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Cut from the same cloth? Comparing Neanderthal processing of faunal resources at Amud and Kebara caves (Israel) through cut-marks analyses

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Amud and Kebara caves (northern Israel) are two broadly contemporaneous Middle Paleolithic sites dated to ca. 70–50 Ka BP, both located in the Mediterranean realm of the southern Levant. Neanderthal occupations at these sites are represented by considerable amounts of lithic artifacts, combustion features and abundant faunal material as well as human remains. As similar mammalian taxonomic distributions were observed in these two Neanderthal cave sites, we explore the complexity and diversity of their animal resources processing techniques by comparing cut-marks characteristics and patterns. A total of 344 animal bone fragments bearing cut-marks were selected from specific stratigraphic contexts from both sites, and studied using macroscopic and microscopic techniques (i.e., Focus Variation microscopy) to quantify, characterize, and measure the cut-marks left on the bones. The observations were compared across the stratigraphic units and between the sites. Despite comparable taxonomic distributions, there are notable differences in the density and layout of cut-marks between the two caves. The micro-morphometric characteristics of these marks also highlight intra- and inter-site differences and similarities. This evidence might suggest distinctive butchering strategies between the Neanderthal populations in Amud and Kebara caves despite comparable occupation intensities, similar lithic technologies, and access to similar food resources. Such discrepancies could possibly reflect inter-group cultural differences related to carcass processing preferences, organization of tasks within the group, or socially transmitted traditions.

KEYWORDS

cut-marks, Middle Paleolithic, Southern Levant, animal resources processing, subsistence practices, bone surface modifications

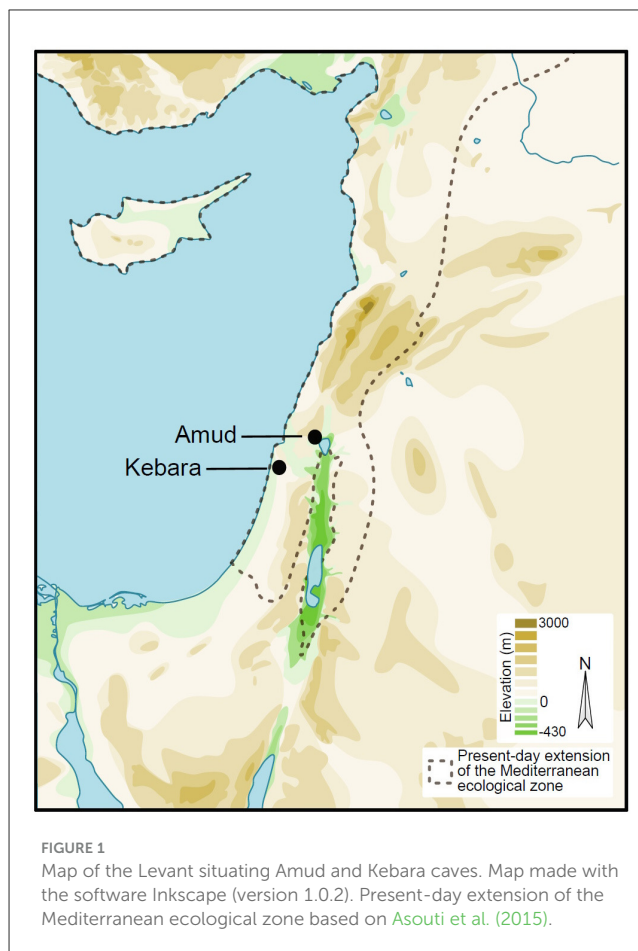
1 Introduction

Neanderthal diet was diverse and flexible, with the composition of faunal assemblages in sites occupied by Neanderthals across Eurasia shown to vary depending on the eco-geographical location of the sites. This suggests that Neanderthals were capable of adapting to different landscapes, environments, and local resources (e.g., [Lorenzen et al., 2011](#); [Blasco et al., 2013, 2016](#); [Morin et al., 2015](#); [Rivals et al., 2022](#); [Romagnoli et al., 2022](#)).

Faunal studies and isotopic analyses demonstrated that the diet of Neanderthal was rich in animal proteins from large and small game, including the consumption of red and yellow bone marrow (Rendu, 2022; Rivals et al., 2022; Vettese et al., 2022 and references therein). Studies of the observed ratios of fallow deer to gazelle in Mediterranean Middle Paleolithic sites have reinforced the already suggested notion of a human bias in favor of gazelles in this region, potentially reflecting a specific human choice of prey (Orbach and Yeshurun, 2021 and references therein). Evidence suggests that the strategies for transport and butchering of animal carcasses adopted by Middle Paleolithic populations were dependent on many factors, including: the distance from residential camps to the hunting locations, the composition and size of the hunting party, the presence of scavenging carnivores near the kill-sites, the number of carcasses to be processed, as well as the size of the prey, and the differential utility of the various body parts (e.g., Binford, 1981; Bunn, 1986; O'Connell et al., 1988, 1990; Metcalfe and Barlow, 1992; Gifford-Gonzalez, 1998, 2018; Monahan, 1998; Faith et al., 2009; Speth, 2012; Schoville and Otárola-Castillo, 2014 and references therein). These factors lead to the hypothesis that large animals were more likely to be butchered at the kill-site, with a selection of body parts with a high yield of meat or fat, while smaller animals were brought whole to the occupation site, a phenomenon commonly referred to as the “schlepp effect” (Gifford-Gonzalez, 1998).

Levantine Late Middle Paleolithic (MP) sites, dated roughly between 75 and 45 Ka BP (corresponding to MIS 4 to MIS 3) are characterized mainly by shared similarities in settlement organization, the overall reduction of exploited territories in comparison to previous periods, as well as similar yet highly variable lithic technological practices (Hovers, 2009; Hovers and Belfer-Cohen, 2013; Abadi et al., 2020). Cave sites usually exhibit evidence for fire use and spatial differentiation of activities. Some of these spatial patterns, for instance the spatial coincidence of knapping activities with hearths, or the presence of specific areas designated for the discard of material and/or deposition of human remains, are common to several sites (Meignen et al., 2006). Reoccurring occupations maintaining consistent locations of these activities over time are also observed, mainly in cave sites (Hovers, 2001; Meignen et al., 2006). These various observations raise the question of knowledge-transmission and specific cultural practices within and between groups. These aspects of MP human behavior, most often discussed with regards to lithic assemblage characteristics, are here investigated from the perspective of animal resources processing. We compare butchery cut-mark patterns from two geographically close and broadly contemporaneous MP sites: Amud Cave and Kebara Cave.

Among the Levantine Middle Paleolithic sites, Amud Cave and Kebara Cave, situated some 70 km apart in Northern Israel (Figure 1), stand out for their richness in lithic artifacts, Neanderthal remains, and faunal remains, which attest to the occupation intensity at the sites. These two sites, located in the Mediterranean ecological zone of the southern Levant, are well-dated and have yielded broadly contemporaneous archeological



layers within the time range of ca. 60–50 Ka BP (Valladas et al., 1987, 1999; Rink et al., 2001; Rebollo et al., 2011). Analyses of dental remains suggested for both sites at the corresponding stratigraphic units that occupations took place mainly between late fall to early spring (Speth and Clark, 2006; Speth and Tchernov, 2007; Rendu and Speth, 2019; Jallon et al., 2025), and that their occupants probably had access to a similar range of food resources. Similarities in the lithic assemblages, the nature of the deposits, and the modalities of occupation of Amud and Kebara caves have been extensively demonstrated by previous studies (Hovers, 1998, 2004, 2007; Albert et al., 2007; Shahack-Gross et al., 2008; Hovers et al., 2011; Meignen and Bar-Yosef, 2019 and references therein; see detailed site descriptions provided in the Section 2 below), making these two cave sites suitable for in-depth comparative analyses. Publications describing the bone assemblages from these two sites reveal that, notwithstanding slight differences, both reflect the Late Middle Paleolithic range of variability, focusing mainly on mountain gazelles, fallow deer, and other middle-to large-sized ungulates. Based on these similarities, we could therefore assume that similar butchering strategies were used at both sites. However, considerable differences were observed in the taphonomic characteristics of both faunal assemblages (Rabinovich and Hovers, 2004; Speth, 2019 and references therein). For instance, at Amud Cave, burnt remains appear to be particularly numerous and the bone material is highly fragmented, which could either

Abbreviations: MP, Middle Paleolithic; BSG, Body-size group; OA, Opening angle; RD, Floor radius; WIS, Width at the surface.

reflect intentional human action (cooking, marrow extraction, or waste management), or be due to post-depositional processes such as trampling and repetitive sets of fireplaces throughout the occupations of the site (Rabinovich and Hovers, 2004; see also Mallol et al., 2013; Pérez et al., 2017; and Gallo et al., 2025 on bone post-depositional fragmentation and burning). Based on previous published work, the two sites also appear to differ in the frequency of butchery marks identified across the assemblages, with only 1%–3% of the remains studied from Amud bearing cut-marks (Rabinovich and Hovers, 2004), against 15% of the identified remains from Kebara (Speth, 2019). These differences in fragmentation and cut-mark frequency could reflect differing human behaviors at the two sites, but they could also be due to differing post-depositional processes, or to differences in zooarcheological analytical strategies and sample sizes. Because of the intense fragmentation, a standard approach to the study of cut-marks is particularly challenging for Amud, since cut-marks are most often observed on undetermined bone fragments. Therefore, in an effort to highlight the potential evidence of site-specific human behaviors and untangle them from taphonomic biases, the present study proposes to complement previous work on the faunal material from Amud and Kebara by focusing our analyses exclusively on the fragments bearing cut-marks and on their macro- and microscopic characteristics. We hypothesize that the absence of differences in cut-mark patterns among the two faunal assemblages may indicate that Neanderthal groups inhabiting the two sites used similar butchering strategies. On the contrary, if different cut-mark patterns can be observed within and between the two faunal assemblages, these differences might reflect differing behaviors. This approach aims to use cut-marks analyses to further explore the complexity and diversity of the animal resources processing techniques adopted at the two sites, despite the challenges inherent to the study of highly fragmented material.

Pioneered by Lartet (1860) and Martin (1909), the study of cut-marks has been widely applied over the last 70 years to explore the traces resulting from various carcass processing strategies, as they can be an important source of evidence to reconstruct ancient butchery practices (e.g., White, 1952; Binford, 1981; Lyman, 1994, 1995; Blumenshine et al., 1994; Domínguez-Rodrigo and Pickering, 2003). Experimental and analytical work led to a better understanding of cut-marks macro- and micro-morphological characteristics, allowing for a better understanding of variations in frequency and morphology of butchery marks resulting from the tools used and the force applied during the butchering process (e.g., Walker, 1978; Potts and Shipman, 1981; Bello and Soligo, 2008; Bello et al., 2009; Bello, 2011; Greenfield et al., 2013; Galán and Domínguez-Rodrigo, 2014; Moretti et al., 2015). The frequency, location, and morphology of cut-marks have been suggested to differ depending on the specific butchery process (i.e., skinning, defleshing, disarticulation, fileting of meat; e.g., Binford, 1981; Vigne, 2006; Soulier and Morin, 2016; Soulier and Costamagno, 2017; Otárola-Castillo et al., 2018; Wallduck and Bello, 2018; Bello and Galway-Witham, 2019; Soulier, 2021). The emergence of new methodologies significantly improved our understanding of ancient butchery activities, providing high-precision microscopic tools for cut-mark identification and analysis (e.g., Bello and Soligo, 2008; Bello et al., 2009, 2013; Bello, 2011;

Maté-González et al., 2017; Yravedra et al., 2017; Bello and Galway-Witham, 2019; Courtenay et al., 2019; Domínguez-Rodrigo, 2019). High-resolution cut-mark analyses therefore have the potential to provide additional insights into ancient human behaviors and how ancient groups exploited the faunal resources available to them. With this approach, we aim to evaluate the potential effects of resource selection (e.g., faunal composition, anatomical parts butchered), differential use of the cave space, and cultural behavior on site-specific butchery practices.

