



HAL
open science

Which predators are responsible for faunal accumulations at the Late Pleistocene layers of El Harhoura 2 Cave (Témara, Morocco)?

Emilie Campmas, Patrick Michel, Sandrine Costamagno, Mohamed Abdeljalil El Hajraoui, Roland Nespoulet

► To cite this version:

Emilie Campmas, Patrick Michel, Sandrine Costamagno, Mohamed Abdeljalil El Hajraoui, Roland Nespoulet. Which predators are responsible for faunal accumulations at the Late Pleistocene layers of El Harhoura 2 Cave (Témara, Morocco)?. *Comptes Rendus. Palevol*, 2017, 16 (3), pp.333-350. 10.1016/j.crpv.2016.08.007 . hal-01891620

HAL Id: hal-01891620

<https://hal.science/hal-01891620>

Submitted on 9 Oct 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Paleontology, Systematics and Evolution (Vertebrate Palaeontology)

Which predators are responsible for faunal accumulations at the Late Pleistocene layers of El Harhoura 2 Cave (Témara, Morocco)?



Quels sont les prédateurs responsables de l'accumulation de la faune des niveaux du Pléistocène supérieur de la grotte d'El Harhoura 2 (Témara, Maroc) ?

Émilie Campmas^{a,*}, Patrick Michel^b, Sandrine Costamagno^a, Mohamed Abdeljalil El Hajraoui^c, Roland Nespoulet^d

^a CNRS UMR 5608 TRACES, University of Toulouse – Jean-Jaurès, 31058 Toulouse, France

^b CNRS UMR 5199 PACEA, University of Bordeaux, 33615 Pessac, France

^c INSAP, Rabat, Morocco

^d CNRS UMR 7194 HHNP, MNHN, 75005 Paris, France

ARTICLE INFO

Article history:

Received 13 March 2016

Accepted after revision 1st August 2016

Available online 24 February 2017

Handled by Lars van den Hoek Ostende

Keywords:

Taphonomy

Carnivores

North Africa

Late Pleistocene

ABSTRACT

El Harhoura 2 cave (Témara, Morocco) has yielded Aterian and Iberomaursian lithic artifacts associated with faunal remains. Both humans and carnivores occupied this cave and non-human predator modifications occurred mainly at the end of the Late Pleistocene. Diverse faunal taxa have been identified, with a predominance of gazelles and various carnivores, particularly canids. The location of the cave and of the excavation area, at the bottom of a cliff of low elevation and in the entrance of the cave, does not correspond to a protected area for large raptor nests or a natural trap. Considering the consumed species, the type of carnivore remains, the skeletal representation of prey, taphonomic alterations such as tooth marks, semi-digested bones and destruction sequences, large canids would be the main cause for faunal modifications. However, North African fossil data attributed to hyena activities present similar results. This paper highlights the difficulty of discriminating between potential accumulators/consumers due to a lack of taphonomic reference data. This study thus demonstrates the necessity of compiling fossil records and neotaphonomic reference data for North African medium-large predators in order to better understand the taphonomic history of North African archaeological and paleontological sites.

© 2016 Published by Elsevier Masson SAS on behalf of Académie des sciences. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

R É S U M É

La grotte d'El Harhoura 2 (Témara, Maroc) a livré des industries lithiques attribuées à l'Atérien et à l'Ibéromaursien, associées à des restes de faune. Les Hommes et les carnivores ont occupé la cavité, mais les modifications dues aux prédateurs non humains sont présentes principalement à la fin de la séquence du Pléistocène terminal. De nombreux

Mots clés :

Taphonomie

Carnivores

Afrique du Nord

Pléistocène supérieur

* Corresponding author.

E-mail address: em.campmas@gmail.com (É. Campmas).

taxons ont été identifiés, avec une prédominance des gazelles et une variété de carnivores, particulièrement des canidés. La localisation de la grotte et de la zone de fouille, à la base d'une falaise de faible élévation et en porche de grotte, ne correspond, ni à une zone protégée privilégiée par les rapaces de grande taille pour nicher, ni à un piège naturel. En considérant les proies, les altérations taphonomiques comme les traces de dents, les restes semi-digérés et les séquences de destruction, nous émettons l'hypothèse que les grands canidés pourraient être les principaux responsables des modifications. Cependant, des assemblages nord-africains similaires sont attribués à l'activité de l'hyène. Cet article met en évidence les difficultés de discrimination des différents prédateurs accumulateurs/consommateurs du fait de lacunes de référentiels. Il montre également la nécessité de compiler les données issues des enregistrements fossiles et de référentiels néo-taphonomiques sur les prédateurs de moyenne à grande taille en Afrique du Nord, afin d'améliorer notre perception de l'histoire taphonomique des assemblages archéologiques et paléontologiques de cette région.

© 2016 Publié par Elsevier Masson SAS au nom de Académie des sciences. Cet article est publié en Open Access sous licence CC BY-NC-ND (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Throughout the Pleistocene in North Africa, hominids and non-human predators frequently used the same caves (e.g., Campmas, 2012; Campmas et al., 2015; Daujeard et al., 2011, 2012; Monchot and Aouraghe, 2009) and were in competition for caves and prey hunting. Consequently, stone tools and faunal remains accumulated by both types of predators are often associated. These accumulations can give rise to misinterpretations of hominid hunting strategies or site functions. In order to understand the history of faunal assemblages and site occupations, it is thus essential to apply taphonomic approaches with the goal of characterizing these accumulations produced by these predators.

At Témara (Morocco), based on the examples of El Harhoura 2 (EH2) and El Mnasra caves, humans and carnivores alternately occupied caves in association with climate shifts (Campmas et al., 2015). During oxygen isotopic stage (OIS) 5, humans occupied these sites “intensively”, undoubtedly in correlation with high sea levels and the proximity of the shore to caves (Campmas, 2012; Campmas et al., 2015, 2016). Throughout climate degradations (OIS 4, 3 and 2), the caves were located further inland and humans occupied these sites more sporadically. Despite the fact that EH2 cave acquired a sepulchral function during the Iberomaurusian (OIS 2), the accumulations of faunal remains, dominated by gazelles, were mainly modified by non-human predators (Campmas, 2012; Campmas et al., 2015).

A diversity of carnivores was recorded in North Africa during the Late Pleistocene, such as: mongoose (*Herpestes ichneumon*), spotted genet (*Genetta genetta*), small cats, small mustelids, large mustelids such as honey badgers (*Mellivora capensis* or *M. carolae*), small canids such as fox (*Vulpes vulpes*) and small jackal (*Canis aureus* and/or *Canis mesomelas*), large canids such as large jackal (*C. aureus* or *Canis* sp.) and perhaps the African wild dog (*Lycaon* sp.?), large felids such as cheetah (*Acinonyx jubatus*), lion (*Panthera leo*) and leopard (*Panthera pardus*), hyenas such as spotted hyena (*Crocuta crocuta*) and striped hyena (*Hyaena hyaena*) and bear (*Ursus* sp.) (e.g., Aouraghe, 2000, 2001; Bougariane et al., 2010; Campmas, 2012; Daujeard et al.,

2011; Michel, 1990; Michel et al., 2009, 2010). Several of these carnivores are still present today in North Africa, such as small mustelids, small felids, foxes and jackals, while others, such as striped hyenas and leopards (e.g., Aulagnier et al., 2008) have become rare or have disappeared recently, such as lions (e.g., Black et al., 2013). It should be noted that recent DNA studies have shown that the large jackal of Egypt and Algeria (*Canis aureus lupaster*) is in fact a wolf (*Canis lupus lupaster*) (e.g., Gaubert et al., 2012; Ruess et al., 2011). Photographs reveal its possible existence in Morocco (e.g., Moliner et al., 2012).

In addition to carnivores, large raptors known to accumulate meso- and macrofaunal remains, such as the bearded vulture (*Gypaetus barbatus*), the Egyptian vulture (*Neophron percnopterus*), the Nubian vulture (*Torgos tracheliotos*) and the griffon vulture (*Gyps fulvus*), are all currently present in Morocco (e.g., Cherkaoui et al., 2006; Eliotout, 2007; Gensbol, 1993; Heinzl et al., 2004; Terrasse, 2006).

This paper's objective is to provide the taphonomic signatures of meso-macrofaunal remains from EH2. It highlights several issues related to the identification of potential non-human predators responsible for faunal accumulations, and subsequently attempts to tackle these issues using an appropriate methodology and actualistic data.

2. Site presentation

EH2 belongs to a complex of several caves, all located in the Témara-Rabat Region (Fig. 1). The main excavation focused on the cave entrance. The stratigraphy of this area is composed of eleven archeostratigraphic layers (Fig. 2). Layer 1 contains deposits dated to the Holocene having yielded Neolithic artifacts. Layer 2 is attributed to the Iberomaurusian culture on the basis of the lithic industries. The underlying layers (3–11) are all attributed to the Middle Stone Age, but the archaeological material is relatively poor (Nespoulet and El Hajraoui, 2012). Only layers 1 to 4A have been excavated on a large surface (~10–20 m²), while the other layers are only known by a test pit.

In layers 4A, 3 and 2 (dated to OIS 4 or 3; Jacobs et al., 2012; Janati Idrissi et al., 2012), anthropogenic

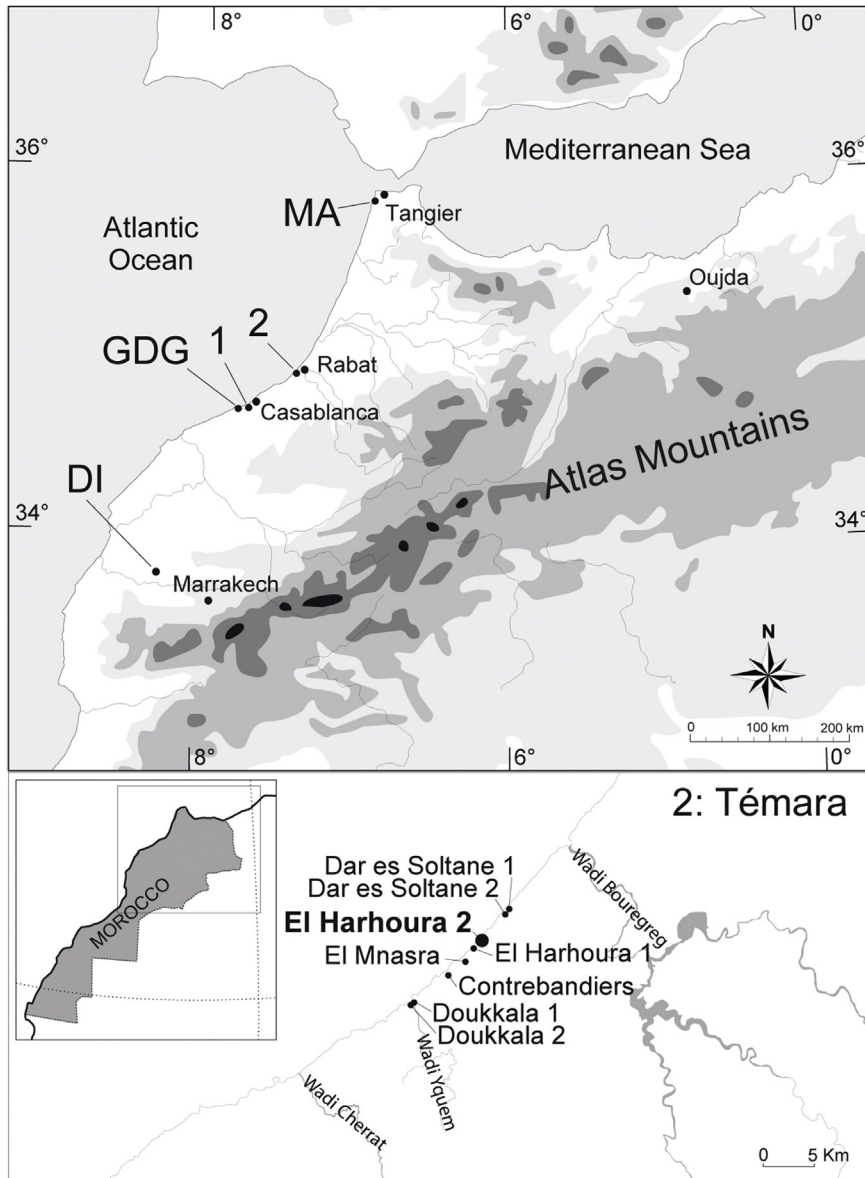


Fig. 1. Top: map of Morocco showing some sites cited in the text (DI: Djebel Irhoud; GDG: Gazelles Cave; 1: Casablanca region, including Hominid, Rhinoceros and Felines Caves. Bottom: Témara region, including El Mnasra, El Harhoura 2 and several other caves; MA: Mugharet el Aliya).

