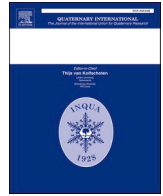




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A reanalysis of the ‘perforated’ scapula from the Boxgrove Horse Butchery Site[☆]

Annemieke Milks^{a,*}, Debra Carr^b, Krishna Godhania^c, Pete Mahoney^d, Simon Parfitt^{e,f},
Gabriele Russo^g, Matt Pope^e

^a University of Reading, Department of Archaeology, Reading, UK

^b Previously at: Impact and Armour Group, Cranfield University, Shrivensham, UK. Now at: School of Applied and Health Science, London South Bank University, 103 Borough Road, London, SE1 0AA, UK

^c Institute of Filipino Martial Arts, Warwick, England, UK

^d Department of Bioengineering, Centre for Injury Studies, Imperial College London, UK

^e Institute of Archaeology, University College London, 31-34 Gordon Square, London, WC1H 0PY, UK

^f Centre of Human Evolution Research, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

^g Paleoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, Eberhard Karls University of Tübingen, 72070, Tübingen, Germany

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ABSTRACT

The archaeological site of Boxgrove (U.K.) represents one of the most detailed records of early Middle Pleistocene hominin activity in Europe. Dated to the end of Marine Isotope Stage (MIS) 13 (~480,000 years BP), it preserves an extensive Acheulean landscape marked by high-resolution evidence of tool manufacture, animal butchery, and hominin remains. Among its key discoveries is the unique archaeological locale of GTP17, known as the Horse Butchery Site, where a single horse carcass was intensively processed by a group of hominins using handaxes and flakes, several of which were knapped adjacent to the carcass at the time of butchery. The archaeological signature also suggests that hammerstones and anvils may have been used to process the horse, probably to access grease and marrow. A fragment of the horse's right scapula features a distinctive curvilinear fracture previously interpreted as a potential hunting lesion caused by a wooden spear—an interpretation that, if confirmed, would push back direct evidence for use of hunting weaponry in Europe and link it with Acheulean bifacial technology. While later sites such as Clacton and Schöningen provide evidence of wooden hunting weapons, the Boxgrove scapula fracture has remained ambiguous, lacking rigorous experimental comparison. This study presents the first comprehensive reassessment of the Boxgrove scapula fragment using both microscopy and quantitative methods. By replicating damage patterns through experiments involving thrust and thrown wooden spear impacts, and hammerstone percussion on scapulae to access marrow and grease, we compare these dynamic impact scenarios with the archaeological evidence. The spear experiments demonstrate that wooden spears used as both thrusting and throwing weapons are capable of creating significant wounds to larger prey such as horses, and can occasionally leave traces in the form of hunting lesions. However, hammerstone percussion on scapulae can also cause curvilinear fractures, and such damage is metrically a better match to the Boxgrove scapula fragment. While the evidence that the butchered horse at Boxgrove was actively hunted by the hominins remains strong, our analysis suggests that the Boxgrove scapula fracture is not indicative of weapon impact, but rather is better aligned to percussion damage from hammerstone use to access within-bone nutrients including grease and marrow.

[☆] Ethical approval was obtained for the spear experiments from the Cranfield University Ethics Committee, Shrivensham, UK (Reference CURES/746/2016), and was waived by UCL. Risk assessments were submitted to both UCL Institute of Archaeology and Cranfield University.

* Corresponding author.

E-mail address: a.g.milks@reading.ac.uk (A. Milks).

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1. Introduction

It is now over 50 years since investigations at Boxgrove (U.K.) commenced (Woodcock, 1981; Pope et al., 2020a; Roberts and Parfitt, 1999). Since its discovery the site has provided a remarkable high-resolution record of the behaviour of an early Middle Pleistocene population, with a Late Acheulean culture, documented at numerous locations within a single landscape (Fig. 1). Multiple excavation areas have revealed a range of well-preserved butchery and workshop locales across a square kilometre, spanning successive intertidal, grassland and periglacial environments. This sequence has been dated, based on biostratigraphy, to the end of Marine Isotope Stage (MIS) 13 (c.480,000 yrs BP) and into the subsequent MIS 12 cold stage (Roberts and Parfitt, 1999). Areas of these landscapes were sampled at over 100 localities, revealing extensive evidence of handaxe manufacture, use, reuse, and discard, alongside the use of hammerstones, stone anvils, flake tools, and unmodified flakes (Pope et al., 2020a; Roberts and Parfitt, 1999). The Boxgrove people also utilised organic materials for technological purposes, such as bone and antler knapping tools (Parfitt and Bello, 2020, 2024). Direct evidence for the use of wood however, including for wooden spears, remains elusive.

Boxgrove has also yielded fossil human remains, a rarity for this period in northern Europe (Stringer et al., 1998; Roberts et al., 1994). At excavation area Q1/B, freshwater silts associated with MIS 13 interglacial conditions preserved two lower incisors. The morphology of these teeth closely resemble those from Sima Los Huesos, Atapuerca (Spain), suggesting that they belong to an individual from an early Neanderthal population (Lockey et al., 2022). From a later deposit at the same site, dating to the transition to colder conditions, a large and robust tibia was recovered. Morphologically, this tibia falls outside the range of variation observed in the Sima Los Huesos hominins (Lockey et al.,

2022). The Boxgrove tibia was previously tentatively attributed to *Homo heidelbergensis* (Roberts et al., 1994), a species that remains poorly defined due to the scarcity of comparative post-cranial material.

During the 1990s the combination of human remains, well-preserved archaeology and widespread media attention led to the Boxgrove discoveries significantly influencing both academic and public perception of this previously opaque part of human prehistory. Central in this perception was ‘Boxgrove Man’, a strong and powerful individual, exhibiting advanced cognition, and considered as a progenitor of both *Homo sapiens* and *Homo neanderthalensis*. This individual was at the top of the food chain, capable of hunting large mammals with weapons at close range (Pitts and Roberts, 1997). Feeding into this portrayal was the emerging interpretation of excavations undertaken at the Geological Test Pit 17 (hereafter GTP17) locality. Here, exceptionally well-preserved archaeological evidence of the extensive butchery of a single adult female horse (*Equus ferus mosbachensis*) (Lister et al., 2010), which had been facilitated by the expert manufacture, and subsequent removal, of a number of handaxes presumed to have been used to butcher the animal. The event took place over a few hours on intertidal mudflats, and the nature of the rapid burial and minor post-burial disturbance resulted in a high-resolution archaeological signature that altered perceptions of the technological and behavioural capacities of hominins in the Middle Pleistocene.

As part of the initial publication of the butchered horse at GTP17, a fragment of its right scapula exhibited an unusual curvilinear fracture margin (Fig. 2). It was proposed that this bone fragment potentially bore a hunting lesion, resulting from impact with a wooden spear (Austin et al., 1999). Labelled a ‘puncture mark’ in the original Boxgrove monograph (Austin et al., 1999), it has also been referred to as an ‘impact point’ (Smith, 2012) and ‘hunting lesion’ (Gaudzinski-Windheuser, 2016) in other studies. This fragment was



Fig. 1. Map of the location of Boxgrove (top), location plan for the Boxgrove quarry.

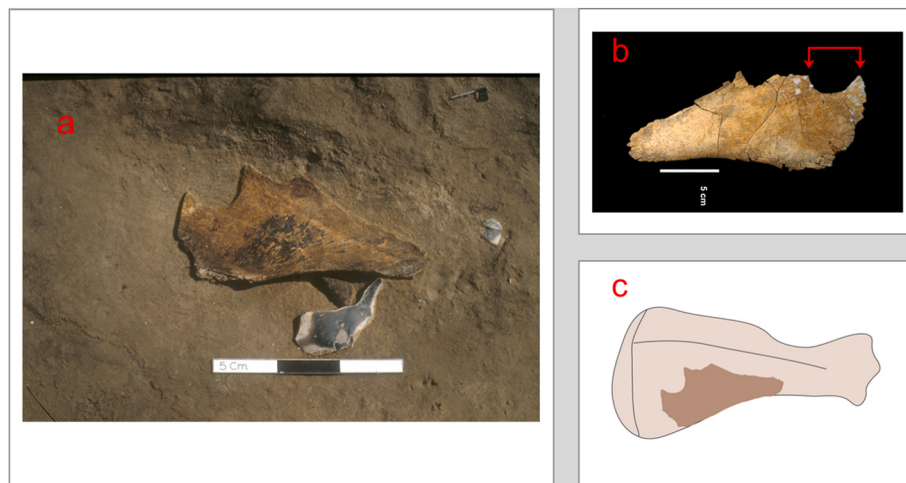


Fig. 2. Boxgrove GTP17 fragment of right horse scapula, bearing potential impact mark. a: excavation image of scapula fragment (lateral side) showing peri-mortem damage prior to post-excavation handling b: medial side of scapula in present condition, with brackets indicating curvilinear fracture, and c: schematic representation of the scapula fragment in relation to a complete right horse scapula.

highlighted as a key piece of evidence not only in support of hunting at Boxgrove but also for the wider European Middle Pleistocene (Stringer et al., 1998; Letourneux and Pétilion, 2008; Pope et al., 2005; Wilkins et al., 2012).

Thieme's (Thieme, 1997) publication of wooden spears and a double-pointed stick from the late Middle Pleistocene site of Schöningen (Germany) a few years later lent weight to the interpretation that Middle Pleistocene hominins were competent hunters of large mammals. The Boxgrove evidence stands alone as the only proposed hunting lesion from the Middle Pleistocene. Unambiguous examples of such lesions are not known until the much later Neanderthal sites in the Late Pleistocene (Gaudzinski-Windheuser, 2016; Boëda et al., 1999; Gaudzinski-Windheuser et al., 2018; Russo et al., 2023). The broken yew spear point from Clacton-on-Sea (U.K.) dated to ca. 400,000 BP (MIS 11), was discovered in 1911, and although it is generally well-accepted as a weapon, its poor find context limits richer behavioural interpretations (Bridgland et al., 1999; Oakley et al., 1977; Warren, 1911) (Fig. 3). There was no further direct evidence of Eurasian Middle Pleistocene hunting weapons until a collection of wooden weapons were uncovered in a cultural horizon at Schöningen (Fig. 3) (Thieme, 1997). Drawing international attention at a time when the Boxgrove excavations were coming to a close, the ongoing excavations and analyses from Schöningen demonstrate a rich behavioural and technological package, including the relatively extensive collection of wooden spears and throwing sticks, additional wooden, osseous and lithic tools, and, key to understanding the presence of all of these technologies, a large number of butchered mammals with a focus on horse (Thieme, 1997; Conard et al., 2015; Julien et al., 2015; Leder et al., 2024; Schoch et al., 2015; Serangeli et al., 2023; Serangeli and Conard, 2015). Re-dating of Schöningen places it within MIS 9 (Richter and Krbetschek, 2015; Van

Kolfschoten, 2014; Van Kolfschoten et al., 2012), two full interglacial cycles later than Boxgrove, representing a gap of some 180,000 years. A recent publication proposed an even younger age for the Schöningen Spear Horizon, in MIS 7 (Hutson et al., 2025). While the evidence at Clacton did (and still does) represent the earliest evidence of Eurasian hunting technologies, it is therefore sandwiched in time between Boxgrove and Schöningen. These latter two have become reference sites for Middle Pleistocene hominin behaviour, thanks to their high-resolution archaeology (Pope et al., 2009, 2020a; Conard et al., 2015; Serangeli et al., 2023). Both are widely known to represent hunting and extensive butchery of equids with GTP17 nicknamed 'The Horse Butchery Site' (Pope et al., 2020a; Austin et al., 1999; Smith, 2012; Pope, 2003; Roberts, 2011; Voormolen, 2008), and Schöningen 13 II-4, dubbed 'The Spear Horizon' (Conard et al., 2015; Van Kolfschoten, 2014; Voormolen, 2008; García-Moreno et al., 2021; Starkovich and Conard, 2015). The evidence at Schöningen clearly indicates repeated visits of hominins who regularly and proficiently hunted large mammals, using single-component but expertly-crafted wooden weapons including spears and throwing sticks (Thieme, 1997; Leder et al., 2024; Schoch et al., 2015; Conard et al., 2020; Milks et al., 2023). While disagreements may persist regarding the nature of the use of those weapons and associated hunting strategies, the debates whether hominins were equipped to be successful hunters from the start of the late Middle Pleistocene (MIS 11) onwards appears largely resolved through the direct evidence of hunting technologies at Clacton-on-Sea and Schöningen.