Our study focuses on the following objectives: firstly, we aim to assess whether cut-mark patterns differ diachronically or spatially within Amud cave, to evaluate whether animal carcasses might have been processed differently over the successive occupations represented in the sequence or within different areas of the cave. Secondly, we explore potential differences in cut-mark patterns in relation to prey-size within Kebara Cave, to evaluate whether specific types of prey could have been processed differently. Finally, we aim to investigate whether strategies of faunal resource exploitation appear similar across the two sites or differed in any way, and, if differences are identified, whether the patterns observed in relation to chronology, site area, or prey size could help explain these discrepancies. Furthermore, an effort is maintained throughout the study to assess the impact of potentially different post-depositional processes between the two sites on cut-mark preservation, in order to formulate our interpretations with caution. However, other factors, and in particular the palimpsest nature of the deposits considered here, limit our ability to confidently explore the full complexity of human behaviors associated with these butchery activities. As such, our objectives are approached as a means of generating informed hypotheses rather than definitive behavioral reconstructions.

2 Archeological sites—background

2.1 Amud cave

Amud Cave is located in the Nahal Amud valley, 5 km northwest of the Sea of Galilee on the edge of the Jordan Valley (Figure 1). It is situated at the top of a steep cliff, ca. 30 m above the present valley floor. The site was first excavated between 1961 and 1964 by a Japanese expedition (Suzuki and Takai, 1970) and re-opened later between 1991 and 1994 by a joint Israeli-American team. The sequence of Amud Cave displays two main stratigraphic units: the uppermost unit A, which mostly consists of mixed Holocene sediments, and, underlying it, unit B formed by anthropogenic Middle Paleolithic sediments (Shahack-Gross et al., 2008; Zeigen et al., 2019; see Supplementary Figure 1). Within this latter stratigraphic unit, four sub-units were identified, well dated by Thermoluminescence and ESR-U series (Valladas et al., 1999; Rink et al., 2001) and numbered B1–B4 from surface to bottom (See Supplementary Data 1.1 for further detail). The uppermost sub-units, B1 and B2, are thought to represent a continuous deposition phase and were dated to ca. 55 Ka BP. The deepest and oldest sub-unit, B4, dated to 68.5–70 Ka BP, is separated from B2 by sub-unit B3, a sterile layer resulting from the collapse of

the cave's roof. The sub-units are not all uniformly distributed among the two main excavated areas of the cave. In particular, sub-unit B1 can be found exclusively in Area (A) along the northern wall of the cave, while sub-unit B4 was encountered mainly in the central part of the cave in the two contingent Areas B and C. All the deposits yielded a large amount of lithic and faunal material, in association with ash, hearths, and other combustion features, especially in the central part of the cave. Taken together, these suggest an intense occupation (Shahack-Gross et al., 2008). In Areas B–C, organized lithic production is associated with hearths, whereas Area A is characterized by higher frequencies of cortical flakes, exhausted, and broken tools, as well as bones in different burning states found within the cemented ash. This led Area A to be interpreted as a discard area (Alpers-Afil and Hovers, 2005; Zeigen et al., 2019). Neanderthal remains were retrieved exclusively from Area A (Hovers et al., 1995, 2000).

In a sample of 5,340 specimens published by Rabinovich and Hovers (2004), one of the main observations was the high degree of fragmentation of the remains resulting in the dominance of small shaft fragments and splinters. This fragmentation pattern considerably constrained taxonomic analyses and the number of identifiable bones available for study. Nonetheless, results from this Rabinovich and Hovers' (2004) study identified the mountain gazelle (*Gazella gazella*) as the most-represented species (12%–14% of the assemblage), which is also part of the most abundant ungulate body size group (BSG) represented in the assemblage (BSG-D: body mass of 15–40 kg, as defined in Rabinovich and Hovers, 2004). Depending on the sub-unit, this size group is between 58% and 60% of the assemblage. Gazelle remains were mostly of juveniles and adults (up to 4–5 years-old). While amounting to <5% of the NISP, the next most represented species are the fallow deer (*Dama mesopotamica*), wild goat (*Capra* sp.), and red deer (*Cervus elaphus*). These taxa were all classified as falling in BSG B and C (80–250 kg and 40–80 kg, respectively, ranging between 5% and 10% of the NISP depending on the sub-units). Other, less abundant taxa included wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). Represented by only a few isolated remains are the common fox (*Vulpes vulpes*) and aurochs (*Bos primigenius*). Rabinovich and Hovers (2004) also suggested the possible presence of larger taxa such as rhinoceros (*Stephanorhinus* sp.), whose remains (mostly long bone splinters) might be misidentified as those of the aurochs, with both taxa falling into the same BSG A (>1,000 kg). Gazelle and fallow deer were shown to be represented by both cranial and post-cranial elements, suggesting that carcasses were likely transported complete to the site, in contrast to larger animals (body mass > 1,000 kg) which were only represented by long bone shafts, fragmented limbs and a few teeth (Rabinovich and Hovers, 2004).

The presence and impact of carnivores was observed to be negligible at Amud cave (Rabinovich and Hovers, 2004), with a notable absence of bone surface alterations caused by carnivores (tooth marks, scratching marks and gnawing marks) on the fauna, a rare phenomenon in Middle Paleolithic cave sites. Burnt bones were reported to represent up to 40% of the identified remains, and the burning colors exhibited were interpreted as likely indicating indirect exposure to fire (Rabinovich and Hovers, 2004). Cut-marks

were observed on long bone shafts on 1%–3% of the total assemblage (Rabinovich and Hovers, 2004).

2.2 Kebara cave

Kebara cave is located on the western flank of Mt Carmel (Figure 1), ca. 60 m above current sea level and 2.5 km from the modern seashore. The excavation campaigns at Kebara were initiated by F. Turville-Petre in 1931 and continued by M. Stekelis between 1951 and 1965. Later campaigns were undertaken between 1982 and 1990 (Bar-Yosef and Meignen, 2007; Meignen and Bar-Yosef, 2019, and references therein). Kebara cave displays a long Mousterian sequence, subdivided into 12 units dated from around 60–48 Ka BP (Valladas et al., 1987; See Supplementary Data 1.2 for further details). Large amounts of lithic material, animal remains as well as laminated hearths were uncovered in most of these units. Given the nature of the sediments, the concentration of combustion features and the density of finds, it has been suggested that the cave served mainly as a base-camp during the Mousterian occupation phases (Meignen et al., 2006, 2017).

Two major Middle Paleolithic occupation episodes were identified on the basis of the faunal remains found at Kebara. The first one, referred to as the “midden period,” corresponds to units XII to VIII and is characterized by an abundance of fauna and lithic material, as well as by high concentrations of burning evidence, such as cemented hearths and charred/burnt bones (Speth, 2019; Supplementary Figure 2). The bones are heterogeneously distributed, with a higher concentration along the northern wall of the cave and a very low density over the cave floor in the other zones, which has been shown to be independent from diagenetic processes (Weiner et al., 1993, 2007). The bone fragments concentrated in the northern zone show a higher incidence of burning, lower fragmentation rate and lower economic utility [according to Binford's (1978) criteria], suggesting that they were intentionally deposited there as a discard midden over successive human occupations of the cave (Speth, 2019). The over-representation of exhausted cores and cortical elements in this zone in comparison to the rest of the lithic assemblage reinforces this interpretation (Bar-Yosef et al., 1992). In contrast, the “post-midden period” (Units VII–V) shows a lower density of bone remains, with a significantly decreased contrast between the central and northernmost areas of the cave (Speth and Tchernov, 2007; Speth, 2019).

The faunal assemblage collected during the latest excavation campaigns (1982–1990) has been studied extensively by Speth (2019, and references therein), who assessed over 20,670 specimens across the seven Middle Paleolithic units. He identified the mountain gazelle (*Gazella gazella*) as being invariably the most abundant taxa, representing 45.6% of the total NISP, the fallow deer (*Dama mesopotamica*) representing 24.7% of the NISP, aurochs (*Bos primigenius*) 14.3% of the NISP, and red deer (*Cervus elaphus*) 8% of the NISP. Other represented taxa are bears (*Ursus* sp., 3.9% of the NISP) and Equids (2.1% of the NISP). Finally, wild goat (*Capra* sp.), roe deer (*Capreolus capreolus*), hartebeest (*Alcelaphus bucephalus*), and steppe rhinoceros (*Stephanorhinus hemitoechus*) represent <1% of the total number of remains.

TABLE 1 Total number of specimens assessed (*N*) per stratigraphic unit for Amud and Kebara caves, with number of specimens bearing cut-marks (*n_{cut-marked}*), and the number of cut-marked specimens selected for further macro- and micro-morphometric analyses (*n_{detailed-sample}*).

Site	Stratigraphic unit	<i>N</i> *	<i>n_{cut-marked}</i>	<i>n_{detailed-sample}</i>
Amud	B1	2,618	10	10
	B2	7,514	107	19
	B4	784	130	14
	Unclear stratigraphic context	569	2	0
	Total Amud	11,485	249	43
Kebara	Unit IX (Total)	1,226	95	34

*Number of specimens assessed, based on the data collected for this study, as well as on published and unpublished data from previous work by R. Rabinovich and J. Speth (Rabinovich and Hovers, 2004; Speth, 2019). Note that for specimens from Amud, *N* refers to the total number of remains (NR), while for those from Kebara, it refers to the number of identified specimens (NISP).

The taphonomic analyses conducted on this assemblage showed no marked difference in the representation of cranial vs. postcranial elements. Evidence of carnivore damage was observed on 9.09% of the NISP in unit IX (Speth, 2019: Table 3.9), and burnt bones were found to represent 9% of the NISP, with burning traces observed more frequently on smaller taxa. The incidence of these burning traces was higher on limbs than on other skeletal elements, and more frequent on diaphysis fragments than on epiphyses, which was interpreted as indication that the burning events were likely related to cooking processes. Cut-marked bones were reported to represent up to 15% of the NISP (excluding dental elements; Speth, 2019).

