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RGZM

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HUMAN BEHAVIOURAL ADAPTATIONS TO INTERGLACIAL LAKESHORE ENVIRONMENTS: AN INTRODUCTION

During the course of human evolution, we have successfully adapted to various environments. Changing climates and landscapes often required new behavioural strategies for survival; human societies indeed came into being against the background of this challenge. Although the connection between human behavioural adaptation and environmental change is well acknowledged, the processes involved are not fully understood. To what extent, how rapidly and at what scale climate and environmental change led to modifications and adaptations in human behaviour are issues that are only just beginning to be intensively addressed. A fundamental problem is the complexity and interdependence of human behaviour and environmental conditions, necessitating the identification of relevant levels of comparability in order to provide a solid foundation on which to base the archaeological record as a product of behavioural adaptation.

In this sense, interglacial environments offer an excellent opportunity to analyse how humans adapted to changing climates and landscapes. Warm environments have traditionally been regarded as a challenge to human survival (Gamble 1987; 1986), mainly due to the limitation that forested landscapes impose on the growth of herds of large herbivores, which are considered to be the basis of Pleistocene hominins diet. However, northern Europe was occupied intensively during interglacials, and recent works highlight the research potential of warm, forested environments in regard to human subsistence (Gaudzinski-Windheuser et al. 2014; Gaudzinski-Windheuser / Roebroeks 2011; Roebroeks / Conard / van Kolfschoten 1992).

On the north European plain, interglacials often correlate with the flooding of basins, resulting in the appearance of lacustrine landscapes with different types of freshwater localities, from small ponds to large lakes. Lacustrine environments offer a broad range of highly predictable resources, such as fish, birds, water plants and regular sources of fresh water (Dinnin / van de Noort 1999; González-Morales 1999; Nicholas 1998; 2006). Freshwater localities are considered to have played a major role in human evolution (Cunnane / Stewart 2010), and therefore hold great potential for studying prehistoric hunter-gatherer behaviour (Nicholas 2006).

The relationship between lakeland environments and human settlement, as well as the consumption of aquatic resources, is clearly demonstrated in the European Mesolithic (Kaiser / Terberger / Jantzen 2000; Jochim 1998; 2006; Naito et al. 2013). In contrast, the consumption of freshwater resources during the Pleistocene is less evident, but hominin diets may have been broader than previously considered (Fiorenza et al. 2015; Villa / Roebroeks 2014). Nevertheless, accepting evidence for a diet mainly based on meat consumption (Richards / Trinkaus 2009) indicates that lacustrine localities would have been essential to hominin subsistence considering the regular presence of ungulates around these areas. Indeed, the expected concentration of ungulates in

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these areas attracted hominins, as demonstrated by the presence of many Palaeolithic sites in lakeland environments (Gaudzinski-Windheuser / Roebroeks 2011).

From an analytical perspective, interglacial wetland deposits often contain high-resolution archives of the past, with favourable conditions for the preservation of archaeological, organic and botanical remains, as well as large-scale, detailed stratigraphic sequences and ecological records (van de Noort 2008). Owing to this excellent preservation, lacustrine deposits permit detailed environmental, chronological and archaeological analyses (Gaudzinski-Windheuser et al. 2014). In the archaeological records, lakeshore sites are well-known as locations for the procurement and butchering of animals, lithic provisioning, gathering vegetal resources, collecting aquatic resources and, occasionally, more permanent visits by hunter-gatherers. In this respect, interglacial lakeshore environments are essential for studying past human behaviour.

The MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution (Neuwied, Germany) has defined one of its core research themes under the title of *"Human behavioural strategies in interglacial environments"*. The aim of this research is to undertake a holistic and diachronic analysis of survival strategies under similar environmental parameters in order to document the evolution of hominin subsistence behaviour and to gauge whether certain subsistence adaptations arose in direct response to distinct environmental conditions. This research focus covers a wide spatial framework and temporal span ranging from the Middle Pleistocene to the Holocene. With this aim in mind, a session titled *"Human behavioural adaptations to interglacial lakeshore environments"* was organized at the XVII Congress of the UISPP, held in Burgos, Spain, in September 2014. The session provided a forum for specialists to present and discuss data from localities of different character, from ephemeral sites to extensive, multi-occupation localities and to highly detailed information preserved at early Holocene sites. The aim of the session was to understand the importance and attractiveness of freshwater localities as focal points for human behaviour during interglacials. This volume gathers some of the lectures given at that session.

For our oldest locale, Turner focuses on the Middle Pleistocene site of Miesenheim I, located on the edge of the Neuwied Basin in the Central Rhineland of Germany. Dating to approximately 500,000 years ago, the site produced an interglacial fauna associated with a small assemblage of lithic artefacts, deposited close to a flood-plain pond. The evidence currently available hints at a transient use of the site by hominins, providing another, ephemeral, facet of human behavioural adaptations in interglacials.

Brasser addresses the issue of whether the accumulations of fauna along the lakeshore at the Lower Palaeolithic locality of Bilzingsleben can be related to human activity or to other factors, such as natural accumulations and / or post-depositional processes. In this case, the presence of cut marks and the prey age profiles proved useful for differentiating the role of hominins from other processes in the creation of the deposit.

The archaeological locality of Schöningen 13II-4 is one of the most well-known examples of a Pleistocene lakeshore site. Here, a series of wooden spears were discovered, considered to be the standard of Palaeolithic organic hunting weapons. In the paper by Hutson and colleagues, the zooarchaeological record of the site is introduced, showing the potential for Schöningen to inform on the use of wooden tools in the Palaeolithic and the development of complex behaviours during the Middle Pleistocene.

Starkovich and Conard evaluate the inclusion of meat into the hominin diet during the Pleistocene. The authors offer a wide, diachronic review of the origins of hominin meat acquisition, a process in which lakeshore environments likely played a major role due to their attractiveness for both ungulates and their predators, including hominin hunters and other carnivores.

On a similar topic, the Eemian locality of Neumark-Nord offers a unique opportunity to approach ungulate carrying capacities and biomass production. With its high-resolution stratigraphic sequence, excellent preservation conditions and archaeological richness, the faunal assemblages of Neumark-Nord, featuring more than 450 hundred large- and medium-sized herbivores, provide the means to evaluate Neanderthal prey selection patterns and subsistence strategies.

Two papers focus on the Mesolithic site of Bedburg-Königshoven. Dated to the beginning of the Holocene interglacial (11,600 BP), in the middle of the Preboreal Pollen Zone, the mammal fauna is already fully temperate in character (e. g. red deer, roe deer, aurochs, wild boar) with possible indicators for surviving open conditions (horse, white stork, crested lark). As Street shows, the waterside location was used by humans for the butchery and disposal of large game, which appears to have been hunted close by. However, there is also evidence for a number of other activities, as indicated by the appearance of antler frontlets, analysed here by Wild.

Finally, Gross examines lakeshore archaeological sites for a detailed reconstruction of prehistoric landscapes. The archaeological locality of Rhinluch is a valuable area for analysing the Early Holocene exploitation of a micro-region. With three contemporaneous archaeological sites, this locality offers promise for the analysis of early Holocene hunter-gatherer-fisher behaviour and for the understanding of Holocene environments.

Taken together, these papers provide a broad, diachronic perspective on the human use of lakeshore environments, from the Middle Pleistocene to the Early Holocene. These environments exhibit remarkable ecological diversity with highly concentrated and predictable resources. With their high-resolution stratigraphic deposits and excellent conditions of preservation, lacustrine localities are exceptional archives for detailed analyses of human adaptations to changing, dynamic environments. In conclusion, interglacial lakeshore archaeological sites are keystones in the long path of human evolution, providing critical insight into what makes us human.

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MONIKA BRASSER

BIG QUESTIONS FOR BIG BONES – EVALUATING THE EXTENT OF HUMAN INFLUENCE AT THE LOWER PALAEOLITHIC SITE OF BILZINGSLEBEN

Abstract

Over 30 years of excavation work at the Lower Palaeolithic site of Bilzingsleben (Thuringia / Germany) yielded several tons of find material. Human remains and engraved animal bones, interpreted as early artwork, made the site world famous. Site formation is an important issue at Bilzingsleben, the key question being the degree of human influence, which is estimated quite dissimilar by different researchers. The debate has to date mainly been based on the geology and lithic material. Therefore a new approach was adopted with the analysis of the megafaunal remains. They make up about 40 % of the total fauna of the site. *Elephas antiquus, Stephanorhinus kirchbergensis / hemitoechus, Bos primigenius / Bison priscus* and as a control group *Ursus* sp. were studied using zooarchaeological, taphonomic and archaeological methods. The human influence that can be seen in the faunal record was addressed and its extent evaluated.

Keywords

Bilzingsleben, megafauna, Lower Palaeolithic, human impact, bone modification

Introduction

The scarcity of well-preserved sites from the Lower and Middle Palaeolithic in Europe poses a great challenge for scientists studying this period of the human past. While analytical methods have developed since the discovery of the site Bilzingsleben more than 45 years ago, using more and more approaches adapted from the natural sciences, the low quantity of existing sites still poses a limiting factor. Therefore comprehensive analyses of the existing sites are crucial. The few sites known (e. g. Boxgrove, Swanscombe, Hoxne) are exclusively from interglacial contexts, frequently displaying a palimpsest of different overlying signals and events often in connection with poor preservation or excavation techniques. Only very few sites yielded large inventories and were excavated using modern methods (Conard et al. 2003; Gramsch 2010). Among these Bilzingsleben is unique in terms of the sheer quantity of well-preserved and documented find material. Because of this a comprehensive analysis and continuing discussion of the site is essential.

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Bilzingsleben

The Lower Palaeolithic site of Bilzingsleben (Thuringia/Germany) was discovered in 1969 and became world famous soon after with the publication of engraved bones, interpreted as early artwork, settlement structures including huts, hearths, bone and stone tools and an artificial pavement (e. g. D. Mania/U. Mania 2005). Those interpretations have recently been challenged by various scientists, who suggest the site was formed mainly by natural processes (Beck et al. 2007).

Dating most likely to OIS 11, Bilzingsleben is one of only a handful of Middle European sites of that period (Steguweit 2003, 28-36; Jöris/Baales 2003; Müller/Pasda 2011, 27).

Excavations were conducted for more than 30 years, covering an area of about 1770 m² (**fig. 1**, numbered squares). Several tons of lithic and faunal materials were unearthed until 2003 (e. g. Gramsch 2003, 13; D. Mania/U. Mania 2001, 10; Müller/Pasda 2011, 25). Later excavations by a different team examined adjacent areas that were not part of this study (Beck et al. 2007, fig. 1 squares A, B, C).

The site is reconstructed as a lake shore environment close to a calcareous spring with a large alluvial fan leading up to a higher, dry area. The actual find layer was buried under 4-6 m of travertine and is extremely well preserved (D. Mania 1997, 43).

One of the key questions at Bilzingsleben has always been the extent of human influence on the site formation processes. Many studies yielded different and often conflicting results, which were controversially discussed by the scientific community (e. g. D. Mania 2003a; 2003b; 2004a; 2004b; 2005; Pasda 2005). Recently an increasing number

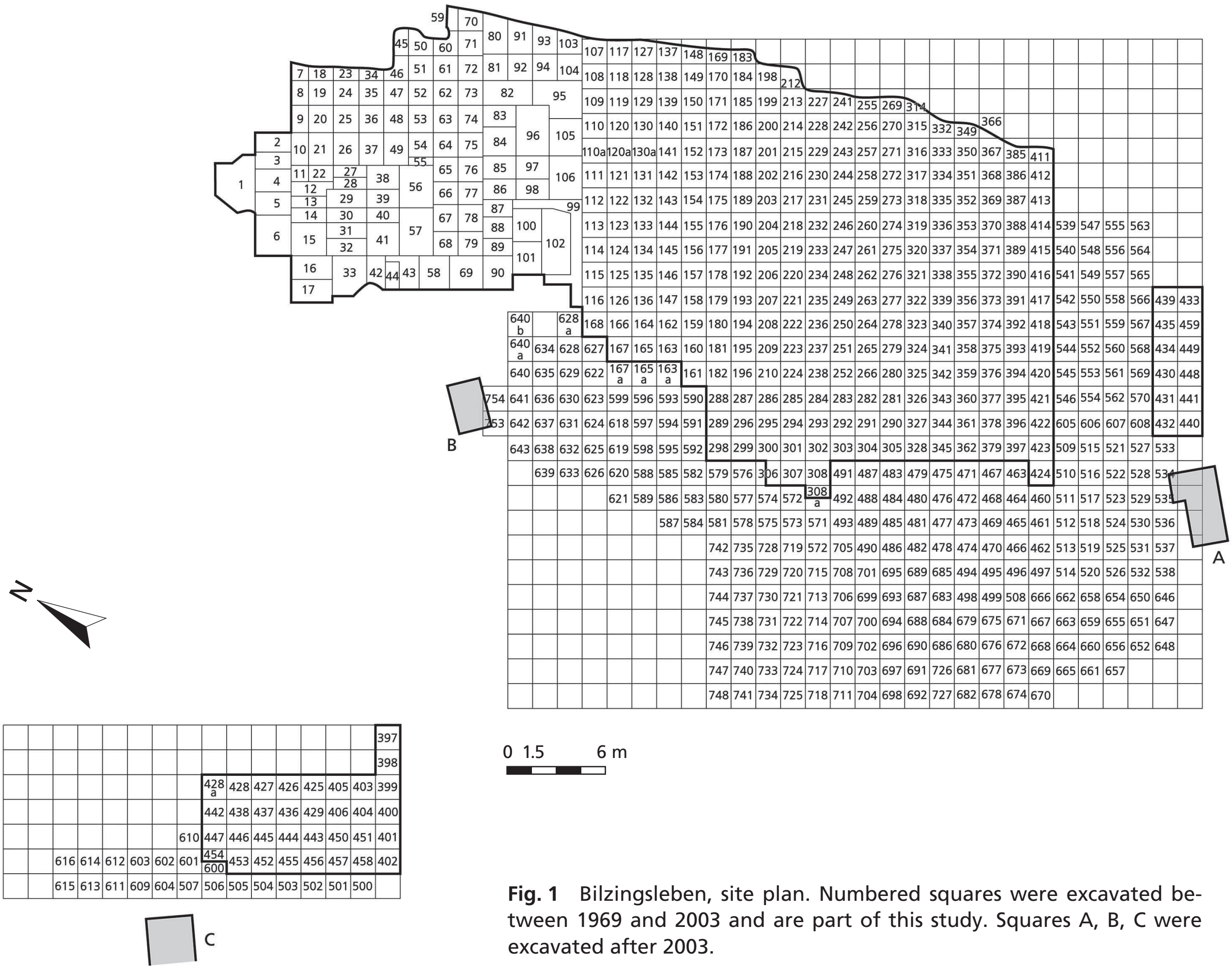

Fig. 1 Bilzingsleben, site plan. Numbered squares were excavated between 1969 and 2003 and are part of this study. Squares A, B, C were excavated after 2003.

of researchers published evidence that biotic and abiotic factors such as fluviatile displacement and carnivores played a more prominent role in site formation than assumed earlier (Beck et al. 2007; Müller/Pasda 2011; Pasda 2012; Vollbrecht 2000).

The debate has so far been based mainly on the geology and lithic material of the site and only to a lesser degree on the animal remains. While single aspects of the fauna have been studied before (most recently the antler remains [Vollbrecht 2000]), they mainly focused on palaeontological questions or limited aspects of taphonomy (see summary in Brasser 2013, 14-22). Therefore a new approach was adopted with the comprehensive analysis of all megafaunal remains.

Material and Methods

Several tons of faunal material were unearthed during the excavations conducted between 1969-2003. Large mammals dominate. However, smaller mammals, reptiles, fish and amphibians were also found (see summary in Brasser 2013, 17-22).

For the current study, all determinable fragments of the megafauna were analyzed and compared. Mammals with a life weight of more than 1000 kg were included here. At Bilzingsleben these are straight tusked elephant (*Elephas antiquus* FALCONER & CAUTLEY, 1847), two species of rhinoceros (*Stephanorhinus kirchbergensis* JAEGER, 1839 and *Stephanorhinus hemitoechus* FALCONER, 1868) and the bovids (*Bison priscus* BOJANUS, 1827 and *Bos primigenius* BOJANUS, 1827). They are best suited to answer the central questions about human influence at Bilzingsleben for two reasons: first of all they are quite abundant, accounting for about 40 % of the total faunal remains (Brasser 2013, 80 f.). This is especially interesting for the rhinoceroses, which are normally considered solitary animals (Laurie 1982, 316). The question here would be whether anthropogenic factors are responsible for their presence. The second important reason for choosing the megafauna was the fact that most of the pieces interpreted and published as bone tools in the past were bones either from elephants or rhinoceroses (U. Mania 1995; D. Mania/U. Mania 1997). In order to ensure that factors which might only influence smaller bones were also considered in the analysis, a smaller species of mammal (*Ursus hercynicus* MUSIL, 2006 and possibly another, smaller bear), was also included. Bears are one of the few smaller species whose bones are abundant at the site.

At present most of the faunal material is kept at a storage facility in Jena (Germany) belonging to the Institut für Ur- und Frühgeschichte of the Friedrich-Schiller-University. About one third of the material is in the depot of the Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt in Halle (Germany). Some pieces are also kept in the permanent exhibitions of the Landesmuseum Sachsen-Anhalt in Halle and the Museum für Ur- und Frühgeschichte Thüringens in Weimar (Germany). All specimens were studied at their present locations by the author. All of the faunal remains were examined but only finds that could be determined to species level were selected for further analysis. The reference collections of the Phyletisches Museum Jena (Germany) and the MONREPOS Archaeological Research Centre and Museum for Human Behavioral Evolution, RGZM in Neuwied (Germany) were consulted where necessary.

The number of allocable fragments for each species is given as NISP (number of identified specimens, Grayson 1984; Lyman 1994b). Each fragment is counted separately as a NISP unless it was a restored (with glue or plaster cast) specimen consisting of several, recently broken fragments. These finds were quite abundant and counted as one specimen. The same applies to other refitting fragments with obvious recent breaks.

Additionally, MNI was tabulated for each bone or tooth (White 1953, 397) taking into consideration age and size ("matching" of possible right and left counterparts, or eliminating matches due to size or state of epiphyseal fusion respectively; Klein and Cruz-Uribe 1984, 26). MNE (minimum number of elements, Binford 1978) and %MAU (minimum animal units necessary to account for the specimens in a collection, Binford 1978, 64-72; Lyman 1994a, 104-

110) were determined in order to characterize skeletal element representation. Fragments of elements were also included in these calculations by observing distinct landmarks on the bones, thus avoiding biasing due to an overlapping of bone parts.

Teeth were used for age determination because there is no reliable data for epiphyseal fusion of most non-domestic animals. In addition the results of dental age analyses cover a greater portion of the overall lifespan (Klein/Cruz-Uribe 1984, 44-62; Steele 2006, 119). For the bovids the method described by Klein and Cruz-Uribe (1984, 44-62) was used. Rhinoceroses were analyzed according to Louguet (2005), elephants according to Haynes (1991) and Roth and Shoshani (1988). Age determination in bears was undertaken following the method of Stiner (1998).

In cases where elephant molars could not be securely determined because of their poor state of preservation, they were allocated provisionally to a particular tooth and distributed equally. This occurred mostly when M V and M VI could not be differentiated due to fragmentation. In these cases, 0.5 was added to the tooth count of M V and M VI respectively. By applying this method, fragmented molars could also be included in the analysis.

For the dental age analysis of the rhinoceroses (Louguet 2005), complete jaw fragments were used rather than single teeth. This method has been shown to produce more reliable results in other species (Turner 2003, 55-58). At Bilzingsleben the large number of such fragments permitted this approach. To avoid duplicate counts of individuals, only the most common jaw element, the left mandibula, was used for the calculation. In cases where tooth abrasion ranged between two stages, both stages were allocated an equal percentage.

Age determination of bovids was conducted using the mandibular M_3 for reasons of preservation. This tooth develops late, only appearing at an age of 24-30 months (Habermehl 1961). Despite this, the M_3 was chosen for this analysis since the only specimen in the collection displaying hardly any abrasion is an M_3. This particular tooth was necessary for the interpretation of different wear stages (Klein/Cruz-Uribe 1984, 46-51). The maximum length (63.34 mm) was measured and used to calculate different wear stages that account for 10 % of the maximum crown height respectively (Klein/Cruz-Uribe 1984, 46). It is not feasible to translate these stages into calendar years, since diverse factors influence the dental wear in bovids (Jones/Sadler 2012, 7). This method is sufficient to enable a comparison of age cohorts between the different species.

In order to compare the age structures of the different animals a ternary plot was constructed (Stiner 1990, 317-321). The spreadsheet TRI-PLOT (Graham/Midgley 2000) was used for this. The position in the diagram is based on the amount of juvenile, adult and senile animals and depicts the variations in age distribution between the different animals for comparative purposes. The classification into three

Tab. 1 Skeletal element representation of *Elephas antiquus, Stephanorhinus kirchbergensis/hemitoechus, Bison priscus/Bos primigenius* and *Ursus* sp.

