

5. THE ESSENTIAL ELEPHANT: NORTHWEST EUROPEAN HOMININ ADAPTATIONS THROUGH THE MIDDLE–LATE PLEISTOCENE AND NEANDERTHAL EXTINCTION

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ABSTRACT

This paper firstly presents the “Ebbsfleet elephant”, an instance of Middle Pleistocene elephant exploitation from the southeast United Kingdom. The find is well-dated to fully interglacial conditions in the early temperate part of MIS 11. The association of hominin activity with the elephant remains is clear-cut. The elephant bones comprise the partial remains of an adult male, occurring in near-life position in one well-defined horizon. A scatter of refitting flint artifacts was found in close association, beside the rib area. Although there is no direct evidence as to how the beast died (and whether it was hunted), it seems inescapable that this find represents hominin exploitation of the carcass. The find is then considered from a wider ecological perspective: firstly, for the importance of elephants (and other megaherbivores) for hominin adaptations to more-seasonal environments of higher latitudes, and northward colonization during post-glacial climatic ameliorations as exemplified in MIS 11; and

secondly for their importance for the persistence of more-northerly populations during pre-glacial climatic deterioration and cold glacial stages. It is suggested that elephant (and mammoth/rhino) exploitation may have been an important enabling factor for settlement of northern latitudes, and may have been a critical constraint upon hominin range during periods of climatic deterioration. This perspective then leads to the conjecture that Neanderthal extinction in northwest Europe during the last ice age was fundamentally caused by the reliance by both modern humans and Neanderthals on a mammoth-niche, and by the unsustainable over-exploitation of this niche by the former leading to the demise of the latter.

5.1 INTRODUCTION

The Volkswagen Symposium “Human-elephant interactions: from past to present”, which took place in Hannover (Germany) 16th-18th October



2019, provided an ideal opportunity to discuss this topic, with a wide variety of contributors gathered from across the world. The diversity of expertise allowed new perspectives to be developed, new critiques of some preconceived ideas, and relevant information to be combined from the varied spheres of the participants. For myself, as a Palaeolithic archaeologist with a primary expertise in lithic artifacts, it provided a valuable opportunity to present the relatively-recent discovery in the UK of the “Ebbsfleet elephant” to a wider audience, and to explore some new ideas about its interpretation. Previous reporting of this find (Wenban-Smith, 2013a) has focused on putting it in a secure Pleistocene dating and palaeoenvironmental framework, reconstructing hominin activity at the site, and considering the lithic remains in relation to wider patterns in the UK and northwest European record. In contrast at the Symposium, I wished to take this level of interpretation as a starting point to consider a wider ecological perspective on the Ebbsfleet elephant find, and on the importance of elephant and other mega-herbivore exploitation for Pleistocene hominin adaptations in the northwest European region.

This approach is followed through in this resulting paper, which presents some conjectures—“conjecture: an opinion or inference based on information that is incomplete or not certain”—for further consideration. The first part (Section 2) recaps the Ebbsfleet elephant find, and summarizes current understanding of its date, and its interpretation in terms of on-the-spot hominin behavior and how the observed lithic technology fits in to the wider UK and northwest European framework. The next section (Section 3) outlines a wider ecological framework for considering Pleistocene hominin adaptations. The history of European Palaeolithic study has been dominated by narratives of lithic technological and typological change (e.g., Bordes, 1950; Breuil and Lantier, 1951; Roe, 1981; Wymer, 1982) across space and through time. However, as increasingly recognised since the later 20th century (e.g., Geist, 1978; Gamble, 1986, 1987, 1993; Roebroeks, 2001), a

deeper understanding of the period has to situate hominin adaptations and evolution within the dynamic ecological framework of changing Pleistocene climate, and the complex network of faunal and floral adaptations that constitute the stage for the slow dispersal of hominins from their Pliocene African cradle to their near-global ubiquity by the end of the Pleistocene.

Having outlined some ecological principles to frame the discussion, Section n.4 puts forward the conjecture that megafaunal exploitation (primarily of elephants, although potentially including other megaherbivores such as rhinoceros) was a key enabling factor that allowed northward expansion into higher latitudes during warmer phases of the Middle Pleistocene. Although (as explicated below) entirely consistent with theoretical ecological principles, this notion was initially inspired as a counter-position to that put forward by Surovell et al. (2005). These authors looked at the broad global patterning of proboscidean kill sites, and suggested that they were preferentially located at the margins of areas occupied by hominins through the Early and Middle Pleistocene. They then suggested that this apparent pattern indicates hominin overkill as a driving factor of regional proboscidean extinction. However, it seems intuitively unlikely that the long-term successful and resilient adaptations of these huge beasts—who could be considered “apex herbivores”, at the top of an evolutionary pyramid of vegetation exploitation, resistant to predation, and bestriding the Pleistocene world in great numbers—would be so vulnerable to the minuscule impact upon their numbers that could have been wrought by the tiny and fragile hominin populations of the era. Rather, the pattern presented by Surovell et al. might be better understood as reflecting the importance of proboscidean exploitation for hominins as they expanded their range, without necessarily having a negative impact upon proboscidean populations. Taking the Ebbsfleet elephant as one exemplar, this notion is further explored through consideration of the wider evidence for hominin expansion, adaptations and elephant presence in Europe in MIS

11, focusing upon the NW region as defined by Gamble (1986: fig. 3.1) comprising the northern part of France and the UK.

Then, having started by outlining an ecological framework that emphasizes the importance of megaherbivores for hominin adaptations and expansion within the context of one ameliorating phase of Pleistocene climate during which hominins became for the first time relatively widespread across northwest Europe, the last part of the paper (Section n.5) considers how northwest European archaic hominin and herbivore adaptations might respond to a cooling climatic phase, and remain resilient through subsequent later Middle and Late Pleistocene climatic oscillations—right up to the point in the middle of the last (Devensian) ice age, when the Neanderthal lineage suddenly (at a deep Pleistocene timescale) disappeared, and was replaced in west and northwest Europe c. 40,000–30,000 BP by anatomically modern *Homo sapiens*.

This replacement—or apparent replacement—has been the topic of substantial debate for many years (e.g., Mellars and Stringer, 1989; Mellars, 1990, 2004; Akazawa et al., 1998; Klein, 2003; Harvati, 2012; Zilhao, 2014). Very few dispute the observed pattern in western Europe of a rapid replacement in the late Middle Pleistocene of a hominin population with physiological attributes that we characterize as “Neanderthal” by a different population with clearly-different attributes that we recognize as anatomically modern humans. However, there remain widely-contrasting, and deeply-entrenched, positions for the explanation of this empirical phenomenon. Some see the Neanderthal-Modern transition as a misleading artifact of the fossil record whereby a single species has undergone rapid evolutionary change, or whereby the coalescence and genetic mixing of native Neanderthals with an incoming anatomically modern population has led to a hybrid population that is physiologically modern but nonetheless retains significant Neanderthal genetic make-up (e.g., Zilhao, 2014). Many (and perhaps most) others, however, accept that the native west/northwest

European Neanderthal population was suddenly replaced by modern humans (e.g., Harvati et al., 2007), although there are widely-varying suggestions for the degree of overlap and the underlying cause of the transition (Soffer, 1994; van Andel and Davies, 2003; Mellars, 2004; Stewart, 2005; Kuhn and Stiner, 2006; Golovanova et al., 2010; Houldcroft and Underdown, 2016; Ko, 2016).

Although it has previously been regularly suggested that the most likely reason for the Neanderthal demise lies in some form of ecological incompatibility for their sustainable co-existence alongside modern humans (e.g., Wenban-Smith, 2007: p. 45; Banks et al., 2008), convincing details as to the precise nature of this incompatibility have yet to be put forward. Here, it is conjectured that, from an ecological perspective, the persistence of the Neanderthal lineage in more-northerly latitudes during cold climatic stages may have been dependent upon exploitation of a mammoth-niche, and the further north, the more dependent. And thus, that the root cause of the Neanderthal demise may have been that they were out-competed in this specific niche by modern humans, who expanded into the Neanderthal world during the middle of the last ice age, providing for the first time direct competition for the specific mammoth-niche that allowed hominin survival so far north in a cold periglacial environment. Direct evidential support for this theoretically-derived scenario is provided in Bocherens and Drucker (this volume) and Germonpré et al. (this volume), complementing previously-published work (Richards et al., 2000; Bocherens, 2009, 2011; Bocherens et al., 2015; Drucker et al., 2017; Wißing et al., 2016, 2019; Wojtal et al., 2019) demonstrating through isotope studies the reliance of both modern human and Neanderthal populations on mammoth meat, and direct instances of mammoth hunting or other exploitation by both groups. This may therefore provide the first instance whereby unthinking modern human over-exploitation of a key resource has had direct and catastrophic impact upon the well-being of a fellow-traveler in the interactive web of adaptation that is life on earth.

5.2 THE EBBSFLEET ELEPHANT

5.2.1. INTRODUCTION AND BACKGROUND TO THE SITE

The “Ebbsfleet elephant” is a partially-complete skeleton of one *Palaeoloxodon antiquus* individual, found and excavated at Southfleet Road on the west side of the Ebbsfleet valley, Swanscombe, Kent (Fig. 5.1). The excavation was part of the

huge program of archaeological work in advance of the HS1 (High Speed 1) rail line, linking the Channel Tunnel at Folkestone with the London terminal at St. Pancras. The site was discovered in late 2003, and excavated in conjunction with Oxford Archaeology through spring-autumn 2004. An interim report appeared quite rapidly (Wenban-Smith et al., 2006), and this was followed in due course by a full report (Wenban-Smith, 2013a). Many details—in particular, the strati-

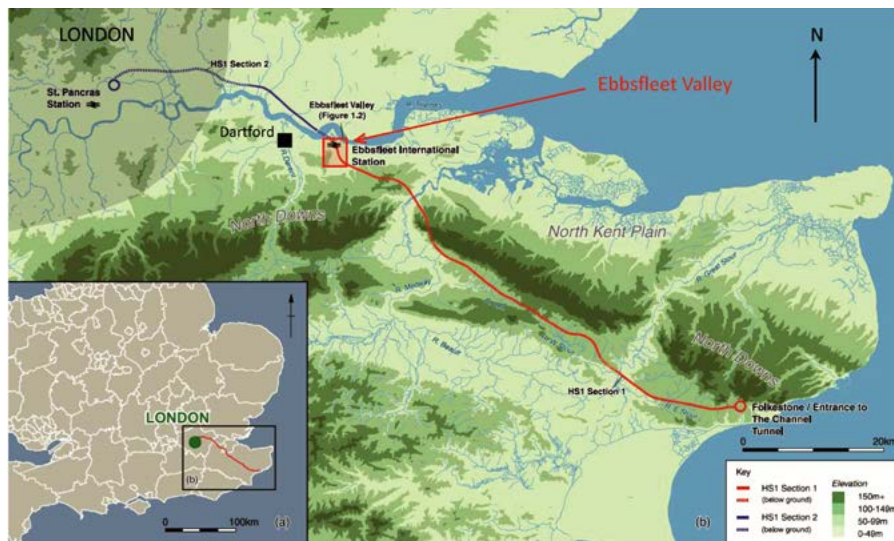


Figure 5.1: HS1 route in the southern UK, and location of Ebbsfleet valley [adapted from Wenban-Smith (2013a: p. 2, fig. 1.1); with permission of Oxford Archaeology and High Speed 1].

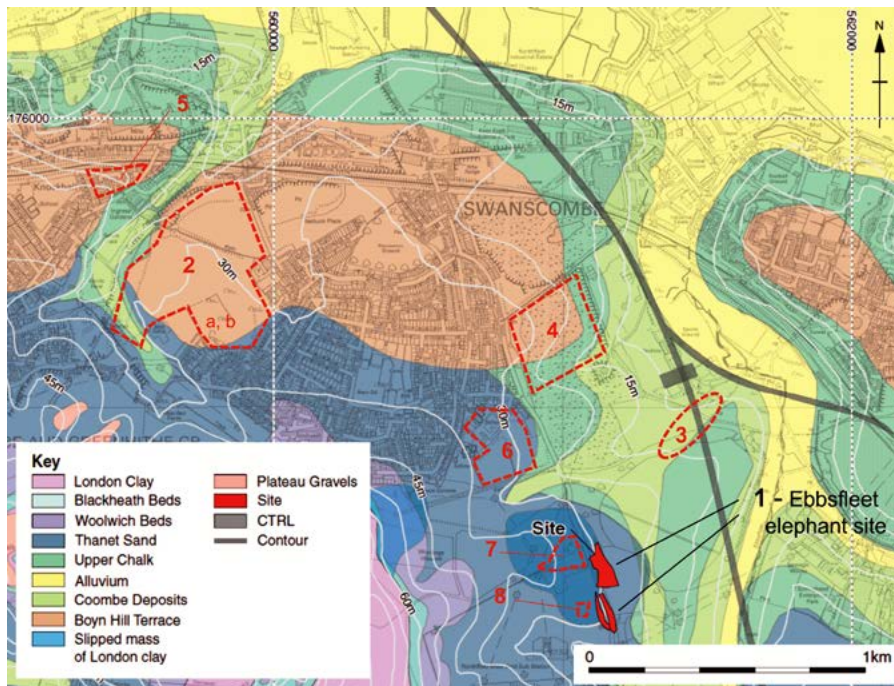


Figure 5.2: The Ebbsfleet elephant site in relation to Pleistocene geological mapping and key local Lower/Middle Palaeolithic sites (see Table 5.1) [adapted from Wenban-Smith (2013a: p. 12, fig. 2.3); with permission of Oxford Archaeology and High Speed 1].