3 Materials and methods

3.1 Identification and taphonomic assessment of cut-marked specimens

Both Amud and Kebara faunal collections are stored and curated at the National Natural History Collections of the Hebrew University of Jerusalem. A comprehensive faunal study of the main stratigraphic units of Amud is currently in progress by one of the authors (A.J.). Data from previous zooarcheological studies (Rabinovich and Hovers, 2004; Speth, 2019) as well as unpublished databases, were combined to these newly collected data to form our faunal assemblage (*N*, Table 1). Within the assemblage, the specimens recorded as bearing cut-marks (*n_{cut-marked}* in Table 1) were identified and re-examined to confirm the presence of cut-marks, following published work on the differentiation of butchery marks from taphonomic damage (e.g., Shipman and Rose, 1983; Behrensmeyer et al., 1986; Andrews, 1995; Blasco et al., 2008; Domínguez-Rodrigo et al., 2009; Fernández-Jalvo and Andrews, 2016). For Amud, the studied specimens derive from stratigraphic sub-units B4, B2, and B1, dated respectively to ca. 70 Ka BP and to ca. 56 Ka BP (Valladas et al., 1999; Rink et al., 2001). Across

the faunal remains assessed to date within these stratigraphic sub-units (*N* = 11,485), 249 bones were identified as bearing cut-marks, accounting for 2.2% of this assemblage (Table 1). For Kebara, we selected specimens from unit IX (*N* = 1,226), which is dated to 58.4 ± 0.4 Ka BP (Valladas et al., 1987) and is therefore broadly contemporaneous with the younger sub-units from Amud Cave. Cut-marks were identified on 95 bone fragments from this unit, representing 8.4% of the identified specimens (Table 1).

The specimens bearing cut-marks (*n_{cut-marked}*, Table 1) were first examined and described to record the following parameters for each cut-marked specimen:

Identifications and prey size classification. Osteological and taxonomic identification was conducted for each specimen using previous identifications provided in the collections databases as well as the comparative osteological and archaeozoological collections housed at the National Natural History Collections at the Hebrew University of Jerusalem. To facilitate comparisons between sites and stratigraphic units and evaluate the influence of prey size on the butchery patterns observed, the specimens were grouped using the following body size classification:

- Prey size 1: Small ungulates, 15–45 kg (e.g., gazelle, roe deer; BSG D in Rabinovich and Hovers, 2004).
- Prey size 2: Medium-sized ungulates, 45–200 kg (e.g., red deer, fallow deer, wild goat, boar; BSG B–C in Rabinovich and Hovers, 2004).
- Prey size 3: Large ungulates, 500–1,200 kg (e.g., aurochs, equids; BSG A in Rabinovich and Hovers, 2004)

General taphonomic assessment. The degree of preservation and alteration of the cut-marked specimens was evaluated using the following parameters:

- Exposure (direct or indirect) to fire, assessed on the basis of surface coloring. Specimens partially or fully carbonized and calcined (corresponding to categories 1–6 of Stiner et al., 1995) were categorized as “burnt,” while cream-colored fresh-looking specimens (category 0 from Stiner et al., 1995) were categorized as “unburnt.” Bone fragments presenting a solid color in shades of brown or orange, which do not show clear signs of charring but whose color is likely the result of indirect exposure to high temperatures, were classified as “likely burnt.”
- Element’s completeness: classification of each specimen into four categories based on the percentage of preserved bone (Rabinovich et al., 2012): less than half the element preserved (<50%); around half of the element preserved (~50%), more than half of the element preserved (>50%), complete or nearly complete element (~100%).
- Evidence of anthropogenic bone fracture: percussion damage (e.g., adhesive flakes, notches, percussion grooves, scraping marks and striations as referred to by Vettese et al., 2020; see also references therein), were identified and recorded when present.
- Presence/absence of other taphonomic alterations that may interfere with the reading of cut-marks (water dissolution,

weathering, root-marks, gnawing etc.) were also recorded using taphonomy manuals and atlases (Fernández-Jalvo et al., 2010; Pokines et al., 2021; Fernández-Jalvo and Andrews, 2016) as well as reference material from the National Natural History Collections of the Hebrew University of Jerusalem.

3.2 Macroscopic and micro-morphometric cut-marks analyses

A sub-sample of specimens bearing cut-marks was further selected for detailed macroscopic assessment and micro-morphometric analyses (hereafter “detailed sample,” Table 1). For the Amud material, 43 specimens were selected in such a way that all of the studied sub-units and spatial areas of the cave would be equally represented, while excluding specimens from disturbed contexts or uncertain stratigraphic attribution (Supplementary Figures 1B, C). For Kebara, 34 specimens were selected for detailed analyses and originate from three squares situated in proximity to the northern cave wall (F19, G19, H19, and I13; Supplementary Figure 2B). Specimens in this sub-sample were measured and analyzed using macro- and microscopic techniques to quantify, characterize, and measure the cut-marks. They represent, respectively, 17.3% and 35.8% of the specimens identified as bearing cut-marks from Amud and Kebara, and account, respectively, for 0.4% and 3% of the total assemblages.

Macroscopic analyses. The selected specimens were first cleaned by applying acetone with a soft brush to remove the sediment embedded in the incisions or overlaying glue residues masking the marks. With the aid of a binocular lens (magnification: 10x–30x), the bone surfaces were assessed, drawn to record the location and morphology of the cut-marks, and measured with a caliper. The following parameters were recorded or calculated:

- Surface area (cm²): Quantification of the cortical surface area of each specimen. The shape of each specimen was simplified as a combination of smaller regular geometric figures (rectangles, isosceles or right-angled triangles, semicircles, etc.) whose areas were calculated separately and added together (Supplementary Figure 3A).
- Number of cut-marks per fragment (n_{cut} , Table 1).
- Cut-marks density per fragment: number of cut-marks per specimen relative to its surface area.
- Linearity of each incision in plan-view: linear (i.e., “straight”) or non-linear (curved, sinuous or drawing a broken-line; Supplementary Figure 3B). The number of linear incisions identified was then divided by the total number of incisions observed on the specimen to calculate the linearity frequency for each specimen (ranging from 0—no incisions are linear, to 1—all incisions are linear).
- Layout of the cut-marks: qualitative description of how the cut-marks were organized (parallel to or overlapping other marks, close or far from each other, etc.), quantitative evaluation of the number of incisions crossing at least

one other incision and the number of intersection points formed.

- Quantitative assessment of complete cut-marks vs. cut-marks interrupted by the breakage of the bone edge (note: cut-marks partially covered by concretions or altered were considered uninformative and not included in this assessment).

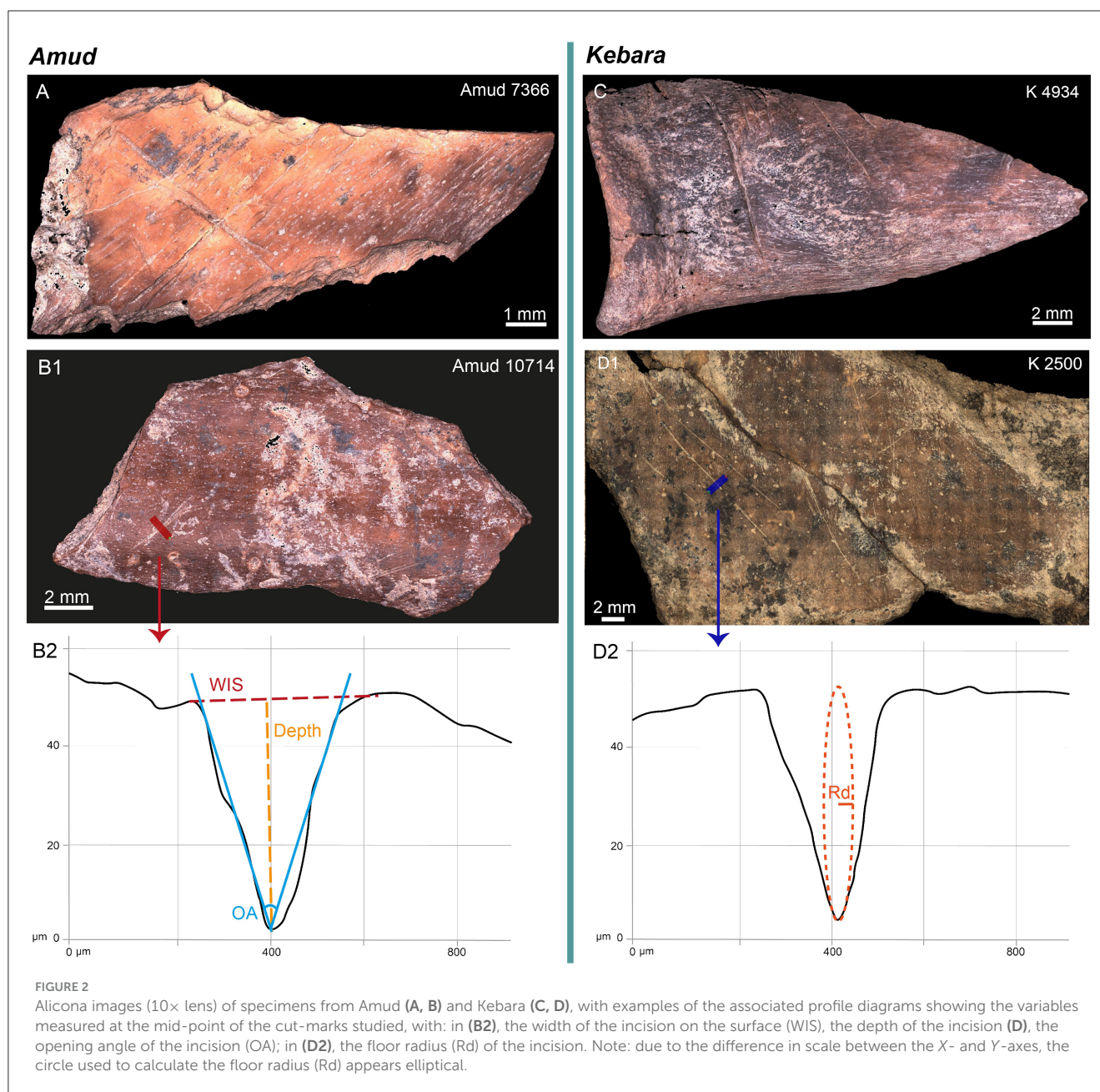
Micro-morphometric analyses. The selected specimens were studied using two Focus Variation microscopes, the Alicona InfiniteFocus G5+ (AIF) and the Portable Alicona RL (ARL) optical surface measurement systems (Optimax Ltd, Market Harborough, UK). These instruments are housed at the Imaging and Analysis Centre, Science Innovation Platforms, at the Natural History Museum (London, UK). The portable ARL system was transported and used directly at the National Natural History Collections of the Hebrew University of Jerusalem for the first phase of data collection. These optical systems allow for the non-destructive and non-invasive three-dimensional (3D) analysis of microscopic surface features. They create a series of individual image planes and overlapping focus levels to produce a virtual reproduction of the object in 3D. The recorded x , y , and z coordinates of each reconstructed pixel can be then used to conduct linear measurements of the surface features using the AIF software IF-MeasureSuite (Bello and Soligo, 2008; Bello and Galway-Witham, 2019). For both microscopes, a 10x lens was used to capture the finer detail of the cut-marks (AIF: working distance = 17.5 mm; numerical aperture = 0.3; vertical resolution = 100 nm; ARL: working distance = 17.5 mm; numerical aperture = 0.3; vertical resolution = 150 nm). Both systems offer the same level of accuracy and precision [finest lateral topographic resolution, AIF = 1.76 μm ; ARL = 2 μm ; Minimum measurable profile roughness (Ra), AIF = 0.5 μm , ARL = 0.55 μm], and are therefore expected to yield comparable outputs.