Fig. 1. En haut : carte du Maroc, avec la localisation des sites cités dans le texte (DI : Djebel Irhoud ; GDG : grotte des Gazelles ; 1 : région de Casablanca, qui comprend les grottes des Hominidés, des Rhinocéros et des Félins. En bas : région de Témara, qui comprend les grottes d'El Mnasra, d'El Harhoura 2 et d'autres cavités, MA : Mugharet el Aliya).

After [Jacobs et al., 2012](#).

marks are very scarce (layers 2–4A: <2% of cut-marks and 4–15% of burnt bones). The information concerning the related human activities is available in [Campmas \(2012\)](#) and [Campmas et al. \(2015\)](#). However, evidence of non-human predator intervention was observed. Tooth marks are scarce but present on all the long bone portions, and digested bones are also observed. These modifications on meso-macrofaunal remains at EH2 are mainly due to non-human predators ([Campmas et al., 2015](#)) Microfaunal and macrofaunal paleontological analyses suggest a semi-wooded steppe environment, relatively humid for layers 4

and 3, and with increasing aridity for the layer 2 ([Stoetzel et al., 2011, 2012a, 2012b, 2014](#)).

3. Material and methods

In this paper, we focus on plotted and identifiable unsorted remains (NR=6707) from layers 4A, 3 and 2 recovered during 2001–2009 excavations. We only present non-human predator activities, as anthropogenic ones are already discussed elsewhere (see [Campmas, 2012; Campmas et al., 2015](#)).

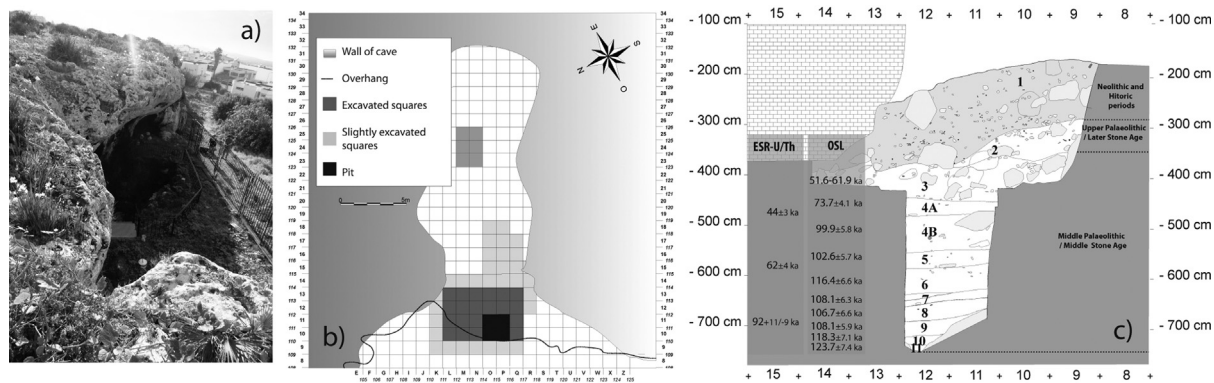


Fig. 2. Excavation at EH2: a: photo of the entrance of the cave; b: map of the excavation area; c: stratigraphy and dating based on Janati Idrissi et al. (2012) for ESR-U/Th and Jacobs et al. (2012) for OSL (infography R. Nespoulet and É. Campmas).

Fig. 2. Fouille à EH2 : a : photographie de l'entrée de la grotte ; b : plan de fouille ; c : stratigraphie et dates d'après Janati Idrissi et al. (2012) pour l'ESR-U/Th et Jacobs et al. (2012) pour OSL (infographie R. Nespoulet et É. Campmas).

In order to identify the non-human predator(s) responsible for the faunal interventions/accumulations, several fossil data were compiled and comparisons were made with actualistic predator behavioral information.

The faunal spectrum provides data on the prey consumed by predators. Species identifications were based mainly on previous works (Michel et al., 2009, 2010; Stoetzel et al., 2012a), in comparison with the modern osteological collection of the “El Harhoura-Témara” mission conserved at the INSAP (containing almost exclusively domestic taxa), as well as osteological atlases and previous paleontological studies (e.g., Aouraghe, 2001; Arambourg, 1957; Assefa, 2006; Barone, 1999; Michel, 1990; Pales and Lambert, 1971; Pales and Garcia, 1981; Walker, 1984). It is expressed in Minimum Number of Individuals [MNI] (Grayson, 1984; Lyman, 1994) and Number of Identified Specimens [NISP] (Lyman, 1994), mainly by size classes (Table 1). We compared the NISP proportions of carnivores among ungulates and carnivores remains, and ungulate size 1 (the main class size) among all ungulate class size.

The presence of coprolites provides evidence of carnivore activities. Morphology and size of complete feces (e.g., Chame, 2003) could give indications of the size of the carnivore. Fragments of coprolites and complete coprolites have thus been taken into account for this study.

The age of the prey provides data on the hunting choices made by the predators. The presence of carnivores with pups points to the use of cavities as maternity dens. Age estimations of both prey and predators are mainly based on tooth eruption and wear (Benatia, 1998; Grant, 1982; Klein and Cruz-Urbe, 1984; Munro et al., 2009). Three age categories have been distinguished (young, mature and old).

The anatomical representation of prey provides information concerning the remains brought into the caves. Bone portion representation allows us to identify missing portions of bones. Skeletal profiles are presented as survival percentages (Lyman, 1994), by bone portions for the main ungulate size (size 1). A non-parametric test, the Spearman's correlation coefficient, was used to assess the degree of correlation between bone portion densities and

skeletal representations (Lam et al., 1999). These correlation tests can shed light on the differential preservation of bones (Lyman, 1984).

Bone surfaces were observed at low magnification ($\times 10$) using a handheld lens. Several taphonomic processes such as weathering, chemical corrosion (soil and roots) or an adhering matrix can alter the surface of bones and hide marks left by the accumulating agents. These biases were taken into consideration and poorly preserved and unreadable bones (with considerable adhering matrix, severe root etching, etc.) were excluded from the percentages of remains with marks. Some of the remains with an invasive adhering matrix were treated with acetic acid, with a concentration of 8% for various times (a few minutes to several hours, depending on the quantity of matrix). Tooth marks and semi-digested bones were counted. To limit misinterpretation of digestive attack, we have only considered partially digested bones with a high degree of modification as digested, since slight alterations could also be due to acetic acid pretreatment. Size, species and anatomical attribution of semi-digested remains are provided. Several notches were identified as “indeterminate” when their morphologies did not allow the identification of the responsible agent, as recommended by Capaldo and Blumenschine (1994). The size of the marks (pits) is an indicator of the consumer carnivore (e.g., Domínguez-Rodrigo and Piqueras, 2003). Even if the size of these marks was not measured, the indication of possible medium-large carnivore actions has been indicated.

Due to their dental morphology and musculature, carnivores such as hyenids, canids or felids do not have the same aptitude to break bones for marrow consumption. To discuss the degree of fragmentation, we identified frequencies of complete remains. We also considered lengths (complete, less than 1/2 or less than 1/4 of the initial shaft length) and circumferences (complete, less than 1/2 of the initial shaft length) of conserved long bone shaft fragments (Villa and Mahieu, 1991). On the long bone shaft fragments, green fractures (curved/oblique and smooth) or dry fractures (transverse right/jagged and rough) were described following Villa and Mahieu (1991). In addition, the

Table 1

Size classes used for the North African ungulates and carnivores.

Tableau 1

Classes de taille utilisées pour les ongulés et les carnivores d'Afrique du Nord.

Size classes	Species	(kg)
Size 1	Gazelles (<i>Gazella dorcas</i> , <i>Gazella cuvieri</i> , <i>Gazella atlantica</i> , <i>Gazella</i> sp.) Reduncinae [reedbuck (<i>Redunca redunca</i>)]	17–50 kg
Size 2	Suidae [warthog (<i>Phacochoerus africanus</i>), wild boar (<i>Sus scrofa</i>)] Alcelaphinae [wildebeest (<i>Connochaetes taurinus</i>) and hartebeest (<i>Alcelaphus buselaphus</i>)] Cervidae Barbary sheep (<i>Ammotragus lervia</i>) Reducinae [Kob (<i>Kobus</i> sp.)] Hippotraginae [scimitar-horned oryx (<i>Oryx dammah</i>), gemsbok (<i>Oryx gazella</i>)] Tragelaphinae (<i>Tragelaphus</i> sp.)	50–200 kg
Size 3	Equidae (<i>Equus algericus</i> , <i>Equus asinus</i> , <i>Equus africanus</i> , <i>Equus melkiensis</i> , <i>Equus mauritanicus</i> , <i>Equus grevyi</i> , <i>Equus</i> sp.)	200–1000 kg
Size 4	Bovinae [ancient buffalo (<i>Pelorovis antiquus</i>), aurochs (<i>Bos primigenius</i>), eland (<i>Taurotragus</i> sp.)] Hippo (<i>Hippopotamus amphibius</i>) Rhinocerotidae [white rhinoceros (<i>Ceratotherium simum</i>) and grassland rhinoceros (<i>Dicerorhinus emitoechus</i>)] Proboscidean [elephant (<i>Loxodonta africana</i>)]	> 1000 kg
Small carnivores	Small mustelids [least weasel (<i>Mustela nivalis</i>), Saharan striped polecat (<i>Ictonyx libyca</i>)] Large mustelids [honey badger (<i>Mellivora capensis</i>)] Viviridae [genette (<i>Genetta genetta</i>)] Herpestidae [mongoose (<i>Herpestes herpestes</i>)] Small felids [caracal (<i>Caracal caracal</i>), serval (<i>Leptailurus serval</i>), sand cat (<i>Felis margarita</i>), african wild cat (<i>Felis libyca</i>), wild cat (<i>Felis silvestris</i>)] Small canids [small jackal (<i>Canis aureus</i> and/or <i>Lupulella mesomellas</i>), red fox (<i>Vulpes vulpes</i>), Rüppell's fox (<i>Vulpes rueppellii</i>), fennec fox (<i>Vulpes zerda</i>)]	30 g–15 kg
Medium carnivores	Large canids [<i>Canis</i> sp. and/or <i>Canis aureus</i> , size of wolf (<i>Canis lupus</i>)]	15–50 kg
Large carnivores	Hyenids [spotted hyena (<i>Crocuta crocuta</i>) and striped hyena (<i>Hyaena hyaena</i>)] Large felids [leopard (<i>Panthera pardus</i>), lion (<i>Panthera panthera</i>)] Ursids (<i>Ursus arctos</i>)	50–300 kg

According to Kingdon (2006) and Aulagnier et al. (2008).

presence of long shaft bone “cylinders” was taken into account. It is important to note that fragmented remains from sieve residues were not included here.

4. Results

The faunal spectrum is diversified, with the presence of many ungulates and carnivores (Table 2). Small size 1 ungulates (gazelles) largely dominate the assemblages (> 70% NISP). Carnivores represent between 10% and 16% of the NISP and are dominated by canids (such as jackal and fox) (Table 2). Large canids (Fig. 3) could correspond to a large jackal such as at Gazelle cave (Bougariane et al., 2012). Other carnivores are also present (Table 2).

Several coprolites are present, some of which have been attributed to a hyena on the basis of their morphology (spherical with a flat side; Fig. 3). In 2008, a crushed pile of coprolites was excavated in layer 3 (Fig. 3).

Layer 3 is the only level with a MNI for gazelles allowing the reconstruction of the mortality profile. We identified all age classes comprising nine young, eleven mature and seven old specimens. For other ungulates, the MNI is too low to reconstruct mortality profiles. However, Alcelaphini, Tragelaphini, Hippotragini and Bovini remains belong mainly to young animals. Canids are the main carnivores and are predominantly represented by remains from mature individuals. One deciduous hyena tooth (layer 3), not recovered during this study, but identified by one of us (P. Michel), belongs to a young animal.