Consequently, confirmation of a hunting lesion at Boxgrove would be significant. If it indeed represents the earliest clear evidence of the use of weaponry in the European archaeological record, it would extend evidence for the use of spears to an earlier interglacial and associate this



Fig. 3. The front points of the Middle and early Late Pleistocene wooden spears from Clacton-on-Sea, Schöningen (labelled Spears I through X), and Leheringen (Germany). Copyright: Leder and Milks (Leder and Milks, 2025).

with an Acheulean culture. Currently, as the associated stone artefact assemblages at both Clacton and Schöningen lack evidence for the manufacture of Large Cutting Tools (Serangeli and Conard, 2015), evidence for hunting with wooden spears at Boxgrove would bring a degree of unity to hunting strategies across different technological cultures, Pleistocene landscapes and periods.

A preference for fat-rich sources including within-bone nutrients such as grease and marrow is well-attested across the Pleistocene (Ben-Dor and Barkai, 2024; Hosfield, 2020) and has persisted among recent hunter-gatherer groups (Binford, 1978; O'Connell et al., 1988). While it is associated both with carcass scavenging and hunting, the benefits of high-quality fats to balance protein intake may have even driven the selection of hominin hunting behaviours (Ben-Dor and Barkai, 2024). 'Cold' marrow processing, where marrow and grease reserves in animal bones are accessed without heating, was practiced by humans before the Upper Palaeolithic (Stiner, 2005), although the application of heat to extract bone grease may have also been practiced by Neanderthals (Kindler et al., 2025). During the Middle Palaeolithic, all medium and large ungulate scapulae recovered from the Mousterian Layer E at Hayonim Cave were opened for marrow and grease exploitation, demonstrating that although marrow extraction usually focuses on long bones, flat bones can also be the focus of such activity (Stiner, 2005). An important context for evaluating the evidence at Boxgrove is that equid marrow has a liquid consistency, likely making it accessible from even small regions of cancellous bone (Outram and Rowley-Conwy, 1998) including from flat bones such as scapulae. Of further significance is the presence of modified and unmodified hammerstones at Boxgrove, and which have been known to be used as percussors to extract marrow and/or grease from bones since the Early Pleistocene (Bunn, 1981; de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005; Assaf et al., 2020).

Until now, the significance of the potential lesion from Boxgrove remained untested by a systematic analysis. In general, experimental work on hunting lesions has thus far focussed on establishing 'diagnostic criteria' and the development of descriptive and qualitative approaches aimed at distinguishing potential lesions from taphonomic signatures such as carnivore gnawing (Gaudzinski-Windheuser et al., 2018; Duches et al., 2016, 2020; O'Driscoll and Thompson, 2014). Quantitative approaches to understand overlaps in impact damage size across a range of causal agents have only recently played a role (Gaudzinski-Windheuser et al., 2018; Russo et al., 2023), and to our knowledge experimental weapon impacts have not yet been directly compared to hammerstone percussion damage. The primary aim of this analysis is to present a microscopic and quantitative analysis of the Boxgrove scapula fragment which is underpinned by experimental testing of two different types of dynamic loading that could be represented on the GTP17 scapula fragment: impact from wooden spears during hunting, and hammerstone percussion to access within-bone nutrients.

1.1. Boxgrove

1.1.1. Significance of the GTP17 signatures

The recently published monograph provides a detailed presentation of the faunal and lithic assemblages from the Horse Butchery Site. While confirming the overall interpretation presented in earlier accounts, a single *in situ* signature relating to the rapid butchery and burial of a single horse carcass (Roberts and Parfitt, 1999; Pope, 2002), it offers a more refined and focused consideration of the full range of activities undertaken, and their implications (Pope et al., 2020a). The evidence shows that approximately 480,000 years ago a group of hominins successfully secured the carcass of a large, adult female horse on intertidal mudflats, beneath flint-bearing chalk cliffs in West Sussex (Pope et al., 2020a).

The lithic assemblage consists of 1797 stone artefacts greater than 20 mm in maximum dimension, including percussors, core elements, tools and debitage (Pope et al., 2020b). Hominins selected high-quality

nodular flint blocks from the chalk cliffs ca. 40–60 m away, and knapped them around the horse carcass, leaving behind nine scatters indicative of biface manufacture. Although all of the knapped handaxes were removed from GTP17 after the butchery of the horse, several flakes, also used in butchery activities, appear to have been left behind. Manuports in the form of beach cobbles and flint nodules were used in percussive activities - some of which were used in stone tool manufacture - and were discarded at the site (Roberts and Parfitt, 1999; Austin et al., 1999; Pope et al., 2020b; Wenban-Smith et al., 1999). In addition to the handaxes shaped on site from the local raw material, at least one handaxe was brought to the site and reworked there. The re-analysis suggests intra-site movement of flakes, apparently as part of the butchery process. This led to the hypothesis that, rather than being the work of a sub-set of the population, the entire group may have participated in the activity (Pope et al., 2020b).

The remains of a butchered horse provide another key element of the GTP17 datasets. Recent detailed study determined that these remains belong to a single large caballine female horse, approximately 4–5 years old at the time of death. The horse was skeletally mature and had reached its adult size (Parfitt, 2020a). The mare is estimated to have weighed around 700 kg and measured between 1.5 and 1.7 m at the withers (Parfitt, 2020a). While signs of malnutrition or systemic illness, indicated by dental hypoplasia, were present, there was no additional clear evidence of pathology (Parfitt, 2020a). The new analysis describes a high level of bone surface preservation, though most of the skeletal elements were highly mechanically fragmented (Parfitt, 2020a). The bones show both cut marks and hammerstone percussion damage from marrow and grease extraction, suggesting the butchery occurred shortly after death (Parfitt, 2020b). Although there are 727 individual bone specimens, very little of the horse's skeleton remains, with spongy bones being particularly underrepresented (Parfitt, 2020a). The presence of a hyaena coprolite and post-butchery carnivore chewing indicates that the remnants left by hominins were subsequently scavenged by hyaenas.

Over a quarter of the bone fragments bear cut marks, alongside evidence of hammerstone impacts on the mandible, vertebrae, pelvis and limb bone fragments (Parfitt, 2020b). The nature of the hammerstone impact damage suggests that hammerstones were used in conjunction with an anvil, possibly a flint nodule or beach cobble. The use of anvils for bone processing has been evidenced elsewhere at Boxgrove, specifically at Q1 GTP8, where an anvil was found with two beach cobble hammerstones and remains from a cervid with butchery marks, including percussion impact notches (Parfitt et al., 1999). None of the bones at GTP17 showed evidence of periosteum removal prior to impact (Parfitt, 2020b). As neither contains significant amounts of marrow, the breakage appears to have been aimed at accessing bone grease within the spongy bone, which can be extracted from a fresh carcass without the use of heat. Regardless of how these within-bone nutrients were consumed, this demonstrates the intensive processing of the horse carcass by the hominins. Further taphonomic analysis shows carnivore involvement, occurring only after hominins had fully de-fleshed and de-marrowed the horse.

Among the identifiable bone elements were two fragments of the right scapula forming part of the neck (F204) and blade (F277). It is the scapula blade fragment, bearing the curvilinear fracture in question, that is the subject of this paper. This fracture was first identified the 1990s, following visual inspection by the forensic pathologist Bernard Knight, who suggested it might be consistent with a hunting lesion caused by a weapon, possibly a wooden spear. Knight noted the presence of internal bevelling, a feature associated with impact in forensic studies of trauma (Pitts and Roberts, 1997; Hale, 1996).

The reanalysis of the horse remains has not resolved the nature of this fracture, nor has it been explained as part of a non-anthropogenic process. Cutmarks are present on the lateral side of the scapula neck fragment, and on the medial side of the blade fragment, the latter containing the curvilinear fracture (Parfitt, 2020b). These marks indicate filleting and scraping to remove the muscle tissue. Furthermore, there is

no evidence of carnivore involvement, nor trampling (Parfitt, 2020b). The most plausible explanation remains that the curvilinear fracture was caused by human activity.

While early interpretations of the faunal assemblage suggested the horse may have been actively hunted (Roberts and Parfitt, 1999; Smith, 2013), the re-analysis left this question somewhat unresolved. It was argued that the evidence indicates that the hominins had primary access to the carcass, while still acknowledging the potential for hunting based on weapon use and hunting evidence elsewhere in the European Middle Pleistocene record (Pope et al., 2020c). The hominin group at GTP17 demonstrated the behavioural capability to secure the horse, whether it was alive or recently dead. This could have occurred in the absence of competing carnivores, though it is more likely that the hominins defended the carcass against wolves and hyaenas present in the surrounding landscape. Regardless, the complete processing of the carcass demonstrates the group's high level of skill, with sufficient time and space to systematically and extensively process the animal (Parfitt, 2020b). Notably, the recent monograph emphasises the need to re-analyse the scapula in light of various lines of evidence including hammerstone use and processing of elements not traditionally considered as marrow-bearing bones (Parfitt, 2020b).

This study primarily focusses on determining whether the curvilinear fracture on the scapula fragment represents evidence of hunting with a spear, or whether it may represent another behavioural facet of hominin activity undertaken at GTP17, such as hammerstone damage for accessing marrow and bone grease. Given that wooden spears are the best-represented Middle Pleistocene weapon technology and were likely to be used for active hunting and aggressive scavenging, we also experimentally explore their potential to lethally wound larger prey. We present a series of three experiments: thrusting wooden spears into a horse carcass, throwing wooden spears into horse carcass, and impacting horse scapulae with flint hammerstones to expose spongy bone and marrow. The resulting spear and hammerstone damage are then metrically and microscopically compared to the perforation on the Boxgrove scapula, alongside published experimental and archaeological hunting lesions.

2. Materials and methods

An experimental programme was designed to address three interrelated objectives: (a) to investigate whether the semicircular damage on the Boxgrove GTP17 horse scapula could have been caused by a wooden spear in a hunting scenario, (b) to explore alternative explanations including use of hammerstones to access nutrients present in bone marrow and spongy bone and (c) to test the broader question of potential effectiveness of wooden spears in wounding larger prey including use as thrusting and throwing spears (javelins).

2.1. Spear experiments

Spear experiments were conducted at Cranfield University/Defence Academy of the United Kingdom (Shrivenham, Oxon, UK) with a team of researchers and technicians possessing expertise in ballistics, weapons testing and mammal anatomy. These experiments made use of the Defence Academy's extensive specialist equipment. The spear thrusting experiment was conducted in the indoor ballistic testing laboratory, while the throwing experiment took place at the outdoor firing range.

2.1.1. Target

A previous experiment demonstrated the capability of wooden spears to penetrate an animal target and damage bone in close-range throwing and thrusting, using a juvenile sheep carcass weighing 15.5 kg (size class 1 animal, following Bunn (1982)) as the target (see also Table S1). While this experiment was relevant to understanding the ability of wooden spears to wound smaller juvenile prey, Boxgrove provides evidence of hominin modification of much larger prey, including the size class 4

horse of GTP17. Larger prey have both larger and thicker bones and soft tissues with higher energy necessary to achieve similar depth of penetration (DoP) (Badenhorst et al., 2012; Frison, 1974, 1989). Additionally, hide thickness and bone mineral density also vary across species, between adults and juveniles, by anatomical location, and individually (Badenhorst et al., 2012; Fenton et al., 2018; Jarman, 1989; Ward et al., 2015). This variability influences the effectiveness of penetrating weapons (Datoc, 2010). There are both advantages and disadvantages to using animal carcasses and homogenous target simulants in prehistoric weaponry experiments. While live animals are not an ethical option for such research, neither animal carcasses, which by nature do not move and therefore cannot reflect a realistic hunting scenario, nor homogenous simulants like gelatine or clay provide a perfect analogy for testing prehistoric weapons (Eren et al., 2024; Eren and Meltzer, 2024; Pettigrew and Bamforth, 2023). Studies involving various target materials such as animal tissues, synthetic and porcine ballistics gelatine, and synthetic bone^{e-g} (Mabbott et al., 2014, 2016; Mahoney et al., 2017), reveal that the different energies involved in early vs. modern weapons may result in very different effects on the target materials.

Central to the current study is determining whether a specific weapon type could produce a distinctive damage signature on a scapula of a size class 4 adult mammal. To address this question, the use of large adult horse carcasses was deemed appropriate as they provided a relevant dataset for evaluating hypotheses related to understanding spears and hunting lesions from the Middle Pleistocene.