	NISP	NISP (%)	MNI	MNI (%)
Elephas antiquus	754	9.11	23	9.39
Stephanorhinus kirchbergensis/hemitoechus	4006	48.38	112	45.71
Bison priscus/ Bos primigenius	1024	12.37	22	8.98
Ursus sp.	2496	30.14	88	35.92
total	8280	100	245	100

NISP: Number of identified specimens, MNI: Minimum number of individuals

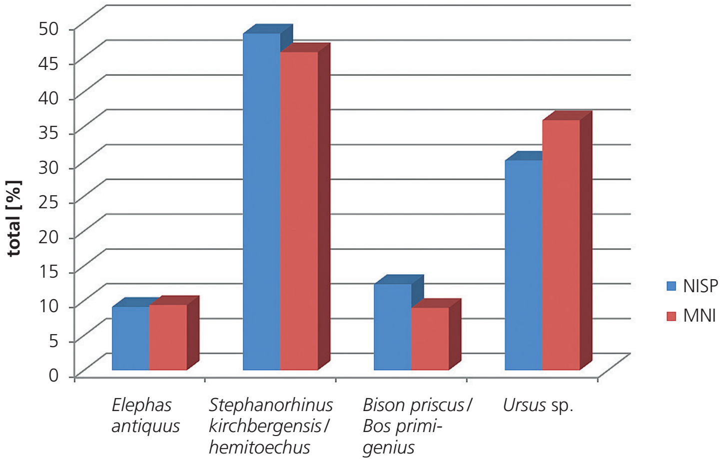

Fig. 2 Abundance of different megafaunal species in the collection (NISP: Number of identified specimens, MNI: Minimum number of individuals).

age stages was undertaken according to Stiner (1998, 312-315) for the bears and analogous for the other animals.

Analyses of bone density were conducted for all species. Lam/Chen/Pearson (1999) showed that there is no significant difference between the density rankings for skeletal elements in different animal species. This principle was applied since there is no data on bone densities of rhinoceroses or elephants. Here the ranking for bovids according to Lam/Chen/Pearson (1999) was applied. The analysis of the ursid bones was undertaken according to Novecosky and Popkin (2005). As suggested by Lam/Chen/Pearson (1998) logarithmized values were used.

A food utility analysis was only possible for the bovids because there are no publications on these analyses for the other species.

In order to determine whether fluviatile processes had an influence on the faunal material, preservation was studied with regard to the Voorhies groups (Voorhies 1969; Behrensmeyer 1975). This method is based on the understanding that certain body parts are transported later than others by streams. For this analysis the MAU of all relevant skeletal parts was used, while single teeth were excluded in order to avoid biasing.

One focus of the analysis was the distinction between natural factors and human influence on the fauna. Carnivores can create marks and patterns on bones that are very similar to human modifications (e.g. Haynes 1991; Johnson 1985; Villa/Bartram 1996, Villa et al. 2004). Therefore these traces have to be distinguished from cut marks and other human modifications. Several authors describe tooth marks from hyenas and other large carnivores in detail (e.g. Haynes 1980; Binford 1981; Lyman 1994a; Suttcliffe 1970; Hill 1989; Villa/Bartram 1996; Villa et al. 2004 and most recently Diedrich 2005a; 2005b; 2005c; 2005d; 2009; 2010a; 2010b; 2010c).

The aim of the archaeological analysis of the find material from Bilzingsleben was to find direct evidence of human modifications and proof of human interaction with the material.

All analyzed bones were searched for cut marks, other butchery marks and traces of the production of organic artefacts. The identification of cut marks was complicated by the vast amount of surface scratches which, due to the embedding matrix, strongly resemble flint induced cut marks. Morphological criteria alone were not sufficient to determine the origin of the cuts. In addition to the general morphology, the anatomical position of the cuts, the number and the overall appearance of the bones were also taken into consideration (Binford 1981, 87-161; Domínguez-Rodrigo et al. 2009; Münzel 1987, 83-101; Olsen/Shipman 1988, 549).

Modifications were only accepted as man-made when other influences could be securely eliminated. This is the case when modifications are neither random nor located next to modification by carnivores.

Tab. 2 Percentages of teeth and bones for all species analyzed. *Elephas* teeth include tusks.

	Elephas antiquus	*Stephanorhinus kirchbergensis/hemitoechus*	*Bison priscus/ Bos primigenius*	*Ursus* sp.
bones (NISP, %)	50.67	40.79	58.11	30.53
teeth (NISP, %)	49.34	59.21	41.89	69.47

NISP: Number of identified specimens

Results

8280 specimens of *Elephas, Stephanorhinus, Bison / Bos* and *Ursus* could be determined (**tab. 1, fig. 2**). The largest proportion is provided by the remains of rhinoceros, which accounts for almost 50 % of the NISP. Bears make up about 30 % of the sample, while elephants and bovids account for about 9 % and 12 % respectively. The overall MNI of 245 is rather high. The distribution is similar to that observed for the NISP, with rhinoceroses accounting for about 45 %, bears for 35 %, and elephants and bovids for about 9 % of the MNI respectively.

Skeletal element representation

Dental elements are the most common finds for all analyzed species (**tab. 2**). While teeth prevail, maxillar and mandibular bones are also quite abundant. Teeth make up for more than two thirds of all *Ursus* remains and thus dominate the bear inventory. The same applies to a somewhat smaller degree to the megafauna, where teeth make up 45 % (bovids), 50 % (*Stephanorhinus kirchbergensis / hemitoechus*) or even 60 % (*Elephas antiquus*) of the total material. For the elephants this number includes tusk fragments, which alone account for 15 % of the total number of teeth. Overall teeth are quite abundant for all species, even though the actual amounts vary. In contrast, the representation of the skeletal elements shows striking differences between the species. For better comparability **figures 3-6** depict the %MAUs of all skeletal elements excluding isolated teeth (see **tab. 3**).

Cranial bones are not very common for any of the species except the bears where they reach 50 %MAU. The same applies to maxillar bones, that have a %MAU of 98.22 in bears, while none are preserved from the bovids. Vertebrae are most common in elephants. Scapulae are hardly preserved in bears but reach a %MAU of almost 50 in elephants. The other species rank in between these counts. Only elephants show higher numbers of pelvic bones (65.22 %MAU), while they are much rarer in the other species.

Differences can also be seen in long bones. While for *Elephas* proximal humeri are more frequent than distal, it is the other way round for the other species, where distal ends prevail markedly. Elephants and bears show even proportions of proximal and distal radii, but the overall numbers are higher for the elephants. Rhinoceroses and bovids yield markedly more proximal than distal ends. Ulnae obtain a %MAU between 22 and 30 in all species.

Proximal femora are more common than distal femora for all analyzed species. However, there are differences in the overall share of this element varying between 5.56 %MAU (*Ursus*) and 43.9 %MAU (*Bison priscus / Bos primigenius*). Patellae are predominantly preserved from bears (25 %MAU) and elephants (17.39 %MAU). There are more proximal elephant tibiae (43.48 %MAU) than distal (21.75 %MAU), while they are generally rare in the rhinoceroses. For the bovids a few medial and a larger amount of distal tibiae could be determined (53.67 %MAU). Bears show a similar pattern with more distal than proximal tibia fragments. However, the overall numbers are lower for these animals. Carpals and tarsals are quite common for the bovids where they account for a %MAU of almost 55, while the number is much lower for all other animals. The same results could be found for the

0 - 25 %MAU ░
26 - 50 %MAU ▒
51 - 75 %MAU ▓
76 - 100 %MAU █

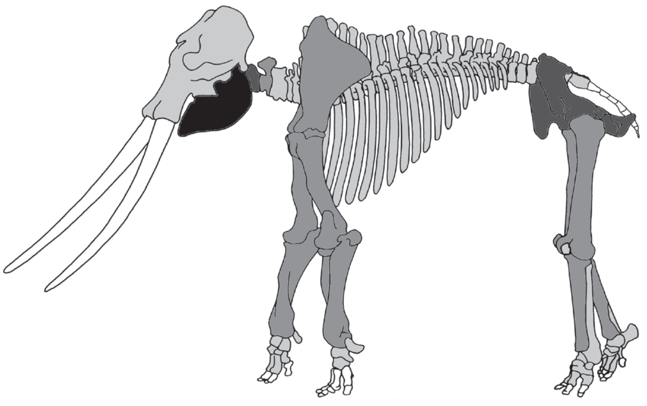

Fig. 3 Illustration of the skeletal element representation for *Elephas antiquus* (%MAU: Minimum number of animal units, percentages based on the total inventory of each species).

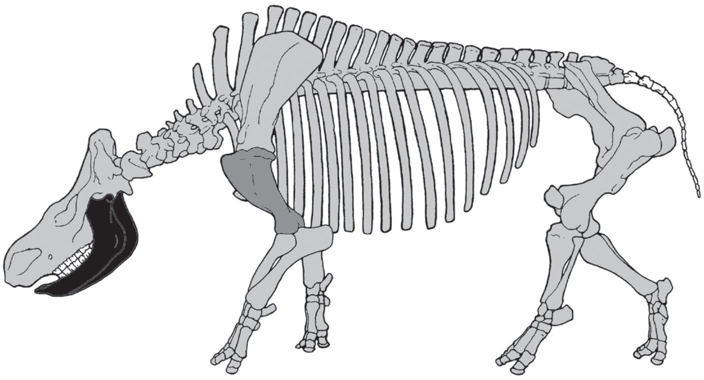

Fig. 4 Illustration of the skeletal element representation for *Stephanorhinus kirchbergensis/hemitoechus* (%MAU: Minimum number of animal units, percentages based on the total inventory for each species).

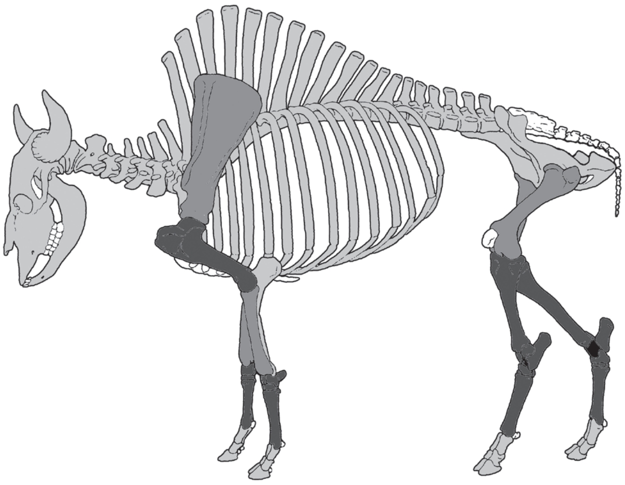

Fig. 5 Illustration of the skeletal element representation for *Bison priscus/Bos primigenius* (%MAU: Minimum number of animal units, percentages based on the total inventory for each species).

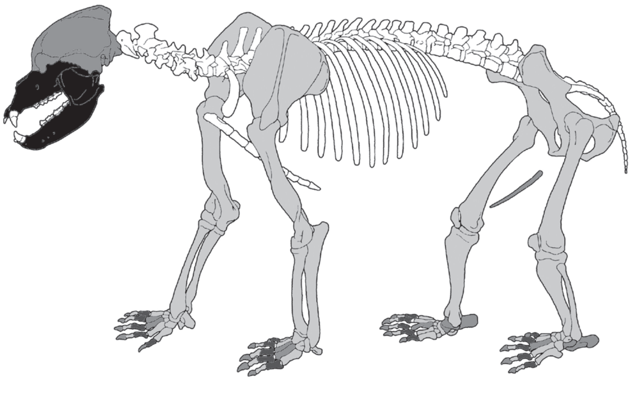

Fig. 6 Illustration of the skeletal element representation for *Ursus* sp. (%MAU: Minimum number of animal units, percentages based on the total inventory for each species).

Tab. 3 Skeletal element representation (without isolated teeth) for all species analyzed.

	Elephas antiquus (%MAU)	*Stephanorhinus kirchbergensis/hemitoechus* (%MAU)	*Bison priscus/ Bos primigenius* (%MAU)	*Ursus* sp. (%MAU)
Cranium	8.7	3.6	4.88	50
Mandibula	100	100	19.51	97.22
Maxilla	13.04	5.86	0	100
Atlas	52.17	3.6	9.76	0
Epistropheus	43.49	4.5	4.88	0
Vertebrae (without atlas and epistropheus)	17.65	3.78	0.39	0
Scapula	47.83	13.96	29.27	2.78
Sternum	17.39	2.7	0	0
Costae	1.3	0.13	0.73	0
Humerus prox.	26.09	9	0	0
Humerus med.	13.04	3.15	2.44	0
Humerus dist.	17.39	33.78	70.73	2.78
Ulna	30.43	23.42	21.95	25
Radius prox.	26.09	19.82	43.9	11.11
Radius med.	0	1.8	0	2.78
Radius dist.	30.43	4.95	21.95	8.33
Carpalia/Tarsalia (without Astragalus and Calcaeneus)	17.39	5.03	54.39	3.89
Sacrum	8.7	0.9	0	0
Pelvis	65.22	23.42	12.2	2.78
Femur prox.	26.09	16.67	43.9	5.56
Femur med.	8.7	10.81	0	0
Femur dist.	34.78	5.86	7.32	16.67
Patella	17.39	0.45	0	25
Tibia prox.	43.48	6.31	0	2.78
Tibia med.	8.7	4.05	2.44	0
Tibia dist.	21.75	9.91	53.67	19.44
Metapodium	5.22	8.11	50.31	35
Astragalus	8.7	14.41	100	30.56
Calcaneus	8.7	9	56.34	36.11
Phalanges	0.43	8.33	20.15	35

%MAU: Minimum number of animal units, percentages based on the total inventory for each species

other autopodials and metapodials. They are rare in elephants and rhinoceroses, while layer quantities of these bones from bovids and bears were preserved.

The patterns of preservation are thus different for each of the analyzed species. Rhinoceros, elephant and bear remains are dominated by mandibular bones. This is particulary true for the assemblage of rhinoceros bones, which has the highest representation of mandibles. Apart from the humerus, all other skeletal elements are represented by less than 25 %MAU. Skeletal representation in the other species is more equal. For *Elephas*, mandibula, pelvis and atlas amount to a %MAU of more than 50. Autopodials, ribs and vertebrae are less common. All long bones (except the fibula) show similar frequencies with %MAUs between 26 and 50. Cranial material, except the mandibula, is rare, a pattern which can also be seen in the other megafaunal species.

Bovids are the only animals analyzed where cranial material does not dominate. Here long bones, and especially metapodials and carpals/tarsals are most common.

Bears show a completely different pattern. Here jaw bones and autopodials clearly dominate. Long bones are present in the sample, but are strongly underrepresented. Ribs and vertebrae are completely absent. In contrast to the other species, maxillar bones are very frequent as well as mandibular bones.

Age

To gain a better impression of age structures at the site, dental age was determined for all species and then compared. The age distribution of the elephant molars shows that most are from young individuals (**tab. 4**). The most common tooth is the M II indicating an age at death between 0.3 and 4.1 years. 14 % of all molars are M I, which are shed between 0.1 and 2.0 years. M III and M IV account for about 20 % of the sample respectively. The results show that elephants over the age of 20 are represented by only about 18 % of all the molars in the sample.

37 left mandibulae containing teeth could be included in the age analysis of *Stephanorhinus* (**tab. 5**). The distribution indicates a "prime dominated" sample. Only a few animals are younger than one year (< 1.5 %). Juvenile animals up to five years of age account for about 11 % of the total. A rise in numbers can be seen for rhinoceroses between 6 and 13 years, which make up for about 75 % of all the determinable specimens. Mature and senile animals are less common. Numbers decrease especially for animals over the age of 22 (2.24 %). Prime age *Stephanorhinus* are thus obviously dominant in the sample.

A total of 27 bovid teeth could be included in the age assessment of *Bison priscus/Bos primigenius* (**tab. 6**). The results show that the greatest number of teeth can be placed in the first half of the maximal tooth lifespan. This indicates that most of the analyzed molars are from adult animals, and that senile bovids are underrepresented. Almost all teeth

Tab. 4 Age distribution of elephants molars including age in years at shedding (according to Haynes 1991).

Molar	NISP	NISP (%)	age in years
M I	21	13.64	0.1-02
M II	41.17	26.73	0.3-04.1
M III	31.42	20.4	2.3-13
M IV	32.25	20.94	5.5-21
M V	17.08	11.09	14.5-40
M VI	11.08	7.19	27.0-61
total	154	100	

NISP: Number of identified specimens

Tab. 5 Age distribution of left rhinoceros mandibulae including age indication (Louguet 2005).

NISP	NISP (%)	age in years
0.5	1.35	<1
2	5.41	1-3
1.5	4.1	4-5
9.66	26.11	6-7
8.66	23.41	8-9
9.5	25.68	10-13
4.33	11.7	14-21
0.83	2.24	>22
37	100	total

NISP: Number of identified specimens

Tab. 6 Age distribution of the M_3 of *Bison priscus/Bos primigenius* including crown height for the different age stages (in mm).

Age stage	crown height (mm)	NISP
Stage 1	63.34-57.01	5
Stage 2	57.00-50.68	2
Stage 3	50.67-44.35	4
Stage 4	44.34-38.02	8
Stage 5	38.01-31.69	4
Stage 6	31.68-25.36	1
Stage 7	25.35-19.03	3
Stage 8	19.02-12.7	0
Stage 9	12.6-6.37	0
Stage 10	< 6.370	0

NISP: Number of identified specimens

Tab. 7 Age distribution of the ursid teeth. Wear stages are according to Stiner (1998).

Stage	NISP	NISP %
II	22	3.17
III	92	13.24
IV	187	26.91
V	143	20.58
VI	128	18.42
VII	64	9.21
VIII	42	6.04
IX	17	2.45
total	695	100

NISP: Number of identified specimens

Tab. 8 Age distribution of the species analyzed based on dental age.

	juvenile (%)	prime (%)	old (%)
Elephas antiquus	60.77	32.03	7.19
Stephanorhinus kirchbergensis / hemitoechus	6.76	79.3	13.94
Bison priscus / Bos primigenius	3.7	85.18	11.11
Ursus sp.	16.41	75.12	8.49

are in the first two thirds of their maximum lifespan. Stage 4 dominates. None of the molars have less than 30 % of the maximum crown height. It can therefore be concluded that adult bovids dominate the sample.

The age distribution of bear teeth shows that most of the bears present died in their prime (**tab. 7**). Juvenile, mature and senile individuals are much less common. Most teeth can be identified in stage IV. The domination of young adult and adult animals is obvious.

The ternary plot, which was used to compare age structures of the species analyzed, shows a distinct difference between *Elephas antiquus* and the other species (**fig. 7, tab. 8**). While *Ursus* sp., *Stephanorhinus kirchbergensis / hemitoechus* and *Bison priscus / Bos primigenius* show a prime dominated distribution, *Elephas* has a U-shaped or attritional distribution (Stiner 1990, 318). This means that very young and older individuals dominate, a pattern that is often linked to natural causes of death where the weakest individuals of a group perish first (Klein / Cruz-Uribe 1984, 56; Stiner 1990, 309). All the other analyzed animals contain less young and very old animals, which can be seen as a sign of non-natural selection (Stiner 1990, 309).

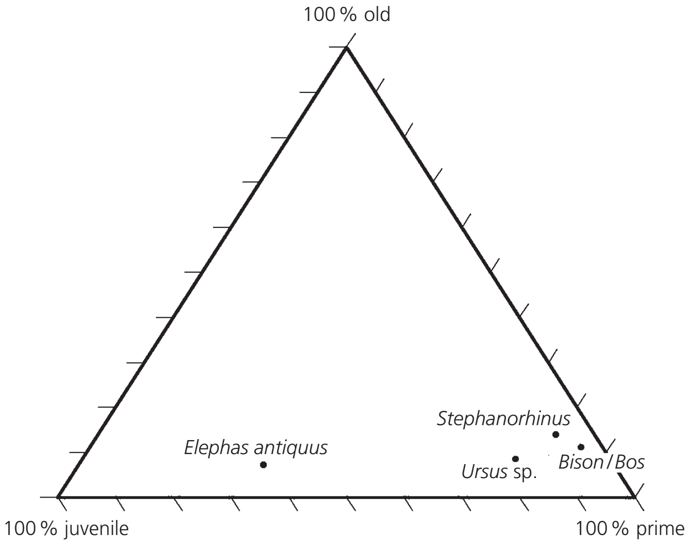

Fig. 7 Age distribution of the species analyzed.

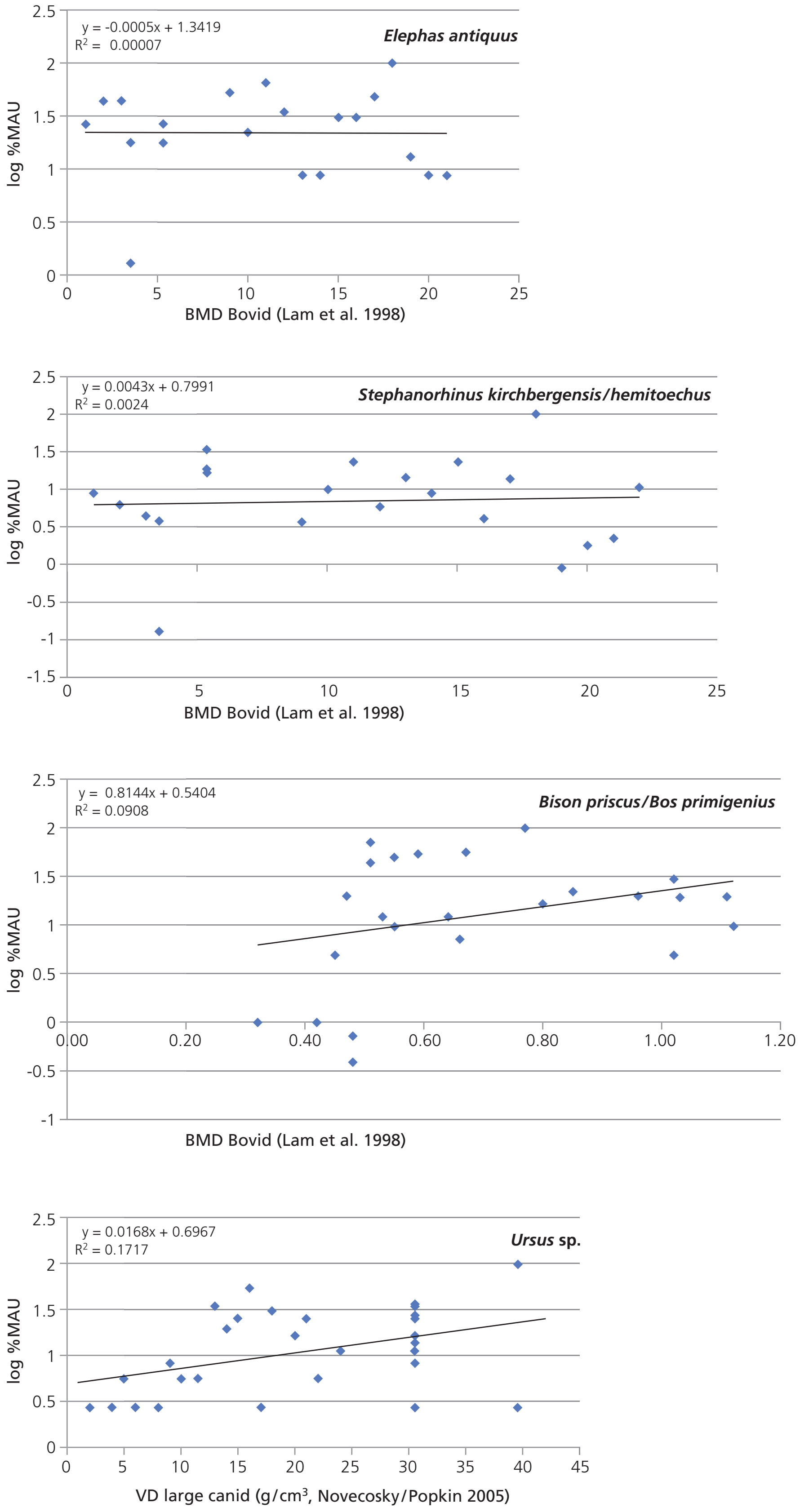

Fig. 8 Assessment of density mediated preservation for all analyzed species. (%MAU: Minimum number of animals units, percentages based on the total inventory of *Elephas antiquus*, BMD: Bone mineral density).