For all layers, all the skeletal parts of the gazelle are present. Survival percentages show an under-representation of the axial skeletal parts. Humerus and tibia shafts, mandibular body, coxal acetabulum, glenoid cavity of the scapula and patella are the best-represented anatomical portions. Short bones (carpal bones, tarsal bones and phalanx) are also well represented (Fig. 4). Teeth are abundant and represent 20–40% of remains (Table 2). The positive correlation with osseous densities of all the skeleton parts, which could indicate a better representation of dense bones, is not significant here (except for layer 4A; $r_s = 0.39$; $P = 0.003 < 0.01$) (Fig. 5). Other ungulates are mainly represented by single teeth and rare post-cranial remains. Canids are mainly characterized by isolated teeth and limb extremities. Other carnivores are identified only on the basis of isolated teeth, except for *Panthera* sp. and hyenas.

The adhering matrix is abundant (Fig. 6a) and occurs on 60% of the remains in layers 3 and 4A and 80% in layer 2. Root corrosion shows the most significant impact, after the adhering matrix, limiting the observation of the osseous surfaces. This concerns 60%–80% of the remains from layers 2, 3 and 4A (excluding remains with extensive adhering matrix, 15–30% of NISP, Table 2).

Carnivore marks, i.e. tooth marks and semi-digested bones, are present (10–13% of remains and 11–17% of ungulate size 1) on all ungulate sizes, as well as on small canids and other carnivore remains (Table 3). However, tooth marks are rare (Table 3; Fig. 6b, c, d and Table 3). On size 1 ungulates, carnivore marks and tooth marks are mainly

Table 2
EH2 faunal spectrum.
Tableau 2
Spectre faunique d'EH2.

	Species	Layer 2		Layer 3		Layer 4A	
Ungulates size 1 ^a	<i>Gazella</i> sp. ^a	7/272	28%/48%	27/1285	46%/67%	5/179	36%/58%
	cf. <i>Gazella</i> sp. ^a	-/79	-/14%	-/232	-/12%	-/74	-/24%
	Caprinae? ^a			1/1	2%/~0%		
	TOTAL NISP^a	351	62%	1518	80%	253	82%
	% NISP Ungulates size 1 (among ungulates)		74%		88%		91%
	% NISP Size 1 (ungulates size 1, small, medium carnivores and indet. Size 1; without other and indet.)		67%		85%		89%
Ungulates size 2 ^a	Suidae ^a	1/5	4%/1%	1/14	2%/1%	2/2	14%/1%
	Alcelaphinae ^a	3/7	12%/1%	4/25	7%/1%	1/2	7%/1%
	Tragelaphinae ^a	1/1	4%/~0%				
	Hippotraginae ^a			1/2	2%/~0%		
	Cervidae ^a			1/1	2%/~0%		
	Alcelaphinae and/or Hippotraginae and/or Cervidae ^a	-/78	-/14%	-/99	-5%	-/17	/5%
	TOTAL NISP^a	91	16%	141	7%	21	
Ungulates size 3 ^a	Equidae ^a	2/9	8%/2%	1/7	2%/~0%		
	cf. Equidae ^a	-/1					
	Bovinae ^a	3/12	12%/2%	4/22	7%/1%	1/2	7%/1%
	cf. Bovinae ^a	-/4	-/1%	-/19	-/1%	-/1	-/~0%
	TOTAL NISP^a	26	5%	48	3%	3	1%
Ungulates size 4 ^a	Rhinocerotidae ^a	1/4	4%/1%	1/9	2%/~0%		
	cf. Rhinocerotidae ^a	-/1					
	Hippo ^a			1/1	2%/~0%		
	TOTAL NISP^a	5	1%	10	1%		
TOTAL NISP Ungulates^a		473	84%	1717	90%	277	89%
Small carnivores ^a	Small carnivores (cf. Mustelidae) ^a			1/7	2%/~0%		
	<i>Felis</i> sp. ^a			1/2	2%/~0%	2/2	14%/1%
	Small canids [cf. fox (<i>Vulpes</i> sp.)/jackal (<i>Canis aureus</i> and/or <i>Lupulella mesomelas</i> ^{a,b})]	3/55	12%/10%	7/111	12%/6%	1/25	7%/8%
	Indet. ^a						
	TOTAL NISP^a	55	10%	120	6%	27	9%
	% NISP Small carnivores/Carnivores		61%		64%		82%
Medium carnivores ^a	Large Canidae (cf. large <i>Canis aureus</i>) = large jackal ^a	2/18	8%/3%	5/44	8%/2%	1/3	7%/~1%
	TOTAL NISP^a	18	3%	44	2%	3	1%
Large carnivores ^a	Hyenidae ^a	1/4	4%/1%	1/4	2%/~0%	1/1	7%/~0%
	<i>Panthera</i> sp. ^a	1/1	4%/~0%	1/1	2%/~0%		
	<i>Ursus</i> sp. ^a			1/2	2%/~0%		
	TOTAL NISP^a	5	1%	7	~0%	1	~0%
Canids indet. ^a		-/12	-/2%	-/17	1%	-/2	-/1%
Total NISP carnivores^a		90	16%	188	10%	33	11%
Total NISP carnivores + s^a		563	100%	1905	100%	310	100%
Other ^a	<i>Hystrix cristata</i> ^a			-/1			
	Leporidae ^a	-/18		-/31		-/3	
	Turtles ^a	-/17		-/88		-/41	
	<i>Struthio camelus</i> eggs ^a	-/6		-/96		-/16	
Size 1 indet. ^a		-/47		-/689		-/142	
Size > 1 indet. ^a		-/65		-/151		-/21	
indet. ^a		-/242		-/1827		-/396	
Carniv. Indet. ^a		-/5		-/8		-/3	
Total NISP ^a		963		4796		932	
Coprolites ^a		1		12		3	
% NISP unreadable excluded for the carnivores marks			28%		22%		15%
% of teeth			40%		28%		26%
% Complete remains			11%		7%		6%

X: presence; MNI/NISP.

^a % calculated with Total carnivores + Total ungulates.

^b Different attribution of small jackals according to several authors, such as Geraads (2011) and Bougariane et al. (2012).

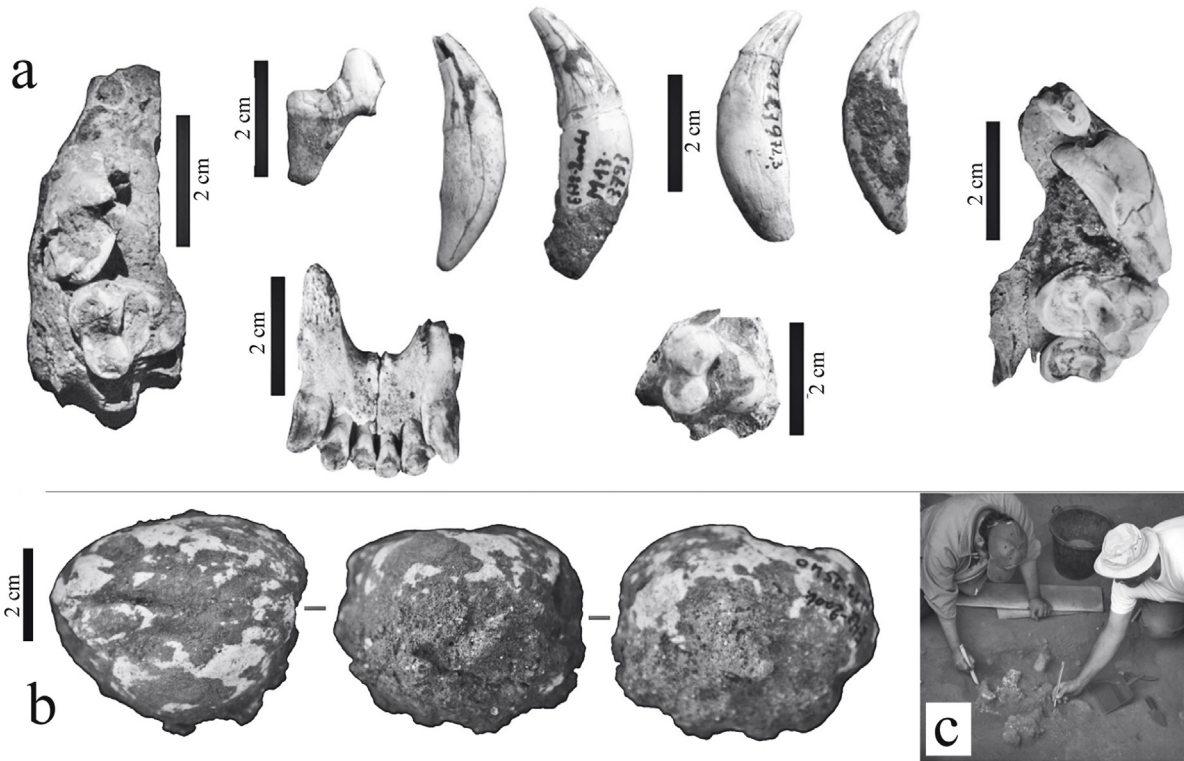


Fig. 3. a : large canid remains from EH2 layers 2, 3 and 4A (picture and infography É. Campmas); b : coprolite found at EH2 and attributed to a hyena (layer 2) (picture N. Hamzaoui and infography É. Campmas); c : excavation of an accumulation of crushed coprolites at EH2 (layer 3) (photo: P. Plailly).
Fig. 3. a : restes de grand canidé d'EH2 couches 2, 3 et 4A (photographie N. Hamzaoui et infographie É. Campmas) ; b : coprolithe d'EH2 attribué à l'hyène (couche 2) (photographie N. Hamzaoui et infographie É. Campmas) ; c : fouille d'un amas écrasé de coprolithes à EH2 (couche 3) (photographie : P. Plailly).

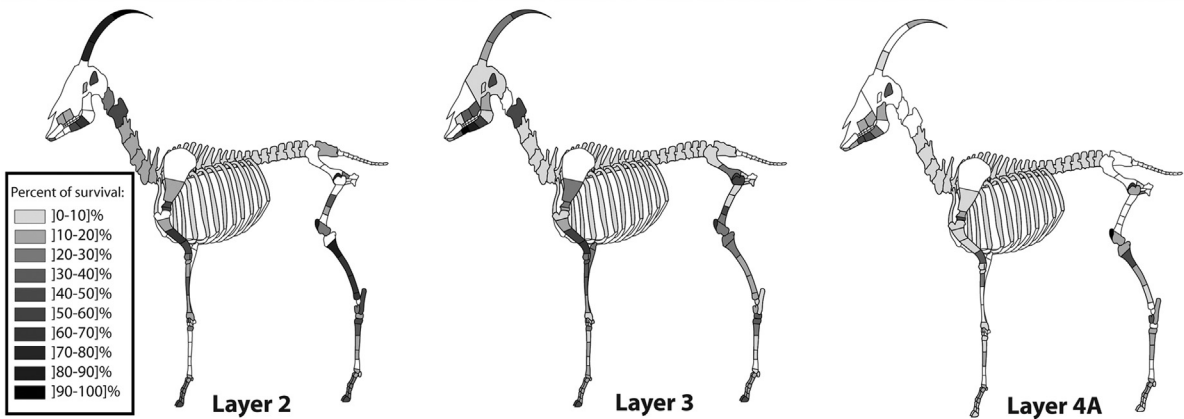


Fig. 4. Skeletal profiles of gazelles from layers 2, 3 and 4A of EH2 in survival percentages.
Fig. 4. Profils squelettiques des gazelles des couches 2, 3 et 4A d'EH2 en pourcentage de survie.

Drawing adapted from Coutureau, 1996.

located on portions with epiphyses although they are also present on shaft portions (Table 3; Campmas et al., 2015). Alterations by digestion are significant (6–9%) (Fig. 6e, f, g, h, i and Table 3) and have been identified mainly on small bones and epiphyses. This effect mainly concerns small remains less than 6 cm long (mostly less than 3 cm).