Linear and profile variables of the cut-marks were recorded following the methodology proposed by Bello and Soligo (2008), Bello et al. (2009), and Bello et al. (2013), by extracting a 2D profile from the mid-point of each incision (Figure 2). The following variables were considered:

- Length: Maximum length of the incision.
- Width of the incision at the surface (WIS): maximal length between the two points where each slope forming the incision intersects with the unaffected bone surface.
- Depth of the incision (D): maximum depth of the incision, measured by drawing a line perpendicular to the WIS from the lowest point of the cut-mark profile.
- Opening angle (OA): angle at the convergence point between two lines fitted onto the left and right slopes of the incision.
- Floor radius (Rd): radius of a circle fitted to the floor of the incision, where the profiles of the left and right slopes start to converge.

3.3 Statistical analyses

The data were analyzed across the sites and stratigraphic units to evaluate whether specific cut-marks patterns could be observed. Results were compared between the Amud and Kebara samples, as



well as between and within the Amud sub-units to assess intra-site spatial and chronological variability for this site. The spatial analysis of cut-marked specimens from Amud focused on sub-units B1–B2, to compare specimens from Area A to specimens from Areas B–C (Supplementary Figure 1).

Descriptive statistics and plots were computed using R Studio (version 2022.12.0+253, Posit Team, 2022; “ggplot” Wickham, 2006), and statistical tests were carried out using Past (version 4.05; Hammer et al., 2001) or R Studio. Statistical comparisons between groups were only carried out for sample sizes ≥ 5 . For quantitative variables, the data was analyzed using non-parametric tests as the data was skewed and did not follow a normal distribution: Mann-Whitney-Wilcoxon or Mann-Whitney U tests (α 0.05) were used for pairwise comparisons, and Kruskal-Wallis tests followed by Dunn tests (where relevant) were used for comparisons between

three groups or more. Qualitative data was analyzed using Chi square tests for independence (α 0.05) to determine whether any observed difference between samples were statistically significant. Chi square *post-hoc* tests include residuals analyses and, when significant differences were revealed for a contingency table of a matrix larger than 2×2 , Fisher’s exact test was applied to the collapsed contingency tables following DeViva (2014; see Sharpe, 2015). In addition, the micro-morphometric measurements were further tested across samples through a series of Principal Component Analyses (PCA) performed in R studio (“factoextra”; Kassambara and Mundt, 2017) on a covariance matrix, using all five variables (length, WIS, depth, OA, and Rd) as a way to assess the overall micro-morphometric variation of cut-marks across samples when analyzed as three-dimensional features. To prepare the data for PCA, the variable OA was converted from circular to linear

data (OA_{linear}) following Courtenay et al. (2021) and Valtierra et al. (2024), to ensure all the variables considered were linear.

4 Results

4.1 Identifications and taphonomic assessment of cut-marked specimens

Species and prey size representation. While the same taxa were exploited at both sites, taxon representation is highly heterogeneous between the two sites (Figure 3A). This is reflected in our cut-marked samples. The Amud sample comprises almost exclusively taxa falling into prey size 1 (73.9%), and fewer from prey size 2 (7.2%) and includes a few unidentified specimens (not included in prey size comparisons). The sample from Kebara is mostly represented by specimens from prey size 1 and 2 (40% and 42.1%, respectively), and comprises also large ungulates (i.e., prey size 3, 17.9%).

Body parts representation. Long bone shafts are the most represented anatomical elements across Amud sub-units, where they constitute 60%–91.6% of the cut-marked specimen. They represent only 35.8% of the Kebara sample, where the distribution of body parts in the Kebara sample is relatively balanced and all body parts are well-represented (Figure 3B).

These proportions are roughly equivalent in the detailed samples (Supplementary Figure 4D). Long bone shafts represent up to 78.6% of the selected specimens from Amud and 29.4% of the Kebara detailed sample. Prey size 1 is the most prominent category represented in the detailed samples of Amud, and represents 50% of the Kebara detailed sample. However, it is worth mentioning that only three specimens of aurochs and equid are present in the detailed sample from Kebara (Supplementary Figure 4).

Exposure to fire. The majority of Amud cut-marked specimens was identified as likely burnt ($n = 172$, 68.5%). Another 52 were recognized as “burnt” (20.7%), and 27 as unburnt (10.7%). The majority of Kebara specimens was classified as unburnt ($n = 90$, 89.1%). An additional seven specimens were identified as heavily burnt (6.9%), and four (<0.1%) as likely burnt (Table 2 and Figure 3C). The differences between the two sites are statistically significant, as well as intra-site differences within Amud, with sub-layer B1 showing less burnt specimens than the other sub-units ($\chi^2 = 202.42$, $df = 2$, $p < 0.001$; Supplementary Table 1).

Element completeness. Out of the 249 Amud cut-marked specimens, the greater majority (97.8%) represent less than half of a complete skeletal element; one was complete (0.4%), three were preserved to more than 50% (1.2%), and four were preserving half of the element (1.6%). Out of the 95 cut-marked specimens from Kebara, 16 items were complete (15.8%), the rest of the specimens (84.2%) preserved less than half of the skeletal element (Table 2 and Figure 3D). χ^2 tests confirmed these inter-sites differences were significant ($\chi^2 = 19.682$, $df = 2$, $p < 0.001$), and reveal further differences within the Amud cut-marked assemblage, with B1 presenting more complete elements than the other sub-units ($\chi^2 = 9.615$, $df = 2$, $p = 0.008$; Supplementary Table 1).

Taphonomic bone surface alterations. Carnivore impact on the faunal remains is practically non-existent at both sites. Other major fossilization alterations, such as striations due to trampling, root-marks, water dissolution and drying cracks are also minimal

and, when present, did not affect the reading of the butchery marks (Table 3).

Anthropogenic bone surface modifications. Considering all sub-units together, specimens bearing cut-marks represent 2.2% of the assessed assemblage for Amud, while they account for 7.8% of the Kebara layer IX assemblage. These numbers are in line with those provided in previous publications of both assemblages, i.e., 1%–3% of the remains studied from Amud depending on the sub-units (Rabinovich and Hovers, 2004), and 15% of the identified remains from Kebara (Speth, 2019). For Amud, we recognized 10 cut-marked bones bearing impact notches. In Kebara, two cut-marked specimens displayed impact notches. Both specimens from Kebara and four from Amud were included in our detailed sample.

The difference observed in the frequencies of burnt and fragmented specimens in both samples, as well as the scarcity of other anthropogenic and non-anthropogenic bone surface modifications, are mirrored in the detailed samples of both sites (Supplementary Table 2 and Supplementary Figure 4).

4.2 Amud cave: spatial and chronological cut-mark variability

4.2.1 Macroscopic analyses

Surface area. At Amud, differences in the dimensions of surface areas were observed between sub-units, with specimens from sub-unit B1 being bigger (median = 5.8 cm², IQR = 3.88) compared to specimens in sub-units B2 (median = 1.65 cm², IQR = 1.45) and B4 (median = 2 cm², IQR = 2.17). The difference is statistically significant [$H_{(2)} = 13.86$, $p < 0.001$; Dunn’s *post-hoc* test $p_{B1/B2} < 0.001$, $p_{B1/B4} < 0.001$, $p_{B2/B4} = 0.468$].

Number of cut-marks and cut-marks density. While the number of cut-marks per specimen is similar across the different sub-units and areas of the site (Tables 4A, C), there are differences in cut-mark density between the two main occupations areas, with a higher density of incisions per fragment on specimens from Areas B–C (median = 0.082; IQR = 0.094) compared to specimens from Area A (median = 0.015; IQR = 0.015; $U = 46$, $p = 0.026$; Figures 4A, B).

Linearity of the incisions. Within the Amud cave sequence, sub-unit B4 significantly differs from B1 and B2, featuring fewer linear incisions ($\chi^2 = 17.787$, $df = 2$, F-exact_{B1+B2/B4} $p < 0.001$, F-exact_{B1/B2} $p = 0.128$; Table 4A and Supplementary Table 3E). No difference was found across the areas of the site (Table 4C and Supplementary Table 3D).

4.2.2 Micro-morphometric analyses

Length of the cut-marks. There is no significant difference in incision length between the Amud sub-units [$H_{(2)} = 1.1629$, $p = 0.559$; Table 5A and Supplementary Table 4E], nor between Amud’s peripheral area (Area A) and the central part of the cave (Areas B and C; $W = 574$, $p = 0.313$; Table 5C and Supplementary Table 4D).

Width of the incisions at the surface (WIS). Significant differences are found between the Amud sub-units [$H_{(2)} = 15.558$, $p < 0.001$], with specimens from B1 presenting wider cut-marks than specimens from B2 and B4 (Table 5A and