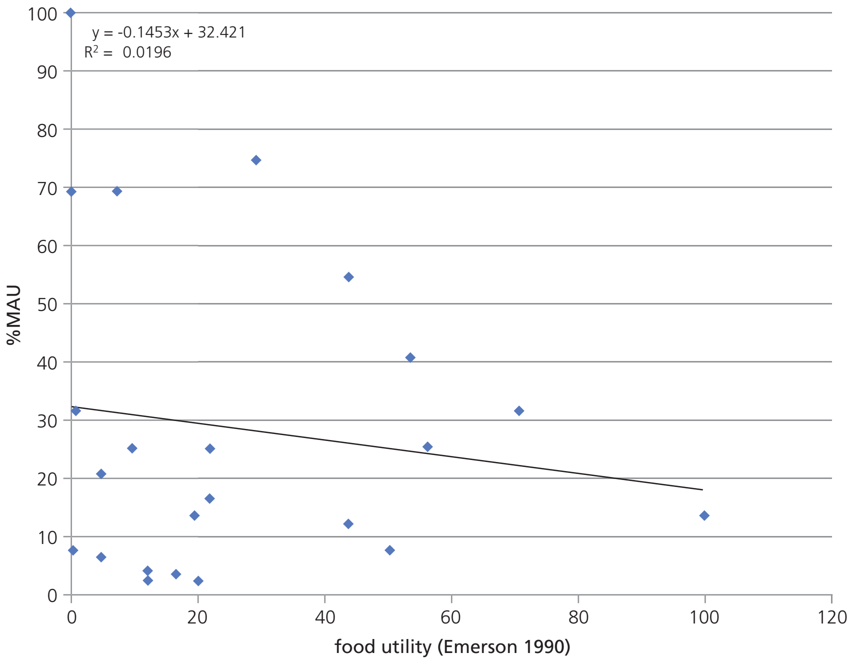

Fig. 9 Food utility, bovids (%MAU: Minimum number of animal units, percentages based on the total inventory of *Bison priscus/Bos primigenius*).

Selection

None of the analyzed species show any connection between bone density and bone frequency (**fig. 8**) and neither positive nor negative correlations were observed. A food utility analysis was only possible for the bovids because there is no data available for the other species. There is no statistically significant correlation between the preservation of the bovids and their food utility (**fig. 9**).

In a further step, it was tested whether fluviatile transport could be responsible for the composition of the Bilzingsleben faunal inventory. The analysis of the Voorhies groups (Voorhies 1969; Behrensmeyer 1975) showed that there are marked differences between the species (**tab. 9, fig. 10**).

Elements from group II, which indicate a winnowed inventory dominate for bovids and elephants, while the distribution is rather equal between groups II and III (lag deposit) for rhinoceroses and bears. However, if skeletal elements in group I/II, which are intermediary between the two groups, are included, it becomes clear that these groups dominate. It can therefore be concluded from the analysis of the Voorhies groups that the inventory has been affected by some fluviatile movement, but is not completely displaced. The ensemble can be considered as winnowed (Voorhies 1969; Behrensmeyer 1975).

Carnivore damage

5.59 % of all analyzed bones from the site show carnivore damage (**tab. 10**). However, there are considerable differences between the species. While more than 7 % of *Elephas* and *Stephanorhinus* remains show gnawing marks, only 4.71 % of *Bison/Bos* are affected. The lowest percentage can be found on the bear bones, where only 1.05 % show traces of carnivore damage. Besides the overall differences between the species, there are also variations in those parts of the skeleton showing the highest traces of gnawing (**tab. 11**). *Elephas* bones yielded the highest number of gnaw marks on the femur (NISP 6) and the pelvis (NISP 8). The other species show less gnaw marks in these areas, which are also less commonly preserved. The same

Tab. 9 MAU representation in the different Voorhies groups (excluding isolated teeth).

Voorhies group	I	I/II	II	II/III	III
Elephas antiquus	9.98	17.44	45.59	0	26.98
Stephanorhinus kirchbergensis/ hemitoechus	4.08	23.28	34.61	1.37	36.53
Bison priscus/ Bos primigenius	2.26	23.11	64.98	0	9.65
Ursus sp.	0	28.82	29.2	7.63	34.35

MAU: Minimum number of animal units

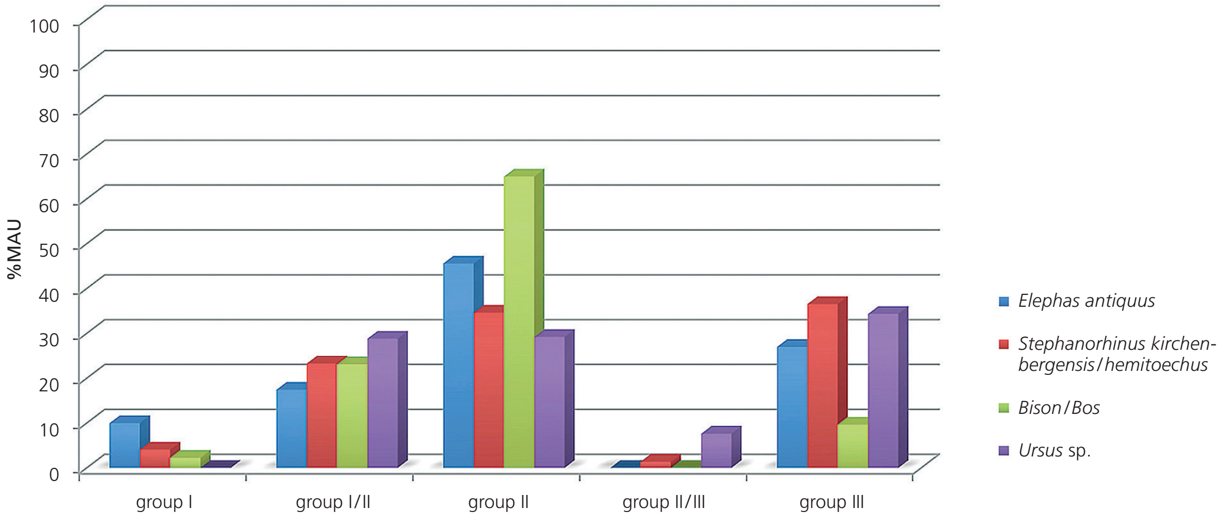

Fig. 10 Distribution of Bilzingsleben animal remains (MAU) in the different Voorhies groups. Isolated teeth are not included (MAU: Minimum number of animal units).

Tab. 10 Counts of bones showing carnivore damage. Total numbers and percentage of the inventory are given for the individual species (left column) and comprehensively for all of the analyzed inventory (right column).

	bones with gnawing marks (NISP)	bones with gnawing marks (NISP %)
Elephas antiquus	35	7.83
Stephanorhinus kirchbergensis/hemitoechus	135	7.18
Bison priscus/ Bos primigenius	28	4.71
Ursus sp.	8	1.05
total	206	5.59

NISP: Number of identified specimens

Tab. 11 Distribution of traces of carnivore damage on skeletal elements (NISP) in comparison to their proportion within the sample (%MAU), including correlation coefficient (R²).

	Elephas (NISP)	*Elephas* (%MAU)	*Stephano-rhinus* (NISP)	*Stephano-rhinus* (%MAU)	*Bison/Bos* (NISP)	*Bison/Bos* (%MAU)	*Ursus* (NISP)	*Ursus* (%MAU)
Cranium	0	8.7	3	3.6	0	4.88	1	50
Mandibula	0	100	13	100	0	19.51	2	97.22
Scapula	5	47.83	5	13.96	1	29.27	0	2.78
Vertebrae	3	17.65	2	3.78	0	0.39	0	0
Costae	4	1.3	6	0.13	0	0.73	0	0
Humerus	2	26.09	40	33.78	9	70.73	1	2.78
Radius	1	30.43	4	19.82	0	43.9	0	11.11
Ulna	1	30.43	12	23.42	2	21.95	1	25
Pelvis	8	65.22	12	23.42	1	12.2	0	2.78
Femur	6	34.78	23	16.67	5	43.9	2	16.67
Patella	1	17.39	1	0.45	0	0	0	25
Tibia	0	43.48	3	9.91	1	53.67	0	19.44
Carpalia/Tarsalia	2	17.39	0	5.03	3	54.39	0	3.89
Metapodium	2	5.22	7	8.11	3	50.31	1	35
Astragalus	0	0	2	14.41	1	100	0	30.56
Calcaneus	0	8.7	1	9	2	56.34	0	36.11
Phalanx I	0	8.7	1	8.33	0	16.49	0	26.39
total	35		135		28		8	
Correlation (R²)		0.0625		0.1706		0.2797		0.3262

NISP: Number of identified specimens, %MAU: Minimum number of animal units, percentages based on the total inventory for each species

Tab. 12 Specimens displaying cut marks.

	Elephas antiquus	*Stephanorhinus kirchbergensis/hemitoechus*	*Bison priscus/ Bos primigenius*	*Ursus* sp.	total
cut marks (NISP)	1	12	0	6	19
cut marks (NISP, % of total inventory per species)	0.12	0.3	0	0.24	0.22

NISP: Number of identified specimens

applies to the ribs, where some gnawing traces were observed on the ribs of both elephants (NISP 4) and rhinoceroses (NISP 6) but are not preserved on bones of bovids and bears. *Stephanorhinus* (NISP 40) and *Bison/Bos* (NISP 9) display a larger number of traces of gnawing on the humerus, a bone which is hardly affected in *Elephas* (NISP 2) and *Ursus* (NISP 1). Only the bovids yielded a larger number of gnawing marks on autopodials. *Stephanorhinus* and *Ursus* are the only species that display gnawing damage in the cranial area.

Some details of the gnawed areas show obvious similarities when compared between the species, however clear patterns of carnivore modification were not observed. Since there is no statistically significant correlation between the most commonly preserved bones and those showing most carnivore damage (see **tab. 11**), it can be concluded that a different selection mechanism must be responsible for the pattern. Correlations with the utilization sequence of large carnivores (Blumenschine 1986) could also not be found.

Human modifications

A total of 19 elements show cut marks (**tab. 12**). One was located on a tusk fragment of *Elephas*, 12 on bones of *Stephanorhinus* and 6 on bones of *Ursus*. These are the only cut marks in the inventory which could be securely identified. Due to a large number of sediment scratches, it is possible that some unambiguous cut marks are no longer identifiable. However, a conservative approach was chosen in the identification in order to avoid biasing.

The marks on rhinoceros bones are concentrated on the front legs (distal scapula, proximal and distal humerus and proximal ulna, see **fig. 11**). A few cut marks were also found on the mandibula and autopodials.

Bear bones are less commonly affected by sediment scratches or abrasion and therefore identification of cut marks was easier. Here a distinct pattern could be seen (**fig. 12**). Three of the specimens showed cut marks located on the buccal side of the maxilla, next to the processus zygomaticus (**fig. 13**). The other three are located on the palmar/plantar side of the metapodials.

Cut marks are regularly found in connection with the butchering of animals. This could be shown for

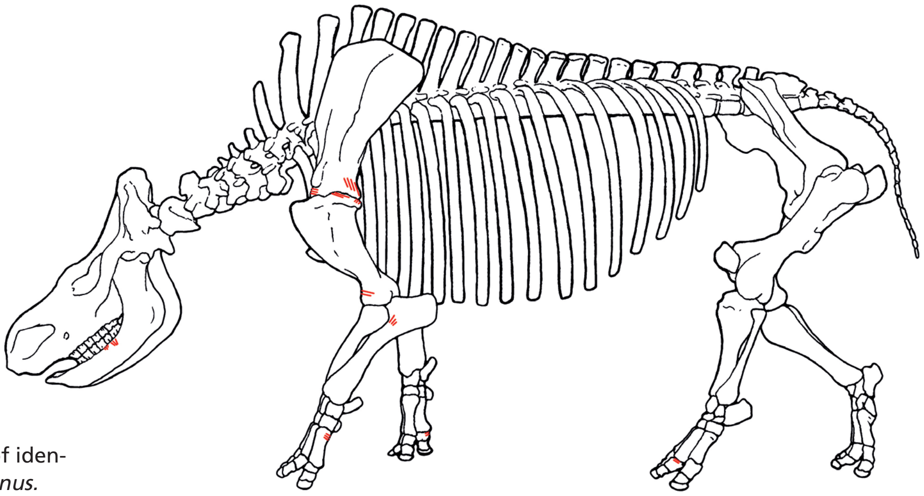

Fig. 11 Schematic illustration of identified cut marks on *Stephanorhinus.*

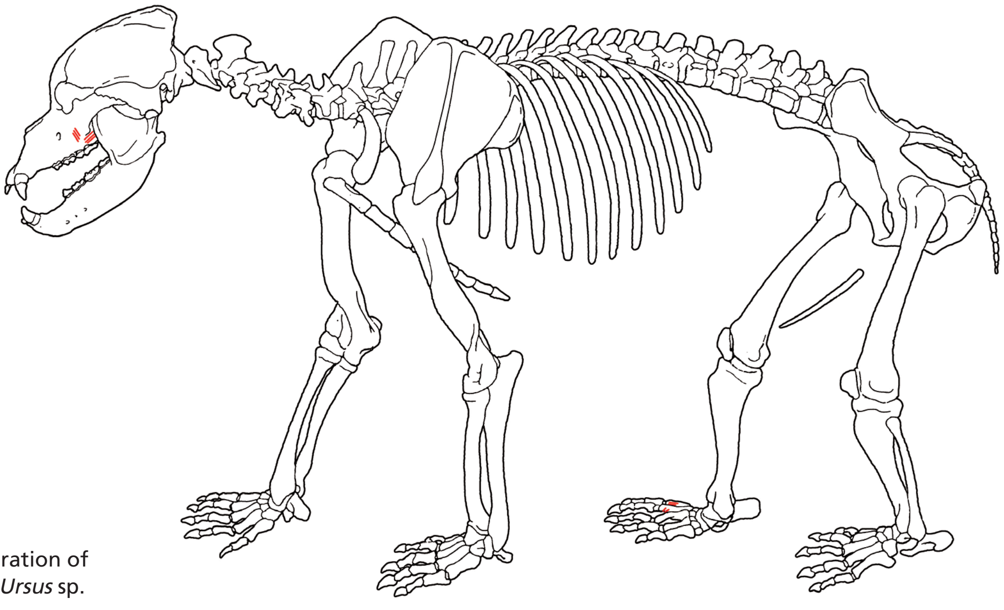

Fig. 12 Schematic illustration of identified cut marks on *Ursus* sp.

Fig. 13 Ursid maxilla with cut marks (indicated by the arrow).

the rhinoceros where the cut marks indicate the dismemberment of the animals. The marks found on the bear bones could also be traces of skinning.

Besides the cut marks there are also other bones that display human modifications. It was assessed whether there are signs of organic artefact production. For this aspect, all bones showing impact marks or any other trace of artificial modification were analyzed individually. These bones are mainly from elephants. Rhinoceros and bovid bones are much less frequent and bear bones show no such traces at all.

In total 364 bones (and some teeth) yield at least one conchoidal flake scar. The agent responsible for these traces could not be identified on most of the specimens, since the pieces only showed single non-diagnostic negatives. Other negatives could be securely attributed to natural processes, mainly because they were found in direct connection with gnawing marks.

Another portion of the bones show impact notches that derived from the deliberate opening of the bone (mainly long bone shafts). A total of 50 bones show interior and/or exterior flakes that were caused by pressure when the bone was opened. Some of these bones contain impact marks that were also caused when the shaft was opened. The question whether humans or animals are responsible for opening these bones can only be answered through analysis of the individual pieces in particular the morphology of the individual negatives. While none of the finds had been retouched, which would have been a clear indicator of human modification, some showed gnawing marks and were therefore considered modified by animals. The diameter of the impact notch could not be taken into consideration for this analysis, because none of them showed any distinct sizing. Therefore, the analysis focussed on the orientation, number and alignment of impacts. A larger number of impact marks with identical orientation in regular intervals should be a strong indicator of human modification. However, the presence of only a single impact does not exclude human handling. Impact marks, induced through dynamic loading, are seen in general as a sign for human interaction with a bone fragment. However, carnivore damage can produce similar patterns (Johnson 1985, 194; Lyman 1994a, 326 f.).

For most of the bones it was not possible to determine whether they had been opened deliberately by humans or animals. However, a total of 9 pieces were quite certainly opened by humans. Here the impact marks are aligned in a way which rules out other possible agents, as can be seen in the example of fragment Bilzingsleben Inv.-Nr. 337,164 (**fig. 14**). All of these pieces show patterns indicating dynamic loading, such as fissures and hackle marks and interior or exterior pressure flakes which developed in connection with the impact when the bone shaft was opened.

Besides these bones there are a number of other specimens that display negatives. For some of them human modifications can be postulated. They contain negatives in one or several rows producing changes of the form of the edge (e.g. **fig. 15, 16**). Natural agents can be ruled out here. There is a total of 6 bones showing these sorts of modifications. They are either from *Elephas antiquus* or could not be securely determined, but are likely to be from elephant because of their size. All of them are large, medial longbone fragments. All but one of the pieces are a slightly less than half as broad as they are long (between 1.77:1 and 1.89:1). While the overall form varies, the proportions remain similar.

Overall the butchering of animals as well as the systematic production of bone artefacts could be verified in Bilzingsleben. When compared to the total count of finds in the assemblage, the number of securely modified pieces is, however, very low.

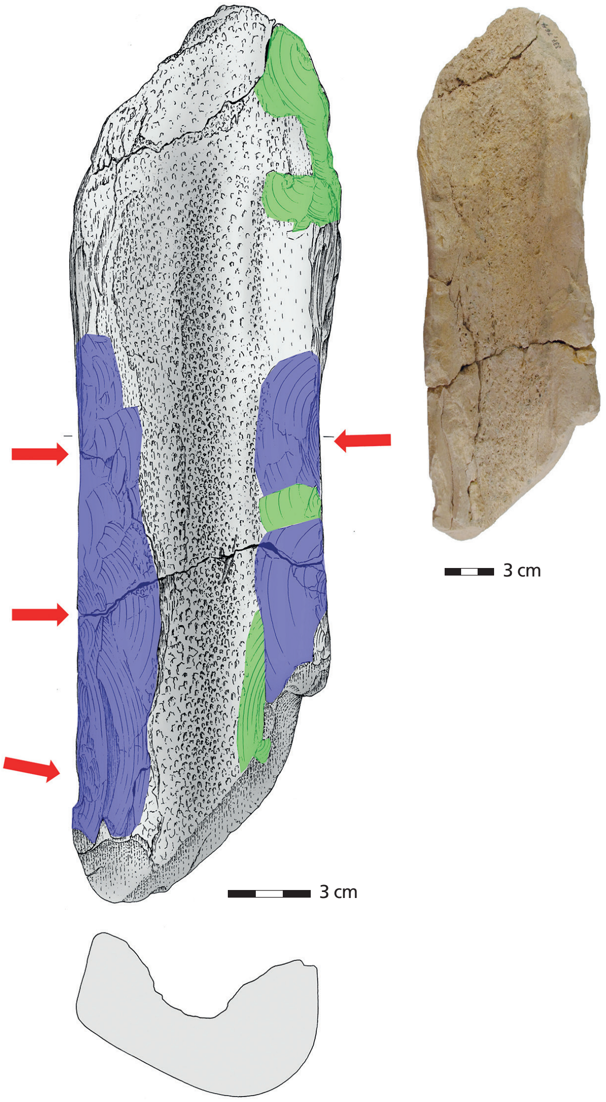

Fig. 14 Bone fragment Bilzingsleben Inv.-Nr. 337, 164 with traces of human modification. Red arrows indicate impact marks, blue areas interior pressure flakes, green areas other negatives. Left: drawing, right: photo.

Discussion

There is conclusive evidence that humans have had the ability to hunt large game as early as the Lower Paleolithic (see summary in Kindler 2012, 3-29). The main question in Bilzingsleben is not whether the humans at this site were able to hunt the megafauna and make use of the carcasses, but rather whether humans actually did hunt at Bilzingsleben and if so to which extent they played a role in the accumulation of faunal material.