Most of the remains are small (less than 4 cm) but very small remains present in sieve residues have not

been integrated here. The percentage of complete remains (including all types of remains, such as small bones, long bones, flat bones, teeth...) is low, lesser than 12% (Table 2). For all layers, less than 2% of gazelle long bones are complete. The lengths and circumferences of preserved shafts are low compared to their original size (for all size classes: 70% of long bones present a shaft length of less than 1/4 of the total length and less than 1/2 of the

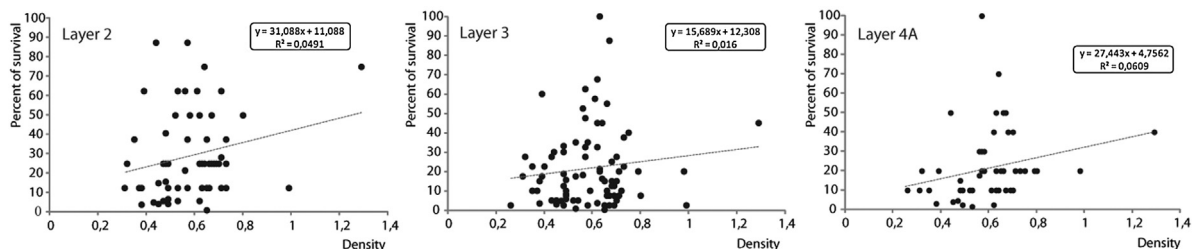


Fig. 5. Scatterplots of survival percentages for gazelles from layers 2, 3 and 4A of EH2 based on densities of *Rangifer tarandus* (Lam et al., 1999) (layer 2: $r_s = 0.22$; $P = 0.09 > 0.05$; layer 3: $r_s = 0.07$; $P = 0.51 > 0.05$; layer 4A: $r_s = 0.39$; $P = 0.003 < 0.01$).

Fig. 5. Pourcentages de survie de gazelles des couches 2, 3 et 4A d'EH2 selon les densités de *Rangifer tarandus* (Lam et al., 1999) (couche 2 : $r_s = 0,22$; $p = 0,09 > 0,05$; couche 3 : $r_s = 0,07$; $p = 0,51 > 0,05$; couche 4A : $r_s = 0,39$; $p = 0,003 < 0,01$).

total circumference). More than 90% of the observed shaft extremities correspond to green fractures. The majority of observed shaft fragments measure less than 10 cm (>80%), and even less than 6 cm (>70%). Five shaft “cylinders” were found in layer 4A, 26 in layer 3 and 10 in layer 2.

5. Discussion – Which predator(s) was(were) responsible for faunal accumulations and modification at EH2?

Regarding faunal remains, several carnivores are represented at EH2: small mustelids (with uncertainty), small

and large canids, small and large felids, and hyenas, which may be the spotted hyena (e.g., Michel et al., 2009) (Table 2). Although large mustelids (honey badger) and striped hyena have not been identified here, these species have been described in other caves of the Témara (Amani et al., 2012; Aouraghe, 2000; Campmas, 2012; Campmas et al., 2015; Michel, 1990; Monchot and Aouraghe, 2009). In addition to small and large carnivores, it is also essential to consider the possible intervention of large raptors, even if bone remains belonging to these taxa were not recovered at EH2. At EH2, contrary to other caves, such as Gazelle (Casablanca), visited by canids and other carnivores with similar results

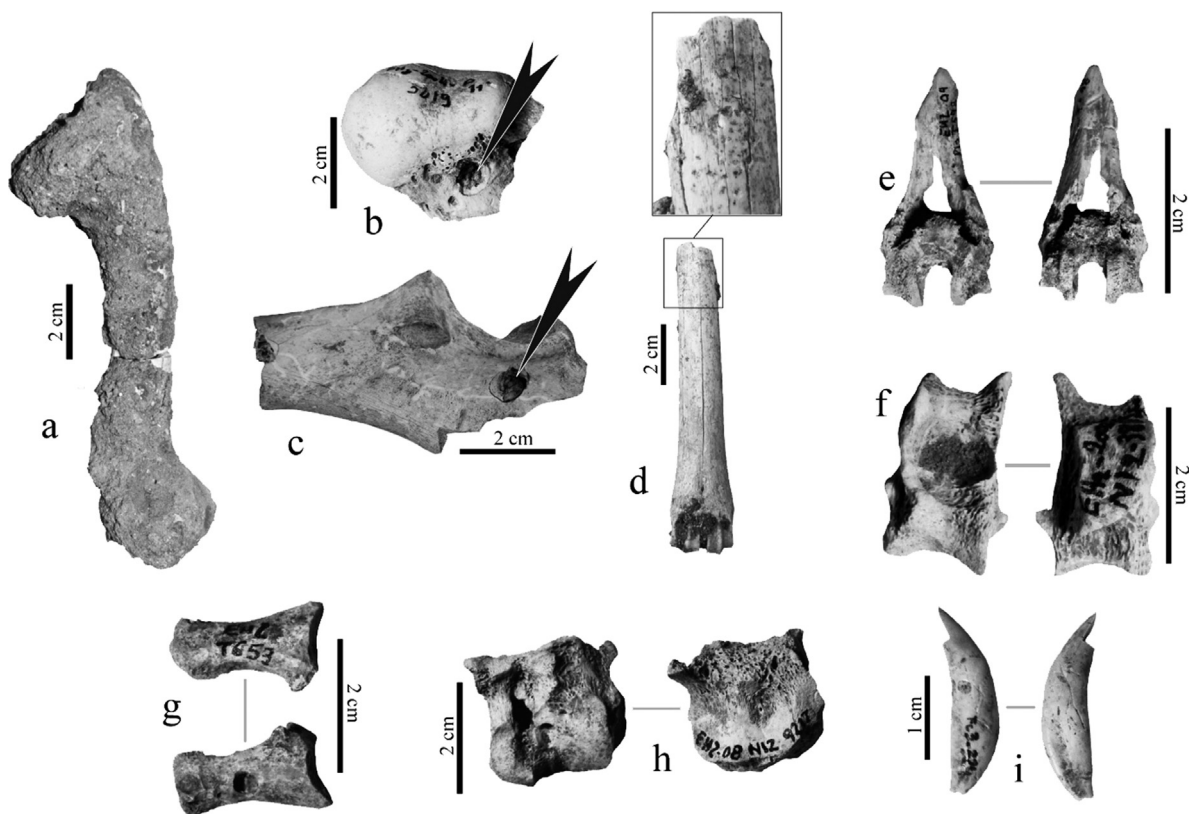


Fig. 6. a: gazelle humerus with adhering matrix; b–h: gazelle remains (tooth marks on: b: femur; c: coxal; d: metapodial; semi-digested: e: metapodial; f: talus; g: phalanx II; h: cubonavicular); i: semi-digested canine of small canid.

Fig. 6. a : humérus de gazelle avec des concrétions ; b–h : restes de gazelle (traces de dents sur : b : fémur ; c : coxale ; d : métapode ; restes semi-digérés : e : métapode ; f : talus ; g : phalange II ; h : cubonavulaire) ; i : canine de petit canidé semi-digérée.

Picture and infography: É. Campmas.

Table 3

Proportions of NR and NISP with non-human predator marks at EH2.

Tableau 3

Proportions des restes (NR et NISP) avec des traces de prédateurs non humains à EH2.

	El Harhoura 2		
	1.2	1.3	1.4A
Carnivore marks (Total)	9%	12%	9%
Carnivore marks (Total) ^a	10%	13%	12%
Tooth marks (te)	4%	4%	3%
Tooth marks ^a (te)	6%	6%	6%
Semi-digested	6%	9%	6%
Carnivore marks on ungulate size 1	11%	17%	15%
Carnivore marks on ungulates size 1 (te)	19%	21%	21%
Carnivore marks on ungulates size 1 ^a (te)	20%	24%	22%
Carnivore marks on long bone of ungulates size 1 ^a			
SH + EP	P	35%	20%
EP	P	43%	P
SH	15%	17%	P
Tooth marks on long bone of ungulates size 1 ^a			
SH + EP	P	16%	P
EP	P	5%	P
SH	13%	13%	15%
Carnivore marks on ungulates size 2	15%	11%	
Carnivore marks on ungulates size 2 (te)	P	17%	
Carnivore marks on ungulates size 2 ^a (te)	P	23%	P
Carnivore marks on ungulates size 3		8%	
Carnivore marks on ungulates size 3 (te)		P	
Carnivore marks on ungulates size 3 ^a (te)		P	
Carnivore marks on ungulates size 4			
Carnivore marks on ungulates size 4 ^a	P		
Carnivore marks on small canids	7%	20%	P
Carnivore marks on small canids (te)	10%	24%	P
Carnivore marks on large canids		P	
Carnivore marks on hyenids	P	P	
Carnivore marks on small felids		P	P

P: presence of marks but less than 30 long bones in total; te: calculation of the percentage of tooth marks excluding teeth; EP: long bones represented by epiphyseal parts; SH: long bones represented by shaft parts; SH + EP: long bones with shaft and epiphyseal parts.

^a With indeterminate notches.

(Daujeard et al., 2011), the location of the main excavation area below the porch, excludes the function of this part of the cave as a natural trap.

5.1. Behaviors of potential non-human accumulators of faunal remains in caves

Large raptors are known to accumulate large mammal bones in their nests (e.g., Robert and Vigne, 2002a, 2002b; Sanchis Serra et al., 2011, 2014). The Témara caves, however, are carved into the base of fossil dunes only a few meters high and were easily accessible to human and large carnivores throughout the Late Pleistocene. Large raptors such as vultures prefer higher and steeper cliffs. These caves were therefore not suitable for nesting and the protection of chicks (e.g., Eliotout, 2007; Heinzel et al., 2004; Terrasse, 2006). Considering small cats and lions, they are not known to bring prey back to their dens (Estes et al., 1991) and can thus be excluded from the potential agents responsible for faunal accumulations at EH2. Other small carnivores, such as honey badger and fox, can bring food back to their den (e.g., Mallye et al., 2008; Mallye, 2007; Castel et al., 2011; Krajcarz and Krajcarz, 2014). Unfortunately, we do not know if the jackal, especially the large jackal, brings their prey back to the den. However, the size of the large canid is similar to that of

the wolf, which is currently present in North Africa (e.g., Gaubert et al., 2012; Rueness et al., 2011). Wolves used cave as dens, and in very rare cases, they bring back isolated remains near the entrance (Binford, 1981; Fosse et al., 2012; Prucca, 2003). Leopards may hide prey in caves as an anti-theft behavior but do not use caves as nurseries (e.g., Brain, 1981; De Ruiter and Berger, 2000, 2001). Present-day spotted and striped hyenas use caves as dens and carry prey back in. Spotted hyena carries prey primarily around the entrance while striped hyena, which is more solitary, accumulates prey inside the den to discourage other predators from stealing (e.g., Fourvel, 2012). In addition to the introduction of prey or portion of prey, these carnivores could bring back ingested remains (e.g., Fourvel, 2012; Mallye et al., 2012). It should be noted that porcupines also bring backbones in their dens (e.g., Brain, 1981). In summary, the faunal accumulation at EH2 can potentially result from the intervention of porcupine, large mustelids, small and large canids, leopards or hyenas.

5.2. Faunal spectrum

In caves used by porcupines, remains of this species are common (e.g., Monchot, 2005; Monchot et al., 2012), which is not the case at EH2 contrary to El Harhoura 1

Cave (Monchot and Aouraghe, 2009). Thus, even if porcupines were present in the region, the intervention of this bone collector is probably minimal at EH2. From a general point of view, as caves are mainly used as caches and not as nurseries by leopards, the absence of leopard remains in cave context is not surprising (e.g., De Ruiter and Berger, 2000), as it is the case at EH2, where large felid remains are scarce in general. However, in a Pleistocene faunal assemblage of Spain attributed to leopard activities, remains belonging to adult leopards were numerous (Sauqué et al., 2014). Unlike in Pleistocene hyena dens in Europe (e.g., Brugal et al., 1997; Fosse, 1995), extant spotted hyena or striped hyena remains are rare in their own dens (Brugal et al., 1997; Kuhn, 2011; Leakey et al., 1999; Monchot and Mashkour, 2010; Pokines and Kerbis Peterhans, 2007; Prendergast and Domínguez-Rodrigo, 2008). However, in fossil assemblages attributed to spotted hyena activities, such as Mugharet el Aliya, Geula or Wezmeh, spotted hyena remains, mainly from young animals, are well represented (Wrinn, submitted; Monchot, 2005, 2008). Only one young hyena remain has been observed at EH2.