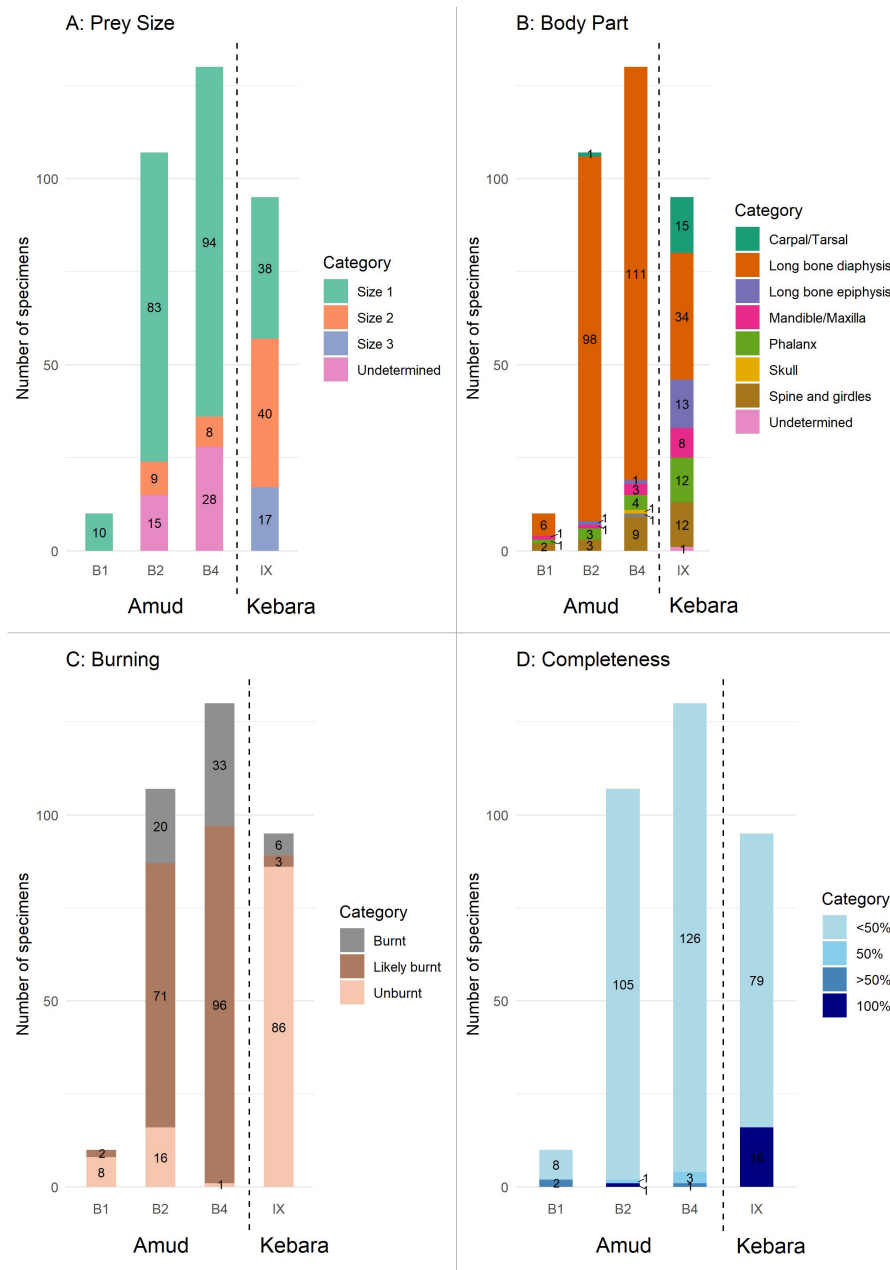


FIGURE 3

Cut-marked assemblage composition and main evidence of anthropic modifications for each site and relevant sub-units. (A) Prey size representation, (B) body part representation, (C) proportion of specimens with identified evidence of exposure to fire/heat source, and (D) completeness of the specimens.

Supplementary Table 4E). WIS values differ between the two areas, with significantly wider cut-marks found in Area A (median = 208.72 μm , IQR = 168.92) compared to Areas B–C (median = 151.24 μm , IQR = 147.48; $W = 1,234$, $p = 0.022$; Table 5C and Supplementary Table 4D).

Depth of the incisions. Depth values are relatively homogenous across sub-units within the Amud sample [$H_{(2)} = 4.8372$, $p = 0.089$; Table 4B and Supplementary Table 4E]. No significant difference was found for the depth of the incisions when comparing cut-marks from Area A to Areas B–C ($W = 1,009$, $p = 0.684$; Table 5C and Supplementary Table 4D).

Opening angle (OA). There are significant differences in OA values across the Amud sub-units [$H_{(2)} = 7.9675$, $p = 0.019$], with B2 presenting significantly lower OA values compared to B1 and B4 (Table 4A and Supplementary Table 4E). Incisions present significantly higher OA values in Area A (median = 134.94°, IQR = 35.66) than in Areas B–C (median = 119°, IQR = 32.98; $W = 1,198$, $p = 0.047$; Table 5C and Supplementary Table 4D).

Floor radius (Rd). Rd was found to differ significantly across the Amud sub-units [$H_{(2)} = 44.858$, $p < 0.001$], with higher values in B1 (median = 53.77 μm ; IQR = 53.06) compared to B2 (median = 26.1 μm ; IQR = 26.23) and B4 (median = 32.81 μm ; IQR = 33.78;

TABLE 2 General taphonomic assessment of the cut-marked samples, for each site/sub-unit.

Site	Unit/sub-unit	Sample size ($n_{cut-marked}$)	Exposure to fire/heat source			State of completeness			
			Burnt	Likely burnt	Unburnt	<50%	50%	>50%	100%
Amud	B1	10	0	2 (20%)	8 (80%)	8 (80%)	0	2 (20%)	0
	B2	107	20 (18.7%)	71 (66.3%)	16 (15%)	105 (98.1%)	1 (0.95%)	0	1 (0.95%)
	B4	130	33 (25.4%)	96 (73.8%)	1 (0.8%)	126 (96.9%)	3 (2.3%)	1 (0.8%)	0
	Unclear	2	0	1 (50%)	1 (50%)	2 (100%)	0	0	0
	All sub-units	249	53 (21.3%)	170 (68.3%)	26 (10.4%)	241 (96.8%)	4 (1.6%)	3 (1.2%)	1 (0.4%)
Kebara	Layer IX	95	6 (6.3%)	3 (3.2%)	86 (90.5%)	79 (83.2%)	0	0	16 (16.8%)

Evidence of exposure to fire/heat source is presented as the total number of specimens identified as “burnt” or “unburnt,” or classified as “likely burnt.” The state of completeness is presented using the following categories: <50% (less than half of the skeletal element is preserved); 50% (about half of the element is preserved), >50% (more than half of the element is preserved), 100% (the element is complete or nearly complete). The percentages provided in parentheses reflect the proportion of specimens displaying the relevant modification, relative to the sample ($n_{cut-marked}$).

TABLE 3 Number of cut-marked specimen bearing additional anthropogenic and non-anthropogenic bone surfaces alterations, per site and stratigraphic unit.

Site	Stratigraphic unit	Sample size ($n_{cut-marked}$)	P	R	E	D	W	G	Total
Amud	B1	10	1 (10%)	0	3 (30%)	0	3 (30%)	0	7 (70%)
	B2	107	1 (0.9%)	5 (4.7%)	11 (10.3%)	2 (1.9%)	5 (4.7%)	0	24 (22.4%)
	B4	130	8 (6.2)	5 (3.8%)	11 (8.5%)	1 (0.8)	7 (5.4%)	0	32 (24.6)
	Unclear	2	0	1 (50%)	0	0	0	0	1 (50%)
	Total Amud	249	10 (4%)	11 (4.4%)	25 (10%)	3 (1.2%)	15 (6%)	0	64 (25.7%)
Kebara	Unit IX (Total)	95	8 (8.4%)	0	6 (6.3%)	0	4 (4.2%)	1 (1%)	19 (20%)

P, percussion notches; R, root marks; E, exfoliated cortical surface; D, water dissolution patches; W, weathering (causing longitudinal cracks and scaling of the cortical surface); and G, Gnawing marks. The percentages provided in parentheses reflect the proportion of specimens displaying the relevant modification, relative to the sample ($n_{cut-marked}$).

Table 5A). Incisions differ significantly in their Rd values between the two main occupation areas ($W = 1,478$, $p < 0.001$), with significantly larger floor radii for specimens from Area A (median = 70.58 μm , IQR = 65.15) compared to Areas B–C (median = 26.19 μm , IQR = 27.88; Table 5C and Supplementary Table 4D).

Principal component analysis. The first two components (PC1 and PC2) explain 37.9% and 32.2% of the variance, respectively (Supplementary Table 5B). PC1 is mostly influenced by OA and Depth, which contribute positively to this component. PC2 is mostly influenced by WIS and Rd, which contribute negatively to this component. When comparing the variability of the incisions’ overall form, cut-marks from B1 display clearly a wider range of values compared to all the other samples (Figures 5B, C).

4.3 Amud and Kebara: comparisons of the butchering marks between sites (detailed sample)

4.3.1 Macroscopic analyses

Surface area. The 43 specimens of Amud selected for further analysis are all fragmented, whereas seven out of the 34 specimens

from Kebara are complete (20.6%). The median fragment surface area is significantly smaller in Amud (median = 2.49 cm^2 , IQR = 2.92) compared to Kebara (median = 17.78 cm^2 , IQR = 20.9; $U = 118$; $p < 0.001$; Figure 4C and Table 4). The surface areas are more variable in Kebara, with fragments ranging from 1.3 to 97.7 cm^2 , while fragment surface areas at Amud are within a much narrower size range (between 0.3 and 9.4 cm^2). As expected, at Kebara, the specimen surface area differs significantly according to prey size [$H_{(2)} = 6.142$, $p < 0.001$], with smaller ungulates producing smaller bone fragments.

To test whether the difference in surface area between the two sites might be due to differences in the prey sizes represented in each sample (i.e., Amud dominated by small ungulates), we compared the surface area of fragments from Amud and Kebara only for specimens attributed to prey size 1. Specimens from Kebara are significantly larger ($U = 95$, $p < 0.001$) and more variable in size compared to those from Amud (Amud: $n = 38$, median = 2.53 cm^2 , IQR = 2.79; Kebara: $n = 17$, median = 7.40 cm^2 , IQR = 18.44).

Number of cut-marks and cut-mark density. Altogether, 936 cut-marks were observed on the 43 specimens studied from Amud, and 736 on the 34 specimens studied from Kebara, which corresponds to an average of 21.3 and 21.4 incisions per specimen, respectively, with comparable variances (Table 4). When scaling the number

TABLE 4 Assessment of the anthropogenic modifications in the detailed-samples for (A) each site/sub-unit, (B) each prey size category, and (C) for each occupation Area at Amud Cave (sub-units B1–B2).

Site	Unit/sub-unit	Sample size (<i>n</i>)	Surface area (mm ²)		<i>n</i> _{cuts}		Cut-marks density		Linearity freq.	
			Median	IQR	Median	IQR	Median	IQR	Median	IQR
(A)										
Amud	B1	10	580.12	387.74	14.50	13	0.023	0.025	0.80	0.27
	B2	19	164.58	145.46	13	14.50	0.082	0.100	0.70	0.44
	B4	14	199.90	216.75	8	41.50	0.051	0.100	0.65	0.48
	<i>All sub-units</i>	43	248.69	291.93	13	18	0.046	0.094	0.70	0.48
Kebara	Layer IX	34	1778.41	2090.45	14	15.75	0.009	0.014	0.90	0.29
(B)										
Amud	Size 1	38	252.87	278.68	13	18.50	0.052	0.094	0.69	0.46
	Size 2	2	498.67	66.30	19	8	0.037	0.011	0.65	0.20
Kebara	Size 1	17	740.30	1844.50	15	15	0.010	0.017	1	0.08
	Size 2	14	2618.46	2242.76	10	14.50	0.008	0.006	0.79	0.17
	Size 3	3	2609.70	1898.88	15	47.50	0.014	0.009	0.67	0.03
(C)										
Amud (B1–B2)	A	4	633.14	394.97	11	16.5	0.015	0.015	0.81	0.08
	B–C	9	164.58	145.20	11	14	0.082	0.094	0.82	0.55

Median values and interquartile ranges (IQR) are reported for each sample when assessing surface area (in mm²), number of cut-marks per fragment (" n_{cuts} "), number of cut-marks per fragment relative to the surface area ("cut-marks density"), and number of linear incisions per fragment relative to curved/sinuuous incisions ("linearity freq.").

of incisions to fragment size (n incisions/cm²), we find that the density of incisions is significantly higher at Amud (mean = 10.34, median = 4.55) compared to Kebara (mean = 1.58, median = 0.89; $U = 211$, $p < 0.001$). Fragments attributed to prey size 1 display a much higher variability in cut-mark density compared to any other prey size categories in either site (Supplementary Table 3 and Figure 4A). When considering prey size 1 only, cut-mark density is higher at Amud (values are, mean = 9.3; median = 5.8) compared to Kebara (are, mean = 2.1, median = 0.9).