The analysis of the bones and teeth of *Elephas antiquus, Stephanorhinus kirchbergensis/hemitoechus, Bison priscus/Bos primigenius* and *Ursus* sp. provided a number of different signals. Some of them supplement, others contradict each other. Since the main goal of this study was to identify human influence at the site, the results presented above will be discussed under this aspect.

A MNI of 245 could be reconstructed from 8280 identifiable specimens. Elephants account for at least 23 individuals, rhinoceroses for 112, bovids 22 and bears for a minimum of 88 individuals. These numbers are large compared to counts from other, even younger, sites. Considering that only a proportion of all species present at the site was studied, the overall number of animals in Bilzingsleben was most likely considerably higher.

Especially striking is the large amount of rhinoceroses, as these are mostly solitary animals, that tend to claim large territories (Hutchins/Kreger 2006, 152f.; Laurie 1982, 316f.). There is no indication in the preservation of the fauna that the material was accumulated over a long period of time, ruling out this possibility. The same applies to the

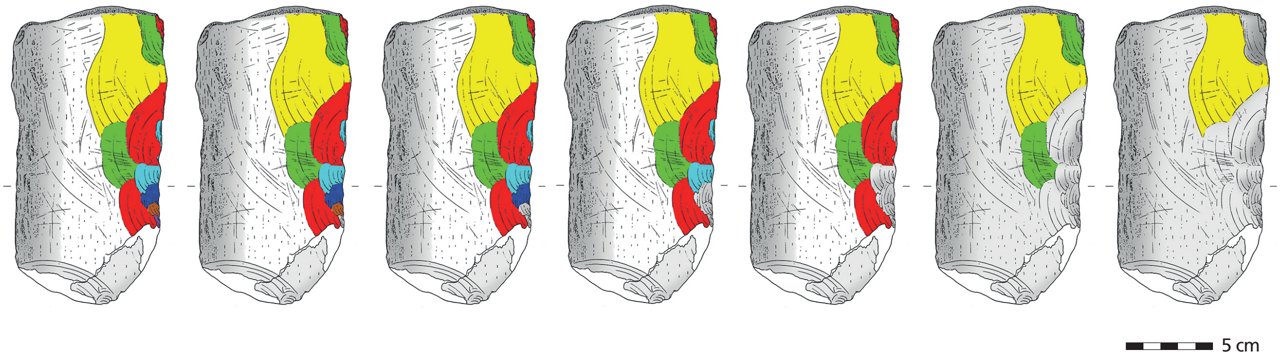

Fig. 15 Colored illustration of the order in which the negatives were created on fragment Bilzingsleben Inv.-Nr. 87, B1 (24.9.70).

bears, who normally also prefer a solitary lifestyle (Hellgren/Vaughan 1989; Dahle/Swenson 2003).

Large mammals often perish close to water sources during droughts (Haynes 1991). Weak bears, however, normally die during hibernation, so that large collections of bones can often be found in winter dens (Stiner 1998, 308f.; Kindler 2012). Large accumulations of dead bears do not naturally occur in the open landscape. Pleistocene open air sites with large amounts of ursid bones are normally interpreted as caused by human hunting activities (e.g. Taubach, see Bratlund 1999 and Biache Saint-Vaast, see Auguste 1995).

The different species all displayed different patterns of skeletal element representation. While the representation of teeth is rather uniform throughout, the largest differences can be found in the bones. The relatively larger overall amount of teeth can be explained with their different mineral structure (Lyman 1994a, 72-80). Another factor is that teeth can often be determined, even when they are strongly fragmented. Thus, at Bilzingsleben, while there were very few teeth that could not be identified, the identification of strongly fragmented long bone shafts of the megafauna was extremely difficult.

The skeletal element representation varies from species to species. A connection with the size of the elements, i.e. larger elements were potentially better preserved, cannot be seen in the material. Smaller pieces are quite common, also for species that were not analyzed here, and it does not seem as if there was a selection towards larger finds. The different patterns of representation for the different species can also not be explained with the overall size of the animals, considering that bovids and rhinoceroses in Bilzingsleben are very similar in size, yet show completely different skeletal representations.

Stephanorhinus kirchbergensis/hemitoechus, Bison priscus/Bos primigenius und *Ursus* sp. show prime dominated age structures, while for *Elephas* young and older animals dominate. The latter pattern is considered a natural death structure since very young and older animals are more vulnerable to natural selection (Lyman 1994a, 118). In the past an active hunting of elephants was postulated at Bilzingsleben (Guenther 1983, 143; D. Mania/U. Mania 1997, 67). The derived age structure indicates otherwise, but must be viewed in connection with the other signals. Haynes (1988, 137f.) writes that subadult elephants often die in larger numbers close to water sources due to droughts, a scenario that should be discussed for the elephants of Bilzingsleben. This would of course not rule out that the carcasses were used by humans.

Natural causes of death most often result in U-shaped death profiles (Stiner 1990, 315), while human hunting practices target mainly prime-age animals and therefore yield prime-dominated age profiles (Stiner 1990, 316f.; 2004, 774). Prime dominated inventories are commonly interpreted in this way (Stiner 1990, 316f.), even though it has been pointed out that the individual behavior of the species of animal has also to be taken into consideration (Lyman 1994a, 128). Wolverton (2006; 2008) describes several sites where prime age bears dominate because they became caught in natural traps. Young, inexperienced bears on the search for new territories are prone to accidents and are therefore dominant at some sites (Wolverton 2006, 541 f.).

While juvenile bears often dominate in caves, open air sites more often show prime dominated age structures, which are interpreted as the results of human hunting (Kindler 2012, 122; Bratlund 1999, 91; Auguste 1995). A natural accumulation of the large amounts of prime age bears in Bilzingsleben is unlikely because of their solitary lifestyle. In addition to this, some of the bones show clear signs of butchering.

The rhinoceros age structure is very similar to that of the bears. The large amount of adult individuals is of key interest here. While there are some very young and older individuals present, the majority died at prime age. However rhinoceroses are more prone to deadly intraspecific conflicts than other herbivores (Mihlbachler 2003, 413 f.). In this context large accumulations of young adult and adult rhinoceros bulls are known from the North American Miocene sites Love Bone Bed and Mixson's Bone Bed (both Florida, Mihlbachler 2003). While there are examples of natural assemblages similar to the Bilzingsleben inventory, these are not very frequent.

On the other hand, the planned exploitation of large amounts of rhinoceroses is only rarely described in Pleistocene contexts. Single rhinoceros bones are regularly found at Pleistocene sites but larger amounts are only known from two other localities in the European Lower and Middle Pleistocene – the sites of Taubach (Germany) and Biache Saint-Vaast (France). This implies that there might be a connection which warrants further research.

The clearest dominance of adult individuals can be seen in the bovids of Bilzingsleben. Here, younger animals are virtually non-existent (only one milk molar was found) while some senile ones are present. The enormous size of the bones, reaching the same dimensions as the rhinoceros specimens, indicates that adult bulls dominate here. The age-structure

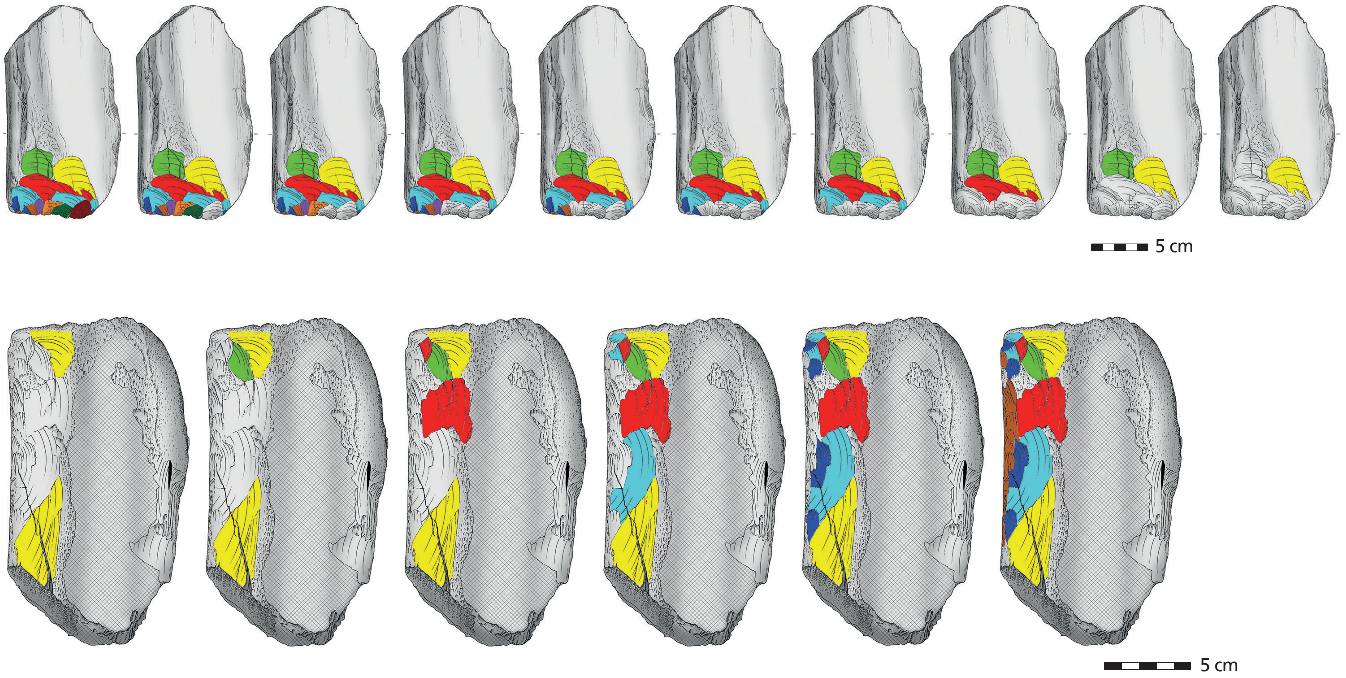

Fig. 16 Colored illustration of the order in which the negatives were created on fragment Bilzingsleben Inv.-Nr. 588, 48. A and B display different sides of the same piece.

also points to a non-natural selection. The overall number of animals is not indicative of a specific selection since bovids are highly sociable and normally live in groups. There are no direct indications for human manipulation on the bones themselves.

Bone density was analyzed for all species using the values published by Lam/Chen/Pearson (1998) and (Novecosky/Popkin 2005). If shaft fragments are not included in bone density analyses, inventories tend to incorrectly display reverse utility caused by the selective analysis (Marean/Assefa 1998, 30f.). Since many of the megafaunal long bones were highly fragmented, a large portion of them could not be identified. However, the representation of the epiphyses does not seem to be connected to bone density for any of the animals studied at Bilzingsleben. Obviously other factors dominate here. The same applies to the meat utility of the bovids, where no connection could be found to the preservation of the bones. Since studies about meat utility do not exist for the other animals, they could not be considered here. The size of elephant and rhinoceros carcasses suggests that butchering and exploitation of these animals would have required different logistical considerations than the butchering of smaller mammals. Therefore it was decided in this analysis to refrain from the application of data derived through studies of smaller species.

Fluviatile sorting was observed in the material by analysis of the Voorhies groups (Voorhies 1969; Behrensmeyer 1975). The large amount of jaw fragments is especially interesting in this regard. The relatively low number of fragments in Voorhies group I is another indicator that there was some shifting of remains. All species show the same patterns of winnowing. This is in so far problematic as it is obvious that more force is necessary to move an elephant than a bear. While the mechanisms of sorting are identical for all animals, a higher current velocity is necessary for larger animals (Behrensmeyer 1975, 500). In Bilzingsleben however, elephants, rhinoceroses and bears show an identical pattern while the bovid inventory is less thinned out. Those differences are mainly caused by the lower number of jaw fragments for the bovids.

The studies of fluviatile mechanisms were conducted on smaller to medium sized carnivores and ungulates (Behrensmeyer 1975; Voorhies 1969) so it is not clear how the properties change if very large mammals are involved. None the less, if flooding played a major role in Bilzingsleben one would expect the smaller animals to be absent, which is obviously not the case. Therefore it can be postulated that there was some minor fluviatile sorting (possibly also shifting within the site) but that the inventory was not transported in its entirely to the site nor removed from it to a great extent. Fluviatile shifting was certainly not the only selective mechanism.

The amount of gnawed bones varies strongly between the different species. Elephants (7.83 % and rhinoceroses (7.18 %) show the highest proportion, bovids (5.59 %) and bears (1.05 %) yield considerably lower numbers of gnawed bones. Hyenas tend to eat smaller mammals whole, so that in hyena dens those bones are less frequently found than fragments of larger animals (see Dusseldorp 2009, 132). It is therefore possible that the low number of gnawed bear bones does not indicate that they were less frequently eaten, but rather that they were more completely consumed. The skeletal element representation of *Ursus* however does not indicate this. There is no direct connection between the skeletal elements present and the consumption sequence of carnivores (Blumenschine 1986). Therefore it is not likely that large portions of the bears were eaten by hyenas. Moreover carnivores generally avoid eating other carnivores if possible (Kruuk 1972). Megafaunal elements genuinely seem to be more often gnawed by carnivores at Bilzingsleben than elements of other animals. The overall amount of gnawed material is quite considerable and it is obvious that carnivores were important agents at the site. In comparison to bones displaying direct anthropogenic modifications, numbers of carnivore-gnawed bones are a lot higher. Less than 0.5 % of all bones show unambiguous traces of direct human influence. Comparable sites where humans are considered the main agent of site formation tend to yield much higher percentages (e.g. Taubach about 25 %, Bratlund 1999; Biache-Saint-Vaast about 30 % "butchering marks", summary Dusseldorp 2009). However the preservation of such marks depends on the overall preservation of the surfaces of the bones, so that differences do not necessarily illustrate the actual intensity of modifications at different sites.

The direct traces on the bones can be considered secure proof of human interaction with bones at Bilzingsleben. They also show that the animals were butchered and used as a source of raw material for the production of bone artefacts.

Conclusion

The analyzed animal species show different patterns of conservation. Some of these are similar, others not. It is obvious that there is not one single factor responsible for the site formation in Bilzingsleben, but a conglomerate of agents.

The skeletal element representation of *Elephas* gives no clear indication of human influence. MNI and age structure are compliant with inventories caused by natural factors. The same applies to the other analyzed factors of selection. The bones show no evidence of butchery marks. However, they display the largest number of unambiguous secondary modifications. Elephant bones, primarily long bone shafts, were used as a raw material for bone artefact production. There is no indication that elephants were actively hunted. At the same time, elephant bones displayed a large amount of carnivore damage. This percentage is much higher than the counts of bones modified by humans, and could be an indication of primary access by carnivores. Humans likely used the remains of elephants not as food, but as sources of raw material.

The signals derived from the analysis of the *Stephanorhinus kirchbergensis/hemitoechus* material paints a slightly different picture. The large amount of individuals of a solitary living species indicates a non-natural cause of accumulation. However, it could be shown for different sites that there are natural processes that can produce patterns in age and numbers of rhinoceros individuals similar to the one recorded at Bilzingsleben (Mihlbachler 2003). Therefore neither the age distribution nor the large numbers of animals pose sufficient evidence of a non-natural accumulation. *Stephanorhinus* is the species that displays the largest proportion of cut marks in the inventory. Even here the total numbers are low, when compared to the total counts in the Bilzingsleben assemblage. They do, however, evidence the butchering of at least three different individuals of rhinoceros. Only a few bones displayed unambiguous evidence of human modification, in contrast to higher counts of carnivore damage. Whether animals had primary access to the carcasses cannot be ascertained. The skeletal representation shows some signs of fluviatile disturbance but cannot be explained by this alone. It is likely that several mechanisms played a role here. Overall, subsistence activities could be shown for the rhinoceroses from Bilzingsleben. A secure verification of the hunting of those animals was not possible.

None of the bovid bones show direct evidence of human modification. Müller and Pasda (2011, 37 f.) describe a bovid specimen with cut marks from a different area of Bilzingsleben, therefore verifying the existence of such modifications at the site. Even so, the overall amount of butchery marks on the bovid bones is still virtually non-existent. The amount of gnawing marks is also lower than in the other megafaunal species. Other differences are apparent in the skeletal part representation. Here mainly the lower number of mandibula fragments and a domination of autopodials can be noted. The age structure indicates that mainly adult animals died at the site, while the overall numbers of individuals are low compared to the other species in this study. The age structure can be seen as an indicator for hunting but other evidence pointing in this direction is lacking. An unambiguous utilisation of bovids by humans in the assemblage analysed in this study could therefore not be shown.

The skeletal part preservation for *Ursus* differs considerably from that of the megafauna species. The pattern of large amounts of head and foot bones is typically found in caves, where it is attributed to animals dying during hibernation over the course of many years (Fosse/Morel/Brugal 2002).

Since Bilzingsleben is an open air site, different taphonomic agents have to be considered. The cut marks found on identical spots on several specimen could be an indication of the skinning of those animals and possible production of furs. It is also possible that the skins were brought to the site from elsewhere. Signs of meat removal could not be found and, considering the good overall preservation of the bone surfaces, such traces are not likely to have been missed. While some accounts of natural accumulations of large amounts of bear bones in open air sites do exist (Wolverton 2006; 2008), they are always connected with a natural trap situation, something that can be ruled out for Bilzingsleben. Overall, there is strong evidence for human influence on at least part of the inventory of bear bones.

Different scenarios can be discussed for the signals derived from the study of the megafauna and bears in Bilzingsleben. In favor of active hunting, by humans as the main agents of site formation, are the large overall amount of (mainly normally solitary living) animals as well as the age structure for all species except *Elephas.* However, the few butchery marks on the bones contradicts this. While it is possible that some marks were abraded by trampling and there is a large amount of sedimentary abrasion scratches on the megafaunal material, this cannot be concluded for the bears. The surfaces of the bones show very few sediment scratches and the overall preservation is good enough to expect butchery marks to survive.

An accumulation over a long period of time in the vicinity of a water source could explain how the large amount of faunal material assembled. However, the preservation of the bones does not indicate that they were exposed on the surface for a considerable period of time, or for different periods of exposure. The age distribution also indicates a non-natural cause of death. A fluviatile influence on the bones is quite likely but it was probably not a major factor and shifting of bones took place within the site or only over short distances.

The butchering of bears and rhinoceroses could be shown to a small extent. A considerably larger amount of bones show traces of carnivore gnawing. This might indicate that humans only had secondary access to the carcasses, a situation especially likely for the elephants. Bears and rhinoceroses could also have been hunted by humans. While there are sites where large amounts of bones from solitary living animals are preserved under natural circumstances, these are almost always under exceptional conditions. While it seems likely, direct proof of a systematic hunting of the animals by humans could not be deduced. Systematic hunting on a larger scale can be ruled out for *Elephas antiquus* and *Bison priscus / Bos primigenius* where no evidence hints at this. It is quite possible that the utilisation of *Elephas* was more passive and / or secondary, e. g. carcasses of already deceased animals were exploited.

Considering that different animal species were affected by different processes at the site, the remaining faunal material and especially the smaller species should be studied in order to gain a deeper understanding of the complete thanatocoenosis.

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ISLANDS IN THE SWAMP. LAKESCAPE-RECONSTRUCTIONS OF MESOLITHIC SITES IN THE RHINLUCH AREA (GERMANY)

Abstract

The Rhinluch area (Havelland District) in the state of Brandenburg, Germany is known for its excellent preservation of early Mesolithic sites. The use of modern remote sensing techniques in combination with detailed stratigraphic analyses provided comprehensive and extensive reconstructions of the early Holocene environment in the area. It is shown how water-level reconstructions, peat-growth models and topographical information were used to reconstruct the lakescape of early Holocene hunter-gatherers. Finally, older environmental reconstructions are compared to the modern results on the basis of water-level and landmass comparisons. The use of GIS software made it possible to simulate and evaluate the improved results and optimize the picture of the Rhinluch in the early Holocene.

Keywords

Early Holocene, Preboreal, Boreal, digital elevation model, environmental reconstruction

Introduction

This paper deals with the geophysical environment of a micro-region in Brandenburg, Germany, where early Mesolithic sites with excellent preservation were excavated at the end of the 20th century. The sites are located in the Rhinluch, which is an extensive fen area that started to form at the beginning of the Holocene. Due to the good preservation of organic artefacts these sites provided extensive information on the palaeo-environment and organic artefact spectrum of early Holocene hunter-gatherers. As several examples show (e.g. Bokelmann 2012; Jessen et al. 2015; Larsson / Sjöström 2010; Mellars 1998; Schuldt 1961; Street 1991; Zhilin 2003), wetland sites are crucial to understanding human behaviours and their interactions with the environment during that time. Therefore, it is also relevant to understanding settlement strategies so that areas with high potential for good preservation can be identified and consequently be more efficiently protected. In this study the results of two excavations were used in combination with a digital surface map to try to model the land-water-proportions during the time of early Holocene settlement.

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Introduction to the study area

The Rhinluch is a region in the state of Brandenburg, Germany characterized by extensive fens which are interrupted by some ground morainic plateaus. It is part of the Warsaw-Berlin ice-margin valley and has been overgrown by peat since the beginning of the Holocene. Until the 16th century, when first ameliorations were conducted (Fontane 1922), it was swampy and consequently not used for agricultural purposes. The area was drained by a small river, the Rhin (also known as Friesacker Rhin) which is a tributary of the River Havel, which itself drains into the Elbe.