In the case of European badger and fox dens, small preys are frequent along with some small young ungulates (Artois, 1989; Castel et al., 2011; Krajcarz and Krajcarz, 2014; Mallye, 2007; Mondini, 1995; Table 4). The jackal hunts and consumes a variety of small preys, including gazelle fawn, but this carnivore has the ability to kill prey two or three times larger than itself (e.g., Estes et al., 1991; Yom-Tov et al., 1995). For example, in social groups, the golden jackal can hunt young cattles (Estes et al., 1991; Yom-Tov et al., 1995; Table 4). In addition, the jackal scavenges prey killed by other carnivores. Wolves, which also live in social groups, consume small and large ungulates. Indeed, this predator can hunt and/or scavenge large adult prey such as reed deer or bison (e.g., Binford, 1981; Esteban-Nadal, 2012; Esteban-Nadal et al., 2010; Fosse et al., 2012; Prucca, 2003). The faunal spectrum at EH2 contains gazelles of all age classes and some other large ungulates. These observations do not seem to correspond to badger and fox behavior but rather to that of large social canids.

The leopard hunts and consumes mainly small prey, such as small antelopes, young individuals of larger species or small and medium carnivores, such as canids (Brain, 1981; De Ruiter and Berger, 2000, 2001). Thus, the faunal spectrum at EH2 could also correspond to leopard consumption.

In modern faunal assemblages resulting from spotted hyena activity, medium ungulates predominate with numerous prime ages (Egeland et al., 2008; Lansing et al., 2009; Pokines and Kerbis Peterhans, 2007; Tables 4 and 5). However, when small ungulates predominate in the environment, the spotted hyena mainly consumes these taxa (Fourvel, 2012; Fourvel et al., 2015; Kuhn, 2011; Kruuk, 1972; Table 5). Thus, accumulations caused by hyenas mostly reflect the local environments and prey availability (e.g., Fourvel et al., 2015). Carnivore remains, belonging to hyenas and canids, are rare in present-day spotted hyena dens (Egeland et al., 2008; Kuhn, 2011; Pokines and Kerbis Peterhans, 2007; Prendergast and Domínguez-Rodrigo, 2008), while canid remains are numerous in

stripped hyena dens (Kuhn, 2011; Leakey et al., 1999; Monchot and Mashkour, 2010; Table 5).

Small ungulates dominate in parallel to the presence of canids at EH2, as it is the case in other North African fossil assemblages attributed to hyena activities, such as at El Harhoura 1 (Monchot and Aouraghe, 2009) and Doukkala 2 (Michel and Wengler, 1993a, 1993b). Similar results were also obtained at Equus cave in southern Africa where Cruz-Uribe (1991) and Klein et al. (1991) suggested that the faunal assemblage was due to the brown hyena (*Parahyena brunnea*) activities. However, in other North African faunal accumulation attributed to large carnivore activities, results differ. At la Felines Cave (Dar Bouazza, Morocco), gazelles are predominant while equids are also abundant (Daujeard et al., 2011). At Mugharet el Aliya (Tangier, Morocco), the faunal accumulations from the lower layers were attributed to spotted hyena activities, and along with gazelles, Alcelaphini/Bovini are also abundant (Wrinn, submitted). At the site of Phacochère (Alger, Algeria), where the identified predator is the spotted hyena, warthogs and Bovini are numerous (Hadjouis, 1994, 2003). How can we explain this variability? It can be both linked to a change in one predator behavior (e.g., hyenas evolving in several environments with different types of prey) or to the occurrence of several predators with different prey selection (e.g., small ungulate assemblages due to canids and larger prey assemblages due to hyenas).

5.3. Bone destruction

If the sequence of bone destruction is similar for all carnivores, in modern leopard caches bones are frequently found complete and in anatomical connection (Brain, 1981; De Ruiter and Berger, 2000), which is not the case at EH2. Present-day data shown that the sequence of bone destruction is more intense for hyenas (Campmas and Beauval, 2008; Fosse et al., 2011; Fourvel, 2012). However, a low degree of fragmentation is described in several stripped and spotted hyena dens with small ungulate bones almost complete (e.g., Fourvel and Mwebi, 2011; Fourvel et al., 2015; Leakey et al., 1999; Monchot and Mashkour, 2010; Prendergast and Domínguez-Rodrigo, 2008). Long bone shaft “cylinders” are generally common in present-day hyena accumulations (e.g., Fosse, 1996; Fourvel, 2012; Fourvel et al., 2015), as well as during the Late Pleistocene, such as at Geula (Monchot, 2005, 2008). Extant stripped and spotted hyena dens studies suggest that “cylinders” can also be rare (Kuhn, 2011). “Cylinders” are scarce at EH2, and the preservation of several long bone epiphyses, particularly from gazelles, does not match with the common high destruction associated with hyena intervention.

5.4. Tooth marks

Bones displaying tooth marks due to porcupine (1 remain) and carnivores (Table 3) are scarce at EH2. Several reasons could explain this phenomenon. Although remains with extensive adhering matrix have been excluded from the counts, adhering matrix is still present on the majority of the remains and potentially hides some marks. However, the small size of the remains at EH2 could also explain

Table 4

Prey consumed by several predators (European badger, fox, jackal, leopard, striped hyena, spotted hyena, large raptor) compared to EH2.

Tableau 4

Proies consommées par différents prédateurs (blaireau, renard, chacal, léopard, hyène rayée, hyène tachetée, grands rapaces) comparées aux observations d'EH2.

	Small prey	Small ungulates	Medium–Large ungulates	Small carnivores	Large carnivores	Observations	References
European badger	++	+	(+)	++		Bones in dens	Mallye, 2007; Mallye et al., 2008; Castel et al., 2011
Fox	++	+	(+)	+	+	Bones in dens and ethological data	Mondini, 1995; Mallye, 2007; Castel et al., 2011; Krajcarz and Krajcarz, 2014
Jackal	++	++	(+)			Ethological data	Brain, 1981; Estes et al., 1991; Yom-Tov et al., 1995
Leopard	+	++	+	+		Bones in dens and ethological data	Brain, 1981; De Ruiter and Berger, 2000, 2001
Striped hyena	++	++	+	++	+	Bones in dens	Brain, 1981; Leakey et al., 1999; Monchot and Mashkour, 2010; Kuhn, 2011; Fourvel, 2012; Fourvel et al., 2015
Spotted hyena		+	++	+	+	Bones in dens	Brain, 1981; Pokines and Kerbis Peterhans, 2007; Egeland et al., 2008; Prendergast and Domínguez-Rodrigo, 2008; Lansing et al., 2009; Kuhn, 2011; Fourvel, 2012; Fourvel et al., 2015
Large raptor	+	++	+	+	+	Bones in dens	Robert and Vigne, 2002a, 2002b; Sanchis Serra et al., 2014
EH2	(++ Brain, 1981) (microfauna)	++	+	+	+	Entrance of a cave	

the scarcity of tooth marks (e.g., Beauval and Morin, 2010; Castel, 2004). When small fragments are excluded, tooth mark frequencies on bones are higher (~15–20% at EH2). Despite the fact that no measurement of the marks was performed, we have observed that some of the tooth marks present at EH2 could have been produced by middle to large-sized carnivores (Fig. 6b and c).

5.5. Semi-digested remains

Semi-digested remains are frequent at EH2 and it is possible that gastric acid attack was underestimated as only remains presenting a high degree of digestion have been considered. In present-day hyena dens, semi-digested bones are present but in low proportions (Fourvel, 2012; Kuhn, 2011). In European Pleistocene hyena dens, these frequencies can also be low (e.g., Fourvel, 2012; Samper Carro and Martínez-Moreno, 2014) or on other cases much higher (Beauval and Morin, 2010; Marra et al., 2004). In wolf scats, juveniles of red deer or roe deer dominate and semi-digested remains measure less than 3 to 2 cm (Esteban-Nadal et al., 2010; Fosse et al., 2012; Mallye et al., 2012). Semi-digested bones produced by hyenas seem to be more diversified with regard to dimensions, species and anatomical portions. They are smaller when they are

contained in scats and they are larger than 3 cm when they result from regurgitations (Fourvel, 2012). At EH2, semi-digested attacks are particularly observed on small ungulates and small canids, and on remains less than 6 cm long (mostly less than 3 cm). Sieve residues contain small faunal remains, but as they are not studied yet, an underestimation of the quantity of digested bones is likely. Finally, the morphology of semi-digested bones of EH2 is similar to what was described by Mallye et al. (2012) for wolves. For example, on talus, digestion marks are located near the articular surfaces with the digging of bone around the *sulcus tali* or proximal portions of femora (head with a shaft fragment) have “nail” morphology. Thus, these semi-digested remains, belonging mainly to small-medium mammals, seem to be close to those produced by canids.

5.6. Coprolithes

A crushed pile of coprolites at EH2 suggests the presence of a small latrine area at the entry of the cave. Coprolites are scarce, however, and may be underestimated as they were not systematically collected. One coprolite from layer 2 has a morphology similar to that of hyenas, with a circular cross-section and with a concave end on one side and a convex end on the other side (e.g., Horwitz and Goldberg, 1989;

Table 5

Prey and marks due to striped and spotted hyena activities and other carnivores in fossil and modern contexts.

Tableau 5

Proies et traces liées à l'activité des hyènes tachetées et rayées, ainsi que d'autres carnivores en contextes actuel et fossile.

	Responsible (actual) and interpretation (fossil)	Localisation	Site (fossil)	Lithic associated (fossil)	% [C/(C + U)]	% [Canid/C]	Species of canids	% [Hy/C]	Species of hyenids	% [US1/U]	Main ungulates	% TM	% DB	References
Current data	Spotted hyena	Kenya			5% NISP	1/2 NISP	<i>Canis familiaris</i>	1/2 NISP	<i>Crocuta crocuta</i>	26% NISP	Bovini	35% NISP	4% NISP; Mainly small size classes	Egeland et al., 2008
		Kenya			1988: < 1% NISP; 1999: 3% NISP	0		1988: 4/6 NISP; 1999: 1/9 NISP	<i>Crocuta crocuta</i>	1988: 28% NISP; 1999: 21% NISP	Wildebeest, impala, buffalo	22% NISP	2% NISP; 6% unidentifiable	Pokines and Kerbis Peterhans, 2007
		Kenya			2% cp	5/7 cp	Jackal	2/7 cp (cubs)	Hyena cubs	25% cp	Wildebeest	–	–	Lansing et al., 2009
		Tanzania			18% NISP	18% NISP	<i>Canis familiaris</i>	82% NISP	<i>Crocuta crocuta</i>	56% NISP	Caprini, bovini	44% NISP	0	Prendergast and Domínguez-Rodrigo, 2008
	Djibouti			0–100% NISP	0–100% NISP	<i>Canis familiaris</i> , <i>Octocyon megalotis</i> , <i>Vulpes rueppellii</i>	0–10% NISP	<i>Crocuta crocuta</i> , <i>Hyaena hyaena</i>	51–100% NISP	Caprini (sometimes camel)	26–40%	0–4%	Fourvel, 2012	
	Southern Africa			0–9% NISP	0% NISP		0–100% NISP	<i>Crocuta crocuta</i>	13–65% NISP	Small antilops or Oryx	20–55% NR	0–9% NR	Kuhn, 2011	
	Jourdan			0–26% NISP	97–100% NISP		0–3% NISP		10–55% NISP	Caprini and/or camel and/or equids	6–40% NR	0%	Kuhn, 2011	
	Djibouti			18% NISP	3% NISP	<i>Canis</i> sp.	97% NISP	<i>Crocuta crocuta</i> , <i>Hyaena hyaena</i>	82% NISP	Caprini	23%	0%	Fourvel, 2012	
Iran			13% NISP	93% NISP	Jackal size	4% NISP	<i>Hyaena hyaena</i>	3% NISP	Equids	4% caprini, 17% equids	–	–	Monchot and Mashkour, 2010	

Table 5
(Continued)