Linearity of incisions. In both detailed samples, the majority of the cut-marks are linear. However, specimens from Amud present significantly more curved or sinuous incisions compared to specimens from Kebara ($\chi^2 = 51.777$, $df = 1$, $p < 0.001$; Table 4). The Amud sample also shows a greater variability per specimen, with more specimens presenting both linear and curved incisions on a same fragment compared to Kebara. Differences between prey size categories also appear for both sites: in Kebara, small ungulates (prey size 1) display more linear cut-marks than other prey size categories, while large ungulates (prey size 3) feature more sinuous incisions compared to the other two prey size classes ($\chi^2 = 12.733$, $df = 2$, F-exact_{1+2/3} $p = 0.012$, F-exact_{1/2} $p = 0.011$). For Amud, the trend is reversed, with small ungulates displaying less linear cut-marks than medium-sized ungulates ($\chi^2 = 13.437$, $df = 1$, $p < 0.001$; note, however, the disparity of sample sizes between the two groups).

Layout and completeness of cut-marks. We counted 191 incisions crossing at least one other mark on the bones from the Amud sample (37.3% of the total number of cut-marks), and 112 on those from the Kebara sample (15.2%). The cut-marks on

specimens in the Amud sample tend to cross other incisions more often than those in the Kebara sample: we counted a minimum of 308 intersection points between incisions on the specimens from Amud, compared to a minimum of 127 intersection points from Kebara (e.g., Figure 6). The completeness of the cut-marks was evaluated for 671 incisions in the Amud sample, and 536 incisions (in the Kebara sample). Similar proportions of complete cut-marks (i.e., uninterrupted by bone fracture) were found at both sites: 465 cut-marks (86.8%) were complete at Kebara, while 559 cut-marks (83.3%) were complete at Amud.

4.3.2 Micro-morphometric analyses

Length of the cut-marks. Cut-mark length differs significantly between the two sites (Amud median = 1.88 mm, $n = 288$; Kebara median = 3.38 mm, $n = 232$; Table 5A and Figure 6). Incisions from Kebara present a higher range of lengths (IQR = 3.7) compared to Amud (IQR = 1.36; $W = 12,219$, $p = 1.341\text{e-}15$). When considering prey size, no significant difference in incision length can be observed between the various prey size categories within the Amud sample ($W = 1765.5$, $p = 0.476$). More variation in lengths can be observed within the Kebara sample [$H_{(2)} = 14.74$, $p = 0.0006$], with longer incisions observed for prey size 2 (median = 3.77 mm, IQR = 4.04) and prey size 3 (median = 4.71 mm, IQR = 5.2; Table 5B). Cut-marks on specimens from prey size 1 are significantly longer at Kebara compared to Amud ($W = 5,958$, $p = 0.001$; Supplementary Table 4B).

Width of the incision at the surface (WIS). No significant difference was found between the two sites (Amud median =

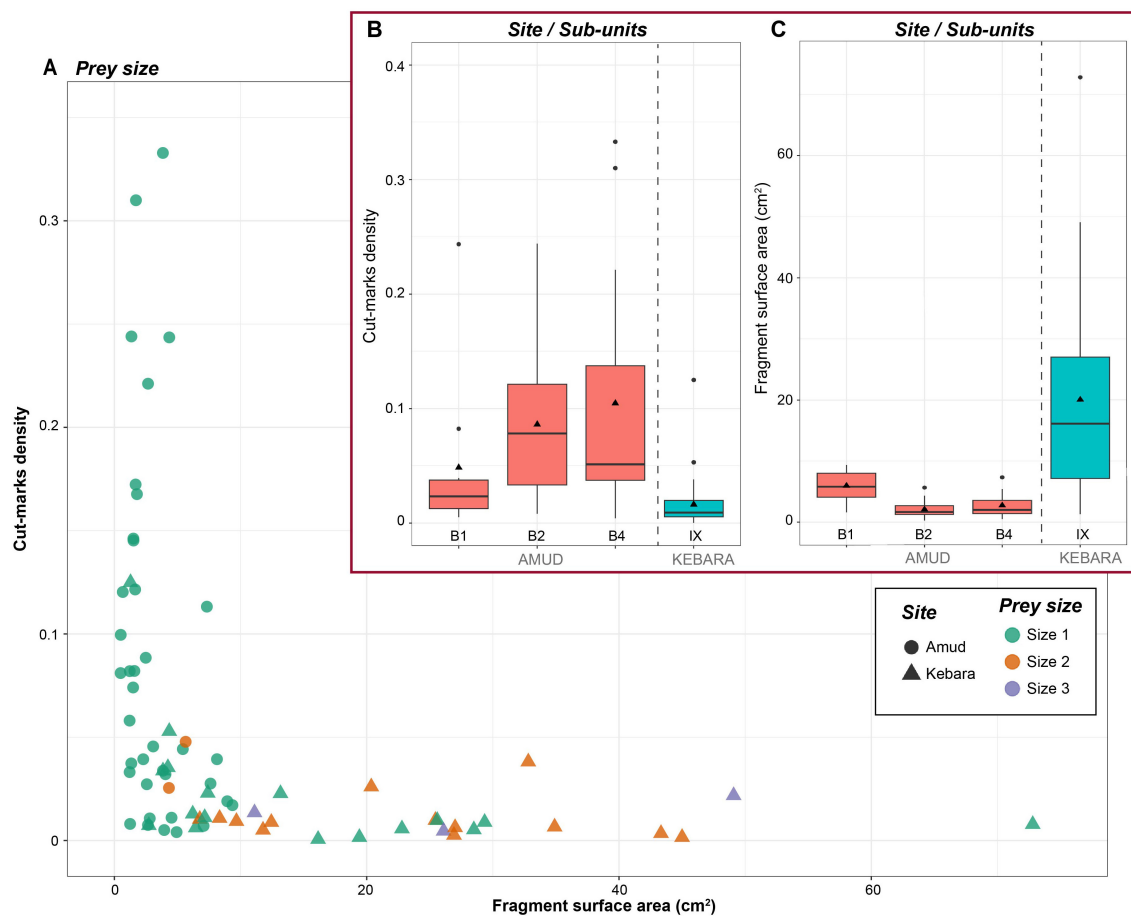


FIGURE 4
Cut-marks density for the Amud and Kebara samples, **(A)** per prey size (Size 1: small ungulates; Size 2: medium-sized ungulates; Size 3: large ungulates), and **(B)** per site and sub-units, and **(C)** Fragment surface area (cm²) per site and sub-units; (boxplots, median and interquartile range; triangles, mean; dots, outliers).

170.04 μm ; IQR = 149.35; Kebara median = 182.33 μm , IQR = 147.3; $W = 29,975$, $p = 0.170$; Table 5A and Figure 6). WIS values are relatively homogeneous across prey size categories within the Amud sample ($W = 1,994$, $p = 0.489$). At Kebara these values are more variable [$H_{(2)} = 11.11$, $p = 0.004$], with significantly wider incisions observed on prey size 3 (i.e., large-sized; median = 294.36 μm , IQR = 166.35) compared to size 2 (median = 166.72 μm , IQR = 114.04) and size 1 (median = 182.01 μm , IQR = 143.23; Table 5B). When focusing on prey size 1, no significant difference in width was found between the Amud and Kebara samples ($W = 11,437$, $p = 0.887$; Supplementary Table 4B).

Depth of the incisions. Cut-marks on specimens from Kebara display a wider range of depths (median = 31.17 μm ; IQR = 54.96) than those from Amud (median = 26.16 μm ; IQR = 34.68), although this difference is not statistically significant ($W = 30,612$, $p = 0.101$; Table 5A and Figure 6). The depth of the incisions differs significantly depending on prey size within the Kebara sample [Kebara: $H_{(2)} = 7.0547$, $p = 0.029$; Amud: $W = 1,773$, $p = 0.089$; Table 4B]: in Kebara, prey size class 3 specimens bear deeper cut-marks (median = 45.33 μm , IQR = 34.67) than size class 2 specimens (median = 26.2 μm , IQR = 50.52). When focusing on prey size 1, no significant difference in depth was

found between Amud and Kebara ($W = 10,931$, $p = 0.164$; Supplementary Table 4B).

Opening angle (OA). The opening angle of the incisions does not differ significantly between the two sites (Amud median = 130.37°, IQR = 32.88; Kebara median = 126.08°, IQR = 38.46; $W = 36,082$, $p = 0.116$; Table 5A and Figure 6). No significant difference in OA values was observed between prey size categories within the Kebara sample [$H_{(2)} = 2.2033$, $p = 0.332$]. In contrast, in the Amud sample, there are significantly higher OA values on specimens from prey size 1 ($W = 3,240$, $p = 0.002$; Table 5B). Prey size 1 specimens in Kebara have significantly lower OA values ($W = 13,874$, $p = 0.029$; Supplementary Table 4B) compared to Amud.

Floor radius (Rd). No significant difference in incision floor radius was found between the two sites (Amud median = 38.22 μm ; IQR = 44.32; Kebara median = 39.71 μm , IQR = 38.71; $W = 29,743$, $p = 0.29$; Table 5A and Figure 6). Rd values are relatively homogeneous across prey sizes within both samples [Amud: $W = 2,155$, $p = 0.910$; Kebara: $H_{(2)} = 2.6993$, $p = 0.259$; Supplementary Table 4C]. When focusing on prey size 1, no significant difference in Rd was found between the Amud and Kebara samples ($W = 11,968$, $p = 0.302$; Supplementary Table 4B).

TABLE 5 Cut-marks micro-measurements per (A) each site/sub-unit, (B) each prey size category represented, and (C) each occupation area (i.e., Area A or Areas B–C) within the Amud sub-units B1–B2.

Site	Sub-unit/layer	n	Length (mm)		WIS (μm)		Depth (μm)		OA (°)		Floor radius (μm)	
			Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
(A)												
Amud	B1	97	1.91	1.19	206.27	178.82	28.91	39.53	133.26	34.16	53.77	53.06
	B2	82	1.94	1.42	153.83	153.96	27.20	31.32	121.96	31.00	26.10	26.23
	B4	109	1.69	1.52	150.35	99.43	23.40	31.53	134.56	31.32	32.81	33.78
	All sub-units	288	1.88	1.36	170.04	149.35	26.16	34.68	130.37	32.88	38.22	44.32
Kebara	Layer IX	232	3.38	3.70	182.33	147.30	31.17	54.96	126.08	38.46	39.71	38.71
(B)												
Amud	Size 1	230	1.94	1.31	171.65	152.08	27.41	34.31	133.59	33.47	39.43	44.73
	Size 2	20	1.85	2.06	194.87	202.71	35.82	50.44	105.62	43.13	44.91	44.44
Kebara	Size 1	105	2.60	2.43	182.01	143.23	32.87	62.49	122.85	40.84	37.58	42.30
	Size 2	98	3.77	4.04	166.72	114.04	26.20	50.52	127.11	39.92	44.93	42.28
	Size 3	29	4.71	5.20	294.36	166.35	45.33	34.67	128.44	45.61	38.92	24.74
(C)												
Amud (B1/B2)	A	48	1.87	0.94	208.72	168.92	44.47	63.29	134.94	35.66	70.58	65.15
	B–C	40	1.96	1.51	151.24	147.48	28.76	30.02	119.00	32.98	26.19	27.88

The median and interquartile range (IQR) is presented for each variable: Length, Width of the Incision at the Surface (WIS), Depth, Opening Angle (OA), and Floor radius. n represents the total number of individual cut-marks measured for each sample.