The Rhinluch is connected in the south to the Havelländisches Luch, forming the Luchland. To the west, the Luchland opens out into the Elbe valley, where run-off water masses from the different ice-margin valleys formed at the end of the last Glaciation (Schneider 1959-1962a, 1106-1113). As a consequence, the Elbe degraded several meters into the basic moraine during the late Pleistocene and early Holocene. The postglacial sea-level rise caused the intrusion of the North Sea into formerly terrestrial areas, while the Elbe was foreshortened. As a result, materials in suspension were increasingly deposited in the middle and upper course of the stream. This led to an accumulation of 10-12 m of gravel and sand as well as 1-2 m of alluvial clay since the Atlantic period (Schneider 1959-1962b, 1189). Due to its less meandering course, the Havel river was not raised in its level to the same extent because most material in suspension had already been deposited in several lakes along its course. As the banks of the Elbe increased in size, drainage of the Havel into the Elbe reduced. The backup water finally led to increasing groundwater levels in the Luchland, which also served as a buffer area for Elbe floods (Schneider 1959-1962a, 1106-1108) (**fig. 1**).

Due to dyke construction along the Elbe the influence of high tides on the Luchland decreased in the 13th century. Until historic times, the high groundwater levels made it impossible to use these low lying areas for agricultural purposes. For this reason drainage was already undertaken in the Rhinluch in the 16th century, whereas the Havelländisches Luch was not drained until 1718 (Eisentraut 2010, 31-38; Fontane 1922, 104; Mundel 2001, 174-181; Mundel 2002, 17). These actions continue intermittently until today.

The base of the Rhinluch is covered almost everywhere with gyttja dating to the Preboreal. This shows a complete inundation of the area in this epoch. At the beginning of the Holocene, groundwater levels had already induced overgrowth by peat (Scholz 1962, 64). In the early Holocene the water level decreased so that elevated spots fell dry and formed islands in large lakes (Gramsch 2002a, 190-191). The overgrowth processes increased up until the late Boreal and the water level became even lower so that only low lying areas and channels provided access to open water (Kloss 1987b, 122-123; cf. Gramsch 2002a). At the same time, the already overgrown areas deteriorated and mixed deciduous forests became established there. In the Subboreal the water level rose again and peat formation increased as a consequence of paludification (Gramsch 2002a, Fig. 3; cf. Kaiser et al. 2012, 133). Several decimeters of peat were formed (Kloss 1987b, 123). Due to the dyke construction along the Elbe the drainage of the Havel was hampered, which again resulted in increasing groundwater levels and increased overgrowth rates (Scholz 1962, 64-65). Until the amelioration of the Rhinluch, the water level rose by ca. 3 m before it decreased to the modern value of 26.5 m asl (Gramsch 2002a, 190-191).

Materials and Methods

The new reconstructions of the palaeosurface are based on a digital surface model (DSM) with data provided by the Landesvermessung und Geobasisinformation Brandenburg (© GeoBasis-DE / LGB [2013]). The area under investigation was mapped by laserscanning with a gridsize of 1 measurement / m² and a height accuracy of ± 0.3-0.5 m (http://www.geobasis-bb.de/GeoPortal1/produkte/dgm-laserscan.htm).

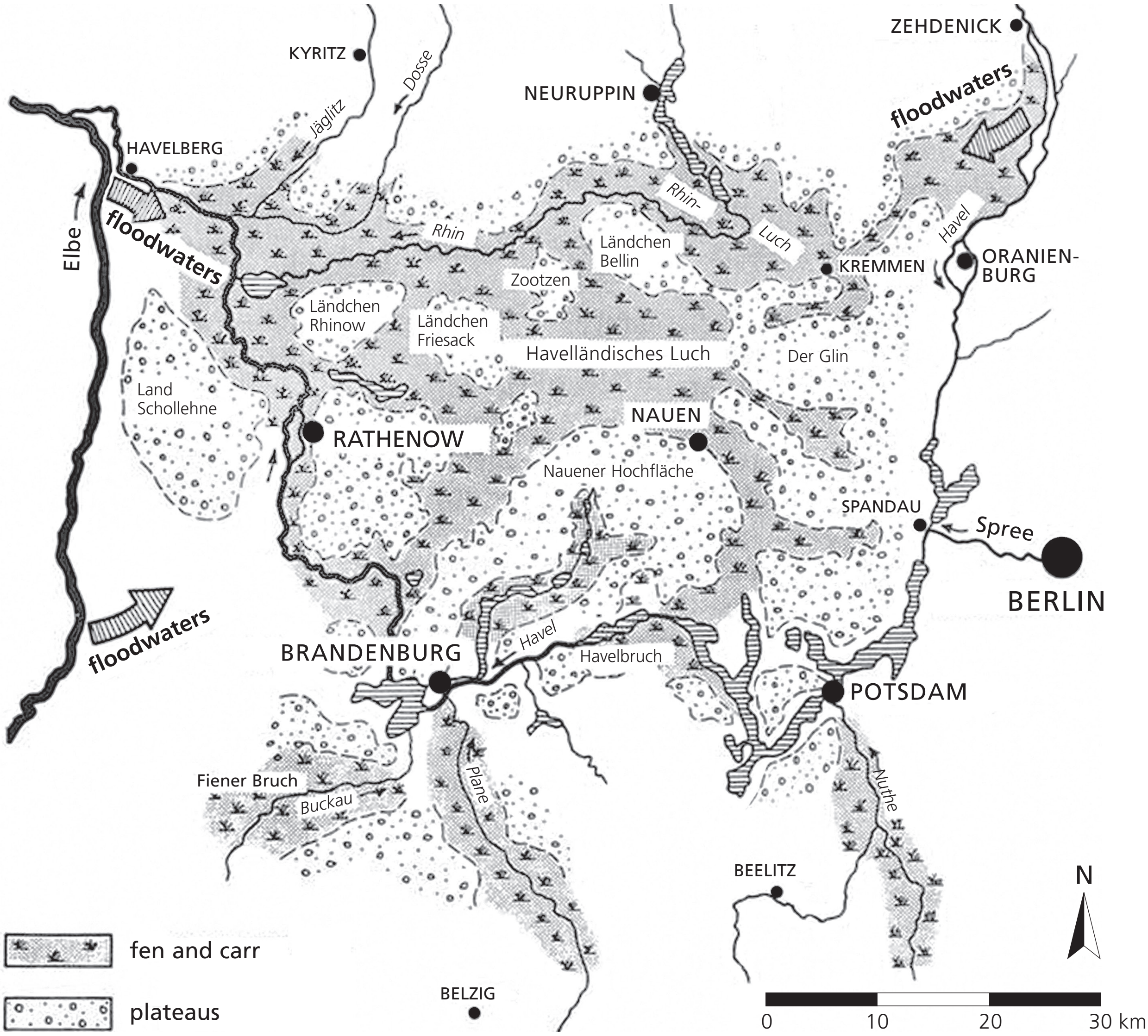

Fig. 1 The landscape of the Rhinluch. Floodwater paths are indicated as well as fen and highmoor areas. The plateaus already served as settlement areas in Medieval times whereas the low lying areas were first used in Modern times after extensive drainage. – (After Eisentraut 2010, fig. 1).

Furthermore, the Prussian *Generalmaßstabskarte* of 1880 (Klockmann 1880) was used for comparative purposes. The latter was especially used to trace the former riverbed of the Friesacker Rhin which was canalized in the 18th century (Itzerott/Kaden 2003). Additionally, the Prussian *Generalmaßstabskarte* enabled us to determine former peat cuttings and differentiate them from natural depressions.

Data such as estimations of peat thickness and its growth rates were included from cores taken during excavations. Additional information was derived from the excavation profiles (Gramsch 2002b; Groß 2017) and water level reconstructions for the area (Gramsch 2002a).

The area in the Rhinluch northwest of the town of Friesack is known for its extraordinary preservation of archaeological material. Between 1977 and 1998 modern excavations took place in the area due to renewed amelioration attempts. Excavations were mainly executed by B. Gramsch (see e.g. Gramsch 2002b), who investigated two Mesolithic sites: Friesack 4 and Friesack 27a (**fig. 2**). Both date to the early Holocene, however Friesack 4 shows a longer occupation sequence than Friesack 27a.

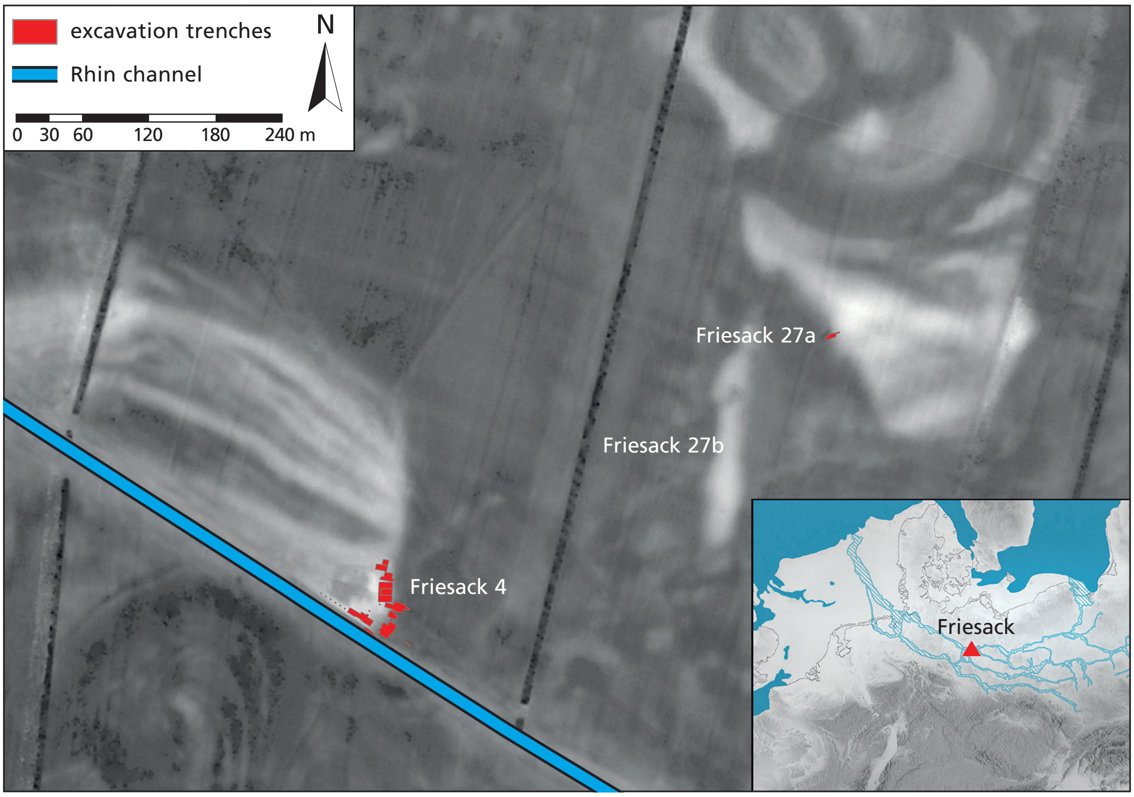

Fig. 2 Location of the excavation trenches of Friesack 4 and Friesack 27a. Friesack 27b is not excavated. The lighter the colour, the higher the surface (range between lowest and highest point: ca. 1.5 m; geobasisdata: © GeoBasis-DE/LGB [2013]). Inset: Location of Friesack in the Preboreal landscape at the Pleistocene/Holocene border. – (Base map: Grimm 2009 after Björck 1995a; Boulton et al. 2001; Brooks 2006; Clarke et al. 2004; Ivy-Ochs et al. 2006; Lundqvist/Wohlfahrt 2001; Weaver et al. 2003; added by Anonymus 1992; Björck 1995b; Björck 1996; Coope et al. 1998, fig. 4H; Gaffney/Thomson/Fitch 2007, 3-7 and 71; Kobusiewicz 1999, 190; Woldstedt 1956).

Synchronous palaeoecological analyses (Kloss 1987a; 1987b) made it possible to gain detailed insights into the environment facing early Holocene hunter-gatherers in that area (see Groß 2017, 79-82). Further understanding was recently achieved by the use of modern remote sensing techniques and its combination with the previous results.

Foremost known is the site Friesack 4, which has been extensively published by B. Gramsch (e. g. 1987; 1992; 2002a; 2002b). The site of Friesack 27a was published recently (Groß 2017). It is located, more or less in a straight line, some 400 m northeast of Friesack 4. At both sites the shorelines of former lakes have been excavated. This resulted in an excellent preservation of archaeological material because it had remained waterlogged since deposition.

Furthermore, it was possible to differentiate several sandy layers that must be connected to human activity at the sites which caused erosion of the sediment. These layers were intercalated with peaty layers which seem to represent times of human absence (Gramsch 2002b, 59-65; Groß 2017, 63-67). Another important aspect for the water-level reconstructions is the fact that the excavations provided evidence of different shorelines and a water-level of 27.5 m asl at the beginning of the Holocene (Gramsch 2002b, 62; 2002b, 62-91; Groß 2017, 58-67).

Apart from the on-site investigations, the botanist in charge, K. Kloss, conducted an extensive coring program with the aim of reconstructing the palaeosurface (Kloss 1987b). Additionally, he carried out extensive palynological analyses (Kloss 1987a). Between 1977 and 1982 K. Kloss managed to record 315 profiles in an area of ca. 7 ha (Kloss 1987b, 121). He concentrated his actions on the area between the sites of Friesack 4 and Friesack 27a and differentiated between peat and the subjacent gyttja. Since he did not differentiate between surface soil and peat, the depths he described have to be used carefully. Additionally, it has to be kept in mind that the peat is still subject to decomposition so that it is not appropriate to use the modern surface heights in combination with the results from more than 30 years ago.

For transferring K. Kloss' peat depths into the new model it was crucial to use height values which are as close to the former level of the surface as possible. For this purpose the initial measurements of Friesack 4 and Friesack 27a were used and compared with the plane survey sheet from 1985 (Militärtopographischer Dienst 1988). In combination with the modern DSM it was possible to approximatively reconstruct the surface level at the time when coring took place. The groundwater levels used in the reconstructions were adopted from B. Gramsch (2002a), who developed a curve based on several archaeological features from the Rhinluch and in the town of Friesack.

Results

The reconstruction of the palaeo-surface was undertaken by subtracting the values for peat depths determined by K. Kloss from the surface at the time of coring. No reconstruction was necessary for areas above 27.5 m asl since these spots were lying above the groundwater level in the early Holocene and hence were overgrown by peat later than the phases in focus. For the deeper areas the peat depths were subtracted so that the palaeo-surface at the beginning of the Holocene could be reconstructed.

Apart from the changing water-level in the Rhinluch during the Preboreal and Boreal chronozone, the overgrowth processes had to be considered in the reconstructions. For this purpose the detailed stratigraphic analyses of site Friesack 27a were used, where up to seven occupations could be differentiated. The intercalations of peat between the sandy occupation layers enabled us to apply a simple age-depth model. For this model a supposed peat accumulation rate of 1 mm per year (1 mm/a) is used (Kloss 1987b, 123) even though K. Dierßen (1990, 145) points out that the peat accumulation rates in fens lags behind those in highmoors (0.12 mm/a to 1.6 mm/a), due to their higher decomposition and density (cf. Rickert 2003, 116-118; Mundel/Trettin/Hiller 1983, 260-261; Overbeck 1975, 49-52). The constantly changing water level might have caused a discontinuous peat growth as well (cf. Kloss 1987b, 122-124). Hence the given peat growth rates and timespans have to be understood as model-like and it is recommended to use the expression of time units (Δt) instead of years (**tab. 1**).

Changes in water-levels were not the only factors affecting overgrowth processes in the area, the surface area changed too. Shallow pools disappeared and larger lakes diminished in size due to peat growth. To include these aspects into the reconstructions, the determined chronological gaps (Δt) were integrated into the reconstructions as peat

# of occupation at Friesack 27a	Δt to previous occupation	water-level asl.	chronozone
7	undetermined	26.75	early Boreal
6	140	27.10	
5	150	27.20	
4	20-50	>27.15	late Preboreal
3	150	27.50	
2	50		
1	—		

Tab. 1 Reconstructed water levels and corresponding occupation events at site Friesack 27a.

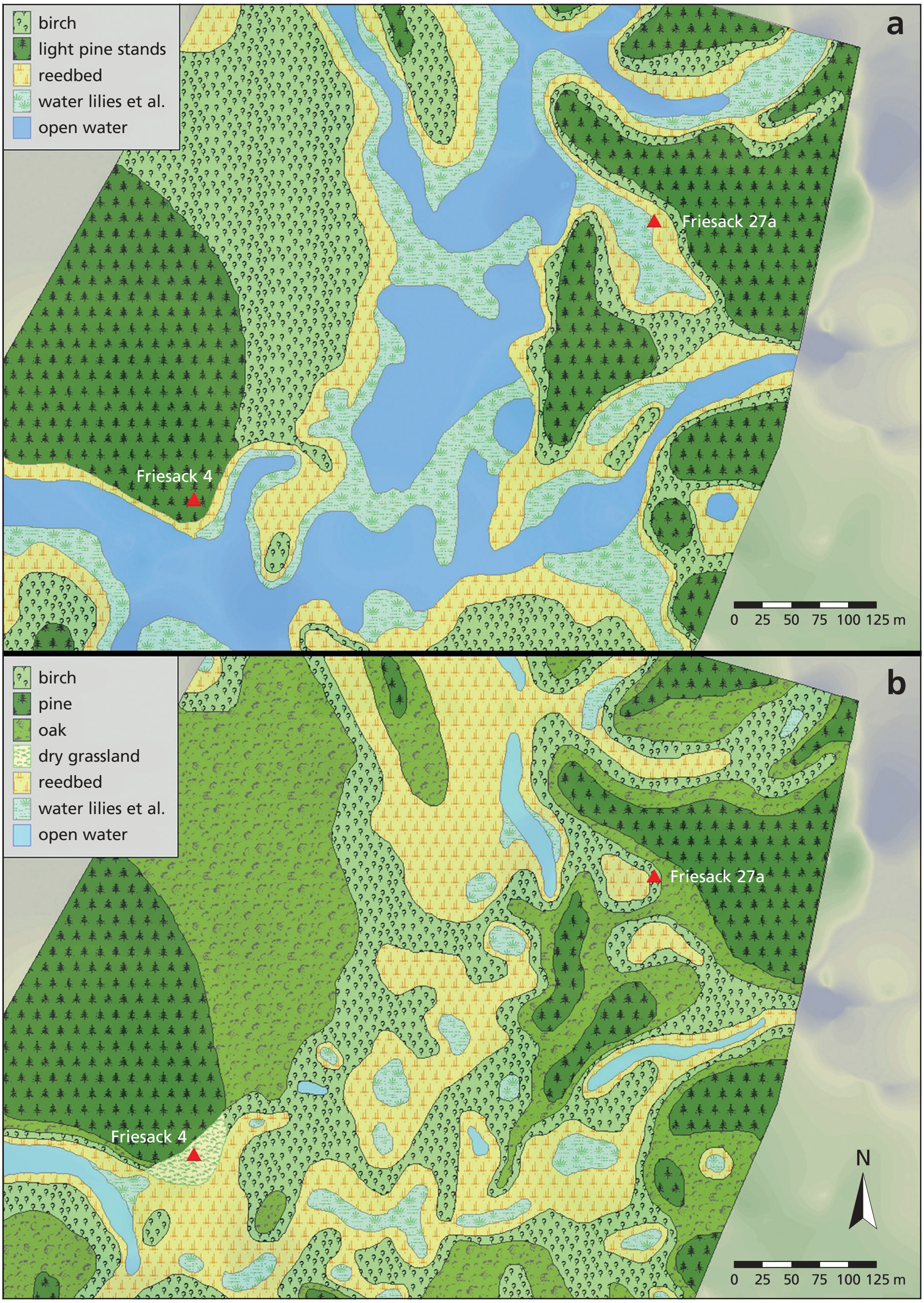

Fig. 3 The vegetation maps by K. Kloss. a) Preboreal, b) Boreal. – (After K. Kloss).

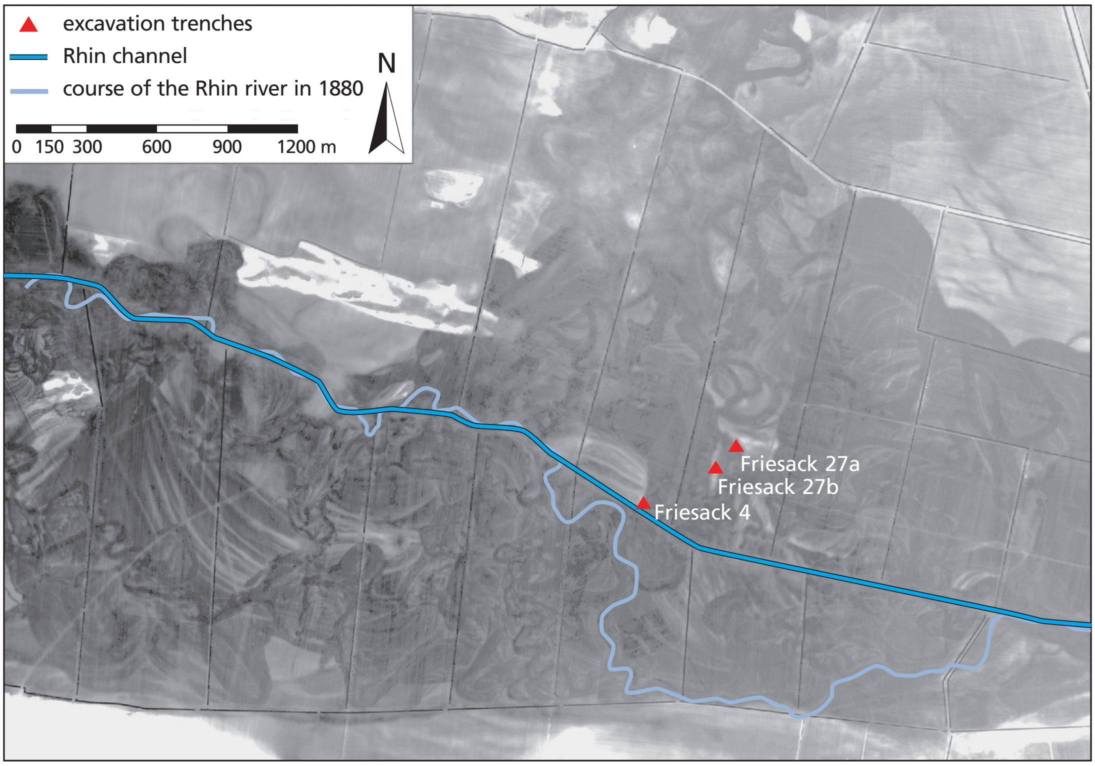

Fig. 4 The DSM clearly shows depressions and former river courses. – (Geobasisdata: © GeoBasis-DE/LGB [2013]).

aggregation. This was basically done by adding the values translated into growth of peat mass to the reconstructed palaeo-surface.