	Responsible (actual) and interpretation (fossil)	Localisation	Site (fossil)	Lithic associated (fossil)	% [C/(C + U)]	% [Canid/C]	Species of canids	% [Hy/C]	Species of hyenids	% [US1/U]	Main ungulates	% TM	% DB	References
		Kenya			8% NISP	78% NISP	Indet.	12% NISP	<i>Hyaena hyaena</i>	81% NISP	Caprini	–	–	Leakey et al., 1999 Prendergast and Domínguez-Rodrigo, 2008 Monchot and Aouraghe, 2009
		Tanzania			0	0		0		8/13 NISP	Gazelles	–	–	
Fossil data	Hyena	Morocco	El Harhoura 1 Cave (EH1)	Mousterian	I.s1: 10%; NISP; I.1: 12%; NISP; I.2: 20% NISP	I.s1: 81%; NISP; I.1: 70%; NISP; I.2: 72% NISP	<i>Vulpes vulpes</i> , <i>Canis aureus</i> , <i>Canis</i> sp.	I.s1: 0; I.1: 0; I.2: 7% NISP	<i>Crocota crocuta</i> , <i>Hyaena hyaena</i>	I.s1: 81% NISP; I.1: 65% NISP; I.2: 80% NISP	Gazelles	P	P	Bougariane et al., 2010 Daujeard et al., 2011
	–		Gazelle Cave (GDG) b	Mousterian/Iberomaurisian	I.inf.: 7% NISP; I.sup.: 10% NISP	I.inf.: 90% NISP; I.sup.: 87% NISP	<i>Vulpes vulpes</i> , <i>Canis aureus</i> , <i>Canis</i> sp. (cf. <i>Canis aureus</i>)	I.inf.: 10% NISP; I.sup.: 13% NISP	<i>Crocota crocuta</i>	I.inf.: 97% NISP; I.sup.: 97% NISP	Gazelles	P	–	
	Natural accumulation visited by carnivores (such as Canids)		Gazelle Cave (GDG) d	Mousterian	4% NISP	90% NISP	<i>Vulpes vulpes</i> , <i>Canis aureus</i>	Another part of the site	<i>Hyaena hyaena</i>	97% NISP	Gazelles	17% NISP (17% gazelles)	–	
			El Harhoura 2 Cave (EH2)	Mousterian/Iberomaurisian	I.4A: 11% NISP; I.3: 10% NISP; I.2: 16% NISP	I.4A: 94% NISP; I.3: 91% NISP; I.2: 91% NISP	Small canids: <i>Vulpes vulpes</i> , <i>Canis aureus</i> and/or <i>Lupulella mesomelas</i> ; Large canids: Cf. Large <i>Canis aureus</i>	I.4A: 3% NISP; I.3: 3% NISP; I.2: 4% NISP	<i>Crocota crocuta</i>	I.4A: 74% NISP; I.3: 88% NISP; I.2: 91% NISP	Gazelles	Size 1: 11–15%; Size 2: 11–15%; Size 3: 8%	6–9% NR	

Table 5
(Continued)

Responsible (actual) and interpretation (fossil)	Localisation	Site (fossil)	Lithic associated (fossil)	% [C/(C + U)]	% [Canid/C]	Species of canids	% [Hy/C]	Species of hyenids	% [US1/U]	Main ungulates	% TM	% DB	References
Large carnivore		Felines Cave (GDF)	Mousterian	I.inf.: 69% NISP; I.sup.: 7% NISP	I.inf.: 4% NISP; I.sup.: 36% NISP	<i>Vulpes vulpes</i> , <i>Canis aureus</i>	I.inf.: 1% NISP; I.sup.: 14% NISP	<i>Hyaena hyaena</i>	I.inf.: 55% NISP; I.sup.: 41% NISP	Gazelles and Equidae/Bovinae	I.inf.: 8% NISP (22% gazelles); I.sup.: 30% NISP (22% gazelles)	Numerous	Daujeard et al., 2011
Different size of carnivores		Hominid Cave (GH)	Acheulean	4% NISP	89% NISP	<i>Lupulella mohibi</i>	3% NISP	Hyenidae	54% NISP	Gazelles and Alcelaphinae	20% NR (size 1–2: 24%)	–	Daujeard et al., 2012
Spotted hyena		Mugharet El Aliya (MA)	Aterian	I.10: 5% NISP; I.9: 19% NISP; I.6: 15% NISP; I.5: 9% NISP	I.10: ¼ NISP; I.9: 59% NISP; I.6: 71% NISP; I.5: 43% NISP	<i>Vulpes vulpes</i> , <i>Canis aureus</i>	I.10: ¾ NISP; I.9: 36% NISP; I.6: 25% NISP; I.5: 55% NISP	<i>Crocota crocuta</i> , <i>Hyaena hyaena</i>	I.10: 16% NISP; I.9: 40% NISP; I.6: 72% NISP; I.5: 87% NISP	Gazelles and Equidae	I.9: 18% NR (5% small size); I.6: 7% NR (2% small size); I.5: 4% NR (0% small size)	–	Wrinn, submitted
Brown hyena	South Africa	Equus Cave (EQ)	MSA	I. 1B: 39% NISP; I. 2A: 36% NISP; I. 2B: 39% NISP	I.1B: 80% NISP; I.2A: 86% NISP; I.2B: 87% NISP	<i>Canis mesomelas</i> , <i>Vulpes chama</i> , <i>Lycaon pictus</i>	I. 1B: 11% NISP; I. 2A: 12% NISP; I. 2B: 12% NISP	<i>Hyaena brunnea</i> , <i>Crocota crocuta</i>	I. 1B: 64% NISP; I. 2A: 64% NISP; I. 2B: 62% NISP	<i>Antidorcas Bondi</i> , <i>Antidorcas marsupiali</i>	I. 1B: 0.3% NR; I. 2A: 0.1% NR; I. 2B: 0.2% NR	I. 1B: 3% NR; I. 2A: 1% NR; I. 2B: 0.4% NR	Cruz-Uribe, 1991
Spotted hyena	Iran	Wezmeh	No lithic (Upper Pleistocene)	79% NISP	48% NISP	<i>Vulpes vulpes</i> , <i>Canis lupus</i>	31% NISP	<i>Crocota crocuta</i>	49% NISP	<i>Ovis orientalis</i>	5% NISP	0	Monchot, 2008
Spotted hyena		Geula	Middle Palaeolithic	15% NISP	21% NISP	<i>Canis aureus</i> , <i>Vulpes vulpes</i>	63% NISP	<i>Crocota crocuta</i>	58% NISP	<i>Dama mesopotamica</i>	2% <i>Dama mesopotamica</i> , 11% <i>Gazella sp.</i> , 29% <i>Capra aegagrus</i> (without teeth)	–	Monchot, 2005

C: carnivores; U: ungulates; Canid: canids; Hy: hyenas; US1: ungulate sizes 1; TM: tooth marks; DB: semi-digested bones; cp: carcass portion.

Larkin et al., 2000). This observation thus argues for the presence of hyena in the cave, without necessarily implying that it was the main occupant.

5.7. Comparison with microfaunal analyses

The caves of the Témara region have also yielded abundant microvertebrate remains. At EH2, the taphonomic study has shown that even if chiroptera and some amphibian and squamate individuals may have died in the cave from natural causes, most of the rodents, shrews, amphibians and squamates from layers 2, 3 and 4A were accumulated by several predators belonging to the Andrew's category 3–4, mainly diurnal raptors and/or small carnivores (Stoetzel, 2009; Stoetzel et al., 2011, 2012a, 2012b). It is thus possible that a small part of the small/medium mammal prey was accumulated by the same type of predator, i.e. a small one such as jackals.

5.8. Synthesis

The topography and the type of faunal accumulation at EH2 cave do not correspond to those of a natural trap. Conversely, several criteria allow us to propose a predator as the main responsible of the accumulation of faunal remains in the cave. The scarcity of porcupine remains and tooth marks suggests that this collector of bones has a very limited involvement. The fragmentation and significant number of digested remains suggest that is not a leopard cat. The dominance of small prey (mainly small ungulates), with all age classes and including all skeletal portions, associated with few remains of larger ungulates (attributed mainly to young animals), together with the presence of tooth marks and digestion marks, allows us to propose large canids as the main authors of the accumulations, without completely exclude contributions of hyenas (with the presence of remains and a coprolite) or small canids (which consume mainly very small prey and young ungulates, and which also display consumption marks). Nonetheless, such small canids could have contributed a small portion of small/medium mammals and very small vertebrate accumulations. Fossil records provide data regarding wild behavior of carnivore in Pleistocene environments. However, analyses frequently assume hyenas to be the main responsible of faunal accumulation. Other carnivores, such as canids, are consequently considered as minor actor. Conversely, present-day data analyses on captive and wild carnivore might be difficult to apply to ancient situation, because carnivores suffered direct or indirect human influence. Even so, these present-day data allow a better recognition of the responsible of fossil record accumulation. Thus, a multiplication of neotaphonomic reference data for canids as well as for leopards will be helpful to refine our interpretation of the EH2 assemblages.

6. Conclusion

The results obtained from the faunal assemblages from EH2 illustrate the difficulty in identifying the carnivores responsible for faunal accumulations in fossil contexts and particularly in the context of the Upper Pleistocene of

North Africa. Based on current and fossil data, we propose that large canids could be predominantly responsible for faunal modifications at EH2. However, several fossil assemblages with similar results have been attributed to hyena activities. In addition, small canids, which were also prey (as they present digestion marks), may have also contributed to a small part in the faunal accumulation, including macro/meso- and microfauna. In several cases, it is difficult to differentiate their taphonomic signatures as there are problems involved in the application of results from neotaphonomic reference studies (for example kill sites, captive records or methodological choices) to fossil assemblages. In addition, there is an important lack of present-day references for several species, such as large North African canids. The multiplication of neotaphonomic studies, both for hyenas and canids, in varied environments and with different biomass availability, is essential to improve interpretations of fossil assemblages and to distinguish the activities of the human and non-human predators responsible for meso- and macrofaunal accumulations in North Africa.

Acknowledgements

Most of this research was funded by the “Agence universitaire de la Francophonie” and the “L'Oréal-France/UNESCO” foundation and hosted by the UMR 5199 PACEA and UMR 5608 TRACES laboratories. We are grateful to the scientific team and all excavators of the El Harhoura-Témara mission. This archaeological mission was conducted under the administrative supervision of the “Institut national des sciences, de l'archéologie et du patrimoine” (Rabat, Morocco) directed by Dr A. Akerraz. We also wish to acknowledge financial support of the mission from the “Ministère des Affaires étrangères et européennes” (France) and the “Ministère de la Culture” (Maroc). We are grateful to E. Stoetzel for discussions concerning faunal remains. Thanks to Louise Byrne and Magen O'Farrell for correcting the English manuscript and SMP3C – CNRS UMR 5608 – TRACES for its funding. We are obliged to C. Daujeard and J.-B. Mallye for their constructive remarks.

References

- Amani, F., Bougariane, B., Stoetzel, E., 2012. Partie 3 : grotte d'El Mnasra. Chapitre XVI. Faunes et paléoenvironnements. In: El Hajraoui, M.A., Nespoulet, R., Debénath, A., Dibble, H.L. (Eds.), La préhistoire de la région de Rabat-Témara. Villes et sites archéologiques du Maroc, Vol. III. Royaume du Maroc, ministère de la Culture, Institut national des sciences de l'archéologie et du patrimoine, Rabat, pp. 110–117.
- Aouraghe, H., 2000. Les carnivores fossiles d'El Harhoura 1, Temara, Maroc. *L'Anthropologie* 104, 147–171.
- Aouraghe, H., (Unpublished PhD thesis) 2001. Contribution à la connaissance des faunes pléistocènes supérieures du Maroc : les vertébrés d'El Harhoura (Témara) comparés à ceux de plusieurs sites du Maghreb. Université Mohamed-I, Oujda, Morocco.
- Arambourg, C., 1957. Observation sur les gazelles fossiles du Pléistocène supérieur de l'Afrique du Nord. *Bull. Soc. Hist. Nat. Afr. Nord*, Alger 48, 49–81.
- Artois, M., 1989. Encyclopédie des carnivores de France, espèces sauvages ou errantes, indigènes ou introduites en métropole et dans les DOM-TOM, Le Renard roux (*Vulpes vulpes* Linnaeus, 1758). Société française d'étude et de protection des mammifères (SFEPM), Bourges.
- Assefa, Z., 2006. Dentitions of East African Ungulates: Digital Archive. Smithsonian Institution NMNH (Human Origins and Archaeobiology). Guide des mammifères d'Europe, d'Afrique du Nord et du