SITE #	NAME	PALAEOLITHIC FINDS	REFERENCES
1	HS1 Southfleet Road - Ebbsfleet elephant site	Undisturbed elephant butchery site (associated with Clactonian material), overlain by a fluvial gravel rich in handaxes	Wenban-Smith (2013a)
2	Barnfield Pit, Swanscombe	Classic sequence of sand, gravel and loam deposits; Clactonian in lower deposits; handaxes („Acheulian“) in upper deposits, along with Swanscombe skull	Wymer (1968: pp. 334–346), Conway et al. (1996)
- a	Barnfield Pit, Skull site, Wymer excavations 1955-1960	Three different parts of Swanscombe skull found close to each other, on separate occasions between 1935 and 1955	Swanscombe Committee (1938), Ovey et al. (1964)
- b	Barnfield Pit, Waechter excavations 1968-1972	Investigation of Lower Gravel and Lower Loam, c. 50 m NE of skull site area	Conway et al. (1996)
3	Baker’s Hole Levallois site	Prolific Levalloisian industry from chalky valley-side slopewash deposits	Smith (1911), Wenban-Smith (1995)
4	Rickson’s Pit	Abundant Clactonian, handaxe and Levalloisian remains recovered, but not with good provenance	Wymer (1968: pp. 351–352)
5	Dierden’s Pit/Yard	Handaxes, flakes, and rich faunal and molluscan preservation, in places	Wenban-Smith (2009); White et al. (2013)
6	Swan Valley Community School	Boyn Hill/Orsett Heath terrace (Swanscombe Middle Gravels) with abundant lithic artifacts (handaxes, cores and flakes) and an elephant tusk	Wenban-Smith and Bridgland (2001)
7	Bevans Wash-pit	22 handaxes and 4 debitage; also reports of elephant/mammoth teeth	Spurrell (1890), Wenban-Smith (2004: Stopes Site 14)
8	Ebbsfleet Green	Undisturbed palaeolandsurface with refitting Clactonian lithic industry, thought to be contemporary with the Ebbsfleet elephant	Wenban-Smith (2014)

Table 5.1: Key Lower/Middle Palaeolithic sites in the Swanscombe area (see Figure 5.2).

graphic phasing and depositional interpretations of some sediment beds, and some lithic artifact counts and interpretations— were substantially revised in the final report, so it is the latter (which is freely downloadable) that should be consulted for further more-detailed information on the site. This section provides a brief recap of the elephant, the associated lithic artifacts relating to its hominin exploitation, and the rich associated palaeo-environmental remains that allow us to locate the elephant and its hominin exploitation precisely in the Hoxnian (MIS 11c, stage Ho IIb-c). It is, however, worth noting that the elephant was just one aspect of the site, which had 11 main stratigraphic phases, and evidence of

Palaeolithic activity spanning from very early in MIS 11 (and perhaps before) through to its end (and perhaps after).

The Ebbsfleet elephant site (Fig. 5.2, Site 1) is located within a rich landscape of surviving evidence from the Lower and Middle Palaeolithic on the southern side of the Thames (Fig. 5.2; Table 5.1), in its lower tidal reaches where it heads east from London towards the North Sea. Here, the higher ground above the southern bank of the river is lined by a series of Middle Pleistocene terrace deposits that have been noted since the late 19th century for their abundant evidence of early hominin activity, in association with mammalian fossils and other palaeo-environmental remains. These de-

DEPOSIT PHASE	MI STAGE	DATE BP	STRATIGRAPHIC UNIT	HEIGHT, MOD	PALAEOLITHIC ARCHAEOLOGY
III	11-10/10/10-8?	?300,000– ?375,000	Upper Gravel	c. 33–35	Uncertain, few reliably-provenanced material other than technologically undiagnostic debitage
			Upper Loam	c. 32–33	
II	11	?375,000– ?400,000	Upper Middle Gravel	c. 28–32	Acheulian - Handaxes (mostly pointed) with thick partly-trimmed butts, often large and well-made, but also small and crude; also occasional cores, debitage and ad hoc flake-tools [Swanscombe Skull was found at the junction between Upper and Lower Middle Gravels]
			Lower Middle Gravel	c. 27–29	
I	11	?400,000– 425,000	Lower Loam	c. 25–27	Clactonian - Cores, debitage, simple flake-tools (often single or double notches), and very occasional crude „proto-handaxes“
			Lower Gravel	c. 23–27	

Table 5.2: Barnfield Pit, Swanscombe: sequence, dating and Palaeolithic industries.

posits—originally categorized as the Swanscombe 100-ft Terrace, or the Boyn Hill Terrace, but now more-properly labelled as part of the Orsett Heath Formation (Bridgland, 1994)—have been investigated at numerous sites, and mostly represent fluvial deposition in the UK’s Hoxnian interglacial (MIS 11). Perhaps the most important site is at Barnfield Pit, Swanscombe (Fig. 5.2, Site 2), located c. 1.5 km to the northwest of the Ebbsfleet elephant site. This was one of the first UK sites where systematic and controlled investigations established changing lithic industries through a deep Middle Pleistocene sequence (Smith and Dewey, 1913, 1914). It is also one of only three British sites where early hominin skeletal remains have been found, represented by an incomplete skull, different parts of which were found on three separate occasions between 1935 and 1955 (Swanscombe Committee, 1938; Ovey, 1964). A further programme of work was carried out at Swanscombe in the 1970s, involving investigation of the lower parts of the sequence—the Lower Loam— which proved to contain a series of undisturbed remains from palaeo-landsurfaces, with a non-handaxe Clactonian lithic industry (Conway et al., 1996). The Barnfield Pit sequence is summarised below (Table 5.2), as it provides an important framework for contextualizing the near-

by Ebbsfleet elephant site within the UK’s MIS 11 Palaeolithic record.

The Ebbsfleet is a small south-bank tributary of the lower Thames. Its valley cuts northward into the Thames through the Boyn Hill/Orsett Heath Formation, and thus its contained deposits—which include the celebrated Baker’s Hole Levalloisian site (Fig. 5.2, Site 3)— mostly post-date MIS 11. However, deposits from MIS 11 are preserved further south up the Ebbsfleet’s valley, higher up the valley on its west side, and it is here that the elephant site is located (Fig. 5.2, Site 1).

5.2.2. DISCOVERY, EXCAVATION, CONTEXT AND DATING

The majority of construction work for HS1 took place in the central and lower parts of the Ebbsfleet valley, relating to installation of the high-speed line and Ebbsfleet International station. The elephant site was discovered during bulk ground reduction for a new access road down from the higher ground to the southwest of the new station. It was very unfortunate that the bulk ground reduction removed the rear half of the elephant, and any associated Palaeolithic artifacts before the

site was discovered. This has unfortunately compromised the eventual scope of interpretation of some aspects of behaviour at the site; in particular, consideration of matters such as group-size, intensity of exploitation of the carcass, and the import/export of lithic tools to the site from elsewhere, are hindered by uncertainty over the missing evidence.

The first sign of the elephant was when the tusks were uncovered by a mechanical excavator (Fig. 5.3a). After this, the rest of the elephant remains were carefully excavated by hand (Fig. 5.3b–d), and they were found to comprise the front half of a single animal. Many bones were in poor condition, although a few were remarkably pristine. The larger bones showed weathering due to pre-burial exposure and had also suffered in situ degradation due to shear stress and compression during their burial. Some smaller bones, especially some of those from the front feet found near the head area of the beast (Fig. 5.3c), were in very good condition; these must have been buried relatively rapidly and their small size made them more resistant to in situ degradation.

The elephant bones were associated with a scatter of approximately 60 mint condition flint artifacts. This scatter was centred immediately beside the rib area, and there were also several flint artifacts amongst the concentration of elephant bones (Fig. 5.3d). The faunal and lithic remains were all found at a well-defined horizon c. 10cm thick within a much thicker (2–3m) bed of grey clay (phase 6) that extended across most of the wider site (Fig. 5.4). The grey clay under the elephant contained various sub-horizontal orange/red bands c. 2cm thick, slightly hardened at their top. These are interpreted as short-lived palaeo-landsurfaces within a build-up of sediment that mostly took place in a wet environment. The elephant horizon was defined by a dark brown organic-rich bed within the grey clay. Enough pollen was found in this bed (Turner et al., 2013) to (a) identify the local environment as a swampy alder carr within a wider landscape that was predominantly-forested, al-

though with some more-open areas, and (b) to attribute the deposits as laid down in the early temperate sub-stage II of an interglacial, and to identify that this was most-likely the Hoxnian interglacial (MIS 11c).

These dating and palaeo-environmental attributions were reinforced by other lines of evidence, in particular by mammalian biostratigraphy and amino acid analysis for dating (Parfitt, 2013a, b; Penkman and Wenban-Smith, 2013), and by interpretation of other mammalian and ostracod faunal remains from the same horizon as the elephant (Parfitt, *ibid.*; Whittaker et al., 2013). The grey clay generally contained rare and widely-scattered identifiable bones of other mammals (such as rhinoceros). However, there was a minor stream channel stratified within one part of the grey clay about 15m to the east of the elephant. This channel was infilled with a white tufaceous silt/sand, which contained small vertebrate and molluscan remains in abundance, as well as some remains of larger vertebrates such as macaque, deer and rhinoceros. Of particular importance was that several articulating bones of one foot of the elephant were found near the bank of this channel, and that another bone from the same foot was found within the channel-fill. This provides a firm foundation for linking the elephant skeleton and its associated pollen remains with the rich palaeo-environmental and dating evidence from the tufaceous channel-fill. It was thus possible to confidently attribute the elephant remains to the early temperate zone HO-II of the UK's Hoxnian interglacial (MIS 11c), and more specifically to relate them to the period covered by sub-zones IIB-c, dating c. 420,000–410,000 BP.

The elephant skeleton was located at the west edge of what would have been the marshy floodplain in the floor of the Ebbsfleet valley, and at the foot of what would have been a slope rising up further to the west, capped by Tertiary clay beds. The model for site formation is that the water level at the valley floor was periodically fluctuating, at the same as there being a —possibly episodic— input of fine-grained slopewash sed-



Figure 5.3: The Ebbsfleet elephant under excavation: (a) shortly after discovery, tusk remnants freshly exposed; (b) tusks fully uncovered, in very poor condition but retaining life position; (c) spread of thoracic, rib and foot bones; (d) flint core amongst elephant bones, note broken bone caused by mechanical excavator before site was discovered.

iment down the slope from the west. Thus the elephant died at a point in the landscape where short-lived dry landsurfaces at the edge of the floodplain were regularly becoming submerged by rising water, and where slopewash deposition was leading to sediment aggradation. The elephant carcass initially lay on a stable dry landsurface at the edge of the floodplain, and then must have remained exposed for several years, enough for some of the bone surfaces of larger bones (skull and limb bones) to have become exposed and weathered (Parfitt et al., 2013). The water level of the floodplain then rose, and they were then covered by clay-silt deposits slipping down onto the wet floor of the floodplain from the west. The bones were probably initially enveloped in a peaty clay-silt deposit forming in a marshy zone at the edge of the valley floor, which subsequently became dried and compressed as overlying sediments continued to accumulate through the ensuing millennia.

As shown below in Figure 4, the elephant remains and the adjacent flint scatter are closely juxtaposed, in an area of the site where other faunal and lithic remains are otherwise very scarce. As outlined above, the elephant skeleton must have been gently buried where the animal first fell, and not been transported or substantially-disturbed post-mortem. Several of the elephant bones are in near-anatomical position in relation to each other, and the overall dispersal of the bone scatter is restricted within an area of 2 m × 5 m, commensurate with minor post-death decay and animal disturbance. The flint artifacts found beside it are all in mint (or very fresh) condition. The lithic assemblage comprised 77 artifacts in total, of which 12 were small chips <2 cm maximum length. Their fresh condition and their recovery from a tight area beside the elephant provided a strong initial indication that these too are undisturbed. It is also beyond reasonable doubt that they were causally linked with the elephant skeleton since the lithic

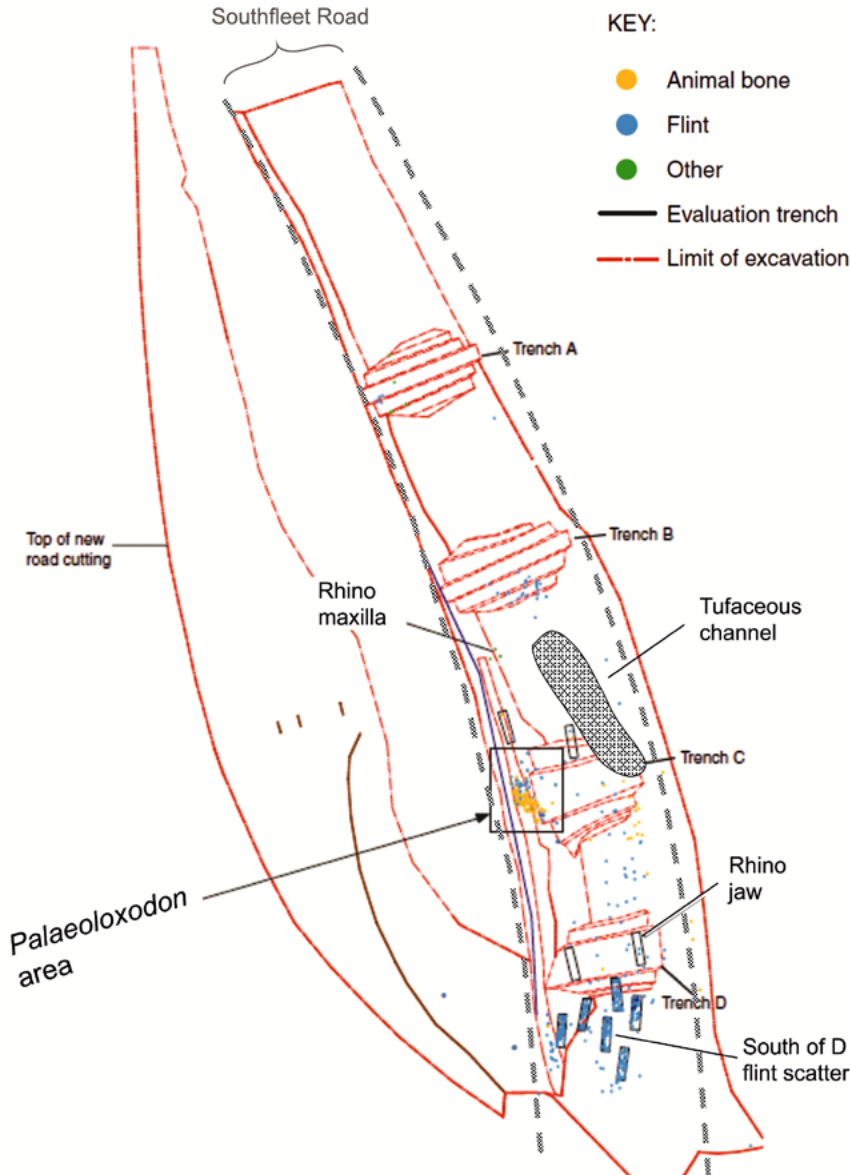


Figure 5.4: The Ebbsfleet elephant site (phase 6): the elephant area in relation to other key aspects of the site [adapted from Wenban-Smith et al. 2006: p. 475, fig. 4d; with permission of Oxford Archaeology].

scatter respects the bone concentration and occurs at the same specific horizon, and these remains occur in an area of the site where lithic and faunal remains are otherwise scarce and widely-dispersed within the phase 6 clay.