K. Kloss prepared two illustrations which show environmental reconstructions for the area between the sites Friesack 4 and Friesack 27a (**fig. 3**). For these he also used the results of his coring and the pollen samples he analysed (Kloss 1987a). The illustrations show the vegetation zones and the corresponding water level in the Preboreal and Boreal, respectively. In a synopsis of the reconstructions based on the DSM and K. Kloss's corings two observations can be made.

First, it becomes obvious that the depressions he revealed are also visible in the modern data. Even though the depressions and differences in height are hardly visible to the naked eye on-site, the DSM shows former channels and depressions very clearly (**fig. 4**). In addition, modern disturbances, like peat cuttings, can be observed and quite accurately determined, especially when historic maps are also considered. The DSM perfectly fits with the coring results but provides much greater detail of the landscape.

Second, the palaeo-vegetation maps drawn by K. Kloss show fairly different water-levels to those in the reconstructions. To reach the levels he used for his maps, values of 25.86 m asl and 25.05 m asl. had to be applied for the Preboreal and Boreal, respectively. As a consequence, there is a water-level difference of 1-1.8 m between the reconstructions and K. Kloss's assumptions.

Since the water levels used in the new reconstructions are based on several archaeological proxies (ancient shorelines, watering holes, wells [Gramsch 1998; Gramsch 2002b]) from different sites they have a high level of confidence. Because of this, the water-levels K. Kloss used for his reconstructions have to be considered as too low. As a consequence, in the early Holocene, especially the Preboreal, Friesack 4 and 27a site were located on an island. The continuous lowering of the water-level until the late Boreal enhanced the overgrowth processes and consequently the reduction of open waters.

Another aspect worth mentioning is the DSM provided indications for the reconstruction of palaeo-rivers. The representation of minimal depressions in the surface enabled a more extensive reconstruction of the palaeo-landscape with respect to K. Kloss' coring results. Starting from the core area of research (the area between Friesack 4 and 27a), former riverbeds which were synchronous to the occupations were deduced. By application and correlation of the morphology of the rivers, such as measures of the meanders, breadths of the rivers, and intersections, a relative chronology of the meanders was applied (cf. Stewart/Lonergan/Hampson 2013, Fig. 6; Mangelsdorf/Scheurmann/Weiß 1990, 93-122) (**fig. 5**).

Discussion

In the case of the water-level reconstructions it could be shown that the water levels K. Kloss assumed were too low. The new reconstructions clearly show that the Mesolithic settlement sites were located on islands, at least during the first occupations. With respect to the more detailed chronology of the sites, radiocarbon datings revealed that the occupation of Friesack 27a probably ceased when the small pond in front of the settlement was completely overgrown by peat (cf. Groß 2014, 3). As a result, the connection to the larger watercourses was interrupted, so that the people settling on the islands had no possibility to easily access open water anymore.

We assume that infrastructural aspects have to be regarded as important for the location of early Mesolithic settlements (cf. Mahlstedt 2015; Mellars 1998; Sergant/Crombé/Perdaen 2009; Terberger 2002). This applies particularly to ice margin valleys and water rich environments since these comprised wide and open spaces in an otherwise forested environment (cf. De Bie/Van Gils 2009, 286; Mellars 1998, 229). Additionally, wetlands and marshes are the most productive landscapes in Central Europe

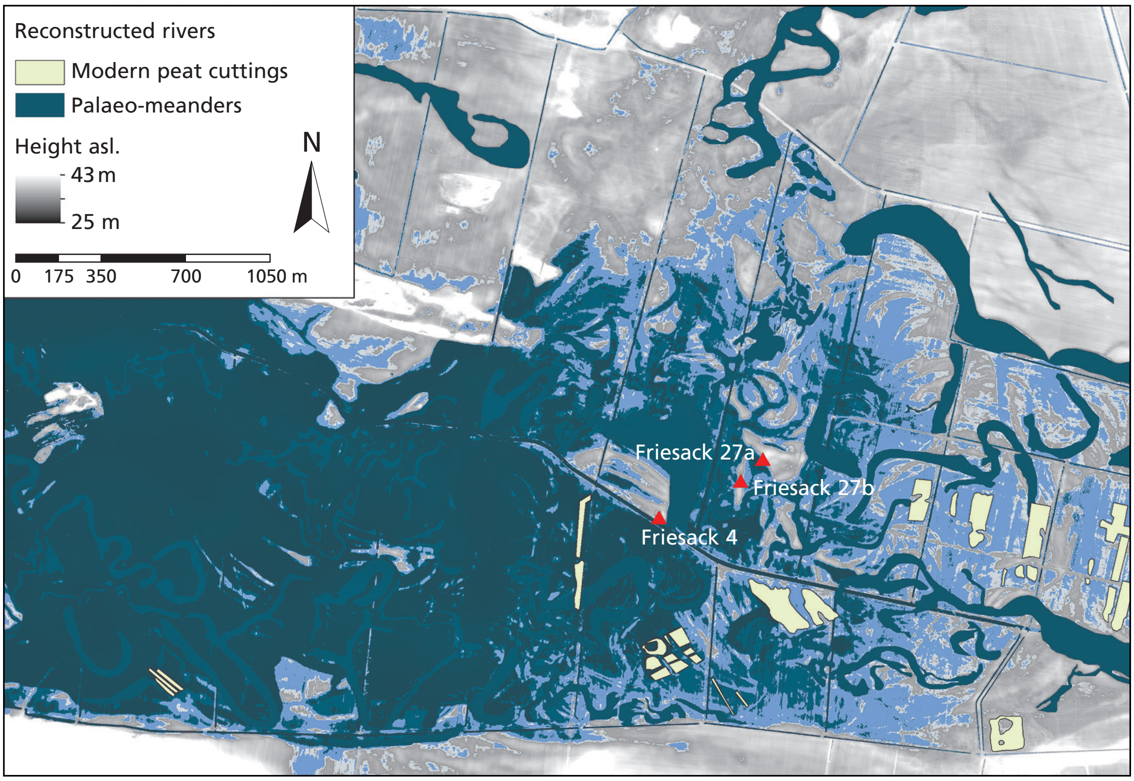

Fig. 5 The morphology of the rivers depict which palaeo-meanders might have existed during times of occupation. – (Geobasisdata: © GeoBasis-DE/LGB [2013]).

Fig. 6 Extensive agricultural use of the ameliorated fen causes the destruction of archaeological sites. At Friesack 27a the former excavation is not covered by grass due to the constant trampling of browsing cows. The destruction of the site is constantly progressing as a consequence.

(Mellars 1998, 227-230; Whittaker 1970, Tab. 4.2) so they might have been preferred for settlement.

As was shown, the use of modern remote sensing techniques is a valuable tool for archaeological investigations. Especially in rural fen areas they bear great potential for survey purposes and environmental reconstructions. For scanning an area of 7 ha K. Kloss needed several field campaigns and 315 corings for his reconstructions (Kloss 1987b). Using airborne laser scanning techniques, efforts can be reduced and much more extensive areas can be surveyed. Even though the use of DSMs and GIS software enhanced the scope of the area under consideration and provided possibilities to prove former assumptions, it still remains useful to apply some corings for dating and stratigraphic purposes. The faster techniques develop, the better and more detailed our reconstructions will become. Nonetheless, it remains important to verify the data by fieldwork.

Conclusion

The analyses showed an aspect that has to be recognized as being a mixed blessing: The reconstruction of former river beds and palaeo-meanders was done well by analysis of the DSM. This was possible due to the deterioration processes that advanced in the area as a result of intensive amelioration attempts and related groundwater lowering. As a result, the peat deteriorated and still deteriorates with increasing speed. Apart from changes in the chemical milieu that might affect the archaeology, as shown in Star Carr (Milner et al. 2011), the sites themselves are subject to visible destruction because they lose their protective cover (**fig. 6**). On the other hand, the decreased peat cover increases the possibility of discovering such wet-land sites. As a consequence it is important to use modern techniques and possibilities to survey and, contrary to many other kinds of archaeological sites, finally excavate wet-land sites. Particularly in extensively used rural areas this becomes an urgent task, as such sites often provide far more insight into prehistory, due to the possibility of organic preservation, than terrestrial sites.

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A ZOOARCHAEOLOGICAL AND TAPHONOMIC PERSPECTIVE OF HOMININ BEHAVIOUR FROM THE SCHÖNINGEN 13II-4 "SPEAR HORIZON"

Abstract

The Schöningen 13II-4 "Spear Horizon" is among the most famous lakeshore archaeological sites dating from the Middle Pleistocene in Europe. Multiple well-crafted wooden spears recovered together with a large assemblage of butchered horse bones at Schöningen stimulated a new outlook of the behavioural capabilities of Palaeolithic hunters. Since these discoveries, a wealth of geological and palaeoecological data have been generated to reconstruct the wider Schöningen interglacial lakeshore environment. Yet, the underlying social and economic behaviours of Middle Pleistocene hominins reflected in the archaeological record itself have received less attention. To address these shortcomings, we began a comprehensive zooarchaeological and taphonomic analysis of the entire large mammalian assemblage from the Schöningen 13II-4 "Spear Horizon", with the goal of re-focusing attention to the "human component" of this important site. Here we present the preliminary results of our research.

Keywords

Schöningen, Middle Pleistocene, zooarchaeology, taphonomy, bone tools, spatial analysis, site formation

Introduction

The Schöningen 13II-4 site came to prominence in the late 1990s with the discovery of multiple wooden spears preserved alongside a large collection of butchered horse remains and small lithic assemblage (Thieme 1997). Dubbed the "Spear Horizon", the site represents one of many Middle Pleistocene interglacial localities unearthed from ancient lakeshore sediments at the open cast lignite mine near the town of Schöningen in Lower Saxony, Germany (**fig. 1**). Geologically, the stacked interglacial deposits within the Schöningen complex of sites formed within an Elsterian tunnel valley and reflect fluctuations in the levels of the Schöningen palaeolake, which was fed by small streams flowing from the nearby Elm ridge (Lang et al. 2012; 2015). Recent radiometric dating (^{230}TH/U) yielded an age of 290 ± 5 ka (Sierralta/Frechen/Urban 2012), and thermoluminescence data suggest a maximum age of 321 ± 16 ka (Richter/Krbetschek 2015). Together, these dates place the "Spear Horizon" within Marine Isotope Stage 9. The interglacial character of the deposits is further documented by numerous pa-

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Fig. 1 Map showing the location of Schöningen in Lower Saxony, Germany, and photograph showing an overview of the current excavations at Schöningen 13II with the open cast mine in the background.

lynological (e. g. Urban 2007; Urban/Sierralta/Frechen 2011; Urban/Sierralta 2012; Urban/Bigga 2015) and biogeographical studies (e. g. van Kolfschoten 2012; 2014). Further geological and palaeoecological data collected from various locations across the open cast mine record the development of the wider Schöningen lakeshore landscape over time (see Behre 2012, and references therein; see also Serangeli et al. 2015).

Since the spears were first uncovered, several competing hypotheses regarding their association with the large assemblage of butchered horse remains have been proposed:

a) Single hunting event: *"… Schöningen II is indeed the product of a single event, a successful interception of a complete herd of wild horses that moved along the shoreline of the lake"* (Thieme 2005, 130);

b) Multiple hunting events: *"… multiple horse kill/butchery events are represented in the Schöningen 13II-4 horse assemblage"* (Voormolen 2008, 128); *"The different lines of available evidence indicate … that the fossil assemblage might correspond to an accumulation of multiple events"* (Julien et al. 2015b, 126);

c) Single hunting events and background accumulation: *"The number of [horse] carcasses is between 20 and 25 … the minimum number of individuals at the entire site is 46 … part of the fossil horse remains should be regarded as natural 'background' accumulation not related to the accumulation of the carcasses of the 20-25 horses"* (van Kolfschoten 2014, 476).

Consistent among these hypotheses is a dual hunting and butchery site situated along the former Schöningen lakeshore. These conclusions, however, are based on observations from a limited sample of the faunal assemblage, with little reference to the cumulative taphonomic factors leading to site formation or spatial arrangements of artefacts across the expansive excavation. The excellent preservation of organic remains within the "Spear Horizon" offers a wealth of possibilities to reconstruct Middle Pleistocene hominin behaviour at a fine scale. A synthesis of Middle Pleistocene hominin activities focusing on the large and extraordinarily well-preserved faunal assemblage recovered from this important site has been lacking until only recently (see Conard et al. 2015, and references therein).

Here we introduce preliminary results of an ongoing investigation of the complete large mammal faunal assemblage from the Schöningen 13II-4 "Spear Horizon" and offer a critical evaluation of the various single and multiple hunting event hypotheses.

Combining a zooarchaeological and taphonomic approach with a GIS-based spatial analysis, we present a holistic view of the site that highlights the "human component" to the Schöningen landscape. With traces of hominin activities as our chief concern, we explore aspects of species representation, bone surface modifications, skeletal part abundances, mortality profiles and seasonality, all from a spatial perspective, to reconstruct the biostratinomic chain of events that led to the creation and preservation of this unique archaeological record of Middle Pleistocene hominin behaviour.

Materials and Methods

For the first time a comprehensive zooarchaeological and taphonomic analysis is planned for the entire large mammalian faunal assemblage from the Schöningen 13II-4 "Spear Horizon". Included for study are all bone specimens excavated between 1994 and 2008 under the direction of Hartmut Thieme and the Niedersächsisches Landesamt für Denkmalpflege. The ca. 3900 m^2 excavation yielded an initial estimate of 25,000 large mammalian faunal remains (Thieme 1997; 2005; 2007; Voormolen 2008), but that total likely reflects conjoinable fragments broken during excavation, processing and storage. Our estimates of the entire faunal assemblage place the total closer to 15,000 specimens, which is in agreement with other assessments (van Kolfschoten 2012; 2014). Taxonomic descriptions and taphonomic summaries of 7946 larger mammal specimens were recently published by van Kolfschoten/Buhrs/Verheijen (2015). Voormolen (2008) provides a more detailed taphonomic analysis, but only studied 4626 remains from a limited spatial extent. The small bone assemblage from the nearby Obere Berme (see Starkovich/Conard 2015), which is thought to represent a southern extension of the "Spear Horizon", is not included in this analysis.

In addition to the material recovered from 1994 to 2008, several dozen bones contained in sediment blocks lifted from the original excavation and transferred to cold storage have been made available for this study. Efforts to process these blocks are currently underway.

The current analysis began in March 2013 with the documentation of specimens selected for exhibition at the Paläon research centre, which has since opened to showcase the finds from the various Schöningen localities. Among the roughly 100 specimens intended for display were numerous complete horse crania and other postcranial remains from a variety of species showing extensive hominin butchery damage. Following that, all specimens listed in the original database as cranial elements and individual teeth (ca. 800 specimens) were analysed and recorded in order to estimate the number of individual animals represented at the site. With those baseline measures established, the bulk of the faunal material has been analysed according to 10 m × 10 m excavation squares. Thus far, our analysis now includes all specimens recovered from the western portion of the Spear Horizon and accounts for roughly half (ca. 8000 specimens) of the estimated bone assemblage from nearly one-third (ca. 1500 m^2) of the entire excavated surface (**fig. 2**).

Each specimen has been individually analysed and documented following standard zooarchaeological methods. All bones were recorded by skeletal part according to Gifford/Crader (1977). Taxonomic designations were made at the highest level possible (i.e., species, genus, family), or otherwise ascribed to a size class based on live body weight (Brain 1974; 1981). As the analysis is in progress, quantifications are limited here to number of identified specimens (NISP) and only cursorily to minimum number of individuals (MNI) defined by Grayson (1984) and Klein/Cruz-Uribe (1984). Measures of skeletal part representation were based on minimum number of elements (MNE) of Binford (1978; 1981) and Bunn (1986), but those calculations are only preliminary and limited to skeletal element survivorship relative to bone density (Lam/Chen/Pearson 1999).

To aid in skeletal element quantification, we developed a simple GIS image-based methodology to automate the process (García-Moreno et al. 2015), similar to that described by Marean et al. (2001). All

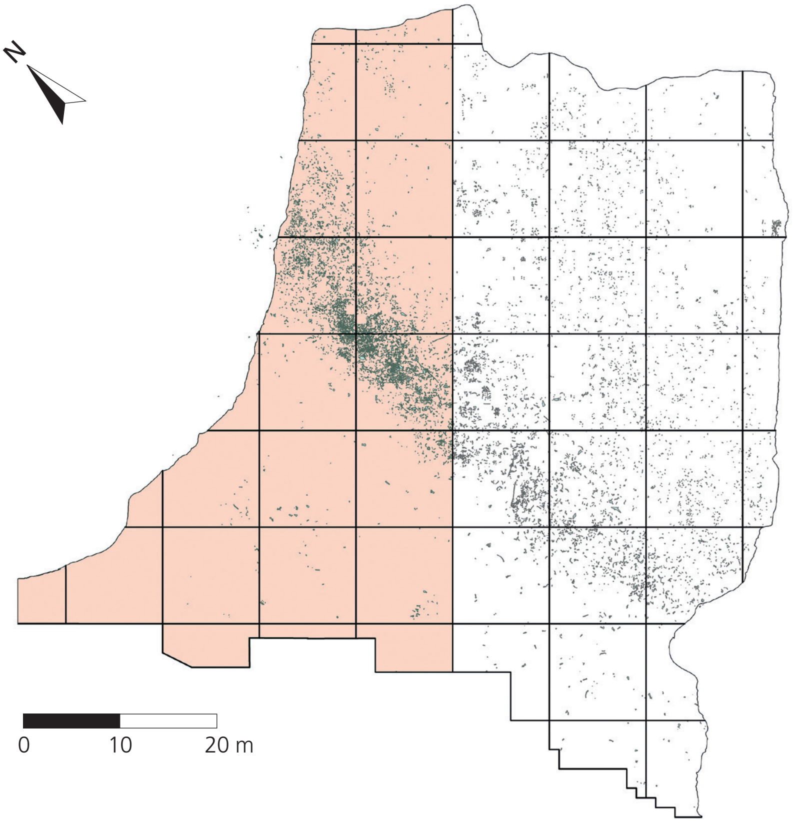


Fig. 2 Plan view of Schöningen 13II-4 showing the distribution of faunal remains. All cranial remains from the complete assemblage have been recorded along with the postcranial remains within the shaded portion of the map. Note that each square represents 10 m².

identifiable bone fragments were drawn on standardized templates unique to each skeletal element, and the MNE was automatically counted with GIS software using the number of overlaps between fragments of each skeletal element. All other calculations, including indices of meat and marrow utility (Outram/Rowley-Conwy 1998), are based on NISP values per skeletal element.

Mortality data was assessed for all specimens when possible, and the methods employed here relate only to the equid assemblage. For dental remains, molar and premolar crown heights provided age at death estimates based on the calculations of Levine (1982) and Fernandez/Legendre (2003) for adult teeth and Bignon (2006) for juvenile dentition. Ages for cheek teeth with incomplete crowns and incisors were estimated according to stages of occlusal wear (Levine 1982). The timing of epiphyseal fusion provided age estimates for postcranial remains (Habermehl 1975).

Bone surface modifications provide direct evidence for hominin butchery and therefore represent an integral component of this analysis. All skeletal elements were examined with a 10× hand lens or 20-40× handheld digital microscope for traces of modification. Hominin-induced butchery marks, including cut marks, scraping marks, and hammerstone impact damage, in addition to carnivore damage, were identified based on diagnostic macro- and microscopic features (Blumenschine 1988; Capaldo/Blumenschine 1994; Lyman 1994; Fisher 1995; Blumenschine/Marean/Capaldo 1996; Pickering/Egeland 2006; Domínguez-Rodrigo et al. 2009). Limb bone fracture patterns were recorded following the system of Villa/Mahieu (1991) and can be used as reliable indicators of pre- and post-depositional processes affecting the assemblage. Weathering can obscure traces of bone surface modifications and prolonged exposure on the ground surface can lead to reduced identifiability of bones. The system of weathering stages developed by Behrensmeyer (1978) was used to assess damage caused by exposure of the faunal assemblage.

The exceptional preservation of the archaeological remains, as well as the large extent of the excavated surface, makes Schöningen 13II-4 a unique site to address a number of issues regarding site formation processes and the patterns in the spatial distribution of bones and artefacts that reflect past hominin butchering activities and social actions (Barceló/Maximiano 2013). This preliminary spatial analysis focuses on three different approaches: point pattern analysis, geostatistics, and refitting.

Despite the fact that point plots are usually an oversimplification of events in space and time (Bevan et al. 2013), plotting artefact distributions provides a good visual overview and statistical foundation to infer general patterns in the spatial arrangement of bones and artefacts across the site. This is especially true in the case of small sample sizes, where poorly represented species can highlight spatial patterns otherwise concealed by the large amount of horse remains (Eixea et al. 2011-2012). To better visualize the spatial distributions, we use kernel density estimation (Barceló 1998; Baxter/Beardah/Wright 1997), which calculates the bi-dimensional density of finds given a set of known locations. This function offers a smooth representation of density and an informal estimation of clusters without imposing any structure on the data.