Principal component analysis (PCA). The first two components (PC1 and PC2) explain 39.6% and 26.7% of the variance, respectively (Supplementary Table 5A). PC1 is mostly influenced by WIS and Depth, which contribute negatively to this component. PC2 is mostly influenced by Rd (positively) and OA (negatively). Visualization of overall cut-marks form patterns through PCAs shows that cut-marks greatly overlap in their measurements across sites and sub-units, although samples from Amud B1 and Kebara IX are the most variable in terms of cut-marks form, while Amud B2 and B4 display consistently shorter, shallower, and narrower cut-marks (Figure 5 and Supplementary Table 5A).

5 Discussion

Within a broader unified technological tradition of the Late MP in the Levant, (e.g., the use of similar flaking methods to produce artifacts of similar shape), the stone tools from Kebara and Amud show some technological variations (e.g., Meignen, 1995) interpretable as local traditions accumulated through social learning (e.g., Hovers and Belfer-Cohen, 2013). Here we investigate whether the exploitation of faunal resources at the two sites, as evidenced in this study, might also reveal local traditions that varied depending on resource selection, differential use of the cave space, and site-specific butchery practices.

Previous studies of the faunal assemblages suggested an overall comparable species composition at both sites for medium- and large-sized ungulates, at the same time highlighting some variations between the two sites. Specifically, large ungulates such as aurochs (*Bos primigenius*) or equids (*Equus* sp.) are better represented at

Kebara compared to Amud (Speth and Tchernov, 2001; Rabinovich and Hovers, 2004). Signs of burning were observed in Kebara on 9% of the identified bone remains (n = 913; Speth, 2019). In contrast, up to 40% of Amud identified remains were burnt [n = 2,124; in addition to another 14% (n = 3,212) observed on unidentifiable bone fragments; Rabinovich and Hovers, 2004]. Finally, specimens from Amud were heavily fragmented, with recorded fragment sizes averaging around 27.4 mm in length but <1 mm in width, while the length recorded for the specimens of Kebara averages around 35.8 mm (Rabinovich and Hovers, 2004; Speth, 2019 and references therein). In the present study, analyses of the cut-marked specimens replicate these observations (Sections 3.1, 3.2), confirming that bone fragments from Amud are significantly smaller in size and more affected by exposure to fire than those from Kebara.

Although the surface area of the Kebara specimens is, on average, generally larger than that of the Amud specimens, both samples display similar numbers of cut-marks per specimen. This results in a much higher cut-mark density on the small bone fragments from Amud and a more clustered appearance of cut-marks, which tend to be placed close to each other and intersect more often than on the cut-marked specimens from Kebara. In addition, a smaller proportion of the observed cut-marks were found to be linear on the bones from Amud, giving an overall impression of clutter in comparison to the specimens from Kebara. Cut-marks from Kebara tend to be significantly longer (see below) and more variable in their depth than those from Amud. Otherwise, the microscopic characteristics of the cut-marks in the detailed samples from the two sites are relatively similar, with comparable values of floor radius, opening angle and width at the surface, which

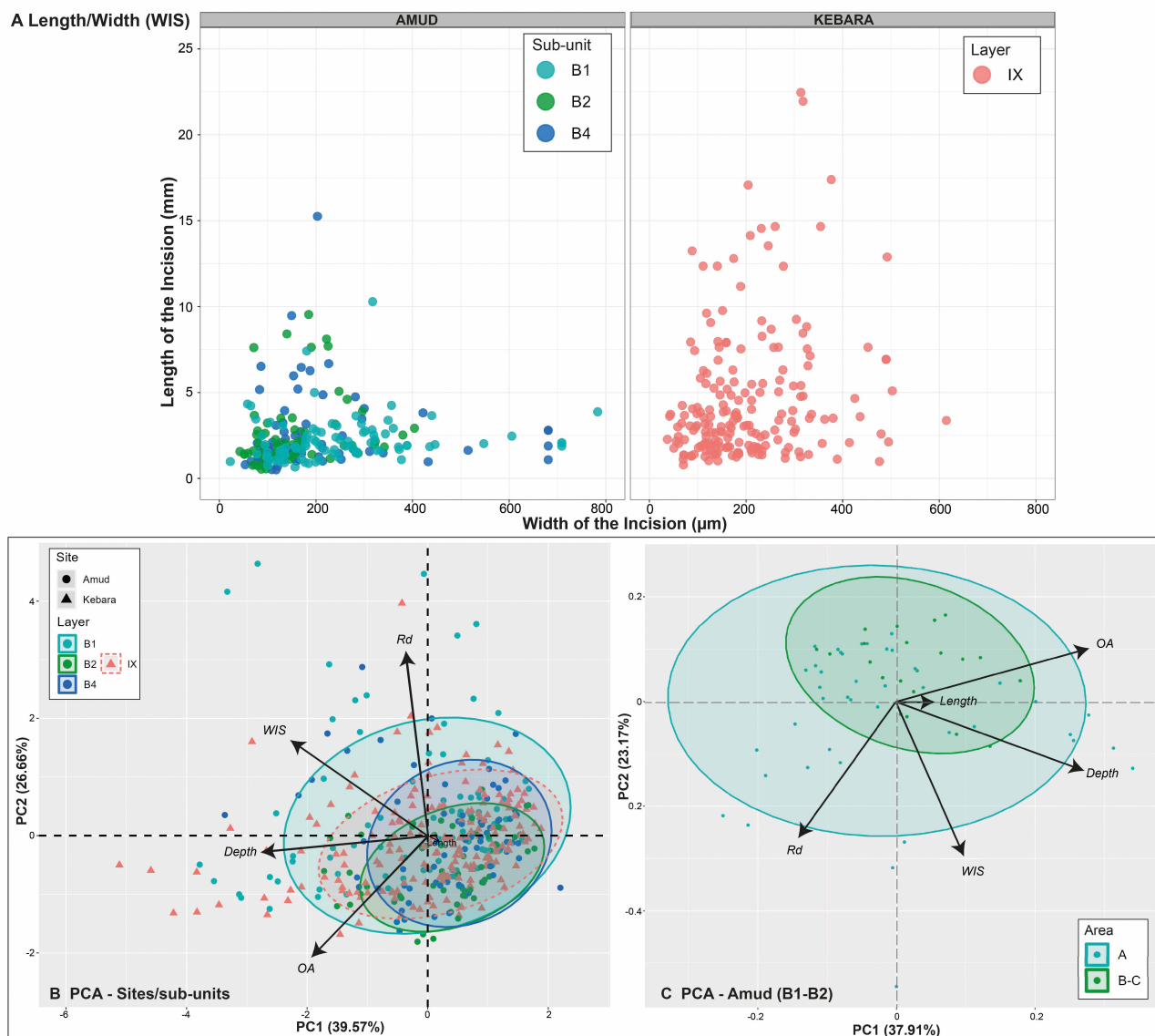


FIGURE 5

Micro-morphometric measurements for the Amud and Kebara samples (as shown in Figure 2). Variation in measurements across site and Sub-units is shown through (A) the length and width at the surface of the incisions (WIS). (B, C) present outputs from Principal Component Analyses (PCA) performed on the dataset using all variables (length, WIS, depth, OA, and floor radius) to assess the overall variation of cut-marks micro-morphometrics across time and space, for (B) the two sites and all sampled Sub-units, and (C) within the Amud B1–B2 sub-sample to compare spatial patterns between the main occupation Areas (A vs. B–C; see Supplementary Figure 6 for boxplots for each variable, and Supplementary Table 5 for PCA results and variable loadings).

further confirms the use of similar tool implements at the two sites (Bello et al., 2009).

In the following sections, we will delve into a detailed discussion of these results, examining the extent to which taphonomic factors or broader site-related differences can account for these patterns, and identifying aspects that likely reflect distinct human behaviors.

5.1 Taphonomic alterations and their influence on butchery patterns

In the framework of the present study, the difference in fragment size between the two sites is significant, and it may have

influenced several of the variables interpreted in the context of butchery behaviors. In particular, fragment size limits the ability to achieve taxonomic identifications and therefore to link butchery marks with prey choice. The strong difference in fragmentation of the two assemblages also likely distorted the comparison of the amounts of cut-marks present in each sample (see Abe et al., 2002; Domínguez-Rodrigo and Yravedra, 2009), despite the small difference observed between the two sites when evaluating the relative proportion of complete cut-marks observed in each sample. This potential bias was corrected in the present study by scaling the number of cut-marks per specimen relative to surface area, shifting the focus to the density of cut-marks per fragment, rather than cut-mark raw counts. Additionally, fragmentation affects the

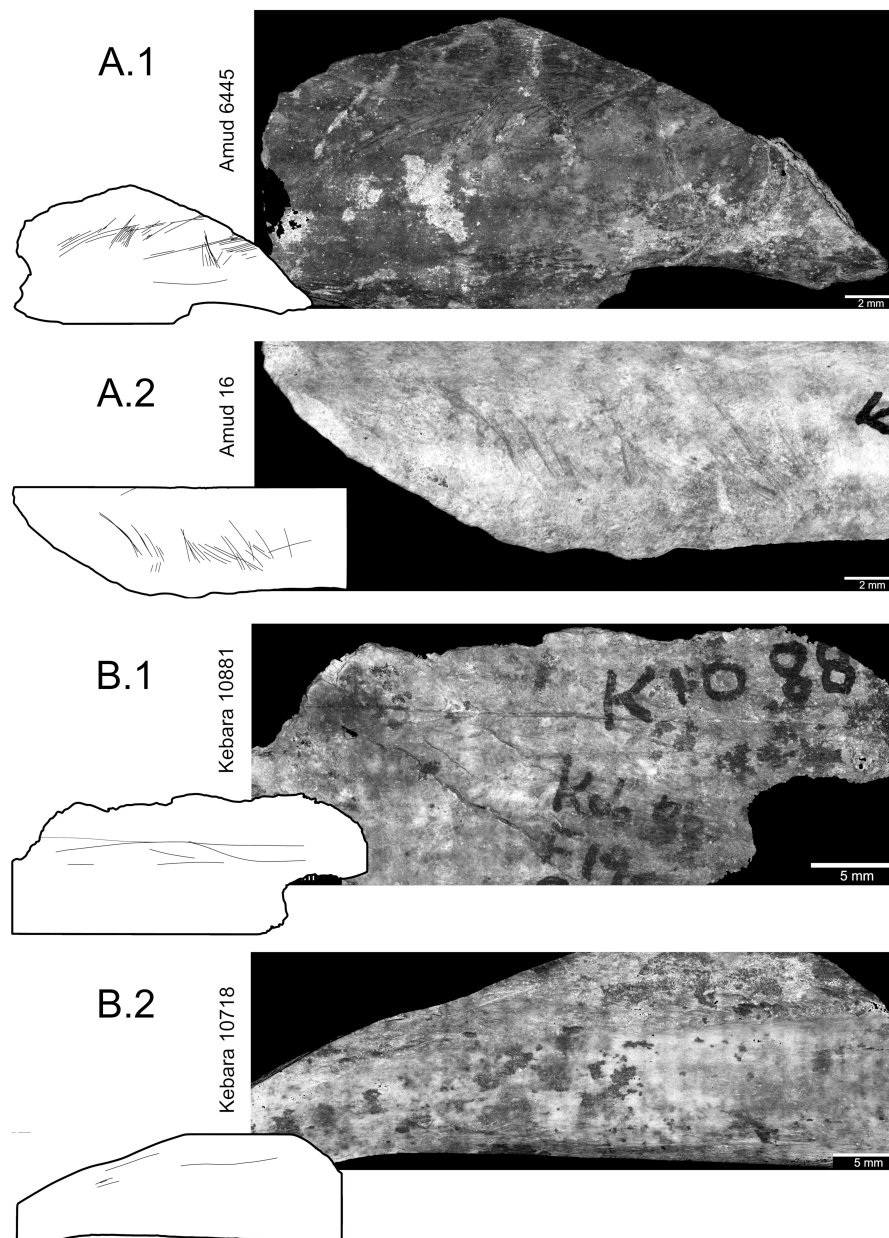


FIGURE 6

Alicona images (10x lens) and schematic sketches for cut-marked specimens from Amud (A) and Kebara (B) caves, illustrating the difference in cut-marks density between the two sites. In the sketches, thick borders represent the outer borders of the specimen, and the thin lines represent the observed cut-marks.

range of cut-mark lengths that could be measured in their entirety potentially leading to an underestimation of cut-mark length at Amud in comparison to Kebara, and thus explaining our results regarding this characteristic.

