might indicate that it is not an area where animals were skinned, but was rather focused on the consumption of carcasses. Additionally, burning should be taken into account as having potentially destroyed remains at level III of Teixoneres, and it is possible that some of the smallest leporid remains recovered from the mesh are mixed with the micro-faunal remains still in process of identification.

Regarding the fragmentation of the assemblage, data from Teixoneres level III is extremely fragmented, unlike the patterns established for raptors and closer to the values produced by lynx (Lloveras et al., 2008b), wolves (Schmitt and Juell, 1994) and humans (Cochard, 2004a; Cochard et al., 2012). Although assemblages produced by foxes normally present moderate degrees of fragmentation (Cochard, 2004a, 2004c; Sanchis, 1999, 2000); there is considerable variability (Lloveras et al., 2012b; Sanchis, 1999, 2000), which is conditioned by the functionality of the place where the remains were found (Cochard, 2004b, 2007; Sanchis, 2000). We therefore cannot dismiss this small carnivore as a possible accumulator.

The presence of shaft cylinders has also been considered and discussed. These elements are usually associated with accumulation by humans, especially when they are present in large numbers (e.g., Allué et al., 2010; Cochard, 2004a; Cochard et al., 2012; Sanchis, 2010). However, carnivores can also produce this morphotype, although in very low proportions (e.g., Cochard, 2004a; Hockett, 1991; Lloveras et al., 2008a; Sanchis, 2010; Schmitt and Juell, 1994). Shaft cylinders found in natural deposits are typically short (Brugal, 2006), while they are usually larger in

human context. This can be used to distinguish them. The dimensions of shaft cylinders found at level III of Teixoneres (< 40 mm), which never overate the 50% of the total bone length, together with the presence of digestive corrosion on some of these bones and their limited presence, suggest that carnivores may possibly have been the agents responsible for these modifications. However, the percentages of digested bones are low compared with those produced by mammal carnivores. Although there are some cases of strong or extreme corrosion in the assemblage (grades 3–4), the pattern fits well with the traces of digestion originated by *Bubo bubo* (Table 4). Nonetheless, the possibility that they were contributed by other agents, such as imperial eagle, or mammal carnivores, cannot be discarded. The percentages of bones that have been slightly digested are, however, higher than those normally produced by these nocturnal raptors (*B. bubo*) (Cochard, 2004a, 2004b; Lloveras et al., 2009a, 2012a; Martínez Valle, 1996; Sanchis, 1999, 2000, 2001). This may be due to a mixture of accumulations from various agents. It is also important to emphasize the case of calcanea, which are the element most closely associated with modification by strong corrosion. For these bones, the values are similar to those from other sites, such as the Arbreda Cave, where the accumulation was attributed to a mammal carnivore, such as lynx, fox or wildcat (Lloveras et al., 2010).

Mechanical modifications to the surfaces of bones are evidenced in similar percentages as those for foxes. Sanchis (2010) and Sanchis and Pascual (2011) carried out a study in Sitjar Baix, where mechanical modifications oscillated between 3.18 and 9.17% range. These values are like those obtained from level III of Teixoneres. Considering the data available to date, there are no other predators that produce similar values of tooth-marks on bone surfaces. Nevertheless, only a few studies have been published for other mammal carnivores and more studies should be carried out to improve this data.

In spite of the significant contribution by carnivores (mammals and raptors) to the leporid assemblage, the analysis of Teixoneres level III provides enough evidence to confirm the butchering and consumption of rabbit remains at the site by groups of humans. This is supported by the presence of:

- cut-marks on limb bones, pelvic girdles and crania;
- burned bones;
- anthropogenic breakage caused by bending and pressure.

Nevertheless, it must be taken into account that burns on bones could reflect other types of intentional actions, such as cleaning activities intended to remove waste, or could be the result of unintended processes, such as accidental cremation. It could even be a consequence of post-depositional damage, for example, thermal alteration by hearths built in the same place where bones fragments are shallowly buried. In the case of Teixoneres, no differential burning patterns have been found, so it is possible that part of the burning might be the result of non-nutritive episodes that occurred following consumption. Although the proportion of bones recorded at level III has shown direct evidence of human consumption is

Table 5

Comparison of different archaeological assemblages to results obtained at Teixoneres level III.

Tableau 5

Comparaison de différents assemblages archéologiques avec les résultats obtenus pour le niveau III de la grotte de Teixoneres.