A series of geostatistical tests, including average nearest neighbour analysis and Ripley's K test, were performed in order to establish if the observed patterns were statistically significant (Barceló/Maximiano 2008). The aim of these tests is to quantify whether the analysed sample follows a clustered, dispersed, or random distribution. Both tests were performed using ArcGIS Spatial Statistics toolbox. In general, nearest neighbour analysis measures the significance of non-random distributions in coordinate data (Blankholm 1991). More specifically, average nearest neighbour analysis compares the average distance between the centroid of each "feature" and its nearest neighbour against the average distance estimated for a hypothetical random distribution. If the observed average distance is smaller or greater than the estimated distance, the distribution can be classified as clustered or dispersed, respectively. Because nearest neighbour analysis is dependent on the extent of the study area (Barceló/Maximiano 2008; Blankholm 1991), a Ripley´s K test was performed to measure the type, intensity, and range of a spatial patterning by comparing the observed distances between each "feature" in the sample against a hypothetical random distribution created using a Monte Carlo simulation (Maximiano 2007). This method defines whether a distribution is aggregated or dispersed, the intensity of aggregation (or dispersion), and how that pattern develops with increasing distance.

Finally, the spatial distribution in relation to skeletal element refits was analysed. Refitting has long been used in archaeology, but the adoption of GIS to archaeological applications has allowed for more detailed analyses (Ortiz Nieto-Márquez 2013; Ortiz Nieto-Márquez/Baena Preysler/Chacón 2014). Refitting of skeletal elements is essential to understand the temporal and spatial relationship of features, such as bone clusters, as well as to approach hominin behaviour (i.e., butchering patterns or food sharing) or post-depositional processes (Conard/Prindiville/Adler 1998; Enloe/David 1992). Here, refits include "breakage refits" that consist of two or more conjoining fragments from one original skeletal element, as well as "anatomical refits" where two or more skeletal elements from the same individual articulate. Refitting efforts are in progress, and the data presented here represent only the unsystematic discovery of refits within or between adjacent 10 m × 10 m excavation units. The spatial analysis of refits entailed calculating the distances and orientations of lines connecting refitting skeletal elements. The orientation pattern of reffiting lines was analysed using Rayleigh test (Davis 2002) to check whether a significant mean orientation could be defined for the refits.

Results

Species representation

In total, 7816 faunal remains from the "Spear Horizon" have been processed and recorded in detail, amounting to roughly half of the estimated total number of remains. **Table 1** shows all species identified to date, along with NISP for each taxon. This provisional species list is similar to those reported by Voormolen (2008) and van Kolfschoten (2012; 2014; van Kolfschoten et al. 2012; van Kolfschoten / Buhrs / Verheijen 2015), but those analyses included different samples of the large mammalian faunal remains. Clearly, the Middle Pleistocene horse, *Equus mosbachensis,* dominates the faunal assemblage, accounting for 65.5 % (5116 of 7816 NISP) of the identified specimens. Add to that bones identified as large ungulate (2337 NISP), most of which are likely large equid based on size, and up to 95 % (7453 of 7816 NISP) of the faunal assemblage may be *Equus mosbachensis* remains. According to van Kolfschoten (2014), the *Equus mosbachensis* assemblage represents a minimum of 46 individuals. Based on our own assessment, this estimate is accurate, but the final number of individuals is likely to increase as more of the assemblage is analysed. A second equid species, the more gracile and small-bodied *Equus hydruntinus*, is also represented by several specimens. Apart from equids, at least two cervidae species are present: mostly red deer (*Cervus elaphus*) and a single giant deer (*Megaloceros giganteus*) specimen. Two bovid species have been identified: a sizeable collection of very robust aurochs (*Bos primigenius*) remains and several remains of steppe bison (*Bison priscus*). The remainder of the large mammal assemblage includes two rhinoceros species, *Stephanorhinus hemitoechus* and *Stephanorhinus kirchbergensis*. Carnivores are represented by wolf (*Canis lupus*), badger (*Meles meles*), and a small weasel species (*Mustela* sp.), and beaver (*Castor fiber*) and mole (*Talpa europea*) have been identified among the small mammal remains. The large variety of waterfowl obviously reflects the site's lakeshore setting, as does the presence of a number of pike (*Esox lucius*) remains.

As a whole, the species list clearly represents a mosaic interglacial environment surrounding the Schöningen palaeo-lakeshore. Most of the large ungulate species identified are grazers typically associated with open habitats, but, based on tooth wear characteristics, cervids and equids are known to adopt variable diets (grazing and browsing) during interglacial time (Rivals / Schulz / Kaiser 2009), which

Tab. 1 Number of identified specimens (NISP) per taxa and proportion (%NISP) of the total analysed sample.

Ungulate	NISP	%NISP
Horse, *Equus mosbachensis*	5116	65.46%
Ass, *Equus hydruntinus*	3	0.04
Steppe bison, *Bison priscus*	6	0.08
Aurochs, *Bos primigenius*	54	0.69
Bovini indet.	84	1.07
Red deer, *Cervus elaphus*	58	0.74
Giant deer, *Megaloceros giganteus*	1	0.01
Cervidae indet.	4	0.05
Stephanorhinus hemitoechus	1	0.01
Stephanorhinus kirchbergensis	1	0.01
Stephanorhinus spp.	2	0.03
Medium ungulate indet.	53	0.68
Large ungulate indet.	2337	29.90
Carnivore		
Wolf, *Canis lupus*	5	0.06
Large carnivore indet.	3	0.04
Badger, *Meles meles*	2	0.03
Weasel, *Mustela* sp.	3	0.04
Small carnivore indet.	1	0.01
Small mammal		
Beaver, *Castor fiber*	3	0.04
Mole, *Talpa europea*	1	0.01
Small mammal indet.	21	0.27
Bird		
Pintail, *Anas acuta*	2	0.03
Teal, *Anas crecca*	4	0.05
Mallard, *Anas platyrhynchos*	3	0.04
Tufted duck, *Aythya fuligula*	2	0.03
Goldeneye, *Bucephala clangula*	1	0.01
Shelduck, *Tadorna tadorna*	1	0.01
Swan, *Cygnus olor*	1	0.01
Water rail, *Rallus aquaticus*	1	0.01
Bird indet.	15	0.19
Fish		
Pike, *Esox lucius*	10	0.13
Fish indet.	14	0.18
Insect		
Beetle, Coleoptera sp.	3	0.04

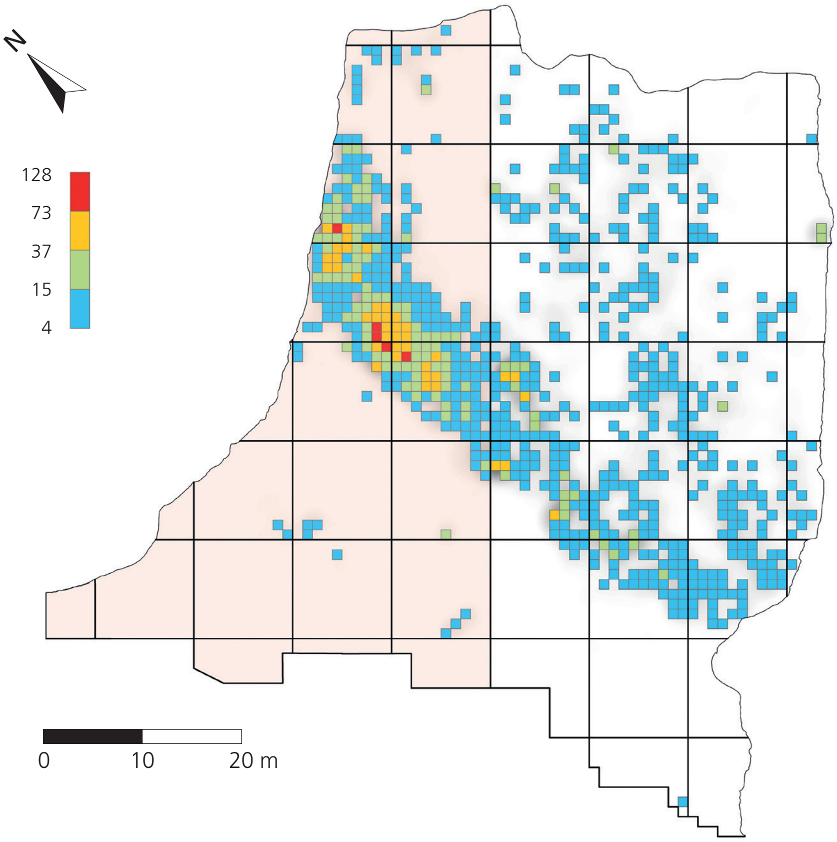


Fig. 3 Plan view showing the number of bones within each 1 m² excavation unit.

also appears to be the case with segments of the Schöningen horse population (Rivals et al. 2015). These dietary signatures imply a grassland habitat with a significant woodland component in the immediate vicinity of the Schöningen palaeo-lakeshore. This mosaic environment is corroborated by numerous palynological studies that show an abundance of grass and arboreal pollen, dominated by pine and birch (e.g. Urban 2007; Urban/Sierralta/Frechen 2011; Urban/Sierralta 2012; Urban/Bigga 2015).

Spatial distribution

The spatial distribution of all faunal remains with accurate horizontal coordinates shows a dense concentration of bones oriented north-to-south across the entire central portion of the site (**fig. 3**). This roughly linear cluster likely represents some aspect of the former lakeshore, with dry land to the west and the deeper part of the lake located to the east. At its widest, the main bone concentration measures roughly 10 m (E-W) wide, and may indicate advancing and receding lake levels during site formation. Regardless of the exact position, a majority of the faunal remains and other artefacts likely accumulated very close to the lakeshore, on dry land or in shallow water, although an accumulation in deeper water cannot be excluded at present (see Stahlschmidt et al. 2015a). Within the main concentration, two distinct clusters appear (denoted by red squares in **fig. 3**): a small cluster located at the northern edge of the excavated area, and a larger cluster positioned just to the south. These two clusters show higher density of bones, in some cases with more than 100/m^2.

Regarding the abundance of large mammal species, horse bones are by far the most abundant, 85 % (4345 of 5116) of which are distributed within the main bone concentration. Both nearest neighbour analysis and Ripley's K test indicate that those remains are significantly clustered (**fig. 4a**). The remains of bovids and cervids show slightly

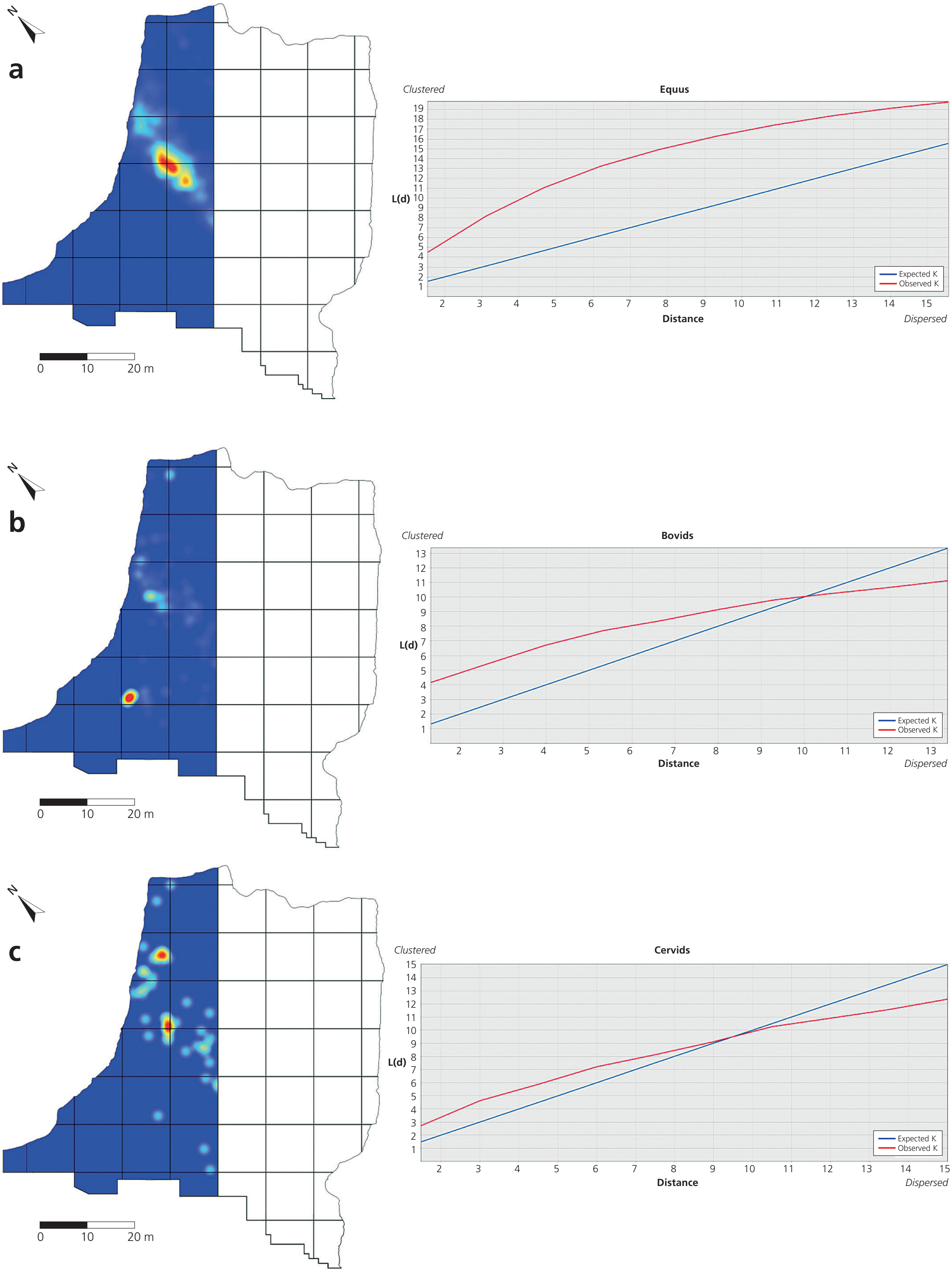


Fig. 4 Kernel density estimation (left) and Ripley's K test (right) of the distribution of equid (a), bovid (b) and cervid (c) remains.

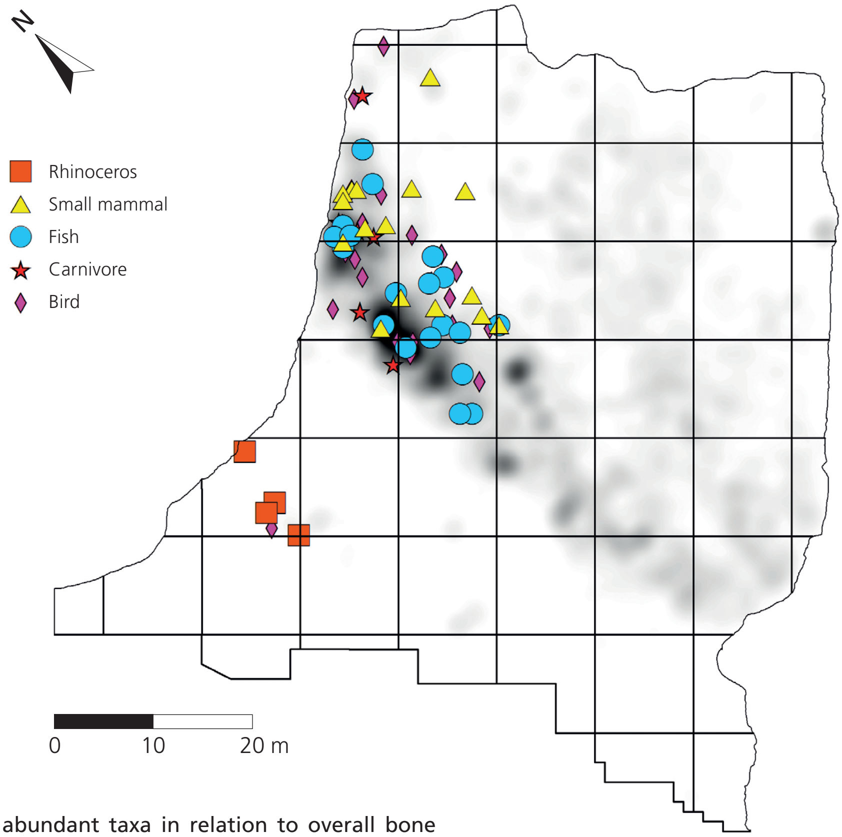


Fig. 5 Distribution of less abundant taxa in relation to overall bone concentration shown as black shaded areas.

different distributions than horses. Bovids are well represented within the main concentration, but occur in higher frequency to the west (**fig. 4b**). Ripley's K function shows that bovid remains are also clustered, but to a lesser extent than horse bones, and up to a certain point become dispersed. On the other hand, cervid bones appear primarily along the main concentration, but are more dispersed than horse remains (**fig. 4c**). A nearest neighbour analysis indicates cervid bones are randomly distributed within the surface area covered here.

Other taxa, such as carnivores, fish, birds, small mammals, and rhinoceros are represented by only a few remains (**fig. 5**). With the exception of rhinoceros, all were recovered within the main concentration, although they are either randomly distributed (birds, fish, small mammals) or dispersed (carnivores, rhinoceros). It is noteworthy that fish remains appear only within the main concentration, but not to the east, an area supposed to represent the deeper part of the lake during the occupation of the site, although taphonomic factors may have led to the absence of fish remains elsewhere. The distribution of rhinoceros bones is also interesting, appearing not in the main concentration, but in a secondary cluster to the west, next to a concentration of bovid remains. Since the spatial analysis presented here only includes the western portion of the site, we can only offer the preliminary hypothesis that large mammals are differently distributed across the site. Thus, the site must include a number of death events occurring over an extended period of accumulation.

Regarding refits within the analysed sample, 37 breakage refits and 118 anatomical refits have been documented (**fig. 6**). Breakage refits primarily include conjoinable limb bone shafts and shaft fragments with ancient breaks indicative of fracture from marrow extraction. Most anatomical refits paired two or more articulating elements from the vertebral column and among carpals and tarsals. A few individual teeth with no associated maxilla or mandible, but with matching wear facets are also counted

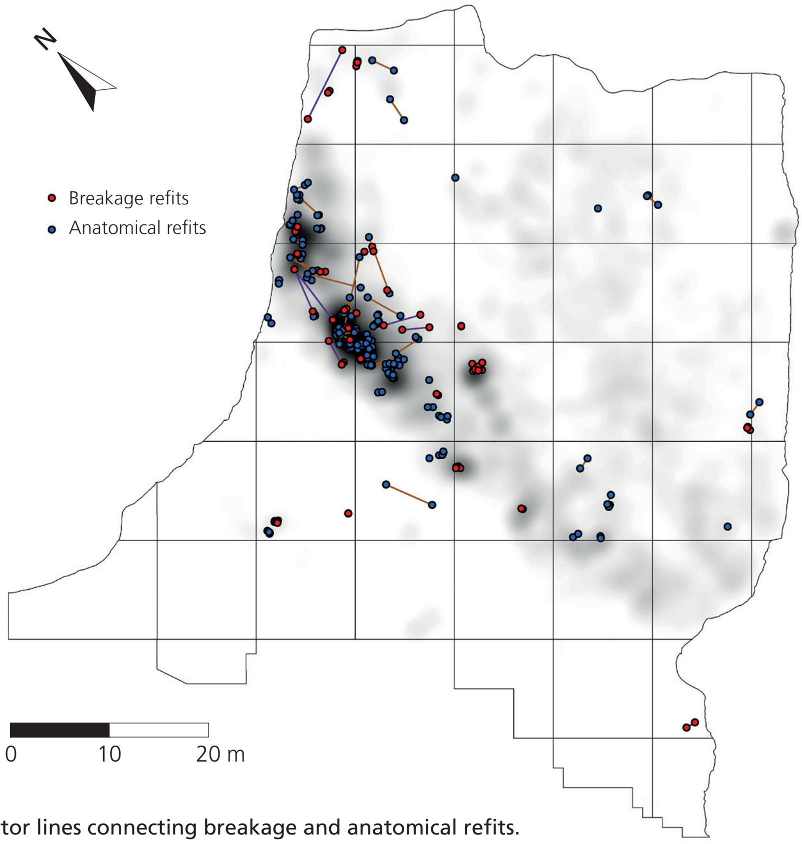


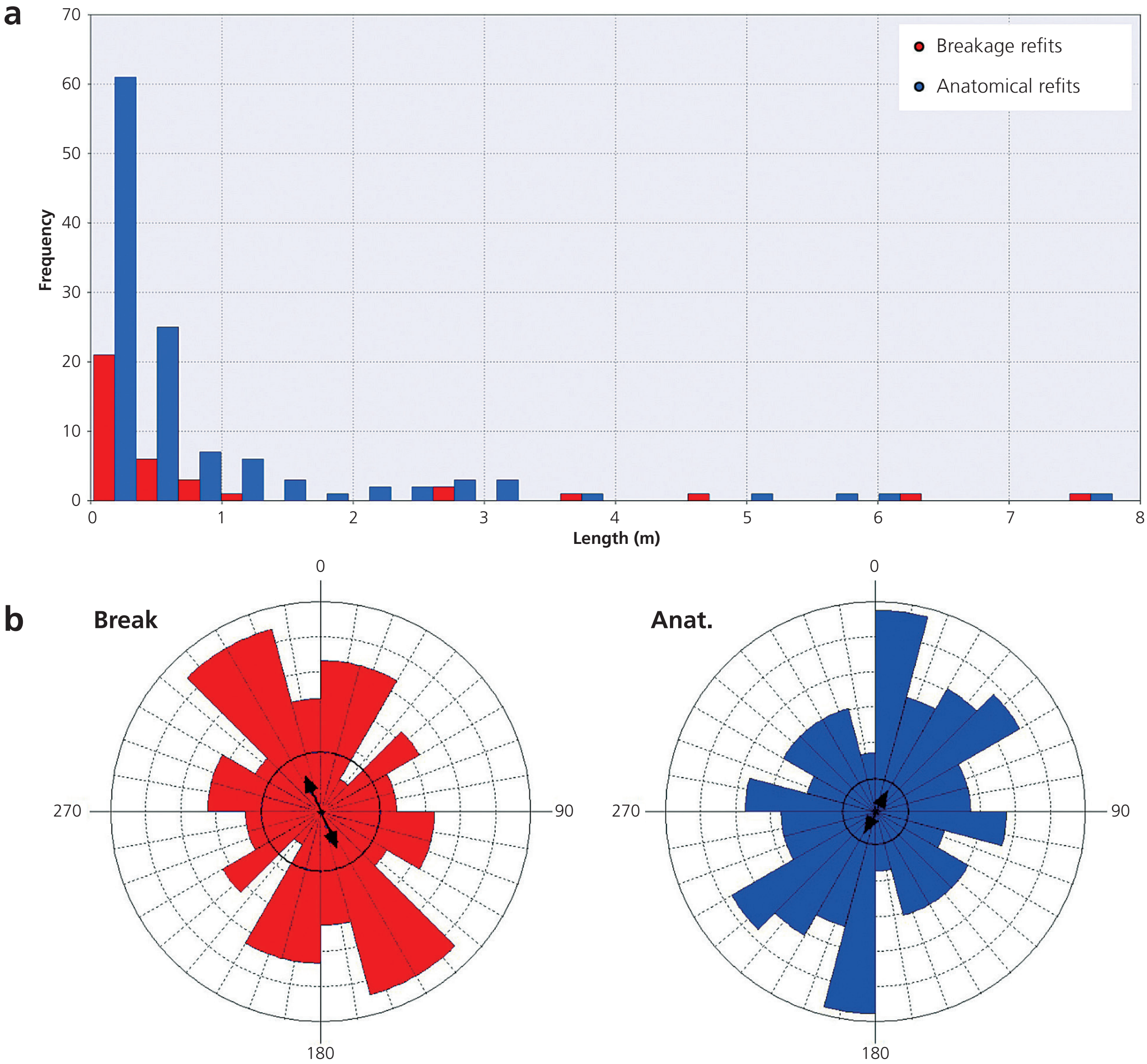
Fig. 6 Plan view with vector lines connecting breakage and anatomical refits.

among the anatomical refits. The mean distance for breakage refits is 1.03 ± 1.82 m (range: 0-7.79 m) and 0.81 ± 1.27 m (range: 0-7.48 m) for anatomical refits. A histogram of refit distances shows that most occur within less than 1 m (**fig. 7a**), likely due to the fact that no refits between distant squares have been considered at this preliminary stage in the zooarchaeological analysis. Considering orientation, the mean vector for breakage refits is 98.51° ± 58.34° and 28.84° ± 59.82° for anatomical refits (**fig. 7b**). Rayleigh's tests show that orientation is significant for breakage refits, but no significant preferential orientations is evident among anatomical refits. These different patterns in refit orientations may indicate two different processes involved in the dispersion of the assemblage, one shaped by regularities in hominin butchery practices in the case of breakage refits, and the other reflecting the natural and random processes of *in situ* disarticulation involved with anatomical refits. But again, our refitting efforts are ongoing and this hypothesis will be tested within a more rigid analytical framework in the future.