5.2.3. LITHIC REMAINS AND ON-SITE BEHAVIOR

A refitting study was carried out (a) to further investigate the degree of disturbance, and (b) to in-

vestigate the hominin activity relating to the lithic remains. The results of the refitting (Table 3; Fig. 5.5) showed that most of the artifacts (nearly 80%, excluding the small chips) were refittable into one of 7 groups A–G. The largest group (C) had 24 constituent pieces, including the core and one flake with visible damage suggesting use as a tool. This refitting group included the full sequence of reduction debitage from very early in the sequence through to the eventual core, which was also present. Some large flakes were missing from the refitted sequence, and it is suggested that these

REFITTING GROUP	SUMMARY DESCRIPTION	ARTIFACTS (N)	TECHNOLOGICAL NOTES
A	Refitting flake sequence, without core	7	Sequence of flakes from early parts of a core's reduction, from distinctive banded grey/white flint with green cortex, but core not found
B	Large core, with several flakes	7	Large remnant cylindrical core, with sequence of refitting flakes from early in its reduction
B?	Debitage, probably related to Group B	1	Cortical irregular waste from end of a cylindrical nodule, probably start of Group B reduction sequence
		1	Small secondary flake, the notch from making notched flake-tool - very similar flint raw material as Group B
C	Moderate-sized core, with numerous flakes	24	Reasonably complete reduction sequence from initial decortication of nodule through to core; refitting sequence includes a flake with use-damage indicating use as a flake-tool
D	Broken percussor	7	Broken flint percussor - appears to have broken in use, and then used further after breaking
E	Broken core	3	Core that has broken into three pieces from one blow, one of these pieces then knapped further, although the flake removed is missing; nor are flakes from earlier stages of reduction present
F	Broken flake	2	Medium-sized flake, partly-cortical, that has broken on knapping
G	Broken cortical flake	2	Small cortical flake that has split during percussion
-	Core	1	Large core on southern fringe of elephant lithic concentration
-	Flake-tools	3	Two utilised flakes and one notched flake-tool, two of them from amongst the elephant bones
-	Flakes	6	Mostly from edge of elephant lithic concentration
-	Irregular waste	2	-
-	Chips <2cm	11	-
Total		77	

Table 5.3: The lithic assemblage by the elephant: refitting groups and other elements.

were selected for tool-use and exported from the immediate area of their manufacture. This is where it becomes particularly frustrating to have lost the rear end of the elephant. They might have been left only a few yards beyond the excavated area, for instance by its rump. Alternatively, they might have been totally removed from the elephant area for use elsewhere. Knowing which of these behaviours took place has major implications for our understanding of hominin capabilities and adaptations at this time, so it is very unfortunate to have lost this evidence here.

Group B (7 pieces, including the core) had a relatively large remnant core of good quality flint,

that had been started at the spot, but then curiously had been abandoned after only a few removals and left substantially unknapped. In contrast, Group D (7 pieces) did not represent a sequence of reduction, but the shattered remnants of a globular flint nodule used as a percussor. It is suggested that this percussor broke while trying/failing to remove a large flake from the Group B core, since this core shows batter marks at a point consistent with an attempted flake removal. The Group A reduction sequence represents the early stages of reduction from raw material that likewise was probably found nearby, although the core and later reduction stages of this sequence were not recovered. Group E,

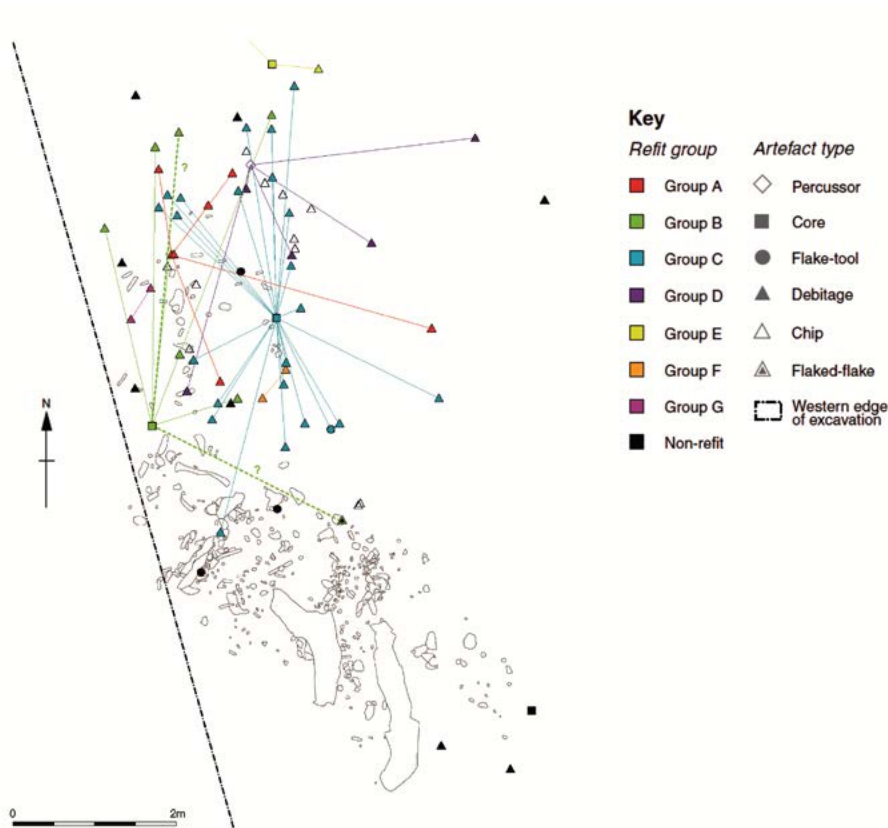


Figure 5.5: The Ebbfleet elephant: skeletal layout and lithic refitting groups [adapted from Wenban-Smith (2013a: p. 344, fig. 17.4); with permission of Oxford Archaeology and High Speed 1].

in contrast, represents a core for which the early stages of reduction were not recovered, and which seems to have been abandoned on the spot after breaking due to an internal flaw.

Three non-refitting flake-tools were identified, as well as the above-mentioned flake-tool that was part of refitting group C. One of these was a small flake that had had a single notch knapped on one side. The other three flake-tools did not have secondary working, but had otherwise-sharp edges with visible zones of minor chipping/scaling interpreted as use-damage. The notched flake-tool was found in the centre of the lithic scatter, but the other three were found at its southern edge, in amongst the elephant bones (Fig. 5.5). There was also evidence of a missing notched flake-tool represented by the secondary flake that produced the notch. Therefore there was direct evidence of 5 flake-tools, and there were also 5–6 medium-large flakes missing from the refitted sequences, which it is suggested were also chosen for use as tools.

The conclusion of the refitting study was that the lithic scatter had undergone minimal or no post-depositional disturbance, and that the flint artifacts were recovered in almost exactly the places they had been left by hominin activity. It seems vanishingly unlikely that, in an area of the site where lithic and faunal remains are otherwise very scarce, this quantity of knapping activity and tool-use could take place right beside (and partly amongst) an elephant carcass and be unrelated to it. The absence of observed cut-marks on any of the elephant bones should not be taken as indicating an absence of human butchery. As observed by Haynes (1991: pp. 185–186) and Crader (1983), exploitation of such large animals as elephants for meat and/or other tissue would often leave no trace on the remnant bones. And in this case, the surfaces of the larger bones have in any case been subject to pre-burial weathering and exposure that would have removed any traces that might have been left. Therefore, the Ebbfleet elephant evidence is confidently interpreted as a location where early

hominins used flint tools to exploit a carcass of *Palaeoloxodon antiquus*.

The lithic remains show that some on-the-spot knapping took place (Groups A, B and D) of flint raw material that was probably collected nearby - there was a good source in the valley-side <50m to the west —as well as some tools and part-knapped raw material (Group E) being brought to the site. The knapping activity involved the production of numerous flakes, and then some seem to have been chosen for use without further modification, and others for simple modification (such as creation of a single notch with one knapping blow) before being used. Functionally, these tools would have been ideal for cutting tasks, even heavy-duty tasks such as cutting elephant hide and flesh, so that is the interpretation of the activity at the site.

Several flakes and flake-tools were found that could not be linked with on-the-spot reduction. Here again, it is frustrating not to have the full site preserved, since this would have revealed whether they were made by the elephant, or brought in. In total, the number of pieces of raw material represented in the surviving lithic assemblage is c. 12. This could be taken as indicative of the number of incidents when the elephant was exploited for meat (or other nutritional elements), although it remains uncertain whether this should be envisaged as having taken place as one event for a larger group, or on repeated occasions by fewer individuals. Considering the amount of food represented, and its nutritional importance in terms of key dietary requirements such as fat and essential vitamins (Ben-Dor et al., 2011; Brown et al., 2013), it would seem likely that it would be repeatedly exploited as long it was nutritionally viable. This period was envisaged as being of the order of weeks in the original report on the site (Wenban-Smith 2013b: p. 367). However, Boschian and Saccà (2015) and Boschian et al. (2019) suggest that parts of a megaherbivore carcass, particularly marrow, could maintain nutritional value for much longer, for many months or even up to a year in certain circumstances. It is also noteworthy

that none of the elephant remains —including the well-preserved foot bones, part of the fatty pad of the foot which would have been desirable to carnivores— showed any sign of animal gnawing, suggesting that the hominins protected access to the carcass from other carnivores.

Based on the evidence that we do have (and thus without agonising on the unknown missing evidence) activity at the site involved a combination of tools made/used/abandoned on the spot, and also tools for which there is no evidence of on-site manufacture; these latter may, therefore, have been brought to the site from elsewhere, in anticipation of their use. Thus the most-plausible model for interpretation of the site is that a fresh carcass was initially exploited, maybe by a band of hominins with as few as 2–4 members, with on-the-spot raw material discovery and tool production/abandonment. And then the carcass was repeatedly visited over the following weeks/months, maybe bringing cutting tools or part-reduced cores to the known carcass location, followed by their export or discard.

Variations on this model might involve less frequent visits by a larger hominin group, or tethering of local mobility to the area of the carcass while it was being exploited, so as to protect it from other carnivores. Unfortunately preservation of Middle Pleistocene archaeological landscapes that allow investigation of behaviour from this era at this level of detail across the landscape almost don't exist; the only exception to my knowledge being the Boxgrove landsurface that survives intermittently over several hectares in the old Eartham Pit (Roberts and Parfitt, 1999). And even at Boxgrove, the excavated areas are too small to encompass more than about 10 seconds of Palaeolithic pedestrian movement to cross them, so this level of interpretation remains out of reach until we find, and fully excavate, a palaeo-landscape of Boxgrove scale. This would have to be envisaged as a major multi-decadal project, requiring huge investment, but with correspondingly major returns in increasing our understanding of Middle Pleistocene hominin adaptations.

5.2.4. PALAEOLITHIC ELEPHANT HUNTING? AND WIDER CONSIDERATIONS

It is uncertain how the elephant died, and what role hominins might have played in its death. It was a large adult male in its prime (c. 45 years old), so this is a beast that would not normally have died from natural causes, and that would have been resistant to carnivore predation. Although it intuitively seems unlikely, there is documented evidence in the modern era of humans killing elephants with simple spears (e.g., Zwilling, 1942), and modern evidence of elephant hunting with (albeit metal-tipped) spears in the eastern Congo Basin by the Mbuti hunter-gatheres (Icjikawa, this volume). It is known from finds at Clacton (Wymer, 1985: pp. 264–285), Schöningen (Thieme, 1997) and Boxgrove (Pitts and Roberts, 1997) that wooden spears were part of the technological capacity of hominins of this era, and the Eemian (MIS 5e) elephant carcass at Lehringen (Adam, 1951; Gaudzinski, 2004) was found with what seems to be a wooden spear in its rib cage, so hunting was a feasible possibility for the demise of the Ebbsfleet elephant, and cannot be ruled out. Also, see the review by Agam and Barkai (2018), which clearly identifies that elephant hunting by Middle Pleistocene hominins was both feasible, and is also documented in the archaeological record. Adult males might also have regularly become injured in the course of fighting each other when in must, and this could have then made them vulnerable to hominin predation. One possibility that can be ruled out, however, is the long-standing trope (e.g., White, 2012) in relation to prehistoric hominin exploitation of elephant remains that the beast was rendered vulnerable by being entrapped in marshy sediment; the elephant bones were resting on a flat and undisturbed palaeo-landsurface, which must have been firm and dry when the carcass first came to rest there.