No animals were harmed in the course of these experiments. Thoracic sections from two semi-feral adult horses, which were humanely killed as part of a sanctioned cull within a UK National Park, were obtained from an abattoir where they were classed as food grade. (Woodcock, 1981). The thoracic sections weighed ca. 140 kg, with an original body weight of ca. 450 kg (size class 4). While the carcasses retained hide, viscera were removed to comply with on-site licencing requirements. The removal of internal organs is consistent with prior experiments testing prehistoric weapons^{e-g} (O'Driscoll and Thompson, 2014; Pargeter, 2007; Smith et al., 2020), and is unlikely to have significantly influenced penetration results, as organ tissue has considerably lower density compared to muscle and bone tissue (Demuth, 1968). To confirm this limited effect of organ removal, test stabs were done into 37 kg blocks of porcine ballistic gelatine (10 % by mass concentration conditioned at 4 °C), as well as one test stab through the horse carcass with a block of porcine ballistic gelatine placed inside the cavity (listed as TEST 1 and TEST 2 in the accompanying dataset). The participants reported that spears impacted gelatine blocks with considerably less resistance compared to the carcass alone. In fact, DoP results exceed those of thrusting on the carcass. Results of these test thrusts are excluded from the dataset.

The thorax of a horse contains vital organs including the heart, lungs, and major arteries with the ribcage serving as a protective barrier for many of these organs. During locomotion, the movement of a horse's front legs expands the ribcage and tightens the overlying hide, potentially facilitating penetration (Friis-Hansen, 1990). Penetration through the ribcage could result in immediate organ failure and/or significant bleeding, making this region a primary target area for hunters seeking a swift and effective kill of an ungulate. The time between the animal's death and the start of experimentation was ca. 24 h, with tests conducted at room temperature. Previous studies demonstrate no difference in penetration when using previously frozen or refrigerated animal tissue in comparison with fresh tissue, provided tests were performed at room temperature (Breeze et al., 2015). Both of these factors should mitigate the effects of *rigor mortis*, which should have dissipated after 24 h in warm conditions. For the thrusting experiment the torso measured ca. 820 mm from stomach to withers, and 960 mm across. The torso was moved throughout the experiment to accommodate the use of different thrusting techniques. For the throwing experiment, as it took place outdoors in high temperatures (mean of 21 °C and maximum of 27 °C) it was necessary to segment the torso into four sections to maintain a

temperature of 18 °C just prior to testing. The segments may have warmed slightly between initial and final shots. The segmenting also facilitated moving the target for shot placement. Each segment was arranged on top of wooden pallets, topped with sandbags, which ensured minimal movement of the target during impact. Strawboard behind segments minimised damage to spears but may have limited DoP.

2.1.2. Spear replicas

Replicas of Schöningen Spear II were crafted from Norwegian spruce (*Picea abies*). The original Schöningen spears, primarily also made of spruce (*Picea* sp.) are the earliest complete weapons in the archaeological record (Thieme, 1997; Leder et al., 2024; Schoch et al., 2015). The lengths and diameters of the complete/nearly complete Schöningen spears vary. Although maximum diameters have since been revised to be slightly less, the revised diameter of Spear II is only 0.4 cm smaller (compare Table 1 in Schoch et al. 2015 with Table S6 in Leder et al. 2024). As accurate tip measurements were not yet available at the time of spear replication, tip diameters were estimated using a scaled photograph of the tip of Spear II (Thieme and Ullrich, 1999). See Table S2 for further details on the spear replica manufacture and measurements.

2.1.3. Experiment protocols

Spear thrusting is both mechanically and biomechanically complex and variable, even amongst a cohort with similar skills and training. Consequently, it is most accurately replicated by trained human participants (Milks et al., 2016). Studies exploring human performance in spear thrusting demonstrate significant variability primarily influenced by experience and to a lesser extent body mass (Milks et al., 2016; Coppe et al., 2019). Mechanical setups replicating thrusting spears^{e-g} (Iovita et al., 2016), have not been adequately validated to accurately represent performance of human participants. For this experiment, two male participants were selected, both highly trained in spear use and in particular Filipino martial arts. Participant 1 (P1) is a professional martial arts practitioner, while Participant 2 (P2) is military personnel with extensive training in Filipino martial arts. To ensure safety, participants were provided with safety glasses and grip gloves. They were given free choice regarding thrusting techniques used, and their hand orientation, gestures, and footwork recorded (see accompanying dataset).

For the ‘throwing’ part of the experiment, spear replicas (javelins), were fired using an air cannon, also known as air guns (Fig. 4), to simulate hand-thrown spears. Detailed information on the air cannon setup can be found in the supplementary materials.

We selected the impact velocities for this experiment based on data recorded for javelin athletes who threw replicas of the same spear (Schöningen Spear II). Impact velocities captured by high speed video

ranged from 12.7 m/s to 33.3 m/s (mean = 17.6 m/s; $n = 31$), with corresponding kinetic energies from 65 J to 444 J (mean = 122.5 J; $n = 31$) (Milks et al., 2019). The recorded impact velocities had minimal variability by distance, although impacts at 20 m and greater achieved slightly higher velocities compared to those recorded at shorter distances of 5–15 m (Fig. S1). Velocities of >20 m/s are recorded in other spear throwing studies: the javelin athlete in Rieder’s (Rieder et al., 2001) experiment achieved similar impact velocities (mean = 23.8 m/s, maximum = 25.5 m/s) while throwing a replica of Schöningen Spear II at a 5 m distance. We replicated impact velocities and corresponding kinetic energy (KE) for wooden spears based on impact velocities (i.e. not the recorded release velocities), setting an upper limit of 25 m/s.

2.1.4. Spear experiment recording and analysis

Experiment recording sheets were used to manually record each impact, and standard digital video and high-speed video (HSV) footage were captured for both experiments (see SI for further details on HSV recording and analysis). Depth of Penetration (DoP) was recorded by marking the spear at the point of maximum penetration before its removal. The marked length was then measured with a calibrated ruler. Spears were photographed in the target, and after removal, photographs further documented wounds.

2.1.5. Analysis of experimental bone lesions

After cleaning the bones by gentle simmering, one of us (AM) examined them with oblique lighting, a hand lens, and a USB microscope (DinoLite Pro, HR AM7000/AD7000), which was also used to photograph relevant microscopic damage. We follow existing definitions (Duches et al., 2016), whereby a puncture is a hunting lesion for which a weapon broke through the bone but does not carry through the other side of the bone, and a perforation represents a lesion that breaks through the bone, resulting in a hole in the bone. Where the cause of the damage is unknown, as with the GTP17 scapula blade fragment, we use the term fracture. Following methods outlined in a previous publication and making use of the dataset therein (Russo et al., 2023) Table S4, we analysed experimental lesions using image analysis software Fiji (Schindelin et al., 2012) for length and breadth, and compared them using the same method to analyse published images of experimental hunting lesions caused by wood and by composite weapons tipped with stone or bone (see accompanying dataset). Area values, used to calculate bevelling, were calculated from photographs using SketchAndCalc™, a software designed to accurately calculate area and perimeter of complex shapes. Both medial and lateral areas were calculated in order to assess bevelling. For both length/breadth (using Fiji) and area (using SketchAndCalc™), when damage consisted of curvilinear fracture edges rather than complete punctures/perforations, a straight line was drawn to close this space between the fracture edges (Fig. S9). For breadth measurements, where there are ‘open’ curvilinear fractures rather than a complete hole these were conservatively measured from the edge of the fracture margin to the intersecting length measurement, thus avoiding an assumption that the original shape would have taken the form of a complete perforation/puncture. For area calculations, the line was digitally drawn around the rim of cortical bone, and areas with crushing were not included.

2.2. Hammerstone percussion experiment

An experimental study using flint hammerstones to impact horse scapulae explored whether curvilinear fractures such as that seen on the GTP17 scapula blade fragment could occur during butchery. The study aimed to address three primary objectives:

- Potential for Curvilinear Fractures: Determine whether lithic hammerstones could produce curvilinear fractures on horse scapulae.
- Assess whether such fractures could result from a single impact or require repeated blows.



Fig. 4. Air cannon experimental setup. A: foam discs used to create a seal between the spear and the barrel. B: The air cannon controller. C: the barrel within which the replicas sit. D: the front point of a wooden spear replica.

- c. Comparison with Spear Damage: Identify macroscopic and microscopic features that might either differentiate hammerstone-induced damage from, or overlap with, damage caused by wooden spears.

This study was not designed to determine causal probabilities (e.g. whether spears, hammerstones or other potential agents were responsible for specific damage), but rather to build an 'interpretative frame of reference' (Gaudzinski-Windheuser, 2016) to aid in evaluating such possibilities. Most previous hammerstone percussion research has concentrated on long bones which contain the highest quantities of marrow (Binford, 1978; Blumenschine and Madrigal, 1993; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Galàn et al., 2009; Pickering and Egeland, 2006). As a result, the characteristics of percussion damage to flat bones like scapulae are less well understood.

2.2.1. Materials

For the hammerstone percussion experiment we sourced six horse scapulae from adult horses (*Equus ferus caballus*) from the Royal Veterinary College (Hatfield, Hert, UK). The horses died a natural death, had no known health conditions affecting the bones, and had existing ethical clearance for research purposes. The scapulae were disarticulated using metal tools, leaving surrounding soft tissues including muscles and cartilage intact. Immediately after disarticulation the scapulae were frozen and were thawed out over a 24-h period within 6 weeks. According to Outram (Outram, 2001; Outram et al., 2002) bones frozen for a limited time and then thawed retain a high 'Freshness Fracture Index'. For tracking purposes, each scapula was assigned an episode number (e.g. IMP 1 = Impact Episode 1). Unretouched flint flakes were used to remove muscle mass while the periosteum was left intact. We collected two types of non-modified flint hammerstones from Sussex beaches and countryside: rolled beach pebbles and cortical nodules (Table S5, Fig. S8). A large cortical flint nodule (273 mm × 175 mm × 162 mm) was used as an anvil. Although the small sample size limited the analysis of probability of specific types of damage, the primary aim was to explore the potential for curvilinear fractures and other damage resulting from hammerstone impacts. These results were then compared with damage caused by weapon impacts to construct an interpretive framework for distinguishing between these types of bone modifications.

2.2.2. Experiment protocols

A healthy adult male with no known shoulder or arm conditions volunteered for the study. The participant was selected based on stature (height: 1.83 m, weight: 90 kg) to replicate the estimated size of the Boxgrove hominin (Stringer et al., 1998). He was allowed to choose hammerstones, with the requirement that he use a different hammerstone for each impact event. Scapulae were impacted on the lateral side, with the medial side resting on the anvil. Impacts were directed at the lateral side of scapulae blades with the aim of exposing the inner cancellous bone containing liquid grease and marrow. It was not the aim to pulverise bone but rather to explore the possibility of curvilinear fractures and/or perforations resulting from intentional impact with hammerstones. Although the controlled conditions of this study may seem artificial, the participant occasionally employed wrenching motions to break apart sections of bone or cartilage, a practice documented ethnographically in butchery and marrow extraction processes (Oliver and Hudson, 1993). Scapulae from impact events 1 through 5 were cleaned using gentle maceration using enzymatic detergent. Scapula 6 was buried in soil for 14 months to provide comparative data. Each scapula was labelled by its impact event with an additional number assigned to individual elements/fragments (e.g. Imp 1/1 = Impact 1, fragment 1).

2.2.3. Analysis of hammerstone bone modifications

As with the spear experiments, a hand-lens with a strong adjustable light source was used in conjunction with a DinoLite Pro HR AM7000/

AD7000 digital microscope to document and photograph microscopic damage on bones. Selected impact areas were further analysed using a scanning electron microscope (Hitachi S-3400N VPSEM).

2.3. Imaging and comparative analysis of the GTP17 specimen

Microscopic analysis of the Boxgrove scapula was conducted using a Nikon SMZ-10 binocular zoom microscope, with magnification up to 50x. Photographs were taken using a Nikon D3100 Digital SLR camera. Image editing and preparation used Adobe Photoshop and Adobe Illustrator. Additionally a CT scan, taken in 2014 by the Natural History Museum (London) contributed to the analysis of bevelling. The measurements used for length and breadth were obtained from an excavation image (with scale) of the Boxgrove scapula (Fig. 2a), before some material at the fracture margin was lost, either during or post-excavation.

Internal bevelling, occasionally referred to in prehistoric hunting lesion studies as diagnostic of weapon impact (Letourneux and Pétillon, 2008; Leduc, 2012; Smith et al., 2007) is a fracture characteristic in which the area of the external surface of the fracture is smaller than the internal surface. This pattern is a typical feature of a ballistic entrance wound (Quatrehomme and Yaşar Işcan, 1998). In rare cases external bevelling, with the opposite pattern, can also occur with entrance wounds (Peterson, 1991) but internal bevelling is the more common and therefore typically indicates direction of impact. While bevelling does occur as a result of projectile impact, it can also result from blunt force trauma (Delannoy et al., 2012; Spatola, 2015) and sharp force trauma (Delannoy et al., 2013). Bevelling ratios were calculated when areas of both lateral and medial sides of damage could be measured using areas calculated (see section 2.1.5).