	Canalettes 4	Bolomor IV	Abri du Maras 4	Caldeirão (Mousterian)	Arbreda I	Teixoneres III
Reference	Cochard et al., 2012	Blasco, 2011 ; Blasco and Fernández Peris, 2012a, 2012b ; Blasco et al., 2013 ; Sanchis, 2010	Hardy et al., 2013	Lloveras et al., 2011	Lloveras et al., 2010	Present work
Anatomical representation	ant. ≈ post.	ant. ≈ post.	–	ant. < post.	ant. < post.	ant. ≈ post.
% complete	Low	Low	–	37,4%	43,4%	13,75%
Shaft cylinders	151 cylinders (39,4%)	71 cylinders (56,8%)	–	9 cylinders (5,5%)	12 cylinders (0,5%)	10 cylinders (0,3%)
Digestions	–	2,13%	–	25,4%	32,4%	9,21%
Mechanical modifications	0,7% (digestions included)	Scarce	–	2,1%	2,53%	8,45%
Anthropic modifications	1% cutmarks 0,4% burnt 0,1% tooth-marks	0,8% cut-marks 8,39% burnt 3,9% tooth-marks	2 remains with cut-marks (40%)	0,08% burnt	0,5% burnt	0,76% cut-marks 0,91% burnt 0,48% tooth-marks/breakage
Agent	Anthropic (principal)/mammal carnivore (sporadic)	Anthropic (principal)/mammal carnivore (scavenger)	Anthropic	Nocturnal raptor/mammal carnivore/anthropic	Mammal carnivore	Mammal carnivore/nocturnal raptor/anthropic

Ant.: anterior; post.: posterior; “X”: presence; “–”: no data.

Ant.: antérieur; post.: postérieur; «X»: présence; «–»: pas de données.

not high, it is important to emphasize that, because of their size, small animals do not present as many direct modifications to bone surfaces as larger ones. They can be processed using only the teeth and hands without any tools, which often makes it difficult to distinguish these modifications from those caused by other predators. Other factors must therefore be taken into account in order to establish whether humans had a significant impact on the remains or not. Nevertheless, and despite tooth-marks associated to human activities were detected on a small proportion, they have always been associated to bending and breakage. It cannot be possible to associate them with other activities, and the clearly high carnivore activity makes to dismiss the possible idea of higher role of hominids on leporid remains. To this end, the Teixoneres assemblage has been compared with other archaeological accumulations (Table 5).

The values presented for level III of Teixoneres are close to those presented at level 4 of Canalettes ([Cochard, 2004a](#); [Cochard et al., 2012](#)), in terms of cut-marks or burned bones. The difference lies in the large number of shaft cylinders – which are associated with human consumption – that were observed at this French site ([Rufà, 2013](#); [Cochard, 2004a](#); [Cochard et al., 2012](#)). The low numbers of digested bones in Canalettes is also significant when comparing it with Teixoneres, where the proportion is higher. The case of level IV of Bolomor Cave is comparable ([Blasco, 2011](#); [Blasco and Fernández Peris, 2012a, 2012b](#); [Blasco et al., 2013](#); [Sanchis, 2010](#)). This site, like level III of Teixoneres, presents low rates of cut-marks on bones. Digested bones are only incidentally present in the

Bolomor assemblage and there are a high number of thermal alterations, confirming the anthropic nature of the contribution. Level 4 of Abri du Maras can also be compared with Teixoneres level III. It presents very few lagomorph remains with butchery marks (NISP=2) and there is no evidence of burned bones, although leporid hair found on stone tools was proposed to demonstrate that they had been processed there ([Hardy et al., 2013](#)). Other analyses carried out of use-wear on stone tools provide evidence of small animal consumption at archaeological sites where there are no cut-marks on the remains. The Middle Palaeolithic of Payre (Ardèche, France) is such a case ([Hardy and Moncel, 2011](#)). Another example to compare it with is the Mousterian assemblage of Gruta do Caldeirão, Tomar, Portugal ([Lloveras et al., 2011](#)), which also contains few bones with cut-marks and no evidence of burning. It presents a comparable percentage of digested bones to level III of Teixoneres and the origin of its accumulation seems to be similar to that of Teixoneres level III. Most of these examples show that, despite the fact that direct evidences are scarce and – in some cases – mixed up with carnivore activity, Neanderthals could access a wide spectrum of prey, including leporids (Table 5).

Although the data from Teixoneres seems to indicate a low level of human activity at the site, it exists. Comparing with other Mousterian levels in the region such as level I of Arbreda Cave, Teixoneres level III shows a higher proportion of anthropogenic activity. Contrary to Arbreda, where mammal carnivore activity clearly predominated ([Lloveras et al., 2010](#)), Teixoneres level III seems to have more assortment in its accumulation.