Technologically, the lithic industry is focused on the production of sharp-edged flakes that could be either be used unmodified as cutting tools, or which were used as blanks for simple notched

flake-tools, also ideal for cutting tasks. While the lithic assemblage by the elephant is maybe too small to characterise a lithic industry, a much more substantial concentration of >1750 flint artifacts was found in the site area “south of D” at the same horizon as the elephant and only 30m to its south. This much larger assemblage showed exactly the same technological characteristics as that beside the elephant (Wenban-Smith, 2013c), and it seems inescapable that they are the contemporary products of the same hominin group, or certainly a broadly contemporary group sharing the same cultural practices.

Within the context of the UK’s culture-historical Palaeolithic narrative, the site is important as providing a clear representation of the Clactonian industry, characteristic of the initial re-occupation of the UK in the Hoxnian climatic amelioration following the end of the Anglian glaciation. Although this topic was the subject of debate in the later 20th century (McNabb and Ashton, 1992; Ashton et al., 1994; Wenban-Smith, 1998), the Ebbsfleet elephant site seems to have moved the dial (McNabb, 2020) in establishing that the early Hoxnian occupants of the UK practised a distinctive non-handaxe core/flake/flake-tool industrial tradition that can be labelled as Clactonian. Handaxe-based Acheulian traditions become prevalent later in the Hoxnian, and the focus of debate should now be whether or not this represents a further influx of settlement into the UK, or whether the observed change represents *in situ* technological development. As previously argued (Wenban-Smith, 1998, 2013d) it seems very unlikely that two contemporaneous and geographically proximal hominin groups could maintain culturally distinct lithic industrial traditions in northwest Europe in the Lower Palaeolithic.

Although a UK-focused instance, this is an example of an interpretive issue of pan-European, and pan-global, Palaeolithic relevance. The “tribal” culture-historical interpretation of the European Palaeolithic record as a narrative of movement around the continent of distinct and culturally conservative hominin groups is deeply rooted in

simplistic 19th and early 20th century perspectives on the archaeological record derived from externalist perspectives on contemporary hunter-gatherer groups such as indigenous first-nation Americans (e.g., Osborn, 1915; Bordes, 1950, 1969). It should also be remembered that the Palaeolithic record has not accumulated steadily through the vast swathes of Pleistocene time, but represents evidence from momentary episodes, interspersed with invisible hiatuses that represent the vast majority of that timespan. What might appear as sudden and drastic technological changes, more-likely represent the telescoped evidence of incremental change over many thousands of years. Thus, rather than invoke an Acheulian invasion to account for the appearance in Britain of handaxe-based industrial traditions later in the Hoxnian (e.g., Ashton et al., 2016), it is more parsimonious, and also more compatible with a realistic understanding of the nature of the Middle Pleistocene archaeological record, to regard this change as representing in situ technological development of the British population - who it should also be remembered were now for the first time cut off on an island from mainland continental Europe (Preece, 1995). And likewise in other parts of the world, we should be wary about a simplistic reversion to culture-historical explanations of synchronous and diachronic material cultural variability, without proper consideration of alternative explanations that take account of the multiplicity of behavioural and contextual factors that can influence material cultural deposition, and without better consideration of the distorting effect of the time-dilated nature of the deep archaeological record.

A contingent question then becomes to consider why did the lithic industrial tradition that sufficed during the initial post-Anglian colonisation of Britain undergo this change. And beyond that, what factors drive lithic technological change through the Palaeolithic across the globe, once one thinks beyond a shallow tribal and culture-historical narrative focusing on the strip of the away team (Gamble, 1986: p. 15). These are not questions that will be addressed in the remainder of this pa-

per, although the ecological framework discussed is without doubt pertinent to them. However, briefly, I suggest that lithic technological practices should be seen as locally-specific solutions to perennial problems of resource distribution —embracing lithic raw materials, other raw materials, animal resources, and plant resources - and adaptive strategy— embracing mobility, demography and technology. Thus, there is potential for high degrees of convergent and repetitive technological evolution through the Palaeolithic. For instance, it seems unnecessary (as well as unconvincing) to invoke continuity of a culturally-transmitted “Acheulian” industrial tradition to explain the connection between a handaxe-making instance in Lower Pleistocene Africa and one in India, or between an instance in the Somme valley of northern France in MIS 15 and one in southern Britain 200,000 years later in later MIS 11. Rather, it seems reasonable to see handaxe development as a recurring solution to a particular set of problems posed for Middle Pleistocene hominin groups living in environments with a certain structure of constraints and potentialities. And likewise, one can equally see that handaxe-making, which is a more difficult technical skill than flake production, may fade away in certain circumstances if a hominin adaptation can flourish without it —as for instance exemplified in the Middle Pleistocene record at Notachirico (Italy), where there appears to be recurring oscillation between horizons with handaxe manufacture and those without (Piperno et al., 1998; Piperno and Tagliacozzo, 2001). In fact, considering the efficacy of a simple unworked flake as a cutting tool, one of the key hitherto-unasked questions of the Palaeolithic has to be: “why did they ever bother with handaxe-making?”, which is not only technically much more difficult, but requires more-carefully-chosen raw material, more-specific and harder-to-source tools such as a soft bone/antler percussor, and, after all that effort, produces a tool with a less acute cutting edge.

In relation to the Ebbsfleet elephant site and the transition from “Clactonian” flake/core lithic industrial traditions to “Acheulian” handaxe-dom-

inated traditions through the Hoxnian in the UK, I have argued (Wenban-Smith, 1998, 2013c) that this may relate to changing patterns of mobility and resource exploitation in relation to the changing availability of lithic raw material through an interglacial period. However, the intention of this contribution is to look beyond this type of site-specific, culture-historical and regionally-contextual interpretation, valuable parts of the subject discourse though these are. Rather, I wish to situate the Ebbsfleet elephant discovery within a wider ecological framework, and to explore the importance, and implications, of megaherbivore exploitation—and in particular elephant exploitation—for Middle Pleistocene hominin adaptations in northwest Europe.

5.3 ECOLOGICAL FRAMEWORK FOR PLEISTOCENE ADAPTATIONS

5.3.1. SOME UNDERLYING PRINCIPLES

Ecology involves understanding the web of interactions between living organisms that allow them to persist in a sustainable manner. The interactions between living organisms are in a constant state of dynamic flux, as they eat each other, compete for resources, and evolve to survive and procreate better. The earth has some fundamental physical parameters that constrain and influence the adaptations of various species. In particular, there is the annual seasonal cycle whereby varying day-length affects the amount of solar radiation received, latitude that affects the angle of the sun's radiation and thus its intensity, and macro-regional factors such as the continentality or the degree of maritime influence. These parameters define the plant growing season and productivity in different parts of the globe, leading to regionally and latitudinally distinctive biomass structure, encompassing primary plant growth, and higher trophic levels of secondary and tertiary animal consumption.

As summarized by numerous authors (e.g., Geist, 1978; Gamble, 1986; Roebroeks, 2001),

increasing seasonality in higher latitudes generally leads to simpler ecosystem structures, with lower diversity of plant and animal species. For moderately-high latitudes primary plant production includes trees and shrubs that lock a substantial amount of received energy into their physical structure, which then shuts down for the winter, and grasses that grow vigorously in the growing season, but which only retain a modest perennial root system and invest most of this energy into producing and dispersing seeds that lie dormant until the next growing season. At even higher latitudes, the constraints of the annual growing season mean that trees are not sustainable, and the primary plant biomass is predominantly grasses, with some shrubs. And at the highest latitudes (such as much of Antarctica), life has not yet evolved to be sustainable, so it is a barren waste of snow and ice. Herbivorous animal communities that are the primary consumers of the plant biomass, and then secondary and tertiary animal consumers, have likewise evolved various adaptations that show regional and latitudinal variation in conjunction with the fundamental patterning of primary plant production.

From the point of view of investigating early hominin adaptations, and the Middle Pleistocene spread of hominins into northwest Europe, this region was peripheral to the lower latitude tropical and sub-tropical core zone of hominin occupation in the late Pliocene and Early Pleistocene, where hominins filled an adaptive niche in ecosystems with higher animal diversity and less seasonality. Through the later Early Pleistocene and the early Middle Pleistocene there seems to have been a pattern of occasional hominin incursions into more northerly latitudes during warmer episodes (Dennell, 2003; Parfitt et al., 2005, 2010), interspersed with long periods of absence when they were unable to sustain a stable adaptation in the higher latitudes with the challenges of greater seasonality, harsher winters and the associated structuring of animal communities. As suggested by Dennell (*ibid.*) these early cycles of northward expansion and then local extinction most likely correspond with the expansion and contraction of the ecozone

in which the earliest European hominins were adapted. It is suggested here—in fact echoing the suggestion of Geist (1978: pp. 281–282) as quoted by Roebroeks (2001: p. 447)—that subsequent hominin success in this evolutionary environment, represented by further and more persistent northward settlement, would have been predicated on development of a new adaptation to a niche focused on megaherbivore exploitation. This would initially have been less-contested by other carnivores in the core inhabited zone, and then would also have been better-suited for sustainable survival in more-northerly latitudes, as outlined in more detail here below.

Two conjectures rooted in this ecological perspective are presented here. One (Conjecture 1) relates to hominin adaptation and range expansion in NW Europe during ameliorating and stable warm climate in MIS 11. And the other (Conjecture 2) relates to Neanderthal range persistence in NW Europe during the Last Glacial, and how this was destabilised by the influx of anatomically humans relying on the same niche in more-northerly areas, but exploiting it more intensively and unsustainably, leading to the local demise of Neanderthals.

5.3.2. CONJECTURE 1: RANGE EXPANSION DURING CLIMATIC AMELIORATION AND STABILITY

Hominins initially evolved in the late Pliocene in tropical and sub-tropical Africa, most-likely filling a marginal scavenging niche against a backdrop of low seasonality and high biological diversity. The plant and animal communities would have had a substantially longer background of co-evolution, so the hominins would have had to find a niche, and then develop new niches, within a context of pre-existing plant/animal adaptations, who had already long been engaged in their own evolutionary arms race. In this context mega-herbivores—such as elephants and rhinoceros—can be construed as “apex herbivores”, with their size and other defenses rendering them immune to carnivore predation,

unless weak or injured, or juvenile and undefended. Once an early hominin adaptation had appeared it could easily spread throughout similar ecozones, although it—along with all interacting elements of the ecosystem—would also have been undergoing a continuous evolutionary process of challenge and development that would lead to persistence and range expansion of the hominin population when successful, but local extinction when not.

A fundamental characteristic of biomass productivity is that the plant growing season becomes shorter and more intense with increased latitude, and the animal communities of higher latitudes are less diverse, although often more-structured into size groups and with each group often very abundant. The herbivore communities have a variety of strategies to sustain their adaptation, with varying degrees of mobility to follow resource opportunity, seasonal fattening-up to withstand the relative paucity of plant resource, and exploitation where feasible of winter plant resources such as tubers. And then the carnivore communities map onto the distribution and adaptations of the herbivores. Although vagaries of elevation and continentality mean that ecozones do not move in a straightforward way in conjunction with Pleistocene climatic change, there is nonetheless a general trend for ecozones characteristic of lower latitudes to expand and spread northward during phases of climatic amelioration, and then to reduce and contract southward during phases of climatic deterioration.

When one considers the nutritional requirements of Pleistocene hominins, it is clear that (without intricate and labour-intensive exploitation strategies, and without carefully-targeted acquisition of certain key nutrients that are often scarce or absent other than from an animal source) these need to be met by the exploitation of animal resources (Gamble, 1986: pp. 97–103). Gamble suggested that the most-suitable niche for hominin exploitation, particularly in the predominantly-open environments of the mid-latitudes of western Europe, would be to compete with carnivores for medium-sized herbivores such as *Bos/Bison*, horse and various deer. Despite the amount of nu-

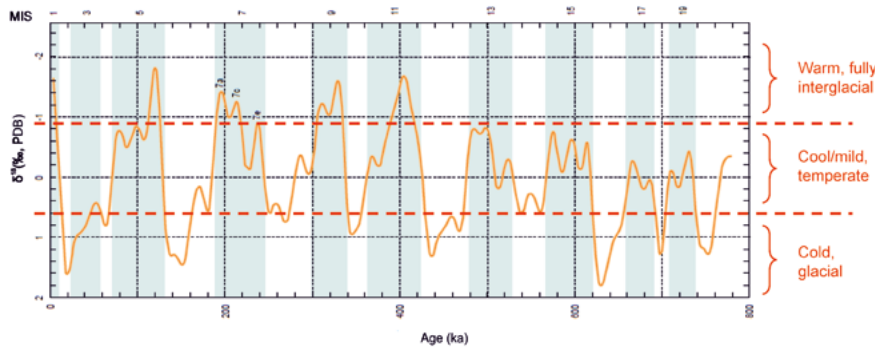


Figure 5.6. Global marine isotope stage (MIS) framework of Pleistocene climatic variations [adapted from Wenban-Smith et al. (2020: fig. 16.3), with permission of Oxford Archaeology and High Speed 1, using SPECMAP stacked data from Imbrie et al., 1984].

trition recoverable from a single individual, he regarded the largest herbivores such as elephant and rhinoceros as too difficult to kill and perhaps also unsustainable as the basis for an adaptation due to their low reproductive potential.