To assess the classification of the Boxgrove GTP17 damage to the scapula within a larger dataset of experimental bone surface modifications (including hunting lesions and the presented hammerstones impacts), we conducted Linear Discriminant Analysis (LDA) using R software (R Core Team, 2021) using length (mm) and breadth (mm) as predictor variables (see associated code, GTP17_R_Stats.R). We separated the Boxgrove GTP17 modification as an unknown category and performed jackknife cross-validation on the remaining groups (Experimental composite weapon, Experimental Hammerstone Impact, and Experimental Wooden Spear) to train the LDA model. The posterior probabilities were calculated to determine the most likely classification of the unknown group. A confusion matrix was generated to evaluate the model's performance.

3. Results

3.1. Spear thrusting experiment

The thrusting experiment resulted in 11 Thrusting Events (TEs; Figs. S2 and S3). Participant 1 (P1) executed six and P2 executed five thrusts. Out of these, seven had high speed videos suitable for analysis for impact velocities. Velocities captured here exceeded those from a previous trial with heavier spears by around 1 m/s (Milks et al., 2016). The two fastest velocities (TE 6 and TE 7) were executed by P1 and P2 respectively, who have extensive training in spear use, and their performance in this experiment was generally comparable.

The mean DoP from spear thrusting was 15.5 cm, with a minimum of 0 cm and a maximum of 32.6 cm (Table 1). Two TE's failed to penetrate the hide (DoP = 0); one of these (TE 5) was aimed at the ribcage while the other (TE 8) aimed for the scapula (Table S4, Figs. S2 and S3). Four (36 %) of TE's reached DoPs of >20 cm, with three of these exceeding 30 cm. Significantly none of the thrusts on scapula (n = 3; TEs 7, 8 and 9; Figs. S2 and S3) achieved a DoP >15 cm (for further details see Table S4 and accompanying dataset).

There was no noticeable macroscopic or microscopic damage to either ribs or scapula from spear thrusting. Participants observed that

Table 1
Descriptive statistics for DoP from spear thrusting experiment. See Table S3 for detailed results by each impact event.

	Min	Max	Mean	SD	n =
DoP (cm)	0	32.6	15.5	13.22	11
Velocity (m/s)	3.5	7.6	5.6	1.33	7

when thrusting into ribs ($n = 8$), the spear slipped around the edges of ribs, pushing through muscle tissue into the thoracic cavity. Thrusts into scapulae ($n = 3$) met significant physical resistance, and though it was possible to penetrate the hide and relatively thick muscle tissue in this area, it was not possible to impact into scapulae. Interestingly, the only time when a spear broke beyond repair occurred when the participant was aiming at the ribs (TE3, DoP = 5.9 cm).

3.2. Spear throwing experiment

We recorded 13 throwing Impact Events (IEs; Figs. S4 and S5). DoP ranged from 4.9 cm to 28.4 cm (Table 2). Three impacts (23 %) achieved >20 cm, and eight impacts >15 cm (Table S4). Impact velocities ranged from 12.25 m/s to 24.89 m/s, and KE from 56.3 J to 232.3 J. These values fall comfortably within the range of impact velocities recorded with replicas of Schöningen Spear II thrown by javelin athletes (Milks et al., 2019; Rieder et al., 2001).

Replica 1D impacted the fifth rib on the left side (IE 2) at a velocity of 25 m/s and KE of 232 J. This impact just missed the scapula and penetrated to a depth of 19.5 cm after shattering the rib. The rib fractured into multiple pieces (Fig. 5), with one bone fragment lost during carcass processing. This impact would have been a fatal injury, as the spear would have penetrated the thoracic cavity, leading to lung collapse. The primary damage includes multiple fractures, which can be best described as a butterfly fracture (Fig. 5) (Kieser et al., 2014; Pechnikova, 2013). A visible impact point is evident with a microflake (Fig. 5, right), and radiating cracks present on both sides of the rib. These fractures exhibit obtuse or acute angles with both sharp and jagged margins.

IE 3 impacted the ridge of the scapula at 18.1 m/s, resulting in a DoP of 8 cm. However, this impact caused no visible damage to the scapula. The subsequent impact (IE 4) struck the same scapula at 17.3 m/s, with only slightly more penetration (10.3 cm). This hit resulted in a damaged spear, and the wound would have been unlikely to be fatal. The area of impact showed light 'bruising' to the scapula blade, which was more evident prior to cleaning and is similar to that illustrated elsewhere (Parsons and Badenhorst, 2004). A microscopic puncture resulted in displacement of cortical bone, and which macroscopically could easily be mistaken for carnivore gnawing (Fig. S6). In at least two cases in the throwing experiment (IE 4 and IE 9), spear points were broken off leaving wood fragments embedded in the muscle tissue (Fig. S7). However there are known cases where animals survived and healed from projectile-inflicted traumas (Oakley et al., 1977; Noe-Nygaard, 1974).

One impact event (IE 9) at a velocity of 17.57 m/s to the right scapula resulted in a perforation at the edge of the supraspinous fossa (Fig. 6), resulting in a curvilinear fracture. A bone fragment remained attached by fibrous connective tissue along the edge of the blade. Laterally there was secondary damage in the form of crushing and cracking, while

Table 2
Descriptive statistics for throwing impacts. See Table S4 for detailed results by each impact event.

	Min	Max	Mean	SD	n =
DoP (cm)	4.9	28.4	15.7	7.21	13
Velocity (m/s)	12.3	24.9	19.1	3.88	13
KE (J)	56.3	232.3	143.1	56.40	13

medially, hinging, flaking and cracking were observed. Two small flakes of cortical bone from the medial side measuring 23 mm and 7.5 mm in length were recovered. This perforation exhibited internal bevelling, with a ratio of 1:1.82. The area of impact occurred on an especially thin area of bone, located on the margin of the blade.

3.3. Summary of spear experiment results

Although the maximum DoP for thrusting was greater, the mean DoPs for thrusting (15.5 cm) and throwing (15.7 cm) were similar. However, throwing impacts resulted in a lower standard deviation, indicating more consistent penetration depths compared to thrusting. This variation may be attributed to the fact that thrusts were performed by human participants, while throws were mechanically projected. Further testing would be required to confirm a true difference. Regardless, wooden spears proved capable of inflicting wounds to a size class 4 carcass with hide intact that are deemed lethal by current standards, and this was true for both thrusting and throwing. These impacts often penetrated into the thoracic cavity containing the vital organs such as heart and lungs. Wounds suggest that impacts, particularly those from throwing, could have caused catastrophic collapse in the thoracic cavity leading to near-instantaneous death. Other locations would have directly punctured the heart. Nevertheless, unlike with lithic-tipped weapons, wooden spears appear to rarely leave identifiable hunting lesions on scapulae and ribs on larger prey. Apart from the small puncture from one throwing event (IE 3), the use of spears did not leave microscopic signatures on bone (as observed with the DinoLite microscope). Hence SEM analysis was unnecessary for the specimens from the spear experiments.

External wounds caused by spear throwing and thrusting of wooden spears resemble those made by bone-tipped projectiles (Wood and Fitzhugh, 2015). Entrance wounds are typically lenticular, measuring ca. 2–3 cm in length. These wounds may have resulted in less bleeding compared to the lacerated and incised wounds caused by stone-tipped weapons (Wood and Fitzhugh, 2015). The intercostal spacing where the wounds were measured, as well as the diameter of the spears at the DoP (20–30 cm) both measure between 20 and 30 mm. External and internal wound measurements are also similar in size. This similarity suggests that wooden spear point design balanced the need for sufficient penetration between ribs with the robustness required to minimise spear tip breakage.

We emphasise that hunting impacts to scapulae would likely be considered a 'miss' by hunters, as even if the weapon penetrated bone, it would result in a significant loss of kinetic energy to soft muscle tissue and organs (Friis-Hansen, 1990). However, in these experiments, scapulae were deliberately targeted to evaluate the ability of hand-delivered wooden weapons to damage these bones. This approach allowed comparison with potential Middle Pleistocene hunting lesions with damage caused by other modes of dynamic impact.

3.4. Hammerstone experiment

Of the six scapulae impacted, four exhibited perforations. These include a curvilinear fracture (Fig. 7, a), and complete perforations entirely or partly characterised by curvilinear fracture margins (Fig. 7b and c and d). Flakes of cortical bone were separated from the scapula in several instances, particularly on the medial side.

All scapulae exhibiting hammerstone-related damage showed some degree of internal bevelling (Table S7). In all impact events, affected areas were smaller on the impacted (lateral) side, and larger on the exit (medial) side, exposing cancellous bone medially (Table S7). Impacts 1, 4 and 5 displayed characteristic microscopic percussion marks around the impact areas (Fig. 8). These marks, consistent with Galán et al.'s (Galán et al., 2009) study on hammerstone use on bone surfaces, include pits, grooves and microstriations, which can occur individually or in combination. In our study, these marks are primarily on the lateral side,

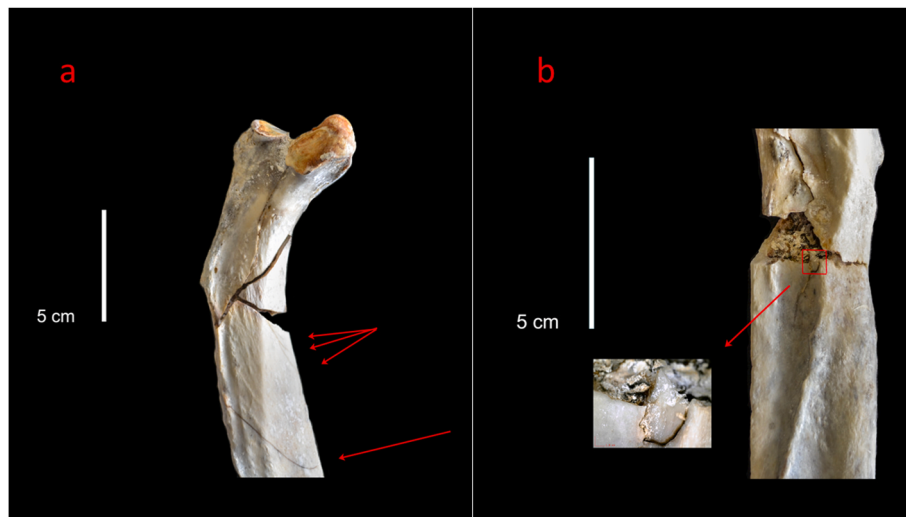


Fig. 5. Left: Rib damaged from a spear throwing impact (IE 2), refitted. Red arrows point to radiating spiral fractures. Right: Close up of rib damaged during spear throwing, including detail of the microflake from the point of impact from the spear. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

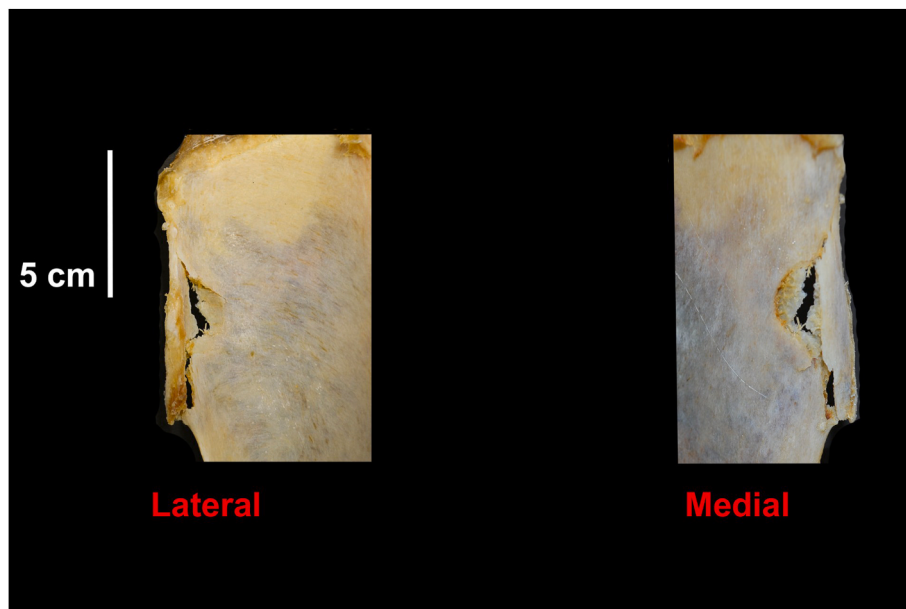


Fig. 6. Damage to the edge of the right scapula in the throwing experiment (IE 9).

with one example observed medially. No microscopic damage was visible on either side of Impact 6. This may be due to the alternative cleaning process used for Impact 6, which resulted in sediment adhering to the bone surface, potentially obscuring microscopic percussion marks. SEM images captured a selection of microscopic damage, including overlapping microstriations around the edge margins of the impact sites.