- Moyen-Orient. Delachaux et Niestlé, Paris <http://humanorigins.si.edu/research/digital-archive-ungulate-and-carnivore-dentition>.
- Aulagnier, S., Haffner, P., Mitchell-Jones, A.J., Moutou, F., Zima, J., 2008. Guide des mammifères d'Europe, d'Afrique du Nord et du Moyen-Orient. Delachaux et Niestlé, Paris.
- Barone, R., 1999. Anatomie comparée des mammifères domestiques, Tome 1. Vigot, Paris.
- Beauval, C., Morin, E., 2010. Les repaires d'hyènes du Lussacois (Lussac-Châteaux, Vienne, France) : apport des sites des Plumettes et des Rochers-de-Villeneuve. In: Buisson-Catil, J., Primault, J. (Eds.), Préhistoire entre Vienne et Charente, hommes et sociétés du paléolithique. Association des publications chauvinoises, Chauvigny, France, pp. 175–190.
- Benatia, M., (Unpublished DEA dissertation) 1998. Étude paléontologique et archéozoologique des populations de gazelles du gisement El Harhoura 1 (grotte Zouhrah), province de Témara, Maroc. Muséum national d'histoire naturelle, Paris.
- Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.
- Black, S.A., Fellous, A., Yamaguchi, N., Roberts, D.L., 2013. Examining the extinction of the Barbary Lion and its implications for felid conservation. *PLoS One* 8, e60174.
- Bougariane, B., Zouhri, S., Ouchau, B., Oujaa, A., 2012. Description et position systématique du grand canidé de Tamaris I (Casablanca, Maroc). *Quaternaire* 23, 149–156.
- Bougariane, B., Zouhri, S., Ouchau, B., Oujaa, A., Boudad, L., 2010. Large mammals from the Upper Pleistocene at Tamaris I "Grotte des gazelles" (Casablanca, Morocco): paleoecological and biochronological implications. *Hist. Biol.* 22, 295–302.
- Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.
- Brugal, J.-P., Fosse, P., Guadelli, J.-L., 1997. Comparative study of bone assemblages made by recent and Pleistocene Hyenids. In: Hannu, L.A., Rossom, L., Winham, R.P. (Eds.), Proceedings of the 1993 Bone Modification Conference Hot Springs, South Dakota, Vol. 1. Archaeology laboratory, Augustana, pp. 158–187.
- Campmas, É., (Unpublished PhD thesis) 2012. Caractérisation de l'occupation des sites de la région de Témara (Maroc) au Pléistocène supérieur et nouvelles données sur la subsistance des hommes du Paléolithique moyen d'Afrique du Nord : exemples des approches taphonomiques et archéozoologiques menées sur les faunes d'El Harhoura 2 et d'El Mnasra. Université Bordeaux-1, Talence, France.
- Campmas, É., Beauval, C., 2008. Consommation osseuse des carnivores : résultats de l'étude de l'exploitation de carcasses de bœufs (*Bos taurus*) par des loups captifs. *Ann. Paleontol.* 94, 167–186.
- Campmas, É., Amani, F., Morala, A., Debénath, A., Nespoulet, R., El Hajraoui, M.A., 2016. Initial insights into Aterian hunter-gatherer settlements on coastal landscapes: the example of Unit 8 of El Mnasra Cave (Témara, Morocco). *Quatern. Int.* 413, 5–20.
- Campmas, É., Michel, P., Costamagno, S., Amani, F., Stoetzel, E., Nespoulet, R., El Hajraoui, M.A., 2015. Were Upper Pleistocene human/non-human predator occupations at the Témara caves (El Harhoura 2 and El Mnasra, Morocco) influenced by climate change? *J. Hum. Evol.* 78, 122–143.
- Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* 59, 724–748.
- Castel, J.-C., 2004. L'influence des canidés sur la formation des ensembles archéologiques : caractérisation des destructions dues au loup. *Rev. Paleobiol.* 23, 675–693.
- Castel, J.C., Mallye, J.-B., Oppliger, J., 2011. Les petits carnivores dans leurs abris temporaires : choix des espèces et caractéristiques taphonomiques. Implications pour l'archéologie. In: Laroulandie, V., Mallye, J.-B., Denys, C. (Eds.), Taphonomie des petits vertèbres : référentiels et transferts aux fossiles. Actes de la table ronde du RTP Taphonomie. British Archaeological Reports, International Series, 2269, Oxford, pp. 77–91.
- Chame, M., 2003. Terrestrial mammal feces: a morphometric summary and description. *Mem. Inst. Oswaldo Cruz* 98, 71–94.
- Cherkaoui, I., Essabbani, A., Rguibi Idrissi, H., 2006. Observation d'un Gypaète barbu juvénile *Gypaetus barbatus* dans le massif du Jbel Ayachi (Haut-Atlas oriental, Maroc). *Go-South Bull.* 3, 4–5.
- Cruz-Uribe, K., 1991. Distinguishing hyena from hominid bone accumulations. *J. Field Archaeol.* 18, 467–486.
- Daujeard, C., Geraads, D., Gallotti, R., Raynal, J.-P., 2012. Carcass acquisition and consumption by carnivores and hominins in Middle Pleistocene sites of Casablanca (Morocco). *J. Taphonomy* 10, 349–372.
- Daujeard, C., Geraads, D., Raynal, J.-P., Mohib, A., Gallotti, R., 2011. Carnivores et/ou hommes dans deux sites moustéro-atériens de Dar Bouazza (Casablanca, Maroc) : les données de la taphonomie. In: Brugal, J.-P., Gardeisen, A., Zucker, A. (Eds.), Prédateurs dans tous leurs états : évolution, biodiversité, interactions, mythes, symboles. In: Actes des Rencontres internationales d'archéologie et d'histoire d'Antibes, octobre 2010, pp. 351–366.
- De Ruiter, D.J., Berger, L.R., 2000. Leopards as taphonomic agents in Dolomitic caves—implications for bone accumulations in the Hominid-bearing deposits of South Africa. *J. Archaeol. Sci.* 27, 665–684.
- De Ruiter, D.J., Berger, L.R., 2001. Leopard (*Panthera pardus* Linnaeus) cave caching related to anti-theft behaviour in the John Nash Nature Reserve. *Afr. J. Ecol.* 39, 396–398.
- Dominguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *J. Archaeol. Sci.* 30, 1385–1391.
- Egeland, A.G., Egeland, C.P., Bunn, H.T., 2008. Taphonomic analysis of a modern spotted hyena (*Crocuta crocuta*) from Nairobi, Kenya. *J. Taphonomy* 6, 275–299.
- Eliotout, B., 2007. Le vautour fauve, description, évolution, répartition, reproduction, observation, protection. Delachaux et Niestlé, Paris.
- Esteban-Nadal, M., 2012. Can archaeozoology and taphonomy contribute to knowledge of the feeding habits of the Iberian wolf? *J. Archaeol. Sci.* 39, 3208–3216.
- Esteban-Nadal, M., Cáceres, I., Fosse, P., 2010. Characterization of a current coprogenic sample originated by *Canis lupus* as a tool for identifying a taphonomic agent. *J. Archaeol. Sci.* 37, 2959–2970.
- Estes, R.D., Wilson, E.O., Otte, D., 1991. The Behavior Guide to African Mammals. University of California Press, London.
- Fosse, P., 1995. Le rôle de l'hyène dans la formation des associations osseuses. 150 ans de controverses : l'apport des anciens textes de préhistoire et de paléontologie du Quaternaire aux études taphonomiques actuelles. *Paléo* 7, 49–84.
- Fosse, P., 1996. La grotte n° 1 de Lunel-Viel (Hérault, France) : repaire d'hyènes du Pléistocène moyen. Étude taphonomique du matériel osseux. *Paléo* 8, 47–79.
- Fosse, P., Avery, G., Selva, N., Smietana, W., Okarma, H., Wajrak, A., Fourvel, J.-B., Madelaine, S., 2011. Taphonomie comparée des os longs d'ongulés dévorés par les grands prédateurs modernes d'Europe et d'Afrique (*C. lupus*, *P. brunnea*). In: Brugal, J.-P., Gardeisen, A., Zucker, A. (Eds.), Prédateurs dans tous leurs états : évolution, biodiversité, interactions, mythes, symboles. In: Actes des Rencontres internationales d'archéologie et d'histoire d'Antibes (octobre 2010), pp. 127–156.
- Fosse, P., Wajrak, A., Fourvel, J.-B., Madelaine, S., Esteban-Nada, M., Cáceres, I., Yravedra, J., Brugal, J.-P., Prucca, A., Haynes, G., 2012. Bone modification by modern wolf (*Canis lupus*): a taphonomic study from their natural feeding places. *J. Taphonomy* 10, 197–217.
- Fourvel, J.-B., (Unpublished PhD thesis) 2012. Hyénidés modernes et fossiles d'Europe et d'Afrique : taphonomie comparée de leurs assemblages osseux. Université Toulouse-2, Toulouse, France.
- Fourvel, J.-B., Mwebi, O., 2011. Hyenas' level of dependence on livestock in pastoralist areas in the Republic of Djibouti and Kenya: relation between prey availability and bone consumption sequence. In: Brugal, J.-P., Gardeisen, A., Zucker, A. (Eds.), Prédateurs dans tous leurs états : évolution, biodiversité, interactions, mythes, symboles. In: Actes des Rencontres internationales d'archéologie et d'histoire d'Antibes (octobre 2010), pp. 157–176.
- Fourvel, J.-B., Fosse, P., Avery, G., 2015. Spotted, striped or brown? Taphonomic studies at dens of extant hyaenas in eastern and southern Africa. *Quatern. Int.* 369, 38–50.
- Gaubert, P., Bloch, C., Benyacoub, S., Abdelhamid, A., Pagani, P., Djagoun, C.A.M.S., Couloux, A., Dufour, S., 2012. Reviving the African wolf *Canis lupus lupaster* in North and West Africa: a mitochondrial lineage ranging more than 6000 km wide. *PLoS One* 7, e42740.
- Gensbol, B., 1993. Guide des rapaces diurnes. Delachaux et Niestlé, Paris.
- Geraads, D., 2011. A revision of the fossil Canidae (Mammalia) of north-western Africa. *Palaeontology* 54, 429–446.
- Grant, A., 1982. The use of tooth wears as a guide to the age of domestic ungulates. In: Wilson, B., Grigson, C., Payne, S. (Eds.), Ageing and Sexing Animal Bones from Archaeological Sites. British Archaeological Reports, International Series, 109, Oxford, pp. 91–108.
- Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Academic Press, New York.
- Hadjouis, D., 1994. Taphonomie des faunes du gisement atérien des phacohères (Alger – Algérie) : Actions anthropiques. In: Outillage peu élaboré en os et bois de Cervidés IV : taphonomie/bone modification.