However, here (following Geist, *ibid.*) it is suggested that the largest herbivores would in fact have been the best resource upon which to base a hominin adaptation in this part of the world, if they could be harvested. Firstly, this would be a new niche, and thus successful exploitation would avoid a continual and draining conflict with other carnivores. Secondly, there is no reason to regard occasional exploitation of adult individuals as in any way threatening the sustainability of the prey resource. If one considers, for instance, the mobility and reproduction strategies of modern elephants in the open areas of Africa, they have a fission/fusion strategy whereby sub-adult and adult males roam singly or as fluid groups of various sizes. In contrast, herds of related females stay together for their full lifespan with juveniles of both genders, protecting them from predation, until the young males are evicted from the matriarchal herd as they approach adolescence and are able to fend for themselves, and having learnt the locations of key resources in their territory. Males and male groups then coalesce in the same locations as female herds for breeding, which habitually involves the bull males fighting for sexual access to a fertile female. A population of this nature would thus be highly resilient to the predation of adult males, and in fact could well produce a supply of injured or weakened males that could be more

vulnerable to predation and wholly outside the breeding chain.

Once a hominin adaptation had developed that was successfully based upon a new niche involving the predation of adult megaherbivores, this would have great potential for the expansion of the hominin range northward into Europe, and during the more-temperate stages of the Pleistocene into the more-northerly western European latitudes where the ecosystem and growing season were so favorable for these animals. And in fact many finds are compatible with this suggestion, such as various early sites in the Middle East (Revadim Quarry —Rabinovich et al., 2012; Gesher Benot —Rabinovich and Biton, 2011), Italy (Notarchirico —Piperno and Tagliacozzo, 2001; Polledrara —Anzidei et al., 2012; Castel di Guido —Saccà, 2012), Spain (Áridos 1 and 2 —Yravedra et al., 2010; PRERESA —Yravedra et al., 2012), Greece (Marathousa 1 —Panagopoulou et al., 2018), Germany (Lehringen and Gröbern —Adam, 1951, Gaudzinski, 2004) and the UK (Ebbsfleet —Wenban-Smith, 2013a) where there is evidence of early hominin exploitation of *Palaeoloxodon*, at times and places compatible with being at the northern limit of the hominin range during warmer stages (Surovell et al., 2005), or refugia during stages of colder climate. This suggestion is further explored below (Section 4) with a brief review of the archaeological record of northern France and southern Britain during the warm climate stage MIS 11, which followed the Anglian cold stage MIS 12, this latter being the most severe cold stage of the Middle

Pleistocene (Fig. 6), with the most prolonged duration of cold conditions and the greatest spread of glacial ice.

5.3.3. CONJECTURE 2: RANGE PERSISTENCE DURING CLIMATIC DETERIORATION

The big picture of Pleistocene climatic change (Fig. 6) provides a saw-tooth curve, whereby major ameliorations happened very rapidly, but deterioration was a more gradual affair. Thus, episodes of amelioration would have provided a wild (north) west scenario, with numerous species extending their adaptations into expanding areas of newly-available terrain. This might in time have led to the new adaptations, but it would initially probably have involved the expansion of the same adaptations into the new terrain, with persistence of existing niches. In contrast, when climate deteriorated, this would have involved a reduction of terrain suitable for the prevailing adaptations. The relatively slow rate of climatic change would have facilitated some adjustment to the more-northerly adaptations. Thus, climatic deterioration need not have led to range reduction if a new adaptation could be achieved. However, changing climate and range reduction for a particular adaptation would have provided evolutionary stress that would have led to local extinction if successful change could not be achieved.

It would not only have been hominin adaptations that would have been subject to these evolutionary stresses, but also the adaptations of the herbivores upon which the hominins depended. The climatic oscillations of the Pleistocene are ultimately driven by orbital factors that dictate the amount and intensity of solar radiation reaching the earth. Thus cold-climate stages are intrinsically associated with reduced growing seasons in more-northerly latitudes. For a particular latitude, the plant biomass would have had a deterioration in the proportion of shrubs/trees and an increase in grasses, which would have had a shorter but intense growing season. The response of the her-

bivore community to this would have been for an increased proportion of the animal biomass to become locked up in larger herbivore herds, and herds of larger herbivores; and the more challenging conditions became in terms of reduced growing season, the greater the adaptive pressure for increased herbivore size. Therefore, for the sub-arctic steppe and tundra that would have developed in northwest Europe during cold glacial episodes, the predominant animal biomass would have been herds of mammoth. For hominins at the northern end of their range, their northerly persistence would therefore become tied up with the extent to which they were able to exploit large herbivores; and the larger the herbivores they were able to exploit, the more northerly their adaptation could persist as climate deteriorated. Thus, it is argued here that, following from a hominin adaptation that was already based upon herbivores and mega-herbivores when climate was temperate but cooling, their ability to exploit mega-herbivores would have been the key determinant of how far north an adaptation could persist during colder and glacial climatic phases. And if they were to persist in northwest Europe during cold glacial episodes, they would have had to be able to exploit a mammoth-based niche. This conjecture is explored below (Section 5), in relation to the evidence for the Neanderthal occupation of northwest Europe in the earlier Devensian glaciation, and the replacement of the Neanderthals by anatomically modern humans in the later part of this glaciation.

5.4 HOMININ RANGE EXPANSION AND SUSTAINABLE ELEPHANT EXPLOITATION IN NORTHWEST EUROPE IN MIS 11

In this section I briefly review some of the data that we have for *Palaeoloxodon* presence in NW Europe before and during MIS 11, and how our data relate to hominin presence and (on occasion) elephant exploitation. While one can rarely provide positive proof of any idea about the Palaeolithic, one can

at least explore the data for falsification. And if no falsifying data can be found, and if an idea is compatible with observations and theoretical perspectives based on the present day, then we can at least go forward with an idea as “not yet ruled out, and compatible with known information”.

Palaeoloxodon was clearly a common element of the fauna of this region both before and after the Anglian glaciation, and likely to have been coeval with the northernmost extent of the hominin range during the Anglian glaciation. The species is present (alongside other elephantid taxa) in Terrace VII (Renancourt) of the Somme at Abbeville, attributed to MIS 16/15 (Tuffreau and Antoine, 1995), although here the contemporaneity of hominin presence is uncertain. It is also present in the southern UK sites of High Lodge (Stuart, 1992), Ostend (Roberts and Parfitt, 1999: p. 304) and (although only as a fragmentary pieces attributable to “elephantid”) at Boxgrove (Roberts and Parfitt, 1999: p. 226), attributed to the intra-Anglian interstadial of MIS 13; here, there is no doubt over the contemporaneity of hominin presence in the UK with *Palaeoloxodon* in MIS 13, although there isn't direct evidence of hominin exploitation.

After the Anglian, there are relatively numerous sites with *Palaeoloxodon antiquus* remains from MIS 11. In southwest France *Palaeoloxodon* is an abundant element of the Argiles du Gurd Formation in the Médoc, attributed to MIS 11 (Beauval et al., 1998; Bosq et al., 2019). In the Somme valley in northern France, there is abundant evidence for the presence of *Palaeoloxodon* contemporary with hominin presence in MIS 11 in Terrace V, Cagny/Garenne (Commont, 1908; Tuffreau and Antoine, 1995). In the UK, there is good evidence in particular from Clacton-on-Sea (Wymer, 1985: pp. 264–284), where abundant remains of *Palaeoloxodon* and hominin presence have been recovered from deposits that date from the late Anglian through to the Late Temperate zone of the Hoxnian, with the lowest and richest horizon even being named “the elephant bed” in light of the abundant presence of *Palaeoloxodon*. Other UK sites where *Palaeoloxodon* is present in MIS 11 alongside hominins are Barn-

ham (Parfitt, 1998), Barnfield Pit in Swanscombe (Conway et al., 1996), Hoxne (Stuart et al., 1993: p. 170) and of course the Ebbsfleet elephant (Section 2). At Barnham, Barnfield Pit and Southfleet Road there is evidence of Clactonian lithic industry in stratigraphically lower horizons contemporary with the *Palaeoloxodon* remains, and attributable to the early temperate zone of MIS 11; and at the latter site there is also, as reviewed above, solid evidence of direct hominin exploitation of an adult elephant. At Barnfield Pit, the only of these sites with deeper stratigraphy preserving both lithic and faunal remains, there is continuing presence of *Palaeoloxodon* (Sutcliffe, 1964; Stuart, 1982) in phase II of the site sequence—the Middle Gravels, see Table 2—alongside lithic artifacts reflecting hominin presence, although the lithic industry of these higher horizons is dominated by handaxe manufacture in contrast to the Clactonian industry of the Phase I levels (Wymer, 1968: pp. 334–343; Ashton and McNabb, 1996). And tusks and molars of *Palaeoloxodon* have regularly been found from other sites in the Swanscombe area where the Phase II deposits have been investigated, such as at the Swan Valley School (Wenban-Smith and Bridgland, 2001). At Hoxne, the horizons that have produced both lithic artifacts and elephant remains are thought to relate to a short reversion to temperate conditions in MIS 11a at the end of the Hoxnian (Ashton et al., 2008), post-dating the Phase II deposits of the Swanscombe sequence.

The overall picture from these data is that *Palaeoloxodon* was present in northwest Europe during more-temperate climate stages between MIS 16 and MIS 10, broadly coeval throughout this period with hominins. The evidence of hominin presence before MIS 12 is sporadic, and there is no direct evidence of hominin exploitation of elephants, although of course this absence of direct evidence cannot be taken as evidence that this did not occur. There seems to have been a marked uptick in the intensity of Palaeolithic occupation in this NW European region in MIS 11 after the Anglian glaciation. Not only are there very numerous sites demonstrating hominin presence from across

southern England and northern France, but there are also quite a few sites that show co-occurrence of hominin activity and elephant presence, notably the specific instance of elephant exploitation at Southfleet Road, early in MIS 11. Importantly, despite the clear-cut evidence for hominin contemporaneity with, and exploitation of, elephant in the early Hoxnian, this does not seem to have affected the continuing presence of elephant through the rest of the Hoxnian (*sensu* MIS 11c) or in the final stages of the Hoxnian as represented at Hoxne itself (MIS 11a), a period spanning maybe 50,000 years (Table 2). Furthermore, despite the general rarity of well-provenanced elephant fossils from northwestern Europe in MIS 11-10 (comprising France, Belgium, Netherlands and UK), the record from Soulac (Gironde) in SW France provides firm evidence that the abundant presence of hominins in this region at this time did not lead to the local extinction of *Palaeoloxodon*. Taken together, these data support the notion that, *contra* Surovell et al. (2005), the observed pattern of proboscidean exploitation sites across the Pleistocene Old World reflects the importance for pioneer hominin adaptations of sustainable elephant exploitation, rather than being a harbinger of their doom.

5.5 LAST GLACIAL ADAPTATIONS IN NORTHWEST EUROPE AND NEANDERTHAL EXTINCTION

We have a much better understanding of the overall pattern of the data for this later period (e.g., Mellars and Stringer, 1989; Mellars, 1990, 2004; Akazawa et al., 1998; Klein, 2003; Harvati, 2012; Zilhao, 2014). However, this does not seem to have led to a consensus view, but rather to an increased multiplicity of suggestions to explain the demise of the Neanderthals (Soffer, 1994; Mellars, 2004; van Andel and Davies, 2003; Stewart, 2005; Kuhn and Stiner, 2006; Golovanova et al., 2010; Houldcroft and Underdown, 2016; Ko, 2016; Degioanni et al., 2019). The generally-accepted data pattern is that Neanderthals were successfully

occupying much of the territory of northwest Europe through much of the period MIS 8–4. The extent to which their often-supposed southwest France heartland is an artifact of 19th–20th century investigation and interpretation is uncertain, but this was without doubt an area of persistent occupation (Bordes, 1972), and probably a refugium in the coldest parts of this stretch of time. There are also good records of Neanderthals themselves, or of their lithic artifactual remains, from much further north, in northern France (e.g., La Chaise —Condemi, 2001; Biache St Vaast —Guipert et al., 2010; Tourville-la-Rivière —Favre et al., 2014; Caours —Antoine et al., 2006, and see Locht et al., 2016 for a general review of Middle Palaeolithic sites), Belgium (Spy, Engis and La Naulette —Fernández-Jalvo and Andrews, 2019), the Channel Islands (Callow and Cornford, 1986; Bates et al., 2013; Scott et al., 2014), the Netherlands (Maastricht-Belvedere —Roebroeks et al., 1992b) and even the UK (White and Jacobi, 2002; Harnham —Bates et al., 2014; Dartford —Wenban-Smith et al., 2010; and Lynford —Boismier et al., 2012).