3.5. Analysis of GTP17 scapula

Given that the damage on the GTP17 scapula is semi-circular in shape, we make a cautious comparison of this feature with both the overall sizes of this with both incomplete curvilinear and complete circular/irregular perforations. We do not directly compare area values for size comparisons due the mixture of complete and incomplete perforations. The Boxgrove specimen's length compares well with experimental hammerstone damage to scapula and is notably longer than all wooden

spear and composite weapon experimental damage (Table S6). The closest weapon damage, in terms of length, is that from the throwing experiment in this paper (Fig. 6). However, while the experimental spear damage on the scapula is indeed long, its breadth is much smaller, as it occurred on the thin margin of the blade.

The results of the LDA are visualized in Fig. 9, highlighting the separation of the groups in the LDA space. The LDA model also predicted the Boxgrove GTP17 perforation as belonging to the "Experimental Hammerstone Impact" category with a posterior probability of 0.7539, followed by "Experimental Wooden Spear" (0.2351) and "Experimental composite weapon" (0.0109). The confusion matrix from jackknife cross-validation revealed an overall accuracy of 76 % (95 % CI: 0.5487, 0.9064), with Kappa statistics of 0.6134, indicating substantial agreement between observed and predicted classifications. Specific performance metrics are summarized in Table S8.

The blade fragment of the horse scapula did not exhibit microscopic percussive damage. However, we note that this was not consistent across

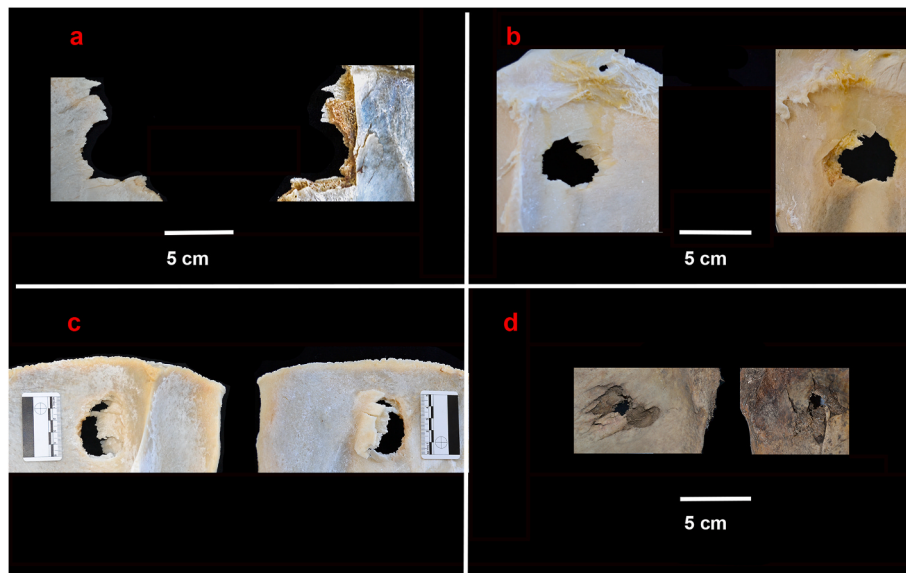


Fig. 7. Lateral (left) and medial (right) views of the four scapulae bearing experimental hammerstone impact damage. a) Impact 1 b) Impact 4 c) Impact 5 d) Impact 6.

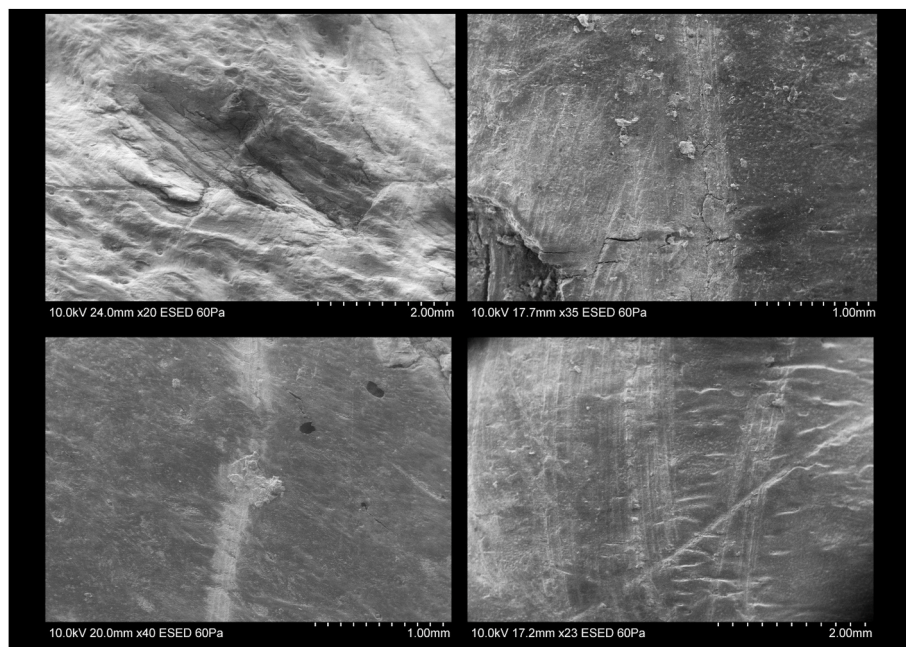


Fig. 8. SEM images of experimental hammerstone percussion. Top left clockwise: a) A pit on Impact 4 with microstriations, b) microstriations on Impact 5, c) microstriations associated with a pit on Impact 5 and d) microstriations and a groove on Impact 5.

all scapulae impacted in the present study. In other experimental hammerstone studies with larger sample sizes, the frequency of percussion-marked fragments when using non-modified hammerstones ranged from 22.3 % to 32.5 % (Galán et al., 2009). The Boxgrove scapula displays a very small amount of external bevelling with a latero-medial ratio of 1.03:1. Three cross-sections of the curvilinear fracture have been taken from the CT scan to provide a visualization of the fracture edge (Fig. 10). These cross-sections illustrate the minimal external bevelling present on the curvilinear damage. Impacts most often result in internal bevelling. Therefore, if the curvilinear fracture on the Boxgrove scapula resulted from an impact, the most likely scenario is that this impact occurred from the medial side. This makes the possibility of impact from a weapon less likely, as spearing through a horse scapula from the inside

would be highly improbable due to its anatomical location on the blade and the structure of the horse's body.

3.6. Methodological reflections

As with all prehistoric weaponry experiments, there were trade-offs between controlled conditions (e.g. using homogenous target materials) and those that allowed examination of the relationship between weapon and target (e.g. the carcasses) (Eren and Meltzer, 2024). Cost and time limited the number of impacts. We opted for a balance between control of variables, such as weapon material and spear design, while exploring the interaction between wooden spears and animals. While this does not represent a 'real life' hunting scenario, the results provide new insight into

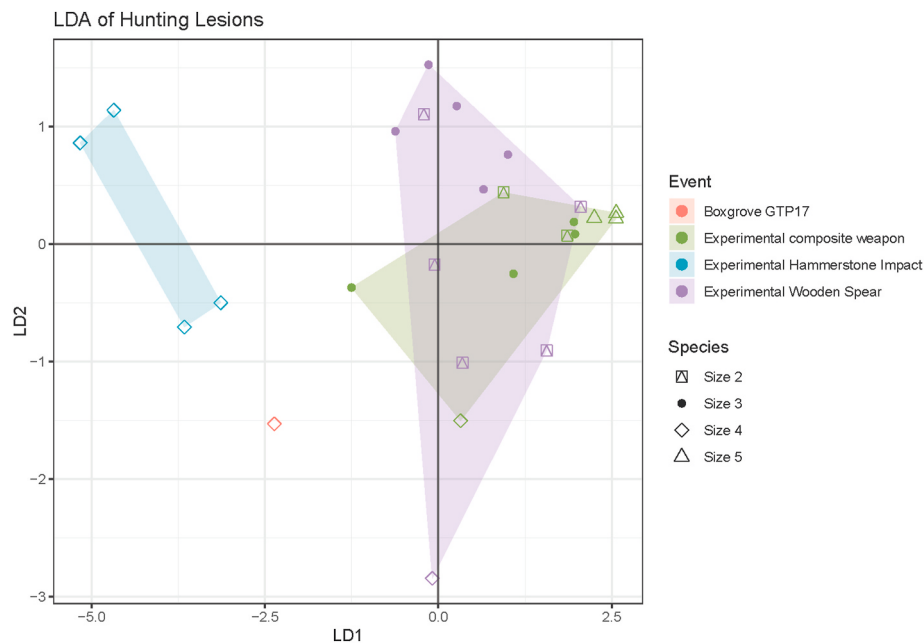


Fig. 9. LDA Visualization of Hunting Lesions. LDA plot showing the separation of experimental groups on different animal size class categories: "Experimental Composite Weapon," "Experimental Hammerstone Impact," and "Experimental Wooden Spear."

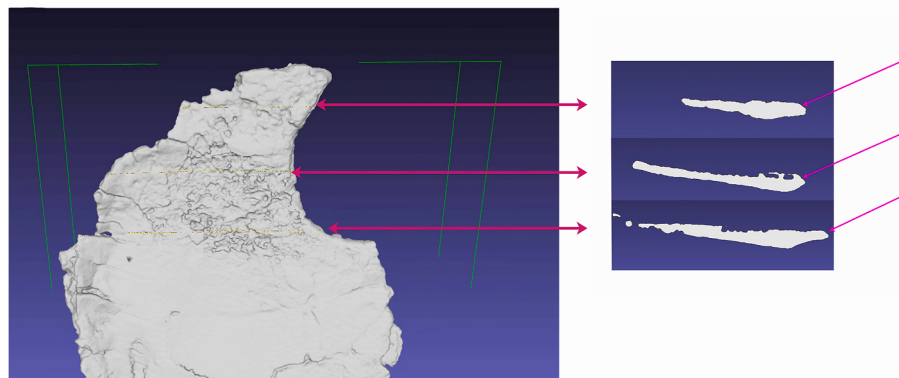


Fig. 10. Left: lateral view of the CT scan of the curvilinear fracture, with arrows indicating location of each slice. Right: three slices of CT scan, with arrows showing small amount of beveling on fracture margin.

the potential of wooden spears to penetrate hide, damage bone, and cause potentially lethal injuries, particularly for large prey. Direct and indirect archaeological evidence, coupled with ethnographic data support the plausibility of these results (Gaudzinski-Windheuser et al., 2018; Russo et al., 2023; Leder et al., 2024; Milks, 2020; Hutson et al., 2024).

A limitation of the hammerstone experiment is small sample size, which limited the ability to explore probability of macro- and microscopic signatures, which would require a much larger experimental sample. Nevertheless, the results indicate the potential for such damage to occur during impact with hammerstones, and provides important data about qualitative and quantitative comparison with both the Boxgrove specimen and weapon impacts.

4. Discussion and conclusion

4.1. An alternative explanation? the processing of cancellous bone for marrow and fat

Numerous ethnographic studies describe the practice of marrow extraction, particularly from long bones (Binford, 1978; O'Connell et al.,

1988; Oliver and Hudson, 1993; Abe, 2005; Hiatt, 1968). Hadza hunters break not only long bones with hammerstones and anvils, but also axial elements, such as zebra ribs at kill sites to extract marrow. For larger prey, hammerstones and anvils were used in 93 % of the breakage events, targeting limb and axial bones (Oliver and Hudson, 1993). Key for understanding the evidence at Boxgrove are ethnographic examples of uncooked cancellous bone being consumed, for example by striking the bone with a hammerstone on an anvil, followed by scraping out the cancellous tissue with a knife, then sucked on or chewed (O'Connell et al., 1988; Oliver and Hudson, 1993). Pulverising and swallowing bone to access nutrients, with or without the added use of heat to extract them (Morin, 2020), is another recorded process, and has been argued to be a strategy employed by later Neanderthals where evidence for the use of hot-rock technology (Abe, 2005; Costamagno et al., 2013; Marean et al., 2005). These practices demonstrate how humans maximise fat and nutrients from marrow and grease locked within cancellous bone, even using bones with smaller reserves. Such a practice during the Lower Palaeolithic may well have preceded the application of heat technology in the Middle Palaeolithic to further maximise nutritional yields.