It might be tempting to argue that the difference in fragment size stems from different butchery strategies. Indeed, when comparing bone surface area in the two sites for only small ungulates (prey size 1), the two samples differ significantly, suggesting that the difference is not related to prey size. One could then argue that the smaller surface area of bone fragments in the Amud detailed sample and its lower size variability (Figure 4C) resulted from specialized butchery strategies meant

to break bones into very small fragments. This interpretation, however, is not consistent with the limited amount of percussion damage observed at Amud relative to the size and number of fragments recovered. Another possible explanation is that the high frequency of burning at Amud (Section 4.1) led to its extreme bone fragmentation. Indeed, as suggested by previous studies, the bone fragments in Amud, burned in large proportions, would have been more friable and thus more susceptible to fragmentation due to post-depositional agents such as sediment compaction (Stiner et al., 1995; Rabinovich and Hovers, 2004; Reidsma, 2022). This topic would require further detailed study.

Despite the higher frequencies of burning, and potentially more post-depositional stresses on the bones of Amud in comparison to Kebara, it would seem that cut-mark morphology was preserved at both sites. At both sites, cut-marks outlines appeared pristine, with visible shoulder effects, internal microstriations and Hertzian cones visible in the SEM images (Supplementary Figure 5).

5.2 Faunal assemblage composition and stone tools: implications for the interpretation of butchery patterns

Cutting tools. One of the most prominent trends observed in the lithic assemblages of both open-air and cave sites in the late Middle Paleolithic in the Levant is the production of subtriangular short blanks, such as triangular flakes and points, often removed from unidirectional convergent Levallois cores. At Amud and Kebara, this similarity in morphology is obtained through slightly different site-specific knapping procedures (Meignen, 1995, 2019; Hovers and Belfer-Cohen, 2013; Krakovsky, 2017). Still, flint was the main raw material used for tool production at both sites. The two lithic assemblages are generally similar also in the preponderance of Levallois flaking strategies and in the production of flakes including points and triangular flakes and the low frequencies of retouched items (Goder-Goldberger, 1997; Hovers, 1998, 2004; Alperson-Afil and Hovers, 2005; Ekshtain et al., 2017; Meignen, 2019 and references therein). The general overlap in cut-mark micro-morphometrics across the two detailed samples (in particular the width and opening angle of the cut) is therefore not surprising when considering the broad similarities of the lithic assemblages (Section 2.1). The similarities in raw material used and in toolkit is a plausible explanation of the inter-assemblage similarities in micro-morphometric characteristics of the cut-marks.

Faunal spectrum, body parts representation and butchering activities. Most of our Amud sample consists of fragments of long-bone diaphysis from small ungulates. These anatomical areas typically undergo a reduced range of butchery activities (e.g., fileting), which would result in a high number of small, clustered cut-marks (as shown in Figure 6; Soulier and Morin, 2016; Soulier and Costamagno, 2017). In contrast, given the higher proportion of medium-sized and large ungulates, as well as the wider range of skeletal elements represented in the Kebara sample, we would expect a wide range of butchering techniques in this sample (such as skinning, disarticulating, and fileting; Speth, 2012 and references therein; Gifford-Gonzalez, 2018). This may explain the greater variability observed in cut-marks length and depth (greater depth of cut as been associated with the cutting of larger muscles; Bello et al., 2009; Wallduck and Bello, 2018) at the two sites.

However, when comparing only small ungulates (prey size 1), we still observe a greater density of incisions, higher proportion of overlapping marks and lower proportion of linear marks in the Amud sample compared to Kebara (Sections 4.3.1). These macroscopic differences cannot be related to the presence of different prey sizes. Moreover, at both sites, prey size 1 includes nearly exclusively mountain gazelles. Thus, taxonomic variation within this group can be considered minimal and unlikely to account for the observed differences between assemblages.

Therefore, these patterns may suggest behavioral differences in the processing of small ungulates (see Section 5.4).

5.3 Intra-site variation within Amud cave

The Amud sample in our study consists of three stratigraphic sub-units. Given their chronologies, we expected that if modes of faunal exploitation changed through time, B1 and B2 (both within MIS 3) would be more similar to one another and differ from the earlier B4 (dated to the end of MIS 4). However, the variations observed in the detailed sample across the various sub-units were contrary to our expectations, with some aspects of the B1 sample differing from the two other sub-units. Firstly, B1 fragments are larger, show a lower density of incisions and are less frequently burnt than in any of the other sub-units. Secondly, specimens from B1 are the most variable in terms of cut-mark micro-morphometrics, bearing generally wider cut-marks with a larger floor radius compared to specimens from B2 and B4. Interestingly, it also appears that within the Amud sample, the sub-sample from sub-unit B1 appears to be the most similar to the Kebara unit IX sample in its micro-morphometric measurements, as well as in terms of cut-marks density (Figure 4B).

It is important to note however that sub-unit B1 is only present in the peripheral area of the cave (Area A; Supplementary Figure 2). Hence the intra-site differences might not necessarily reflect chronological variation, but might instead relate to differential use of the space in each cave, with different butchery activities being carried out in the central occupation area (Areas B–C; represented in our sample by specimens attributed to sub-unit B2) compared to the peripheral area of the cave (Area A; represented in our sample by specimens attributed to sub-unit B1). Indeed, Alperson-Afil and Hovers (2005) suggested that in sub-unit B2, knapping and living activities were carried out in Area C, while Area A was used as a refuse area. This interpretation was further supported by archaeomagnetic data (Zeigen et al., 2019) documenting variable heating intensities in this area. Thus, the presence of relatively large bone fragments variably exposed to heat (based on bone coloration) in sub-unit B1 may be explained as the result of cleaning of the central area. Interestingly, previous publications have suggested that the concentrations of bones along the northern wall during accumulation of unit IX in Kebara likely represented a discard midden (Speth, 2019). It is therefore possible that the similarities between Kebara IX and Amud B1 stem from the similar use of the two areas as discard area. Still, we are unable to explain the differences in cut-mark densities within the Amud sample through this spatial functional perspective.

5.4 Potential cultural differences in carcass processing at Amud and Kebara sites

Experimental work combined with ethnographic and archeological case studies have shown that cut-marks may attest to behavioral variations. While the processes leading to these phenomena are not well-understood (Domínguez-Rodrigo et al., 2017), several authors noted behavioral variations related to

modes of exploitation and processing of the hunted fauna. For example, humans may opt for different timing and ways of obtaining meat off carcasses (i.e., preparing drying, boiled or rotten meat as opposed to fresh meat; e.g., Abe, 2005; Soulier and Morin, 2016; Soulier, 2021; Wallduck and Bello, 2018; Speth and Morin, 2022). Differences in group organization and social modes of food sharing were also suggested as underlying drivers of variation in the patterning of cut-marks (Stiner et al., 2009, 2011). Interestingly, experimental work on differences between expert vs. novice butchers suggested that skill cannot be correlated with the amount and morphologies of cut-marks (Pobiner et al., 2018; Soulier, 2021). For this reason, we consider that an interpretation suggesting that butchers were generally less skilled at Amud compared to butchers at Kebara does not sufficiently explain the higher density, clustered appearance and lower linearity of the cut-marks in Amud compared to Kebara.

Possibly, differences between cut-marks in the Amud and Kebara samples could stem from a more intensive exploitation of the carcasses at Amud cave. Such behavior could have resulted from a higher pressure on resources in a somewhat drier environment at Amud compared to Kebara (Section 1). Alternatively, more intensive occupations in Amud Cave, estimated through lithic frequencies per volume per duration (cf. Hovers, 2001, p. 133), could have necessitated a higher intensity of carcass use. However, experimental work has suggested that the frequencies of cut-marks are poorly correlated with the intensity of butchering activities (Egeland, 2003; Pobiner et al., 2018).

Another possible explanation for differences in cut-mark density and linearity between the two sites is that the butchering of meat in more advanced states of decomposition took place in Amud, but less frequently in Kebara. It has been shown that decaying carcasses tend to be more difficult to process, often resulting in the production of haphazard, deep, and sinuous cut-marks (Speth, 2017; Wallduck and Bello, 2018). The higher frequencies of non-linear marks in the Amud samples, compared to Kebara, could therefore suggest that the acquisition of meat off the prey was approached differently in the two sites, with, for example, decaying carcasses being processed more often at Amud Cave than at Kebara. Further experimental research and comparative work is needed to better assess the influence of these factors on cut-mark patterns. Additional variables, such as group organization (e.g., number of individuals involved simultaneously in butchering one carcass, see Egeland et al., 2014) and the types of gestures employed by the butcher(s) would also benefit from further investigation, which could help identifying the range of factors that could result in high frequencies of cut-marks.

6 Conclusion

The Amud samples show a number of patterns that are repeated over time and, despite observed intra-site variations, differ from Kebara IX. We discussed the similarities and differences in cut-marks patterns observed between the Amud and Kebara samples, from environmental, functional, and site-use perspectives. While we cannot fully untangle the various factors that resulted in the cut-mark patterns reported in this study, our results do suggest that the broadly contemporaneous groups of Neanderthals that

occupied Amud and Kebara caves exploited similar communities of ungulates in nuancedly different ways. Our study suggests that animal exploitation can leave archeological evidence that reflects group-specific butchering strategies. Thus, detailed analysis of butchery marks can provide useful information to our understanding of group-specific action choices. This hypothesis can be tested by future comparative studies to reveal potential underlying patterns of socially-transmitted traditions—as it is the case with lithic technology.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

AJ: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. LC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. SB: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing. EH: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing. RR: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Gen AI was used in the creation of this manuscript.

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