Data from macromammals at Teixoneres level III also suggests that both humans and carnivores used the cave and performed actions linked to their consumption sequences (Rosell et al., 2010a, 2010b). In the case of hominins, the final phases of the butchery sequence took place in the cave. This has been determined from cut-marks related mainly to defleshing, although evidence of skinning and disarticulation have also been detected, as well as intentional bone breakage associated with marrow extraction. Thermal alterations are important, specifically those associated with double colorations, which suggest that bones were roasted when they still had meat adhering to them (Rosell et al., 2012).

In addition to this, the analysis of the rabbit assemblage could be linked to an occupational pattern and provide information about it. In the case of level III, it should be taken into account that leporids are just one group among a wide variety of species present at the site. This diversity may be a consequence of the hominins having better control and knowledge of the territory, which would indicate a pattern of long-term occupancy or a succession of short occupations where encounter rates play an important role (Blasco et al., 2013; Jones, 1983; Martínez, 2009).

The age and sex-ratio profiles of leporid population proposed by Jones (2006) and applied by Cochard et al. (2012) and Blasco et al. (2013) can be of assistance in determining the procurement system, which may have been related to knowledge of environment and, indirectly, to occupational pattern. These authors assume that an assemblage with high proportions of females (and, in many cases, infant leporids) might be linked to trapping near the burrows and, consequently, a good knowledge of the landscape. In contrast, higher or equal numbers of adult males might commonly be associated with individual acquisition of prey, more closely linked to encounter rates, and occurring opportunistically. In that respect, Teixoneres patterns seem to be related to individual acquisition of prey, because no sex profile predominates (Fig. 2). This pattern is similar to that observed at levels XI and XVII of the Bolomor Cave and TD10-1 of Gran Dolina (Blasco et al., 2013) and differs from the data presented at Bolomor IV (Blasco et al., 2013) and Canalettes 4 (Cochard et al., 2012). Nevertheless, these results should be taken as an approximation, because most of the lagomorph remains recovered at level III of Teixoneres were brought there by small mammal carnivores, or probably, *B. bubo*.

Regardless, the high levels of carnivore activity observed not only on leporid remains but also on ungulate remains (Rosell et al., 2010a, 2010b) reinforce the idea of successive short-term human occupations forming palimpsests (Sánchez-Hernández, 2013; Sánchez-Hernández et al., 2014). This is concluded from the facts that, first, there is no evidence of interaction between hominids and carnivores and, second there are very few bones with hominid and carnivore alterations on the same surface, so any overlapping appears to have been occasional.

Eagle owl and fox activity, and possibly the activity of other mammals (such as lynx or wolf) are strongly associated with situations of alternated occupation of the cave with hominins. Additionally, the taphonomic study,

linked to the occupational patterns and the presence of a high diversity of taxa that were consumed by hominins at the site – not only ungulates, but also leporids and other small prey – confirms that there was a broad spectrum of resources available for consumption by Neanderthals. This diversity of prey species also indicates the Neanderthals' adaptability to several different landscapes and, their overall knowledge of the environment. This was previously demonstrated by Henry et al. (2011) and Hardy et al. (2012), who found evidence of the use and consumption of plants from studies of phytoliths and microfossils in dental calculus taken from Neanderthal specimens. In the case of the Spanish site of El Sidrón, this vegetable component in the diet not only had nutritional value but also medicinal properties (Hardy et al., 2012), reflecting the Neanderthals' capabilities and their behavioral complexity.

5. Conclusions

The accumulation of leporid remains from level III of Teixoneres Cave is an example of a mixed assemblage in which different agents were active, forming a palimpsest. This study confirms that the assemblage was produced by a mix of contributions, in which carnivores played an important role. Fox (*V. vulpes*) and eagle owl (*B. bubo*) seem to have been the carnivores principally responsible for modifying the remains, as is demonstrated by modifications produced both mechanically and by digestive processes. However, other carnivores such as lynx cannot be discounted as agents that had a role in producing the assemblage.

Humans also took part in producing the assemblage, as is evidenced by cut-marks, intentional breakage to release fat/marrow, and burned bones. Human activity may possibly have been under-represented, because leporids can be processed without the use of tools. This study has proven that Neanderthals had a broad spectrum of animals available to them that they could potentially exploit. Of these, the leporids were not exceptional. Other species of ungulates were consumed at the site, and, on the basis of the encounter rates, leporids may well have been hunted. The wide variety of animals consumed by humans, together with the sex-ratio and age profiles of leporids and the presence of multiple carnivores might be linked to the idea of short-term occupational patterns at Teixoneres. These conclusions also reflect the Neanderthals' ability to adapt to new and different environmental conditions.

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