Marrow is highly caloric and rich in fat, making it an essential dietary

component for humans subsisting on high protein, low carbohydrate diets, which would particularly be the case in cooler temperate periods in high latitudes (Hosfield, 2020; Outram, 2001). Increased processing of animals, especially for marrow, is known to coincide with resource stress. This practice reflects the need to maximise returns from the animal while accessing fat reserves that persist even in lean or starving animals; bones retain fat as the body metabolises other stores first (Stiner, 2005; Outram, 2001). Equids were a dietary staple of hominins throughout the Pleistocene (Voormolen, 2008; Hutson et al., 2024; Forsten and Moigne, 1998; Domínguez-Rodrigo et al., 2015) and although the amount of marrow yield from horses is lower compared to other ungulates (Blumenshine and Madrigal, 1993) it contains a high concentration of essential polyunsaturated fats (Outram and Rowley-Conwy, 1998), which are healthier compared with the saturated fats in most animal marrow. Ethnographic evidence suggests that humans consume marrow from relatively low-yield animals, such as equids, not only due to nutritional benefits but also for taste preferences (Outram and Rowley-Conwy, 1998; Oliver and Hudson, 1993).

Hominins regularly processed long bones and mandibles for marrow, including from equids, and may have exploited lower-yield elements such as scapulae under certain circumstances. The faunal assemblages from other localities at Boxgrove supports the interpretation that hominins regularly consumed marrow and grease from spongy bones, including scapulae. Notably as the horse at GTP17 showed signs of malnutrition shortly before its death and may have provided fewer calories through consumption of lean meat, the humans may well have sought to exploit more of the carcass by exposing the cancellous bone in the scapula blade, neck and glenoid cavity to access the healthy liquid marrow and grease. This can be achieved using a simple and readily available technology of unmodified hammerstones with or without the use of an anvil. Indeed, the overall pattern of exploitation of the carcass appears to show a heavy focus on marrow exploitation, including of other skeletal elements, in the form of extreme fragmentation including long bone shafts, mandible, and the pelvis (Parfitt and Bello, 2020; Parfitt, 2020b; Smith, 2013).

A new interpretation of the Boxgrove GTP17 scapula can now be proposed: as part of an extensive strategy for accessing marrow and grease, hominins deliberately smashed the scapula open with a hammerstone. Questions around its size and morphology have been addressed here, including the proposed bevelling. Our analysis shows that only a very small amount of external bevelling is present, and such as it is, this likely indicates impact from the internal side of the blade countering the interpretation of a weapon impact. Although microscopic evidence of hammerstone impact is absent on the archaeological specimen, this could be due to the low percentage rates in experimental tests of this phenomenon, coupled with taphonomic effects on the bone. Finally, statistically the Boxgrove specimen is a better match to the hammerstone damage than to experimental weapon impacts, as is exemplified in the LDA.

We emphasise that the GTP17 horse may well have been hunted with a wooden spear before its butchery by the human group. Bearing in mind the limitations outlined in our experimental testing, our results demonstrate that Middle Pleistocene wooden spears are capable of creating lethal wounds to size class 4 prey animals, even if evidence in the form of hunting lesions from such weapons is rare. However, the analogical reasoning, supported by our experiments and archaeological comparisons, suggests that the curvilinear fracture on the Boxgrove horse scapula aligns more closely with hammerstone percussion than with weapon-induced damage.

Boxgrove occupies an important space in interpreting Middle Pleistocene hominin behaviour, providing a high-resolution record of the interaction with hominins and an array of materials to effectively and expertly navigate their environments, and provision themselves through primary access to large carcasses. The period of 600 to 400 ka is crucial for understanding human evolution in Europe. Within this period we have the first clear evidence of the control of fire, the spread of handaxe

technologies, and the use of organic materials for tools including for flintknapping and hunting (Ashton and Davis, 2021). These technologically-dependent behaviours, many of which are evidenced directly and indirectly in the material culture of Boxgrove, likely reflect social and cognitive advances that enabled occupation of these northern environments. The interpretation of a larger group involvement at GTP17 is supported here by our re-interpretation of the horse scapula damage as hammerstone impact for marrow access. A high-quality diet including fat, amino acids and essential fatty acids is especially important for females during pregnancy and breastfeeding, as well as in infancy and adolescence – life-history events that are particularly susceptible to negative impacts of nutritional stress (Nowell, 2021). Marrow and grease represent excellent nutritional resources, and so evidence of full exploitation of the GTP17's nutritional yield supports previous interpretations of the site as a focus for a larger, demographically diverse group including infants. The expert and near-complete exploitation of the horse carcass may reflect engagement and consumption by a wider group of hominins, including of all ages and sexes, maximising the nutritional yield while also indicating their confident control of the carcass over a number of hours in this open landscape. In spite of the lack of direct evidence of hunting in the form of a hunting lesion or a preserved weapon, the likelihood remains that the horse was actively hunted by the hominin group, or at the very least secured within a matter of minutes of its death, as the presence of carnivores at the site mean the carcass would have been quickly consumed by wolves and/or hyenas, who would have left clear signs of first access through tooth marks and gnawing. As early as MIS 13, the Boxgrove archaeological record evidences early human adaptive behaviours that are often suggested to appear at much later Pleistocene sites. Furthermore, behaviours such as large-game hunting are in evidence in other European Lower Palaeolithic sites, such as Gran Dolina (Atapuerca) (Rodríguez-Hidalgo et al., 2015, 2017). These include the strategic use of landscapes that attracted both hominins and predators in search of herbivores, a rich body of knowledge and skill to exploit local resources and a wide range of materials for technological purposes, expert butchery, and group cooperation. It remains a key site for understanding these origins of behaviours in human evolution and, even in the absence of a clear hunting lesion confirming use of weaponry, a site with important potential for research into the origins of hunting by human populations.

CRedit authorship contribution statement

Annemieke Milks: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Debra Carr:** Writing – review & editing, Visualization, Project administration, Formal analysis, Conceptualization. **Krishna Godhania:** Investigation. **Pete Mahoney:** Writing – review & editing, Investigation. **Simon Parfitt:** Writing – review & editing, Visualization, Resources, Investigation. **Gabriele Russo:** Writing – review & editing, Formal analysis, Data curation. **Matt Pope:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

- Abe, Y., 2005. *Hunting and Butchery Patterns of the Evenki in Northern Transbaikalia, Russia* [PhD Thesis].
- Ashton, N., Davis, R., 2021. Cultural mosaics, social structure, and identity: the Acheulean threshold in Europe. *J. Hum. Evol.* 156, 103011. <https://doi.org/10.1016/j.jhevol.2021.103011>.
- Assaf, E., Caricola, I., Gopher, A., Rosell, J., Blasco, R., Bar, O., Zilberman, E., Lemorini, C., Baena, J., Barkai, R., Cristiani, E., 2020. Shaped stone balls were used for bone marrow extraction at lower Paleolithic Qesem Cave, Israel. *PLoS One* 15 (4), e0230972. <https://doi.org/10.1371/journal.pone.0230972>.
- Austin, L.A., Bergman, C.A., Roberts, M.B., Willemsen, K.H., 1999. Archaeology of excavated areas. In: Roberts, M.B., Parfitt, S.A. (Eds.), *Boxgrove: a Middle Pleistocene Hominid Site at Eartham Quarry, Boxgrove, West Sussex*. English Heritage, pp. 312–378.
- Badenhorst, S., 2012. Cause and effect: the impact of animal variables on experimentally produced bone lesions. In: Seetah, K., Gravina, B. (Eds.), *Bones for tools—Tools for Bones*. McDonald Institute for Archaeological Research, pp. 65–71.
- Ben-Dor, M., Barkai, R., 2024. A matter of fat: hunting preferences affected Pleistocene megafaunal extinctions and human evolution. *Quat. Sci. Rev.* 331, 108660. <https://doi.org/10.1016/j.quascirev.2024.108660>.
- Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press.
- Blumenschine, R.J., Madrigal, T.C., 1993. Variability in long bone marrow yields of east African ungulates and its zooarchaeological implications. *J. Archaeol. Sci.* 20 (5), 555–587. <https://doi.org/10.1006/jasc.1993.1034>.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 333 (6175), 763–765. <https://doi.org/10.1038/333763a0>.
- Boëda, E., Geneste, J., Griggo, C., 1999. A levallois point embedded in the vertebra of (*Equus africanus*): hafting, projectiles and Mousterian hunting weapons. *Antiquity* 73, 394–402.
- Breeze, J., Carr, D.J., Mabbott, A., Beckett, S., Clasper, J.C., 2015. Refrigeration and freezing of porcine tissue does not affect the retardation of fragment simulating projectiles. *Journal of Forensic and Legal Medicine* 32 (C), 77–83. <https://doi.org/10.1016/j.jflm.2015.03.003>.
- Bridgland, D.R., Field, M.H., Holmes, J.A., McNabb, J., Preece, R., Selby, I., Wymer, J., Boreham, S., Irving, B., Parfitt, S.A., Stuart, A., 1999. Middle Pleistocene interglacial Thames–Medway deposits at Clacton-on-Sea, England: reconsideration of the biostratigraphical and environmental context of the type Clactonian industry. *Quat. Sci. Rev.* 18 (1), 109–146. [https://doi.org/10.1016/S0277-3791\(97\)00092-9](https://doi.org/10.1016/S0277-3791(97)00092-9).
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291, 574–577.
- Bunn, H.T., 1982. *Meat-Eating and Human Evolution: Studies of the Diet and Subsistence Pattern of Plio-Pleistocene Hominids* [PhD Thesis].
- 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 (4), 724–748. <https://doi.org/10.2307/282345>.
- Conard, N.J., Serangeli, J., Böhner, U., Starkovich, B.M., Miller, C.E., Urban, B., Van Kolschoten, T., 2015. Excavations at Schöningen and paradigm shifts in human evolution. *J. Hum. Evol.* 89 (C), 1–17. <https://doi.org/10.1016/j.jhevol.2015.10.003>.
- Conard, N.J., Serangeli, J., Bigga, G., Rots, V., 2020. A 300,000-year-old throwing stick from Schöningen, northern Germany, documents the evolution of human hunting. *Nature Ecology & Evolution* 4, 690–693. <https://doi.org/10.1038/s41559-020-1139-0>.
- Coppe, J., Lepers, C., Clarenne, V., Delaunoy, E., Pirlot, M., Rots, V., 2019. Ballistic study tackles kinetic energy values of Palaeolithic weaponry. *Archaeometry* 2 (4), 107–124. <https://doi.org/10.1111/arc.m.12452>.
- Costamagno, S., 2013. Bone grease rendering in Mousterian contexts: the case of noisetier cave (Fréchet-Aure, Hautes-Pyrénées, France). In: Clark, J.L., Speth, J.D. (Eds.), *Zooarchaeology and Modern Human Origins Human Hunting Behavior During the Later Pleistocene*. Springer, Netherlands, pp. 209–225. https://doi.org/10.1007/978-94-007-6766-9_13.
- Datoc, D., 2010. Finite Element Analysis and Modeling of a .38 Lead Round Nose Ballistic Gelatin Test. Master's Theses and Project Reports. <http://digitalcommons.calpoly.edu/cgi/viewcontent.cgi?article=1284&context=theses>.
- Delannoy, Y., Becart, A., Colard, T., Delille, R., Tournel, G., Hedouin, V., Gosset, D., 2012. Skull wounds linked with blunt trauma (hammer example). A report of two depressed skull fractures—elements of biomechanical explanation. *Leg. Med.* 14 (5), 258–262. <https://doi.org/10.1016/j.legalmed.2012.04.006>.
- Delannoy, Y., Colard, T., Becart, A., Tournel, G., Gosset, D., Hedouin, V., 2013. Typical external skull beveling wound unlinked with a gunshot. *Forensic Sci. Int.* 226 (1–3), e4–e8. <https://doi.org/10.1016/j.forsciint.2012.12.001>.
- Demuth, W.E., 1968. High velocity bullet wounds of the thorax. *Am. J. Surg.* 115 (5), 616–625. [https://doi.org/10.1016/0002-9610\(68\)90087-1](https://doi.org/10.1016/0002-9610(68)90087-1).
- Dominguez-Rodrigo, M., Rayne Pickering, T., Semaw, S., Rogers, M., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *J. Hum. Evol.* 48 (2), 109–121. <https://doi.org/10.1016/j.jhevol.2004.09.004>.
- Dominguez-Rodrigo, M., Barba, R., Soto, E., Sesé, C., Santonja, M., Pérez-González, A., Yravedra, J., Galán, A.B., 2015. Another window to the subsistence of Middle Pleistocene hominins in Europe: a taphonomic study of Cuesta de la Bajada (Teruel, Spain). *Quat. Sci. Rev.* 126, 67–95. <https://doi.org/10.1016/j.quascirev.2015.08.020>.
- Duches, R., Nannini, N., Romandini, M., Boschin, F., Crezzini, J., Peresani, M., 2016. Identification of late epigravettian hunting injuries: descriptive and 3D analysis of experimental projectile impact marks on bone. *J. Archaeol. Sci.* 66 (C), 88–102. <https://doi.org/10.1016/j.jas.2016.01.005>.
- Duches, R., Nannini, N., Fontana, A., Boschin, F., Crezzini, J., Peresani, M., 2020. Experimental and archaeological data for the identification of projectile impact marks on small-sized mammals. *Sci. Rep.* 10 (1). <https://doi.org/10.1038/s41598-020-66044-3>. Article 1.
- Eren, M.I., Meltzer, D.J., 2024. Controls, conceits, and aiming for robust inferences in experimental archaeology. *J. Archaeol. Sci.: Report* 53, 104411. <https://doi.org/10.1016/j.jasrep.2024.104411>.
- Eren, M.I., Bebbler, M.R., Mukusha, L., Wilson, M., Boehm, A.R., Buchanan, B., Miller, G. L., Skoglund, M., Hayes, J., Barta, M., Bates, S., Callaghan, R., Floyd, C., Morris, S., Neuhauser, S., Newcomb, C., Rinella, S., Schneider, C., Smith, M.M., et al., 2024. Experimental bison butchery using replica hafted Clovis fluted points and large handheld flakes. *J. Archaeol. Sci.: Report* 55, 104480. <https://doi.org/10.1016/j.jasrep.2024.104480>.
- Fenton, L.A., Horsfall, I., Carr, D.J., 2018. Skin and skin simulants. *Aust. J. Forensic Sci.* 1–11. <https://doi.org/10.1080/00450618.2018.1450896>.
- Forsten, A., Moigne, A., 1998. The Horse from the Middle Pleistocene of Orgnac-3 (Ardeche, France) [Les chevaux du site du Pléistocène moyen d'Orgnac 3 (Ardeche, France)]. <https://doi.org/10.3406/quate.1998.1613>.
- Friis-Hansen, J., 1990. Mesolithic cutting arrows: functional analysis of arrows used in the hunting of large game. *Antiquity* 64 (244), 494–504. <https://doi.org/10.1017/S0003598X0007839X>.
- Frison, G.C., 1974. *The Casper Site: Hell Gap Bison Kill on the High Plains*. Academic Press.
- Frison, G.C., 1989. Experimental use of Clovis weaponry and tools on African elephants. *Am. Antiq.* 54 (4), 766–784. <https://doi.org/10.2307/280681>.
- Galán, A.B., Rodríguez, M., de Juana, S., Dominguez-Rodrigo, M., 2009. A new experimental study on percussion marks and notches and their bearing on the interpretation of hammerstone-broken faunal assemblages. *J. Archaeol. Sci.* 36 (3), 776–784. <https://doi.org/10.1016/j.jas.2008.11.003>.
- García-Moreno, A., Hutson, J.M., Villaluenga, A., Turner, E., Gaudzinski-Windheuser, S., 2021. A detailed analysis of the spatial distribution of Schöningen 13II-4 'Spear Horizon' faunal remains. *J. Hum. Evol.* 152, 102947. <https://doi.org/10.1016/j.jhevol.2020.102947>.
- Gaudzinski-Windheuser, S., 2016. Hunting lesions in Pleistocene and early Holocene European bone assemblages and their implications for our knowledge on the use and timing of lithic projectile technology. In: *Multidisciplinary Approaches to the Study of Stone Age Weaponry*. Springer, Netherlands, pp. 77–100. https://doi.org/10.1007/978-94-017-7602-8_6.