Although the pattern of occupation may be distorted by its focus on the more-visible cave and rock-shelter sites, there are also several open-sir sites (such as Harnham, Biache-Saint-Vaast, Maastricht-Belvedere, Tourville-La-Rivière, Caours, Dartford and Lynford). More-northerly occupational evidence seems intermittent in the period MIS 8–6 (Roebroeks and Tuffreau, 1999; Roebroeks et al., 2011), and also, curiously, in the warm interglacial conditions of MIS 5e, the reason for which there has been much debate (Gamble, 1986; Roebroeks et al., 1992; Roebroeks and Speleers, 2002). Bearing in mind the dating imprecision of most sites from this period, La Cotte de St Brelade, on Jersey, is perhaps a good representative example of northerly occupation by Neanderthals in this period, with numerous superimposed occupational levels that attest episodic presence from MIS 7 through to the Last (Devensian) Glacial (Bates et al., 2013; Scott et al., 2014). The main occupation horizons date to within MIS 7, and there

is interesting evidence of two “bone heaps” —a “lower” heap in the bottom part of layer 3, and an “upper” heap in the bottom part of layer 6. These bone heaps— which are dominated by bones of mammoth and rhino - abut, and partly merge into, the underlying occupation horizons: layers A and 5 respectively. Both bone heaps are covered by loessic deposits without evidence of human activity that are thought to represent cold climate, and too cold for hominin survival here, perhaps a stadial within MIS 7 for the lower loess bed, followed by layer 6 representing loess accumulation in MIS 6. Towards the end of MIS 6, pulses of climatic warmth coincided with the northward expansion of Neanderthals (van Andel et al., 2003), and their re-settlement in northern Europe, at the site of Veldwezelt-Hezerwater in Belgium (Bringmans, 2007). There are, however, indications of presence in MIS 6 in Biache-Saint-Vaast, and in Beavais (La Justice) (Roebroeks and Tuffreau, 1999). Later, there is evidence of Neanderthal presence near the Normandy coast during MIS 5e, at the site of Caours in the lower Somme valley (Antoine et al., 2006). The evidence suggests that, although Neanderthals did have some adaptations to cold climate, they did not necessarily prefer it, and their population increases and northward range expansions corresponded with episodes of relative climatic warmth (van Andel et al., 2003; Hublin and Roebroeks, 2009; Locht et al., 2016), although still by no means fully temperate. Once they arrive this far north in MIS 5, there are relatively numerous sites in northern France from the post-Eemian cooler periods MIS 5d–5a, representing the early part of the Devensian glaciation (Antoine, 1993; Vallin and Masson, 2004; Bringmans, 2007; Locht et al., 2016). And there is also one site in southern England from this period, near Dartford (Wenban-Smith et al., 2010), suggesting that the Neanderthal range occasionally extended into the UK, when the barrier of the channel area could be crossed, which, when not marine, would have been marshy badlands with a major river along its main axis. Later in the Devensian, towards the end of MIS 4 and in MIS 3, there is further evidence of increasingly abundant

Neanderthal occupation in northern Europe and southern UK, at sites such as Spy and Goyet caves in Belgium (Wißing et al., 2019), Arcy-sur-cure in France (Leroi-Gourhan and Leroi-Gourhan, 1964; Higham et al., 2010) and Lynford Quarry in England (Boismier et al., 2012). And then there is consistent evidence that this thriving adaptation was suddenly interrupted c. 40,000–35,000 BP, and replaced by anatomically humans, often in the same sequence as at most of these afore-mentioned sites (the exception being Lynford, where the only evidence is from the Neanderthal era).

The focus of this section is not, however, to provide a comprehensive review of the evidence, but to float a speculative idea on the eventual demise of the Neanderthals in the later part of the Last Glacial, rooted in the preceding ecological discussion (Section 3) but also supported by recent data. In accordance with the ecological basis of this northerly Neanderthal adaptation, numerous analyses of Neanderthal diet (e.g., Stiner, 1994; Villa, 2009; Gaudzinski-Windheuser and Niven, 2009; Bocherens, 2009, 2011; Macdonald et al., 2009; Richards and Trinkaus, 2009) demonstrate a major reliance upon nutritious herbivores, with significant skeletal representation of mammoth and rhino bones, as well as other herbivores such as horse, bovid and deer. Although there is often spirited debate on the precise nature of human-mammoth interactions, probably with a general tendency to see the evidence as reflecting hunting rather than otherwise —e.g., for Lynford Quarry, compare the analysis of Smith (2012) with that in the main volume (Schreve et al., 2012)— there is no doubting the importance of mammoths, and important recent and new evidence for this was presented, or referenced, at the Symposium (Wißing et al., 2016, 2019; Jaouen et al., 2019).

My own presentation suggested that the importance of mammoths for a sustainable northerly Neanderthal adaptation might have gone beyond their nutritional value, and that their spongy fat-rich bones might, especially in relatively treeless landscapes, have been an important source of fuel for fires, which would have been a key technolo-

gy for sustaining adaptations in a cold climate. I thus drew attention to the published data from La Cotte (Callow and Cornford, 1986; Callow et al., 1986) which showed a significant presence of charred and intensely-heated scraps of mammoth bone in the main occupational layers A and 5, and suggested that the abutting and immediately-overlying mammoth bone heaps could perhaps be understood as associated stashes of “firewood” ready and waiting. Although they date earlier than the Last Glacial, they nonetheless may represent another, non-dietary, aspect of the importance of the mammoth for northerly Neanderthal adaptation in cold climatic periods. As identified by Callow et al. (*ibid.*) burnt bone fragments occur frequently throughout the occupational sequence, and especially in the associated layers A and 5, and are clearly interpretable as having been deliberately burnt, rather than cooked. The blue-white color of many of the burnt bone fragments reflects a high combustion temperature, as would be expected given the spongy structure and high fat content of mammoth limb-bone. This could therefore, have been a vital survival resource in cold landscapes without abundant trees. Of course other possibilities abound, as put forward during the meeting.

The importance of mammoth exploitation for both late Neanderthals and early modern humans is further highlighted by other recent work. Wojtal et al. (2019) demonstrated the smoking gun—or perhaps “quivering spear”—for modern human mammoth hunting, with evidence of a flint point embedded in a mammoth rib. Evidence from faunal remains and stable isotope analysis (Wißing et al., 2016, 2019) also shows the importance of mammoth year-round for Neanderthals and modern humans - in particular of tender, fatty and nutritious baby mammoths which must have been a sought-after treat. Bocherens and Drucker (this volume) review further isotope analyses that demonstrates the predominance of mammoth meat in the diet of both modern humans and Neanderthals, and also that for modern humans it was even greater. They drew attention to the potential ecological impact of this hyper-exploitation of mammoths by

the earlier modern human colonizers of central and northwest Europe. As also suggested by Wojtal et al. (2019), these authors propose that the intensity of their exploitation may have been sufficient to challenge the sustainability of the mammoth populations, and that it may have affected the wider herbivorous niche structure and provided a dietary subsidy to other carnivores. They did not however, consider the impact upon pre-existing Neanderthal adaptations of the sudden arrival of a direct and unsustainably-successful competitor for the megaherbivore exploitation niche. Likewise, Wißing et al. (2019) concluded that since Neanderthals and modern humans were eating the same thing, dietary differences could not explain Neanderthal extinction. However, it could be argued that it was precisely this dietary similarity that caused extinction, rather than any difference. As argued above (Section 3), the nutritional resource vital for Neanderthal survival would have been increasingly held in megaherbivore—and especially mammoth—herds as climate deteriorated, so the northerly limit of a Neanderthal adaptation could have been defined by their ability to exploit this megaherbivore resource. And thus when a direct competitor appeared who was (a) exploiting the same resource more intensely and (b) also perhaps significantly reducing the presence of mammoth overall, then the Neanderthal adaptation in northwest Europe may have become unsustainable, leading to their local extinction.

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REFERENCES

- ADAM, K. D., 1951. Der Waldelefant von Lehringen, eine Jagdbeute des diluvialen Menschen. *Quartär* 5, 79–92.
- AGAM, A., Barkai, R., 2018. Elephant and mammoth hunting during the Paleolithic: A review of the relevant archaeological, ethnographic and ethno-historical records. *Quaternary* 1, 3.
- AKAZAWA, T., Aoki, K., Bar-Yosef, O. (Eds.), 1998. Neandertals and modern humans in Western Asia. Plenum Press, New York and London.
- VAN ANDEL, T. H., Davies, S. W. G., 2003 (Eds.). Neanderthals and modern humans in the European landscape during the Last Glaciation. McDonald Institute for Archaeological Research, Cambridge.
- VAN ANDEL, T. H., Davies, S. W. G., Wenninger, B., 2003. The human presence in Europe during the Last Glacial period I: human migrations and the changing climate, in: van Andel, T. H., Davies, S. W. G. (Eds), Neanderthals and modern humans in the European landscape during the Last Glaciation. McDonald Institute for Archaeological Research, Cambridge, pp. 31–56.
- ANTOINE, P. 1993. L'environnement des occupations humaines au Paléolithique Moyen récent dans la France septentrionale. *Bulletin de la Société Préhistorique Française* 90, 320–323.
- ANTOINE, P., Limondin-Lozouet, N., Auguste, P., Loch, J. L., Ghaleb, B., Reyss, J. L., Escude, E., Carbonel, P., Mercier, N., Bahain, J. J., 2006. The Caours tufa (Somme, France): evidence from an Eemian sequence associated with a Palaeolithic settlement. *Quaternaire* 17, 281–320.
- ANZIDEI, A. P., Bulgarelli, G. M., Catalano, P., Cerilli, E., Gallotti, R., Lemorini, C., Milli, S., Palombo, M. R., Pantano, W., Santucci, E., 2012. Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human–elephant relationships. *Quaternary International* 255, 171–187.
- ASHTON, N. M., McNabb, J., 1996. The flint Industries from the Waechter excavation, in: Conway, B., McNabb, J., Ashton, N. M. (Eds.), Excavations at Barnfield Pit, Swanscombe, 1968–72. British Museum (Occasional Paper Number 94), London, pp. 201–236.
- ASHTON, N. M., McNabb, J., Irving, B., Lewis, S., Parfitt, S., 1994. Contemporaneity of Clactonian and Acheulian flint industries at Barnham, Suffolk. *Antiquity* 68, 585–589.
- ASHTON, N., Lewis, S. G., Parfitt, S. A., Penkman, K. E., Coope, R. G., 2008. New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. *Quaternary Science Reviews* 27, 652–668.
- ASHTON, N., Lewis, S. G., Parfitt, S. A., Davis, R. J., Stringer, C., 2016. Handaxe and

- non-handaxe assemblages during Marine Isotope Stage 11 in northern Europe: recent investigations at Barnham, Suffolk, UK. *Journal of Quaternary Science* 31, 837–843.
- BANKS, W. E., d’Errico, F., Peterson, A. T., Kageyama, M., Sima, A., 2008.** Neanderthal extinction by competitive exclusion. *PLoS ONE* 3, e3972.
- BATES, M., Pope, M., Shaw, A., Scott, B., Schwenninger, J. L., 2013.** Late Neanderthal occupation in North-West Europe: rediscovery, investigation and dating of a last glacial sediment sequence at the site of La Cotte de Saint Brelade, Jersey. *Journal of Quaternary Science* 28, 647–652.
- BATES, M. R., Wenban-Smith, F. F., Bello, S. M., Bridgland, D. R., Buck, L. T., Collins, M. J., Keen, D. H., Leary, J., Parfitt, S. A., Penkman, K., Rhodes, E. J., Ryssaert, C., Whittaker, J., 2014.** Late persistence of the Acheulian in southern Britain in an MIS 8 interstadial: evidence from Harnham, Wiltshire. *Quaternary Science Reviews* 101, 159–176.
- BEAUVAL, C., Patrick, M., Tastet, J. P., 1998.** L’éléphant antique de Soulac (Gironde, France). *Quaternaire* 9, 91–100.
- BEN-DOR, M., Gopher, A., Hershkovitz, I., Barkai, R., 2011.** Man the fat hunter: the demise of *Homo erectus* and the emergence of a new hominin lineage in the Middle Pleistocene (ca. 400 kyr) Levant. *PLoS ONE* 6, e28689.
- BOCHERENS, H., 2009.** Neanderthal dietary habits: review of the isotopic evidence, in: Hublin, J. J., Richards, M. P. (Eds.), *The evolution of hominin diets*. Springer, Dordrecht, pp. 241–250.
- BOCHERENS, H., 2011.** Diet and ecology of Neanderthals: implications from C and N isotopes, in Conard, N. J., Richter, J. (Eds.), *Neanderthal lifeways, subsistence and technology: one hundred and fifty years of Neanderthal study*. Springer, Dordrecht, pp. 73–85.
- BOCHERENS, H., Drucker, D. G., this volume.** Isotopic insights on ecological interactions between humans and woolly mammoths during the Middle and Upper Palaeolithic in Europe.
- BOCHERENS, H., Drucker, D. G., Germonpré, M., Lázníčková-Galetová, M., Naito, Y. I., Wißing, C., Brůžek, J., Oliva, M., 2015.** Reconstruction of the Gravettian food-web at Predmosti I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quaternary International* 359–360, 211–228.
- BOISMIER, W. A., Gamble, C. S., Coward, F. (Eds), 2012.** Neanderthals among mammoths: excavations at Lynford Quarry, Norfolk. *English Heritage*, Swindon.
- BORDES, F., 1950.** L’évolution buissonnante des industries en Europe occidentale: considérations théoriques sur le Paléolithique Ancien et Moyen. *L’Anthropologie* 54, 393–420.
- BORDES, F., 1969.** Reflections on typology and technology in the Palaeolithic. *Arctic Anthropology* 6, 1–29.
- BORDES, F., 1972.** *A tale of two caves*. Harper and Row, New York.
- BOSCHIAN, G., Saccà, D., 2015.** In the elephant, everything is good: Carcass use and re-use at Castel di Guido (Italy). *Quaternary International* 361, 288–296.
- BOSCHIAN, G., Caramella, D., Saccà, D., Barkai, R., 2019.** Are there marrow cavities in Pleistocene elephant limb bones, and was marrow available to early humans? New CT scan results from the site of Castel di Guido (Italy). *Quaternary Science Reviews* 215, 86–97.
- BOSQ, M., Bertran, P., Beauval, C., Kreutzer, S., Duval, M., Bartz, M., Mercier, N., Sitzia, L., Stéphan, P., 2019.** Stratigraphy and chronology of Pleistocene coastal deposits in northern Aquitaine, France: a reinvestigation. *Quaternaire* 30, 275–303.
- BREUIL, H., Lantier, R., 1951.** *Les Hommes de la Pierre Anciennes*. Payot, Paris.
- BRIDGLAND, D. R., 1994.** *Quaternary of the Thames*. Chapman & Hall, London.
- BRINGMANS, P. M. M. A., 2007.** First evidence of Neanderthal presence in Northwest Europe during the Late Saalian ‘Zeifen Interstadial’ (MIS 6.01) found at the VLL and VLB Sites at Veldwezelt-Hezerwater, Belgium. *PalArch’s*