- Éditions du Centre d'études et de documentation archéologiques, Artefacts 9, Treignes, pp. 183–191 (9).
- Hadjouis, D., 2003. La faune quaternaire d'Algérie. Dossier Archeol. 282, 42–53.
- Heinzel, H., Fitter, R., Parslow, J., 2004. Guide Heinzel des oiseaux d'Europe, d'Afrique du Nord et du Moyen-Orient. Delachaux et Niestlé, Paris.
- Horwitz, L.K., Goldberg, P., 1989. A study of Pleistocene and Holocene hyaena coprolites. *J. Archaeol. Sci.* 16, 71–94.
- Jacobs, Z., Roberts, R.G., Nespoulet, R., El Hajraoui, M.A., Debénath, A., 2012. Single-grain OSL chronologies for Middle Palaeolithic deposits at El Mnasra and El Harhoura 2, Morocco: implications for Late Pleistocene human–environment interactions along the Atlantic coast of Northwest Africa. *J. Hum. Evol.* 62, 377–394.
- Janati Idrissi, N., Falguères, C., Haddad, M., Nespoulet, R., El Hajraoui, M.A., Debénath, A., Bejjit, L., Bahain, J.-J., Michel, P., Garcia, T., Boudad, L., El Hammouti, K., Oujaa, A., 2012. Datation par ESR-U/Th combinées de dents fossiles des grottes d'El Mnasra et d'El Harhoura 2, région de Rabat-Temara. Implications chronologiques sur le peuplement du Maroc atlantique au Pléistocène supérieur et son environnement. *Quaternaire* 23, 25–35.
- Kingdon, J., 2006. Guide des mammifères d'Afrique. Delachaux et Niestlé, Paris.
- Klein, R.G., Cruz-Urbe, K., 1984. *The Analysis of Animal Bones from Archaeological Sites*. The University of Chicago Press, Chicago, IL, USA.
- Klein, R.G., Cruz-Urbe, K., Beaumont, P.B., 1991. Environmental, ecological, and paleoanthropological implications of the Late Pleistocene Mammalian Fauna from Equus Cave, northern Cape Province, South Africa. *Quat. Res.* 34, 94–119.
- Krajcarz, M., Krajcarz, M.T., 2014. The Red Fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. *Int. J. Osteoarchaeol.* 24, 459–475.
- Kruuk, H., 1972. *The Spotted Hyena. A study of Predation and Social Behavior*. The University of Chicago, Chicago, IL, USA.
- Kuhn, B., 2011. *Hyaenids: Taphonomy and Implications for the Palaeoenvironment*. Cambridge Scholars Publishing, Newcastle Upon Tyne, UK.
- Lam, Y.M., Chen, X., Pearson, O.M., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *Am. Antiq.* 64, 343–362.
- Lansing, S.W., Cooper, S.M., Boydston, E.E., Holekamp, K.E., 2009. Taphonomic and zooarchaeological implications of spotted hyena (*Crocuta crocuta*) bone accumulations in Kenya: a modern behavioral ecological approach. *Paleobiology* 35, 289–309.
- Larkin, N.R., Alexander, J., Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, UK. *J. Archaeol. Sci.* 27, 19–31.
- Leakey, L.N., Milledge, S.A.H., Leakey, S.M., Edung, J., Haynes, P., Kiptoo, D.K., McGeorge, A., 1999. Diet of striped hyaena in northern Kenya. *Afr. J. Ecol.* 37, 314–326.
- Lyman, R.L., 1984. Bone density and differential survivorship of fossil classes. *J. Anthropol. Archaeol.* 3, 259–299.
- Lyman, R.L., 1994. Quantitative units and terminology in zooarchaeology. *Am. Antiq.* 59, 36–71.
- Mallye, J.-B., (Unpublished PhD thesis) 2007. Les restes de blaireau en contexte archéologique : taphonomie, archéozoologie et éléments de discussion des séquences préhistoriques. Université Bordeaux-I, Talence, France.
- Mallye, J.-B., Cocharde, D., Laroulandie, V., 2008. Accumulations osseuses en périphérie de terriers de petits carnivores : les stigmates de prédation et de fréquentation. *Ann. Paleontol.* 94, 187–208.
- Mallye, J.-B., Costamagno, S., Boudadi-Maligne, M., Prucca, A., Laroulandie, V., Thiébaud, C., Mourre, V., 2012. Dhole (*Cuon alpinus*) as a bone accumulator and new taphonomic agent? The case of Noisetier cave (French Pyrenees). *J. Taphonomy* 10, 317–347.
- Marra, A.C., Villa, P., Beauval, C., Bonfiglio, L., Goldberg, P., 2004. Same predator, variable prey: taphonomy of two Upper Pleistocene hyena dens in Sicily and SW France. *Rev. Paleobiol.* 23, 787–801.
- Michel, P., (Unpublished PhD thesis) 1990. Contribution à l'étude paléontologique des vertébrés fossiles du Quaternaire marocain à partir de sites du Maroc atlantique, central et oriental. Museum national d'histoire naturelle, Paris.
- Michel, P., Campmas, É., Stoetzel, E., Nespoulet, R., El Hajraoui, M.A., Amani, F., 2009. La macrofaune du Pléistocène supérieur d'El Harhoura 2 (Témara, Maroc) : données préliminaires. *L'Anthropologie* 113, 283–312.
- Michel, P., Campmas, É., Stoetzel, E., Nespoulet, R., El Hajraoui, M.A., Amani, F., 2010. Upper Palaeolithic (layer 2) and Middle Palaeolithic (layer 3) large faunas from El Harhoura 2 Cave (Témara, Morocco): paleontological, paleoecological and paleoclimatic data. *Hist. Biol.* 22, 327–340.
- Michel, P., Wengler, L., 1993a. Un site paléontologique avec des vestiges archéologiques : la carrière Doukkala II (région de Temara, Maroc atlantique). *Paléoécologie des faunes et contribution à la connaissance du comportement humain*. *Paléo* 5, 11–41.
- Michel, P., Wengler, L., 1993b. Le site paléontologique et archéologique de Doukkala II (Maroc, Pléistocène moyen et supérieur) : premier jalon en Afrique du Nord d'un comportement humain assimilable à un charognage contrôlé et actif. *C. R. Acad. Sci. Paris, Ser. II* 317, 557–562.
- Moliner, V.U., Ramirez, C., Gallardo, M., Idrissi, H.R., 2012. Detectan al lobo en Marruecos gracias al uso del foto-trampeo. *Quercus* 317, 14–15.
- Monchot, H., 2005. Un assemblage original au Paléolithique moyen : le repaire à hyènes, porcs-épics et hominidés de la grotte Geula (mont Carmel, Israël). *Paleorient* 31, 27–42.
- Monchot, H., 2008. Des hyènes tachetées au Pléistocène supérieur dans le Zagros, grotte Wezmeh, Iran. In: Vila, E., Gourichon, L., Choyke, A.M., Buitenhuis, H. (Eds.), *Archaeozoology of the Near East VIII*. Maison de l'Orient et de la Méditerranée, Lyon, France, pp. 65–78.
- Monchot, H., Aouraghe, H., 2009. Deciphering the taphonomic history of an Upper Paleolithic faunal assemblage from Zouhrah Cave/El Harhoura 1, Morocco. *Quaternaire* 20, 239–253.
- Monchot, H., Mashkour, M., 2010. Hyenas Around The city (Kashan, Iran). *J. Taphonomy* 8, 17–32.
- Monchot, H., Fernandez, P., Gaillard, J.-M., 2012. Paleodemographic analysis of a fossil porcupine (*Hystrix refossa* Gervais, 1852) population from the Upper Pleistocene site of Geula Cave (Mount Carmel, Israel). *J. Archaeol. Sci.* 38, 3027–3038.
- Mondini, N.M., 1995. Artiodactyl prey transport by foxes in Puna rock shelters. *Curr. Anthropol.* 36, 520–524.
- Munro, N.D., Bar-Oz, G., Stutz, A.J., 2009. Aging mountain gazelle (*Gazella gazella*): refining methods of tooth eruption and wear and bone fusion. *J. Archaeol. Sci.* 36, 752–763.
- Nespoulet, R., El Hajraoui, M.A., 2012. Partie 2 : grotte d'El Harhoura 2. Chapitre III. Présentation du site et archéostratigraphie. In: El Hajraoui, M.A., Nespoulet, R., Debénath, A., Dibble, H.L. (Eds.), *La préhistoire de la région de Rabat-Témara. Villes et sites archéologiques du Maroc*, Vol. III. Royaume du Maroc, ministère de la Culture, Institut national des sciences de l'archéologie et du patrimoine, Rabat, pp. 27–30.
- Pales, L., Garcia, M.A., 1981. Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire. II: Tête – rachis, ceintures scapulaires et pelvienne, membres, herbivores, vol. 2. CNRS, Paris.
- Pales, L., Lambert, C., 1971. Atlas ostéologique pour servir à l'identification de mammifères du Quaternaire. I: Les membres, herbivores, vol. 1. CNRS, Paris.
- Pokines, J.T., Kerbis Peterhans, J.C., 2007. Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. *J. Archaeol. Sci.* 34, 1914–1931.
- Prendergast, M.E., Domínguez-Rodrigo, M., 2008. Taphonomic analyses of a hyena den and a natural-death assemblage near lake Eyasi (Tanzania). *J. Archaeol. Sci.* 6, 301–335.
- Prucca, A., (Unpublished DEA Mémoire) 2003. Caractérisation de l'impact des loups sur des ossements d'herbivores (cerfs de Virginie, originaux, bisons) : étude des modifications infligées par des loups captifs et sauvages nord-américains. Université de Provence, Aix-en-Provence, France.
- Robert, I., Vigne, J.-D., 2002a. The bearded vulture (*Gypaetus barbatus*) as an accumulator of archaeological bones. Late glacial assemblages and present-day reference data in Corsica (Western Mediterranean). *J. Archaeol. Sci.* 29, 763–777.
- Robert, I., Vigne, J.-D., 2002b. Bearded vulture *Gypaetus barbatus* contributions to the constitution of two different bone assemblages: modern reference data and an archaeological example in Corsica. *Acta Zool. Cracov.* 45, 319–329.
- Ruerness, E.K., Asmyhr, M.G., Sillero-Zubiri, C., Macdonald, D.W., Bekele, A., Atickem, A., Stenseth, N.C., 2011. The cryptic African wolf: *Canis aureus lupaster* is not a golden jackal and is not endemic to Egypt. *PLoS One* 6, e16385.
- Samper Carro, S.C., Martínez-Moreno, J., 2014. Who let the hyenas out? Taphonomic analysis of the faunal assemblage from GL-1 of Cova del Gegant (Sitges, Spain). *Quatern. Int.* 330, 19–35.
- Sanchez Serra, A., Morales Pérez, J.V., Pérez Ripoll, M., Ribera, I., Gomez, A., 2011. À la recherche d'un référentiel pour l'étude des restes de petits vertébrés provenant d'accumulations de rapaces diurnes rupicoles : les ensembles des grottes-fenêtre de la rivière Tueiljar (Chlva, Valencia, Espagne). In: Laroulandie, V., Mallye, J.-B., Denys, C. (Eds.), *Taphonomie Des Petits Vertébrés : Référentiels et Transferts Aux Fossiles*. Actes de la table ronde du RTP Taphonomie. British Archaeological Reports, International Series, 2269, Oxford, pp. 57–63.
- Sanchez Serra, A., Real Margalef, C., Morales Pérez, J.V., Pérez Ripoll, M., Tormo Cuiat, C., Carrión Marco, Y., Pérez Jordá, G., Ribera Gómez, A.,

- Bolufer Marqués, J., Villaverde Bonilla, V., 2014. Towards the identification of a new taphonomic agent: an analysis of bone accumulations obtained from modern Egyptian vulture (*Neophron percnopterus*) nests. *Quat. Internat.* 330, 136–149.
- Sauqué, V., Rabal-Garcés, R., Sola-Almagro, C., Cuenca-Bescós, G., 2014. Bone Accumulation by Leopards in the Late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain). *PLoS One* 9, e92144.
- Stoetzel, E., (Unpublished Ph.D. Thesis) 2009. *Les microvertébrés du site d'occupation humaine d'El Harhoura 2 (Pléistocène supérieur – Holocène, Maroc) : systématique, évolution ; taphonomie et paléoécologie*. Muséum national d'histoire naturelle, Paris.
- Stoetzel, E., Bougariane, B., Campmas, É., Michel, P., 2012a. Partie 2 : grotte d'El Harhoura 2. Chapitre V. Faunes et paléoenvironnements. In: El Hajraoui, M.A., Nespoulet, R., Debénath, A., Dibble, H.L. (Eds.), *La préhistoire de la région de Rabat-Témara. Villes et sites archéologiques du Maroc, Vol. III. Royaume du Maroc, ministère de la Culture, Institut national des sciences de l'archéologie et du patrimoine*, Rabat, pp. 35–51.
- Stoetzel, E., Campmas, É., Michel, P., Bougariane, B., Ouchaou, B., Amani, F., El Hajraoui, M.A., Nespoulet, R., 2014. Context of modern human occupations in North Africa: contribution of the Témara caves data. *Quatern. Int.* 320, 143–161.
- Stoetzel, E., Denys, C., Bailon, S., El Hajraoui, M.A., Nespoulet, R., 2012b. Taphonomic analysis of amphibian and squamate remains from El Harhoura 2 (Rabat-Témara, Morocco): contributions to palaeoecological and archaeological interpretations. *Int. J. Osteoarchaeol.* 22, 616–635.
- Stoetzel, E., Marion, L., Nespoulet, R., El Hajraoui, M.A., Denys, C., 2011. Taphonomy and palaeoecology of the Late Pleistocene to Middle Holocene small mammal succession of El Harhoura 2 cave (Rabat-Témara, Morocco). *J. Hum. Evol.* 60, 1–33.
- Terrasse, F., 2006. *Le Gypaète barbu, description, mœurs, observation, réintroduction, mythologie*. Delachaux et Niestlé, Paris.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48.
- Walker, R., 1984. *A Guide to Post-Cranial Bones of East African Animals*. Hylochoerus Press, Norwich.
- Wrinn, P.J., submitted. Reanalysis of the Pleistocene Archaeofauna from Mugharet El Aliya, Tangier, Morocco: implications for the Aterian. In: Miller, R. (Ed.). In: *Actes du XIV^e congrès de l'Union internationale des sciences préhistoriques et protohistoriques*, Liège 2001.
- Yom-Tov, Y., Ashkenazi, S., Viner, O., 1995. Cattle predation by the golden jackal *Canis aureus* in the Golan Heights, Israel. *Biol. Conserv.* 73, 19–22.