- Gaudzinski-Windheuser, S., Noack, E.S., Pop, E., Herbst, C., Pflöging, J., Buchli, J., Jacob, A., Enzmann, F., Kindler, L., Iovita, R., Street, M., Roebroeks, W., 2018. Evidence for close-range hunting by last interglacial Neanderthals. *Nature Ecology & Evolution* 2, 1087–1092. <https://doi.org/10.1038/s41559-018-0596-1>.
- de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., Woldegabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284 (5414), 625–629.
- Hale, C., 1996. *The Butchers of Boxgrove*. BBC [Documentary].
- Hiatt, B., 1968. The food quest and the economy of the tasmanian aborigines (Continued). *Oceania* 38 (3), 190–219. <https://doi.org/10.2307/40329716>.
- Hosfield, R., 2020. *The Earliest Europeans A Year in the Life: Seasonal Survival Strategies in the Lower Palaeolithic*. Oxbow Books. <https://books.casematepublishers.com/The Earliest Europeans.pdf>.
- Hutson, J.M., Bittmann, F., Fischer, P., García-Moreno, A., Gaudzinski-Windheuser, S., Nelson, E., Ortiz, J.E., Penkman, K.E.H., Perić, Z.M., Richter, D., Torres, T., Turner, E., Villaluenga, A., White, D., Joris, O., 2025. Revised age for Schöningen hunting spears indicates intensification of Neanderthal cooperative behavior around 200,000 years ago. *Sci. Adv.*
- Hutson, J.M., Villaluenga, A., García-Moreno, A., Turner, E., Gaudzinski-Windheuser, S., 2024. Persistent predators: zooarchaeological evidence for specialized horse hunting at Schöningen 13II-4. *J. Hum. Evol.* 196, 103590. <https://doi.org/10.1016/j.jhevol.2024.103590>.
- Iovita, R., Schönekeß, H., Gaudzinski-Windheuser, S., Jäger, F., 2016. Identifying weapon delivery systems using macrofracture analysis and fracture propagation velocity: a controlled experiment. In: Iovita, R., Sano, K. (Eds.), *Multidisciplinary Approaches to the Study of Stone Age Weaponry*. Springer, pp. 13–28. <https://www.dropbox.com/home/Chapters>.
- Jarman, P.J., 1989. On being thick-skinned: dermal shields in large mammalian herbivores. *Biol. J. Linn. Soc.* 36 (1–2), 169–191. <https://doi.org/10.1111/j.1095-8312.1989.tb00489.x>.
- Julien, M.-A., Hardy, B., Stahlschmidt, M.C., Urban, B., Serangeli, J., Conard, N.J., 2015. Characterizing the lower Paleolithic bone industry from Schöningen 12 II: a multi-proxy study. *J. Hum. Evol.* 89, 264–286. <https://doi.org/10.1016/j.jhevol.2015.10.006>.
- Kieser, D.C., Riddell, R., Kieser, J.A., Theis, J.-C., Swain, M.V., 2014. Bone micro-fracture observations from direct impact of slow velocity projectiles. *Journal of Archives in Military Medicine* 2 (1), 1–6. <https://doi.org/10.5812/jamm.15614>.
- Kindler, L., Gaudzinski-Windheuser, S., Scherjon, F., García-Moreno, A., Smith, G.M., Pop, E., Speth, J.D., Roebroeks, W., 2025. Large-scale processing of within-bone nutrients by Neanderthals, 125,000 years ago. *Sci. Adv.* 11 (27), ead1257. <https://doi.org/10.1126/sciadv.adv1257>.
- Leder, D., Milks, A., 2025. In search of the origins of distance hunting—the use and misuse of tip cross-sectional geometry of wooden spears. *Journal of Paleolithic Archaeology* 8 (9). <https://doi.org/10.1007/s41982-024-00206-x>.
- Leder, D., Lehmann, J., Milks, A., Koddenberg, T., Sietz, M., Vogel, M., Böhner, U., Terberger, T., 2024. The wooden artifacts from Schöningen's spear horizon and their place in human evolution. *Proc. Natl. Acad. Sci.* 121 (15), e2320484121. <https://doi.org/10.1073/pnas.2320484121>.
- Leduc, C., 2012. New Mesolithic hunting evidence from bone injuries at Danish maglemosian sites: lundby mose and mullerup (Sjælland). *Int. J. Osteoarchaeol.* 24 (4), 476–491. <https://doi.org/10.1002/oa.2234>.
- Letourneau, C., Pétillon, J.M., 2008. Hunting lesions caused by osseous projectile points: experimental results and archaeological implications. *J. Archaeol. Sci.* 35 (10), 2849–2862.
- Lister, A.M., Parfitt, S.A., Owen, F.J., Collinge, S.E., Breda, M., 2010. Metric analysis of ungulate mammals in the early middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy. *Quat. Int.* 228 (1–2), 157–179. <https://doi.org/10.1016/j.quaint.2010.05.014>.
- Lockey, A.L., Rodríguez, L., Martín-Francés, L., Arsuaga, J.L., Bermúdez De Castro, J.M., Crété, L., Martínón-Torres, M., Parfitt, S., Pope, M., Stringer, C., 2022. Comparing the Boxgrove and Atapuerca (Sima de los Huesos) human fossils: do they represent distinct paleodemies? *J. Hum. Evol.* 172, 103253. <https://doi.org/10.1016/j.jhevol.2022.103253>.
- Mabbott, A., Carr, D.J., Caldwell, E., Miller, D., Teagle, M., 2014. Bony debris ingress into lungs due to gunshot. *The International Symposium on Ballistics Atlanta, GA* 1–9.
- Mabbott, A., Carr, D.J., Champion, S., Malbon, C., 2016. Comparison of porcine thorax to gelatine blocks for wound ballistics studies. *Int. J. Leg. Med.* 130 (5), 1353–1362. <https://doi.org/10.1007/s00414-015-1309-9>.
- Mahoney, P.F., Carr, D.J., Miller, D., Teagle, M., 2017. The effect of helmet materials and simulated bone and tissue layers on bullet behaviour in a gelatine model of overmatch penetrating head injury. *Int. J. Leg. Med.* 131 (6), 1765–1776. <https://doi.org/10.1007/s00414-017-1665-8>.
- Marean, C.W., 2005. From the tropics to the colder climates: contrasting faunal exploitation adaptations of modern humans and Neanderthals. In: d'Errico, F., Backwell, L. (Eds.), *From Tools to Symbols: from Wierly Hominids to Modern Humans*. Witwatersrand University Press, pp. 333–371.
- Milks, A., 2020. A review of ethnographic use of wooden spears and implications for Pleistocene hominin hunting. *Open Quat.* 6 (1). <https://doi.org/10.5334/oq.85>, 79–20.
- Milks, A., Champion, S., Cowper, E., Pope, M., Carr, D., 2016. Early spears as thrusting weapons: isolating force and impact velocities in human performance trials. *J. Archaeol. Sci.: Report* 10, 191–203. <https://doi.org/10.1016/j.jasrep.2016.09.005>.
- Milks, A., Parker, D., Pope, M., 2019. External ballistics of Pleistocene hand-thrown spears: experimental performance data and implications for human evolution. *Sci. Rep.* 9 (1), 820. <https://doi.org/10.1038/s41598-018-37904-w>.
- Milks, A., Lehmann, J., Leder, D., Sietz, M., Koddenberg, T., Böhner, U., Wachtendorf, V., Terberger, T., 2023. A double-pointed wooden throwing stick from Schöningen, Germany: results and new insights from a multianalytical study. *PLoS One* 18 (7), e0287719. <https://doi.org/10.1371/journal.pone.0287719>.
- Morin, E., 2020. Rethinking the emergence of bone grease procurement. *J. Anthropol. Archaeol.* 59, 101178. <https://doi.org/10.1016/j.jaa.2020.101178>.
- Noe-Nygaard, N., 1974. Mesolithic hunting in Denmark illustrated by bone injuries caused by human weapons. *J. Archaeol. Sci.* 1 (3), 217–248. [https://doi.org/10.1016/0305-4403\(74\)90024-7](https://doi.org/10.1016/0305-4403(74)90024-7).
- Nowell, A., 2021. *Growing up in the Ice Age: Fossil and Archaeological Evidence of the Lived Lives of Plio-Pleistocene Children* (Paperback). Oxbow Books.
- Oakley, K.P., Andrews, P., Keeley, L.H., Clark, J.D., 1977. A reappraisal of the clacton spearpoint. *Proc. Prehist. Soc.* 43, 13–30. <https://doi.org/10.1017/S0079497X00010343>.
- Oliver, J.S., 1993. Carcass processing by the Hadza: bone breakage from butchery to consumption. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, pp. 200–227. Occasional Paper No. 21.
- Outram, A.K., 2001. A new approach to identifying bone marrow and grease exploitation: why the “Indeterminate” fragments should not be ignored. *J. Archaeol. Sci.* 28 (4), 401–410. <https://doi.org/10.1006/jasc.2000.0619>.
- Outram, A.K., 2002. Bone fracture and within-bone nutrients: an experimentally based method for investigating levels of marrow extraction. In: Miracle, P., Milner, N. (Eds.), *Consuming Passions and Patterns of Consumption*. McDonald Institute for Archaeological Research, pp. 51–63.
- Outram, A.K., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (Equus). *J. Archaeol. Sci.* 25 (9), 839–849. <https://doi.org/10.1006/jasc.1997.0229>.
- O'Connell, J.F., Hawkes, K., Blurton Jones, N., 1988. Hadza hunting, butchering, and bone transport and their archaeological implications. *J. Anthropol. Res.* 44 (2), 113–161.
- O'Driscoll, C.A., Thompson, J.C., 2014. Experimental projectile impact marks on bone: implications for identifying the origins of projectile technology. *J. Archaeol. Sci.* 49 (C), 398–413. <https://doi.org/10.1016/j.jas.2014.05.036>.
- Parfitt, S., 2020a. 6 aspects of the life history and ecology of the GTP17 horse. In: *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove, UK*. SpoilHeap Publications, pp. 79–83.
- Parfitt, S., 2020b. 7 the taphonomy of the horse remains. In: *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove, UK*. SpoilHeap Publications, pp. 85–104.
- Parfitt, S., Bello, S., 2020. 8 the manufacture and use of bone tools. In: *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove, UK*. SpoilHeap Publications, pp. 105–122.
- Parfitt, S., Bello, S., 2024. Bone tools, carnivore chewing and heavy percussion: assessing conflicting interpretations of lower and upper Palaeolithic bone assemblages. *R. Soc. Open Sci.* 11 (1), 231163. <https://doi.org/10.1098/rsos.231163>.
- Parfitt, S.A., Roberts, M.B., 1999. Human modification of faunal remains. In: Roberts, M. B., Parfitt, S.A. (Eds.), *Boxgrove: a Middle Pleistocene Hominid Site at Earham Quarry, Boxgrove, West Sussex*. English Heritage, pp. 395–415.
- Pargeter, J., 2007. Howiesons poort segments as hunting weapons: experiments with replicated projectiles. *S. Afr. Archaeol. Bull.* 62 (186), 147–153. <https://doi.org/10.2307/20474970>.
- Parsons, I., Badenhorst, S., 2004. Analysis of lesions generated by replicated Middle Stone Age lithic points on selected skeletal elements: research letter. *South Afr. J. Sci.* 100 (July/August), 384–387.
- Pechnikova, M., 2013. Forensic analysis of bone fractures caused by blunt force trauma. PhD Thesis]. http://is.muni.cz/th/109015/prif_d/DP_Pechnikova.pdf.
- Peterson, B., 1991. External beveling of cranial gunshot entrance wounds. *J. Forensic Sci.* 36 (5), 1592–1595.
- Pettigrew, D.B., Bamforth, D.B., 2023. On the (Non-)Scalability of target media for evaluating the performance of ancient projectile weapons. *Open Archaeol.* 9 (1), 20220295. <https://doi.org/10.1515/opar-2022-0295>.
- Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33 (4), 459–469. <https://doi.org/10.1016/j.jas.2005.09.001>.
- Pitts, M., Roberts, M.B., 1997. Fairweather Eden: Life in Britain Half a Million Years ago as Revealed by the Excavations at Boxgrove. Century Books.
- Pope, M.I., 2002. The Significance of bifacial-rich Assemblages: an Examination of Behavioural Controls on Lithic Assemblage Formation in the Lower Palaeolithic [PhD Thesis]. <http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.270401>.
- Pope, M., 2003. Placing Boxgrove in its prehistoric landscape. *Archaeol. Int.* 7, 13–16. <https://doi.org/10.5334/ai.0705>.
- Pope, M., Roberts, M.B., 2005. Observations on the relationship between Palaeolithic individuals and artefact scatters at the middle Pleistocene site of boxgrove, UK. In: Gamble, C., Porr, M., Gamble, C., Porr, M. (Eds.), *The Hominid Individual in Context: Archaeological Investigations of Lower and Middle Palaeolithic Landscapes, Locales, and Artefacts*. Routledge, pp. 81–97.
- Pope, M., Roberts, M., Maxted, A., Jones, P., 2009. The valdov: archaeology of a locality within the boxgrove palaeolandscape, west sussex. *Proc. Prehist. Soc.* 75, 239–263. <https://doi.org/10.1017/S0079497X00000360>.
- Pope, M., Davis, R., Evans, A., 2020. 5 technological, refitting and microwear analysis of the stone artefact assemblage. In: *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove, UK*. SpoilHeap Publications, pp. 51–78.