- Journal of Archaeology of Northwest Europe 1, 1–15.
- BROWN, A. G.**, Basell, L. S., Robinson, S., Burdge, G. C., 2013. Site distribution at the edge of the Palaeolithic world: a nutritional niche approach. *PLoS ONE* 8, e81476.
- CALLOW, P.**, Cornford, J. M. (Eds.), 1986. La Cotte de St. Brelade 1961–1978: excavations by C.B.M. McBurney. Geo Books, Norwich.
- CALLOW, P.**, Walton, D., Shell, C. A., 1986. The use of fire at La Cotte de St. Brelade, in: Callow, P., Cornford, J. M. (Eds.), La Cotte de St. Brelade 1961–1978: excavations by C.B.M. McBurney: 193–195. Geo Books, Norwich.
- COMMENT, V.**, 1908. Les industries de l'ancien Saint-Acheul. *L'Anthropologie* 19, 527–572.
- CONDEMI, S.**, 2001. Les Néandertaliens de La Chaise. Comité des Travaux Historiques et Scientifiques, Paris.
- CONWAY, B. W.**, McNabb, J., Ashton, N. (Eds.), 1996. Excavations at Barnfield Pit, Swanscombe, 1968–72. British Museum Occasional Paper 94, British Museum Press, London.
- CRADER, D. C.**, 1983. Recent single-carass bone scatters and the problem of “butchery” sites in the archaeological record, in: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and archaeology: 1. Hunters and their prey*. BAR International Series, Oxford, pp. 107–141.
- DEGIOANNI, A.**, Bonenfant, C., Cabut, S., Conde mi, S., 2019. Living on the edge: Was demographic weakness the cause of Neanderthal demise? *PLoS ONE* 14, e0216742.
- DENNEL, R.**, 2003. Dispersal and colonisation, long and short chronologies: How continuous is the Early Pleistocene record for hominids outside East Africa? *Journal of Human Evolution* 45, 421–440.
- DRUCKER, D. G.**, Naito, Y. I., Péan, S., Prat, S., Crépin, L., Chikaraishi, Y., Ohkouchi, N., Puaud, S., Lázničková-Galetová, M., Patou-Mathis, M., Yanevich, A., Bocherens, H., 2017. Isotopic analyses suggest mammoth and plant in the diet of the oldest anatomically modern humans from far southeast Europe. *Scientific Reports* 7, 6833.
- FAIVRE, J. P.**, Maureille, B., Bayle, P., Crevecoeur, I., Duval, M., Grün, R., Bemilli, C., Bonilauri, S., Coutard, S., Bessou, M., Limondin-Lozouet, N., Cottard, A., Deshayes, T., Douillard, A., Henaff, X., Pautret-Hormerville, C., Kinsley, L., Trinkaus, E., 2014. Middle Pleistocene human remains from Tourville-la-Rivière (Normandy, France) and their archaeological context. *PLoS ONE* 9, e104111.
- FERNÁNDEZ-JALVO, Y.**, Andrews, P., 2019. Spy cave (Belgium) Neanderthals (36,000 y BP). Taphonomy and peri-mortem traumas of Spy I and Spy II: murder or accident. *Quaternary Science Reviews* 217, 119–129.
- GAMBLE, C. S.**, 1986. The Palaeolithic settlement of Europe. Cambridge University Press, Cambridge.
- GAMBLE, C. S.**, 1987. Man the shoveler: alternative models for Middle Pleistocene colonisation and occupation in northern latitudes, in: Soffer, O. (Ed), *The Pleistocene Old World: regional perspectives*. Plenum Press, New York, pp. 81–98.
- GAMBLE, C. S.**, 1993. *Timewalkers: the prehistory of global colonization*. Alan Sutton, Penguin Books, UK.
- GAUDZINSKI, S.**, 2004. A matter of high resolution? The Eemian Interglacial (OIS 5e) in north-central Europe and Middle Palaeolithic subsistence. *International Journal of Osteoarchaeology* 14, 201–211.
- GAUDZINSKI-WINDHEUSER, S.**, Niven, L., 2009. Hominin subsistence patterns during the Middle and Late Palaeolithic in northwestern Europe, in: Hublin, J. J., Richards, M. P. (Eds.), *The Evolution of hominin diets: integrating approaches to the study of Palaeolithic subsistence*. Springer, Dordrecht, pp. 99–111.
- GEIST, V.**, 1978. *Life strategies, human evolution, environmental design: toward a biological theory of health*. Springer, New York.
- GERMONPRÉ, M.**, Bocherens, H., Bessudnov, A., Lázničková-Galetová, M., Reynolds, N., Sablin, M., Wißing, C., this volume. Seasonality

- at Middle and Upper Palaeolithic sites based on the presence and wear of deciduous premolars from nursing mammoth calves.
- GOLOVANOVA, L. V., Doronichev, V. B., Cleg-horn, N. E., Koulkova, M. A., Sapelko, T. V., Shackley, M. S., 2010.** Significance of ecological factors in the Middle to Upper Paleolithic transition. *Current Anthropology* 51, 655–691.
- GUIPERT, G., de Lumley, M. A., Tuffreau, A., Mafart, B., 2010.** A late Middle Pleistocene hominid: Biache-Saint-Vaast 2, north France. *Comptes Rendus Palevol* 10, 21–33.
- HARVATI, K., 2012.** What happened to the Neanderthals? *Nature Education Knowledge* 3, 13.
- HARVATI, K., Gunz, P., Grigorescu, D., 2007.** Cioclovina (Romania): morphological affinities of an early modern European. *Journal of Human Evolution* 53, 732–746.
- HAYNES, G., 1991.** Mammoths, mastodons and elephants: Biology, behavior, and the fossil record. Cambridge University Press, Cambridge.
- HIGHAM, T., Jacobi, R., Julien, M. A., David, F., Basell, L., Wood, R., Davies, W., Ramsey, C. B., 2010.** Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. *Proceedings of the National Academy of Sciences* 107, 20234–20239.
- HOULDCROFT, C. J., Underdown, S. J., 2016.** Neanderthal genomics suggests a Pleistocene time frame for the first epidemiologic transition. *American Journal of Physical Anthropology* 160, 379–388.
- HUBLIN, J. J., Roebroeks, W., 2009.** Ebb and flow or regional extinctions? On the character of Neanderthal occupation of northern environments. *Comptes Rendus Palevol* 8, 503–509.
- ICHIKAWA, M., this volume.** Elephant hunting by the Mbuti hunter-gatherers in the eastern Congo Basin.
- IMBRIE, J., Hays, J. D., Martinson, D. G., McIntyre, A., Mix, A. C., Morley, J. J., Pisias, N. G., Prell, W. L., Shackleton, N. J., 1984.** The orbital theory of Pleistocene climate: support from a revised chronology of the marine $\delta^{18}\text{O}$ record, in: Berger, A., Imbrie, J., Hays, J., Kukla, G., Salzmann, B., (Eds.), *Milankovitch and climate, part I.* Plenum Reidel, Dordrecht, pp. 269–305.
- JAOUEN, K., Richards, M. P., Cabec, A. L., Welker, F., Rendu, W., Hublin, J. J., Soressi, M., Talamo, S., 2019.** Exceptionally high $\delta^{15}\text{N}$ values in collagen single amino acids confirm Neanderthals as high-trophic level carnivores. *Proceedings of the National Academy of Sciences*: 116, 4928–4933.
- KLEIN, R. G., 2003.** Whither the Neanderthals? *Science* 299, 1525–1527.
- KO, K. H., 2016.** Hominin interbreeding and the evolution of human variation. *Journal of Biological Research-Thessaloniki* 23, 17.
- KUHN, S., Stiner, M., 2006.** What's a mother to do? The division of labor among Neanderthals and modern humans in Eurasia. *Current Anthropology* 47, 953–980.
- LEROI-GOURHAN, A., Leroi-Gourhan, A., 1964.** Chronologie des grottes d'Arcy-sur-Cure (Yonne). I: Climats du quaternaire récent. II: Industries du Paléolithique supérieur. *Gallia Préhistoire* 7, 1–64.
- LOCHT, J. L., Hérissou, D., Goval, E., Cliquet, D., Huet, B., Coutard, S., Antoine, P., Feray, P., 2016.** Timescales, space and culture during the Middle Palaeolithic in northwestern France. *Quaternary International* 411, 129–148.
- MACDONALD, K., Roebroeks, W., Verpoorte, A., 2009.** An energetics perspective on the Neanderthal record, in: Hublin, J. J., Richards, M. P. (Eds.), *The evolution of hominin diets: integrating approaches to the study of Palaeolithic subsistence.* Springer, Dordrecht, pp. 211–220.
- MELLARS, P., 1990 (Ed).** *The emergence of modern humans: an archaeological perspective.* Edinburgh University Press, Edinburgh.
- MELLARS, P., 2004.** Neanderthals and the modern human colonization of Europe. *Nature* 432, 461–465.
- MELLARS, P., Stringer, C., 1989 (Eds).** *The human revolution: behavioural and biological per-*

- spectives on the origins of modern humans. Edinburgh University Press, Edinburgh.
- MCNABB, J.**, 2020. Problems and pitfalls in understanding the Clactonian, in: Groucutt, H. S. (Ed.), *Culture history and convergent evolution: Can we detect populations in prehistory?* Springer, Cham, pp. 29–53.
- MCNABB, J.**, Ashton, N. M., 1992. The cutting edge: bifaces in the Clactonian. *Lithics* 13, 4–10.
- OSBORN, H. F.**, 1915. *Men of the Old Stone Age*. Scribner, New York.
- OVEY, C. D.** (Ed.), 1964. *The Swanscombe skull: a survey of research on a Pleistocene site*. Royal Anthropological Institute, London: Occasional Paper No. 20.
- PANAGOPOULOU, E.**, Turloukis, V., Thompson, N., Konidaris, G., Athanassiou, A., Giusti, D., Tsartsidou, G., Karkanis, P., Harvati, K., 2018. The Lower Palaeolithic site of Marathousa 1, Megalopolis, Greece: Overview of the evidence. *Quaternary International* 497, 33–46.
- PARFITT, S. A.**, 1998. The interglacial mammalian fauna from Barnham, in: Ashton, N. A., Lewis, S. G., Parfitt, S. (Eds.), *Excavations at the Lower Palaeolithic site at East Farm, Barnham, Suffolk 1989–94*. British Museum Press, London, pp. 111–147.
- PARFITT, S. A.**, 2013a. The vertebrate remains from Southfleet Road: introduction, taphonomy and palaeoecology, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet Elephant: excavations at Southfleet Road, Swanscombe in Advance of High Speed 1, 2003–4*. Oxford Archaeology Monograph No. 20, Oxford Archaeology, Oxford, pp. 149–203.
- PARFITT, S. A.**, 2013b. Mammalian biostratigraphy, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet Elephant: excavations at Southfleet Road, Swanscombe in Advance of High Speed 1, 2003–4*. Oxford Archaeology Monograph No. 20, Oxford Archaeology, Oxford, pp. 233–262.
- PARFITT, S. A.**, Barendregt, R. W., Breda, M., Candy, I., Collins, M. J., Coope, G. R., Durbidge, P., Field, M. H., Lee, J. R., Lister, A. M., Mutch, R., Penkman, K. E. H., Preece, R. C., Rose, J., Stringer, C. B., Symmons, R., Whittaker, J. E., Wymer, J. J., Stuart, A. J., 2005. The earliest record of human activity in northern Europe. *Nature* 438, 1008.
- PARFITT, S. A.**, Ashton, N. M., Lewis, S. G., Abel, R. L., Coope, G. R., Field, M. H., Gale, R., Hoare, P. G., Larkin, N. R., Lewis, M. D., Karloukovski, V., Maher, B. A., Peglar, S. M., Preece, R. C., Whittaker, J. E., Stringer, C. B., 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466, 229–233.
- PARFITT, S. A.**, Bello, S. M., Stewart, J. R., Hewitt, R., Herridge, V. H., Wenban-Smith, F., 2013. The elephant skeleton and the question of human exploitation, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003–4*. Oxford Archaeology Monograph No. 20, Oxford Archaeology, Oxford, pp. 205–232.
- PENKMAN, K.**, Wenban-Smith, F. F., 2013. Amino acid dating, in: Wenban-Smith, F. (Ed.) *The Ebbsfleet Elephant: excavations at Southfleet Road, Swanscombe in Advance of High Speed 1, 2003–4*. Oxford Archaeology Monograph No. 20, Oxford Archaeology, Oxford, pp. 307–318.
- PIPERNO, M.**, Tagliacozzo, A., 2001. The elephant butchery area at the Middle Pleistocene site of Notarchirico (Venosa, Basilicata, Italy), in: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M. R. (Eds.), *The world of elephants-1st International Congress*. Consiglio Nazionale delle Ricerche, Rome, pp. 230–236.
- PIPERNO, M.**, Lefèvre, D., Raynal, J. P., Tagliacozzo, A., 1998. Notarchirico. An early Middle Pleistocene site in the Venosa basin. *Anthropologie* 36, 85–90.
- PITTS, M.**, Roberts, M. B., 1997. *Fairweather Eden: Life in Britain half a million years ago as revealed by the excavations at Boxgrove*. Century, London.
- PREECE, R. C.**, 1995 (Ed.). *Island Britain: a Quaternary perspective*. Geological Society Special Publication, vol. 96.

- RABINOVICH, R.**, Biton, R., 2011. The early Middle Pleistocene faunal assemblages of Gesher Benot Ya'aqov: Inter-site variability. *Journal of Human Evolution* 60, 357–374.
- RABINOVICH, R.**, Ackermann, O., Aladjem, E., Barkai, R., Biton, R., Milevski, I., Solodenko, N., Marder, O., 2012. Elephants at the Middle Pleistocene Acheulian open-air site of Revadim Quarry, Israel. *Quaternary International* 276–277, 183–197.
- RICHARDS, M. P.**, Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proceedings of the National Academy of Sciences* 104, 16034–16039.
- RICHARDS, M. P.**, Pettitt, P. B., Trinkaus, E., Smith, F. H., Paunovic, M., Karavanic, I., 2000. Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *Proceedings of the National Academy of Sciences* 97, 7663–7666.
- ROBERTS, M. B.**, Parfitt, S. A., 1999 (Eds.). *Boxgrove: a Middle Pleistocene hominid site*. English Heritage, London.
- ROE, D. A.**, 1981. *The Lower and Middle Palaeolithic periods in Britain*. Routledge & Kegan Paul, London.
- ROEBROEKS, W.**, 2001. Hominid behaviour and the earliest occupation of Europe. *Journal of Human Evolution* 41, 437–461.
- ROEBROEKS, W.**, Tuffreau, A., 1999. Palaeoenvironment and settlement patterns of the Northwest European Middle Paleolithic, in: Roebroeks, W., Gamble, C. (Eds.), *The Middle Palaeolithic Occupation of Europe*. University of Leiden, Leiden, pp. 3–22.
- ROEBROEKS, W.**, Speleers, B., 2002. Last interglacial (Eemian) occupation of the North European plain and adjacent areas, in: Tuffreau, A., Roebroeks, W. (Eds.), *Publications du CERP, Université des Sciences et Technologies de Lille, Villeneuve-d'Ascq*, pp. 31–39.
- ROEBROEKS, W.**, Conard, N. J., van Kolfschoten, T., 1992. Dense forests, cold steppes, and the Palaeolithic settlement of northern Europe. *Current Anthropology* 33, 551–586.
- ROEBROEKS, W.**, Hublin, J. J., MacDonald, K., 2011. Continuities and discontinuities in Neanderthal presence: a closer look at northwestern Europe, in: Ashton, N. M., Lewis, S. G., Stringer, C. B. (Eds.), *Developments in Quaternary Science* 14, 113–124. Elsevier, Amsterdam.
- SACCÀ, D.**, 2012. Taphonomy of *Palaeoloxodon antiquus* at Castel di Guido (Rome, Italy): proboscidean carcass exploitation in the Lower Palaeolithic. *Quaternary International* 276–277, 27–41.
- SCHREVE, D. C.**, Brothwell, D. R., Stuart, A. J., 2012. The vertebrate assemblage, in: Bois-mier, W. A., Gamble, C. S., Coward, F. (Eds.), *Neanderthals among mammoths: excavations at Lynford Quarry, Norfolk*. English Heritage, Swindon, pp. 157–205.
- SCOTT, B.**, Bates, M., Bates, R., Conneller, C., Pope, M., Shaw, A., Smith, G., 2014. A new view from La Cotte de St Brelade, Jersey. *Antiquity* 88, 13–29.
- SMITH, R. A.** 1911. A Palaeolithic industry at Northfleet, Kent. *Archaeologia* 62, 515–532.
- SMITH, G. M.** 2012. Middle Palaeolithic subsistence: the role of hominins at Lynford, Norfolk, UK. *Quaternary International* 252, 68–81.
- SMITH, R. A.**, Dewey, H., 1913. Stratification at Swanscombe: report on excavations made on behalf of the British Museum and H.M. Geological Survey. *Archaeologia* 64, 177–204.
- SMITH, R. A.**, Dewey, H., 1914. The High Terrace of the Thames: report on excavations made on behalf of the British Museum and H.M. Geological Survey. *Archaeologia* 65, 185–212.
- SOFFER, O.**, 1994. Ancestral ways of life in Eurasia: the Middle and Upper Palaeolithic records, in: Nitecki, M. H., Nitecki, D. V. (Eds.), *Origins of anatomically modern humans*. Plenum Press, New York, pp. 101–119.
- SPURRELL, F. C. J.**, 1890. Excursion to Swanscombe. *Proceedings of the Geologists' Association* 11, 145.
- STEWART, J. R.**, 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. *Quaternary International* 137, 35–46.

- STINER, M., 1994. Honor among thieves: a zoo-archaeological study of Neanderthal ecology. Princeton University Press, Princeton.
- STUART, A. J. 1982. Pleistocene Vertebrates in the British Isles. Longman, London.
- STUART, A. J., 1992. The High Lodge mammalian fauna, in: Ashton, N. M., Cook, J., Lewis, S. G., Rose, J. (Eds.), High Lodge: excavations by G. de G. Sieveking 1962–68 and J. Cook 1988. British Museum Press, London, pp. 120–123.
- STUART, A. J., Wolff, R. G., Lister, A. M., Singer, R., Egginton, J. M., 1993. Fossil vertebrates, in: Singer, R., Gladfelter, B. G., Wymer, J. J. (Eds.), The Lower Palaeolithic site at Hoxne, England. The University of Chicago Press, London, pp. 163–206.
- SUROVELL, T., Waguespack, N., Brantingham, P. J., 2005. Global archaeological evidence for proboscidean overkill. *Proceedings of the National Academy of Sciences* 102, 6231–6236.
- SUTCLIFFE, A. J., 1964. The mammalian fauna, in: Ovey, C. D. (Ed.), The Swanscombe skull: a survey of research on a Pleistocene site. Royal Anthropological Institute, Occasional Paper 20, 85–111.
- SWANSCOMBE COMMITTEE, 1938. Report on the Swanscombe skull: prepared by the Swanscombe Committee of the Royal Anthropological Institute. *Journal of the Royal Anthropological Institute* 68, 17–98.
- THIEME, H., 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385, 807–810.
- TUFFREAU, A., Antoine, P., 1995. The earliest occupation of Europe: continental northwestern Europe, in: Roebroeks, W., van Kolfschoten, T. (Eds.), The earliest occupation of Europe. University of Leiden, Leiden, pp. 147–163.
- TURNER, C., Silva, B., Wenban-Smith, F. F., 2013. Pollen, in: Wenban-Smith, F. (Ed.), The Ebbsfleet Elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003–4. Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford, pp. 291–306.
- VALLIN, L., Masson, B., 2004. Behaviour towards lithic production during the Middle Palaeolithic: examples from Hermies Le Champ Bruquette and Hermies Le Tio Marché (Pas-de-Calais, France), in: Walker, E. A., Wenban-Smith, F. F., Healy, F. (Eds.), *Lithics in action: Proceedings of the Lithic Studies Society Conference held in Cardiff, September 2000*. Lithic Studies Society Occasional Paper No. 8. Oxbow Books, Oxford, pp. 6–25.
- VILLA, P., 2009. Lower and Middle Paleolithic faunal exploitation in Europe, in: Hublin, J. J., Richards, M. P. (Eds.), *The evolution of hominid diets: integrating approaches to the study of Palaeolithic subsistence*. Springer, Dordrecht.
- WENBAN-SMITH, F. F., 1995. The Ebbsfleet Valley, Northfleet (Baker's Hole), in: Bridgland, D. R., Allen, P., Haggart, B. A. (Eds.), *The Quaternary of the Lower Reaches of the Thames: Field guide*. Quaternary Research Association, Durham, pp. 147–164.
- WENBAN-SMITH, F. F., 1998. Clactonian and Acheulian industries in Britain: their chronology and significance reconsidered, in: Ashton, N., Healy, F., Pettitt, P. (Eds.), *Stone Age archaeology: essays in honour of John Wymer*. Oxbow Books, Oxford, pp. 90–97.
- WENBAN-SMITH, F. F., 2004. The Stopes Palaeolithic Project: final report. English Heritage Research Project 3338, <https://doi.org/10.5284/1000268>.
- WENBAN-SMITH, F. F., 2007. The Palaeolithic archaeology of Kent, in: Williams, J. H. (Ed.), *The archaeology of Kent to AD 800*. The Boydell Press, Woodbridge, pp. 25–64.
- WENBAN-SMITH, F. F., 2009. Henry Stopes (1852–1902): engineer, brewer and anthropologist, in: Hosfield, R. T., Wenban-Smith, F. F., Pope, M. I. (Eds.), *Great Prehistorians: 150 years of Palaeolithic research 1859–2009*, *Lithics* 30, 65–85.
- WENBAN-SMITH, F. F., 2013a (Ed). *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1*,

- 2003-4. Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford.
- WENBAN-SMITH, F. F., 2013b. Lithic artefacts: Phase 6, the elephant area, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003-4*: Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford, pp. 339–367.
- WENBAN-SMITH, F. F., 2013c. Lithic artefacts: Phase 6, the concentration south of Trench D and other more scattered pieces, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003-4*: Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford, pp. 369–413.
- WENBAN-SMITH, F. F., 2013d. Discussion and conclusions: Clactonian elephant hunters, north-west European colonisation and the Acheulian invasion of Britain?, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003-4*: Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford, pp. 447–474.
- WENBAN-SMITH, F. F., 2014. Ebbsfleet Green, newly revealed Middle Pleistocene deposits to the west of the Southfleet Road elephant site (NGR 561060 173310), in: Bridgland, D. R., Allen, P., White, T. (Eds.), *The Quaternary of the Lower Thames and Eastern Essex: Field guide: 199-204*. Quaternary Research Association, London.
- WENBAN-SMITH, F. F., Bridgland, D. R., 2001. Palaeolithic archaeology at the Swan Valley Community School, Swanscombe, Kent. *Proceedings of the Prehistoric Society* 67, 219–259.
- WENBAN-SMITH, F. F., Allen, P., Bates, M. R., Parfitt, S. A., Preece, R. C., Stewart, J. R., Turner, C., Whittaker, J. E., 2006. The Clactonian elephant butchery site at Southfleet Road, Ebbsfleet, UK. *Journal of Quaternary Science* 21, 471–483.
- WENBAN-SMITH, F. F., Bates, M. R., Schwenninger, J. L., 2010. Early Devensian (MIS 5d-5b) occupation at Dartford, southeast England. *Journal of Quaternary Science* 25, 1193–1199.
- WENBAN-SMITH, F. F., Bates, M. R., Stafford, E., Parfitt, S. A., 2020. Landscape, environment and dating framework, in: Wenban-Smith, F. F., Stafford, E., Bates, M. R., Parfitt, S. A. (Eds.), *Prehistoric Ebbsfleet: excavations and research in advance of High Speed 1 and South Thameside Development Route 4*. Oxford Wessex Archaeology Monograph 7 (High Speed 1 series), pp. 279–293.
- WISSING, C., Rougier, H., Crevecoeur, I., Germonpré, M., Yuichi, I. N., Semal, P., Bocherens H., 2016. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. *Quaternary International* 411, 327–345.
- WISSING, C., Rougier, H., Baumann, C., Comeyne, A., Crevecoeur, I., Drucker, D. G., Gaudzinski-Windheuser, S., Germonpré, M., Gómez-Olivencia, A., Krause, J., Matthies, T., 2019. Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in Europe. *Scientific Reports* 9, 4433.
- WHITE, M. J., 2012. The lithic assemblage, in: Boismier, W. A., Gamble, C. S., Coward, F. (Eds.), *Neanderthals among mammoths: excavations at Lynford Quarry, Norfolk*. English Heritage, Swindon, pp. 219–261.
- WHITE, T. S., Preece, R. C., Whittaker, J. E., 2013. Molluscan and ostracod successions from Dierden's Pit, Swanscombe: insights into the fluvial history, sea-level record and human occupation of the Hoxnian Thames. *Quaternary Science Reviews* 70, 73–90.
- WHITTAKER, J. E., Horne, D. J., Wenban-Smith, F. F., 2013. Ostracods and other microfossils, in: Wenban-Smith, F. (Ed.), *The Ebbsfleet elephant: excavations at Southfleet Road, Swanscombe in advance of High Speed 1, 2003-4*: Oxford Archaeology Monograph No. 20. Oxford Archaeology, Oxford, pp. 275–289.
- WOJTAL, P., Haynes, G., Klimowicz, J., Sobczyk, K., Tarasiuk, J., Wrońskie, S., Wilczyńska, J.,

2019. The earliest direct evidence of mammoth hunting in Central Europe – The Kraków Spadzista site (Poland). *Quaternary Science Reviews* 213, 162–166.
- WYMER, J. J., 1968. *Lower Palaeolithic Archaeology in Britain as represented by the Thames Valley*. John Baker, London.
- WYMER, J. J., 1982. *The Palaeolithic Age*. Croon Helm, London.
- WYMER, J. J., 1985. *The Palaeolithic Sites of East Anglia*. Geo Books, Norwich.
- YRAVEDRA, J., Domínguez-Rodrigo, M., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Baquedano, E., 2010. Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). *Journal of Archaeological Science* 37, 2469–2476.
- YRAVEDRA, J., Rubio-Jara, S., Panera, J., Uribe-larrea, D., Pérez-González, A., 2012. Elephants and subsistence. Evidence of the human exploitation of extremely large mammal bones from the Middle Palaeolithic site of PRERESA (Madrid, Spain). *Journal of Archaeological Science* 39, 1063–1071.
- ZILHAO, J., 2014. The Neanderthals: evolution, palaeoecology, and extinction, in: Cummings, V., Jordan, P., Zvelebil, M. (Eds.), *The Oxford handbook of the archaeology and anthropology of hunter-gatherers*. Oxford University Press, Oxford, pp. 191–213.
- ZWILLING, E. A., 1942 (4th edition). *Unvergessenes Kamerun: zehn Jahre Wanderungen und Jagden: 1928-1938*. Paul Parey, Berlin.