- Pope, M., Roberts, M., Parfitt, S., 2020a. 10 the behavioural and social implications of the GTP17 horse butchery episode. In: *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove*, UK. SpoilHeap Publications, pp. 133–137.
- Pope, M., Roberts, M., Parfitt, S., 2020b. *The Horse Butchery Site GTP17: a high-resolution Record of Lower Palaeolithic Hominin Behaviour at Boxgrove*, UK. SpoilHeap Publications.
- Quatrehomme, G., Yaşar Işcan, M., 1998. Analysis of beveling in gunshot entrance wounds. *Forensic Sci. Int.* 93 (1), 45–60.
- R Core Team, 2021. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Richter, D., Krbetschek, M., 2015. The age of the lower Paleolithic occupation at Schöningen. *J. Hum. Evol.* 89 (C), 46–56. <https://doi.org/10.1016/j.jhevol.2015.06.003>.
- Rieder, H., 2001. Erprobung der Holzspeere von Schoeningen (400000 Jahre) und Folgerungen daraus. In: Wagner, G.A., Mania, D. (Eds.), *Frühe Menschen in Mittel Europa: Chronologie, Kultur, Umwelt*, pp. 91–98. Shaker.
- Roberts, M.B., 2011. Where now for Boxgrove? *Archaeol. Int.* 11, 28–32. <https://doi.org/10.5334/ai.1109>.
- Roberts, M.B., Parfitt, S.A. (Eds.), 1999. *Boxgrove: a Middle Pleistocene Hominid Site at Earham Quarry, Boxgrove, West Sussex*. English Heritage.
- Roberts, M.B., Stringer, C.B., Parfitt, S.A., 1994. A hominid tibia from middle Pleistocene sediments at Boxgrove, UK. *Nature* 369 (6478), 311–313. <https://doi.org/10.1038/369311a0>.
- Rodríguez-Hidalgo, A., Saladié, P., Ollé, O., Carbonell, E., 2015. Hominin subsistence and site function of TD10.1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. *J. Quat. Sci.* 30, 679–701. <https://doi.org/10.1002/jqs.2815>.
- Rodríguez-Hidalgo, A., Saladié, P., Ollé, O., Arsuaga, J.-L., Bermúdez de Castro, J.M., Carbonell, E., 2017. Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain). *J. Hum. Evol.* 105, 89–122. <https://doi.org/10.1016/j.jhevol.2017.01.007>.
- Russo, G., Milks, A., Leder, D., Koddenberg, T., Starkovich, B.M., Duval, M., Zhao, J.-X., Darga, R., Rosendahl, W., Terberger, T., 2023. First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals. *Sci. Rep.* 13 (1). <https://doi.org/10.1038/s41598-023-42764-0>. Article 1.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D.J., Hartenstein, V., Eliceiri, K., Tomancak, P., Cardona, A., 2012. Fiji: an open-source platform for biological-image analysis. *Nat. Methods* 9 (7), 676–682. <https://doi.org/10.1038/nmeth.2019>.
- Schoch, W., Bigga, G., Böhner, U., Richter, P., Terberger, T., 2015. New insights on the wooden weapons from the Paleolithic site of Schöningen. *J. Hum. Evol.* 89 (C), 214–225. <https://doi.org/10.1016/j.jhevol.2015.08.004>.
- Serangeli, J., Conard, N.J., 2015. The behavioral and cultural stratigraphic contexts of the lithic assemblages from Schöningen. *J. Hum. Evol.* 89, 287–297. <https://doi.org/10.1016/j.jhevol.2015.07.004>.
- Serangeli, J., Verheijen, I., Rodríguez-Álvarez, B., Altamura, F., Bigga, G., Schoch, W.H., Urban, B., van Kolfschoten, T., Venditti, F., Conard, N.J., 2023. Schöningen: a reference site for the middle Pleistocene. *Journal of Mediterranean Earth Sciences* 15, 369–387. <https://doi.org/10.13133/2280-6148/1815>.
- Smith, G., 2012. Hominin-carnivore interaction at the lower Palaeolithic site of Boxgrove, UK. *Journal of Taphonomy* 10 (3–4), 373–394.
- Smith, G., 2013. Taphonomic resolution and hominin subsistence behaviour in the lower Palaeolithic: differing data scales and interpretive frameworks at Boxgrove and Swanscombe (UK). *J. Archaeol. Sci.* 40 (10), 3754–3767. <https://doi.org/10.1016/j.jas.2013.05.002>.
- Smith, M.J., Brickley, M.B., Leach, S.L., 2007. Experimental evidence for lithic projectile injuries: improving identification of an under-recognised phenomenon. *J. Archaeol. Sci.* 34 (4), 540–553.
- Smith, G., Noack, E.S., Behrens, N.M., Ruebens, K., Street, M., Iovita, R., Gaudzinski-Windheuser, S., 2020. When lithics hit bones: evaluating the potential of a multifaceted experimental protocol to illuminate middle Palaeolithic weapon technology. *Journal of Paleolithic Archaeology* 126–156. <https://doi.org/10.1007/s41982-020-00053-6>.
- Spatola, B.F., 2015. Atypical gunshot and blunt force injuries: wounds along the biomechanical continuum. In: *Skeletal Trauma Analysis: Case Studies in Context*. Wiley & Sons Ltd, pp. 7–26.
- Starkovich, B.M., Conard, N.J., 2015. Bone taphonomy of the Schöningen 'Spear Horizon South' and its implications for site formation and hominin meat provisioning. *J. Hum. Evol.* 89 (C), 154–171. <https://doi.org/10.1016/j.jhevol.2015.09.015>.
- Stiner, M.C., 2005. The Faunas of hayonim Cave, Israel: a 200,000-year Record of Paleolithic Diet, Demography, and Society. with Contributions by Ofer Bar-Yosef. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, Mass.
- Stringer, C.B., Trinkaus, E., Roberts, M.B., Parfitt, S.A., Macphail, R.I., 1998. The middle Pleistocene human tibia from Boxgrove. *J. Hum. Evol.* 34 (5). <https://doi.org/10.1006/jhevol.1998.0215>, 39–39.
- Thieme, H., 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385, 807–810.
- Thieme, H., 1999. Lower palaeolithic throwing spears and other wooden implements from Schoeningen, Germany. In: Ullrich, H. (Ed.), *Hominid Evolution: Lifestyles and Survival Strategies*. Gelsenkirchen Germany : Edition Archaea, pp. 383–395.
- Van Kolfschoten, T., 2014. The Palaeolithic locality Schöningen (Germany): a review of the mammalian record. *Quat. Int.* 326–327, 469–480. <https://doi.org/10.1016/j.quaint.2013.11.006>.
- Van Kolfschoten, T., Knul, M., Buhrs, E., Gielen, M., 2012. Butchered large bovids (*Bos primigenius* and *Bison priscus*) from the Palaeolithic throwing spear site Schöningen 13 II-4 (Germany). A Bouquet of Archaeozoological Studies 12, 32–45. Groningen Archaeological Studies.
- Voormolen, B., 2008. Ancient hunters, modern butchers: Schöningen 13 II-4, a kill-butchery site dating from the northwest European lower Palaeolithic. *Journal of Taphonomy* 6 (2), 71–141. <https://doi.org/10.1002/9781118659991>.
- Ward, J., Mathias-Davis, H., Cooper, S., Crawford, E., Wheeler, M., Asher, G., 2015. Evaluation of production traits of red deer skins in the deer progeny test. *Proc. N. Z. Soc. Anim. Prod.* 75.
- Warren, S., 1911. Proceedings: 'first Published Report and exhibition of the specimen, May 10th, 1911'. *Quarterly Journal of the Geological Society* 67 (1–4), XCIX. <https://doi.org/10.1144/GSL.JGS.1911.067.01-04.02>.
- Wenban-Smith, F.F., 1999. Knapping technology. In: Roberts, M.B., Parfitt, S.A. (Eds.), *Boxgrove: a Middle Pleistocene Hominid Site at Earham Quarry, Boxgrove, West Sussex*. English Heritage, pp. 384–395.
- Wilkins, J., Schoville, B.J., Brown, K.S., Chazan, M., 2012. Evidence for early hafted hunting technology. *Science* 338 (6109), 942–946. <https://doi.org/10.1126/science.1227608>.
- Wood, J., Fitzhugh, B., 2018. Wound ballistics: the prey specific implications of penetrating trauma injuries from osseous, flaked stone, and composite inset microblade projectiles during the Pleistocene/Holocene transition, Alaska U.S.A. *J. Archaeol. Sci.* 91, 104–117. <https://doi.org/10.1016/j.jas.2017.10.006>.
- Woodcock, A., 1981. The lower and middle Palaeolithic periods in Sussex. *BAR Br. Ser.* 94.