Bone surface modification

A wide array of bone surface modifications has been recorded in the faunal assemblage, providing critical information for reconstructing site formation processes and the role of hominins in the accumulation of the faunal assemblage. Taken together, bone surface modifications indicate primary access to carcasses by hominins, likely through active hunting along the Schöningen palaeo-lakeshore.

Among the horse remains, the entire sequence of hominin butchery activities is preserved, from filleting of meat to disarticulation and marrow extraction. Overall, cut and scraping marks are concentrated on limb elements along the midshafts and epiphyses, corresponding to the removal of meat, dismemberment, and preparation of bones to facilitate access to marrow. Similar marks on some non-meat-bearing skeletal elements (crania and lower limbs) suggest skinning activities (Binford 1981; 1984), but most hominin-induced damage is focussed on the major meat- and marrow-bearing elements of the appendicular skeleton. Vertebrae show comparatively few butchery traces, along with most other elements of the axial skeleton. A high incidence of cut-marked ribs has been recorded; however, this observation is less relevant to the overall treatment of carcasses when considering the relative abundance of ribs in a single horse skeleton (ca. 36 per individual). Numerous bovid and cervid bones also show butchery traces, indicating horses were not always the primary focus of hominin hunters along the Schöningen lakeshore, but systematic butchery of those species is likely masked by the small sample size.



Refit type	Min. distance	Max. distance	Mean distance	Mean vector	Concen-tration	Circular variance	Rayleigh's z	p
Breakage	0.02 m	7.79 m	1.03 + 1.82 m	98.51° ± 58.34°	1.49	0.40	13.12	0.000
Anatomical	0.02 m	7.48 m	0.8 + 1.27 m	28.84° ± 59.82°	0.23	0.44	1.50	0.222

Fig. 7 Histogram of refit distances (a) and rose diagram of refit vectors (b), with statistical comparisons between breakage and anatomical refits.

Impact notches and other associated damage related to marrow extraction are common on horse limb bones and mandibles. Fresh bone fracture characteristics are abundant, providing solid evidence for breakage while bones were still fresh and greasy. Many of these notches occur repeatedly in the same locations on limb shafts, suggesting a systematic process of bone breakage. Figure 8 shows damage to femora shafts on the anterior surface adjacent to the third trochanter, a relatively thin area on an otherwise very dense limb shaft. Tibiae, humeri, and radio-ulnae also show similarly consistent locations of bone breakage. Often impact notches are paired with damage to the opposite side of the limb shaft, indicating the possible use of anvils in the fracturing process. Whereas impact notches on limb bones occur regularly in the same locations, impact damage does not follow a standardized pattern related to food utility. More specifically, there is no correlation between the frequency of impact marks and the amount of marrow within a particular limb bone. If maximum returns were the only goal of the Schöningen hominins, bones containing the most marrow would be broken more often and should preserve more traces of impact. In general, femora and humeri contain the most marrow among horse limb bones (Outram/Rowley-Conwy 1998), but impact damage is preserved more frequently on tibiae and radii fragments (based on NISP). Furthermore, impact damage is almost as frequent in metatarsals as femora despite the lowest marrow content for metatarsals among the major limb bones. Reduced frequency of damage to the highest-ranking limb bones may simply reflect the large amounts of trabecular bone in the marrow cavities of equid femora and humeri, which can pose difficulties for marrow removal (Blumenschine/Madrigal 1993).

On the other hand, perhaps such maximizing behaviours should not always be expected among Middle Pleistocene hominins. In the case of Schöningen, patterns of impact damage to limb bones and the lack of butchery marks on much of the axial skeleton do not follow predictions for the maximization of food resources. With so many horse carcasses present at the site, maximizing returns may have been unnecessary, and the resulting patterns reflect a strategy to meet short-term subsistence needs. Clearly meat yields, marrow content, and the like, have some influence over butchery, but as we analyse the entire assemblage and begin to form a clearer picture of the overall pattern of modification, we must look beyond quantitative comparisons to food utility and explore alternative explanations for the observed butchery patterns and measures of skeletal part representation.

In addition to the identification of several carnivore remains in the assemblage, carnivore presence is also indicated by numerous tooth scores, pits, punctures, and other related damage on the horse bones. Bovid and cervid bones also preserve the distinct traces of carnivore gnawing, but considerably less than in the horse assemblage. Several lines of evidence indicate carnivore access to horse carcasses was secondary to that of hominins. In general, hominin butchery marks are most common on horse limb elements (477 of 1130 NISP, 42.2 %), but large portions of the axial skeleton were completely ignored (203 of 2171 NISP with butchery marks, 9.4 %). Carnivore damage is present on some horse limb bone shafts and epiphyses (110 of 1130 NISP, 9.7 %), but slightly more abundant on ribs, vertebrae, and other axial elements (241 of 2171 NISP, 11.1 %). This contrast between the locations of hominin and carnivore damage is statistically significant ($\chi^2=119.34$; $p < 0.0001$), and suggests early access to carcasses by hominins followed by carnivore scavenging. Furthermore, 71 horse bones include both cut marks and carnivore damage, and in a few cases tooth pits or scores are preserved directly on top of cut or scraping marks. No cut or scraping marks occur directly on top of carnivore damage.

In addition to cut, scrape, and impact marks that clearly identify a systematic pattern of hominin butchery, the Schöningen faunal assemblage also includes a large collection of bones interpreted as bone retouchers and soft hammers used in the manufacture and maintenance of lithic tools. Eighty-eight such bone tools have been reported by van Kolfschoten et al. (2015). We have identified additional retouchers and soft hammers not previ-

Fig. 8 *Equus mosbachensis* right femur shaft fragments showing consistent patterns of breakage.

ously reported. The Schöningen retouchers are most frequently made from limb bone shaft fragments and display characteristic pits and scores indicative of forceful percussion applied to the edges of stone flakes or tools (Chase 1990; Patou-Mathis 2002; Mallye et al. 2012; Daujeard et al. 2014; Abrams et al. 2014). A few rib shaft fragments also show similar damage along the dense portion of the medial shaft at the neck. Some examples made from limb bones also include small stone flakes imbedded within the bone surface. Consistent with the dominance of horse bones in the overall assemblage, most retouchers are made from horse remains, and only a few are fashioned from bovid and cervid bone. Specifics regarding the gross morphology of retouching marks and associated breakage patterns (Mallye et al. 2012) indicate that most retouchers appear to have been used in a relatively fresh state, with only a few possible specimens showing evidence of use while dry, or at least defatted (**fig. 9**). We are currently analysing these implements in greater detail in order to differentiate the markings from other biotic and abiotic modifications and confirm their use as retouchers. In the end we expect the total number of bone retouchers to exceed 100, a remarkable number considering the age of the site.

An additional collection of limb bones preserve damage to the epiphyses related to use as soft hammers (**fig. 10**), primarily on the proximal and distal ends of horse metapodials. Based on our own limited experimental studies, we hypothesize that the bone retouchers were used in light-duty tasks of trimming tool and flake edges, while the soft hammers were better served as heavy-duty implements, either for working stone or breaking other bones for marrow, as suggested by van Kolfschoten et al. (2015).

With such a wide variety of bones used to shape and modify lithic tools, bone was a useful resource for Middle Pleistocene hominins at Schöningen. Furthermore, the relative scarcity of metacarpals and metatarsals in the overall assemblage may indicate the selective removal of metapodials for later use at other locations across the landscape. As the lithic assemblage at Schöningen is relatively small – only 1500 fragments of chert, mostly retouching debris (Thieme 2007; Serangeli / Conard 2015) – it is possible that bone retouchers and soft hammers supplanted stone hammers in the manufacture and maintenance of lithic tools or as hammerstones used to process the numerous animal carcasses. Substantial variability in form and damage produced implies a variety of functional uses for these implements during different stages in the lithic reduction and butchery process. Such diversity also indicates the use of bone as a raw material was a well-established behaviour by 300,000 years ago.

Skeletal part representation

As the analysis of the Schöningen 13II-4 faunal assemblage is still progressing, interpretations of skeletal part representations are only preliminary. Thus far, all of cranial remains listed as such in the original database have been analysed, but only the postcranial remains from the western portion of the site have been processed (see **fig. 2**). Because many statistical correlations rely heavily on the differential survival of skeletal elements, i. e., the relationship between the number of observed bones and the number of expected bones, meaningful calculations cannot be made in reference to the analysed sample. The minimum number of elements (MNE) can be calculated from the number of identified specimens (NISP), but it would be misleading to compare those totals against the expected totals from an unknown minimum number of individuals (MNI). However, certain trends of skeletal part representation can be evaluated in terms of NISP and MNE, without reference to MNI or other derived measures of abundance.

In general, all elements of the horse skeleton are preserved in various quantities, from the most dense teeth and limb bone shafts to the very thin and fragile hyoid bones and sternebrae. Although all elements are represented, the survival frequency of different skeletal elements and portions of skeletal elements is highly influenced by density, at least for the postcranial skeleton. From a sub-sample of

Fig. 9 Retouch damage on large mammal limb shaft fragments. Specimen on the left was likely used as a fresh bone; specimen on the right was likely used in a relatively dry or defatted state.

Fig. 10 *Equus mosbachensis* metapodial with damage to distal condyles from use as a soft hammer.

1857 adult horse postcranial remains (estimated MNE = 765), survivability is highest among the densest portions of the skeleton and lowest in the least dense skeletal elements. For example, humerus midshafts, with a calculated bone mineral density of 1.10 g/cm^3 (Lam/Chen/Pearson 1999), are represented by 38 MNE, while only seven proximal humeri (0.23 g/cm^3) were preserved based on MNE. This pattern is repeated in nearly all of the limb bones, as well as other elements of the appendicular and axial skeleton. From a different sample of bones, Voormolen (2008) found no correlation between survivorship and bone density; however, those calculations were based on average density for each bone rather than individual bone portion.

Density-mediated attrition is pervasive in the fossil record (e. g. Brain 1967; 1969; Lyman 1984; 1993; Grayson 1989), and carnivore feeding behaviour has also been shown to follow this same pattern of density-mediated survival of skeletal parts (e. g. Faith/Marean/Behrensmeyer 2007; Marean/Spencer 1991; Marean et al. 1992). In fact, many of the carnivore tooth pits, scores, punctures, etc., are concentrated at the least dense limb bone epiphyses and portions of the axial skeleton. Thus, a combination of pre- and post-burial taphonomic processes likely account for the resulting skeletal part representation at Schöningen, wherein the diagenic effects of prolonged burial have amplified the effects of carnivore ravaging following hominin discard of the bone assemblage.

Despite the apparent density-mediated survival of skeletal parts, a clear pattern in the representation of horse limb bones appears to have endured the effects of burial and carnivore ravaging. This pattern, coupled with the high frequency of hominin-induced modifications to the bones, provides critical insight into the carcass acquisition strategies, butchery practices, and possible transport decisions of Middle Pleistocene hominins. **Figure 11** depicts the representation of horse front and hind limb bones with corresponding NISP values per element. In both front and hind limbs the upper limbs (humerus and femur) are abundant, and the highest NISP values are shown in the tibia, followed by radius. Representation of the lower limbs substantially decreases in sequence from the metacarpals and metatarsals through to the phalanges. The data

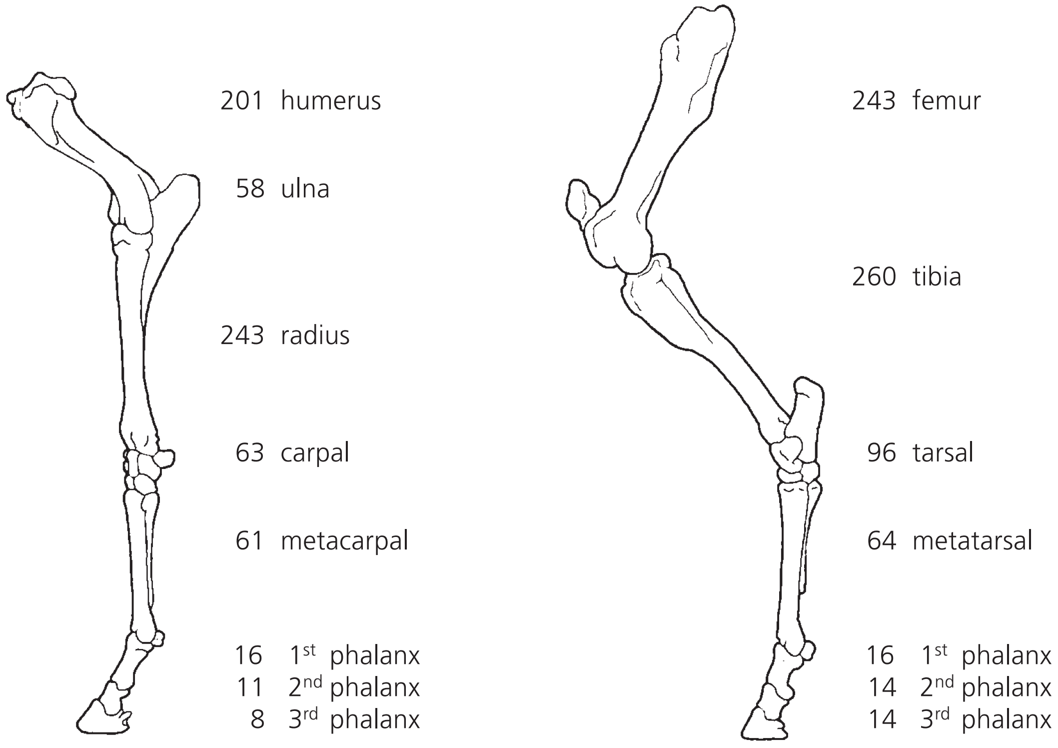


Fig. 11 Horse front and hind limb bone representation based on number of identified specimens (NISP).

presented are only based on NISP values, but this representation of front and hind limb bones does not fit the pattern of a strictly density-mediated assemblage. Among limb bones, metapodial midshafts rank as the most dense bone portions at 1.10 g/cm^3 (Lam/Chen/Pearson 1999), equal to that of humerus mid-shafts. While humeri are quite abundant, metapodials are comparatively scarce. Metapodial midshaft fragments may be more difficult to identify to side, portion, and segment than humerus midshafts, and therefore may not be counted in the analysed sample with the same reliability, but the overall pattern of limb bone representation appears more pervasive than a simple matter of identifiability.

Experimental results of carnivore feeding on simulated hominin-created bone assemblages shows that phalanges of small ungulates (sheep) are often completely consumed when present (Marean et al. 1992). This could explain the scarcity of phalanges in the assemblage. However, metapodials were only rarely consumed by carnivores in the experiments, which would argue against their absence as a result of carnivore ravaging. These simulated assemblages involved hyena consumption of sheep bones, which may not be exactly relevant to the taphonomic history of the Schöningen assemblage since horse phalanges are significantly more robust than those of sheep. Carnivores with a comparable ability to completely destroy or consume entire bones or bone portions like hyenas are absent from the Schöningen site, and similar experiments to determine the effects of carnivores on horse limb bones are not available. Additionally, only a low percentage of identified metapodials (6 of 125 NISP) and first phalanges (4 of 32 NISP) in the Schöningen assemblage show any damage from carnivores. As density and carnivore ravaging do not fully explain the resulting pattern of limb bone survival, it is probable that skeletal part representation reflects the butchery and transport decisions of Middle Pleistocene hominins.

The open-air, lakeshore setting at Schöningen is not a likely place for a residential site. There are no indications for long-duration occupations, but shorter-term encampments could be possible given the range of artefacts recovered. The most likely scenario is that the site represents an overlapping series of hunting episodes followed by intensive butchery activities. In such a case, the hominin discard of the bone assemblage potentially came with the selective removal of skeletal parts away from the site for nutritional purposes or otherwise. As a number of proximal and distal metapodials show damage related to their use as heavy-duty implements, Middle Pleistocene hominins certainly recognized the utility of these specific bones as soft hammers. Other skeletal parts do not show such consistent use as tools. It is possible that metapodials, along with the attached phalanges, were separated from the carcasses and transported away from the site for use as tools at other locations across the landscape. In fact, of the 443 bones recovered from nearby site 12II-2 (stratigraphically above the "Spear Horizon"), only one bone was identified as large cervid (likely *Megaloceros*) – a metapodial shaft fragment with traces of use as a retoucher at both ends (Julien et al. 2015a). Neither the proximal or distal epiphyses of the bone are present, but its singularity and its use as a tool suggest that the bone may have been transported to the site.

Mortality Profiles

From the cranial remains, van Kolfschoten (2014) identified a minimum of 46 *Equus mosbachensis* individuals; we expect this total to increase as our analysis progresses. Breaking down the available sample into age classes according to broad life history stages, the horse population includes an abundance of prime age adults, numerous subadults, and few old adults based on tooth crown heights and tooth wear characteristics. Comparing the resulting mortality profile against theoretical models there is a strong correspondence between the Schöningen horse assemblage and a pattern of catastrophic mortality (see Lyman 1987; Stiner 1990) or the Juvenile-Prime-Old (JPO) model described by Discamps/Costamagno (2015). This suggests that the cumulative age at death mirrors the living structure of a stable horse population. In other words, horse mortality at Schöningen occurred independently of age. Such a pattern is most easily imagined as resulting from any number of large-scale catastrophic events – floods, fires, volcanic eruptions, disease, etc. – where the probability of death is equal across the population regardless of age. Catastrophic mortality can also result from the additive effects of predation, when prey animals are killed according to their proportional live abundance (Stiner 1990). There is no indication of a natural, catastrophic event at Schöningen, and the presence of individuals distributed across all age classes likely rules out a single, mass-kill event. In terms of hominin hunting preferences, the horse population at Schöningen does not appear to be selectively hunted, but rather killed in accordance to their live abundance during multiple hunting events along the lakeshore. Furthermore, the Schöningen horse population includes a minimum of five prime adult males, the presence of which would suggest multiple bands of horses. A typical horse herd usually includes a single prime adult male over the age of five or six, a harem of 2-6 breeding adult females, and their offspring (Klingel 1974; Levine 1983; Berger 1986). Bachelor herds can consist of 2-15 males aged 2-4.5 years; older males may remain solitary after 4.5 years of age, but most leave the bachelor group to form their own family groups. Several bands may join to form one large herd at certain times of year, but it is more likely that the horse population reflects multiple individual bands, portions of which were killed along the Schöningen lakeshore during chance encounters with Middle Pleistocene hominins.

Looking to the seasonality of death among the subadult horses (**fig. 12**), a slight drop in deaths occurred in spring, during and following the birthing period in May, but in general, all seasons are equally represented. No deaths are recorded for November, but overall autumn deaths are equal to those occurring during the winter and summer. No distinct seasonal pattern was found in ^{18}O and ^{13}C isotopic variations of adult horse teeth (Julien et al. 2015b). The exact month of birth and death is not entirely relevant, but the wide range of crown heights and wear stages recorded in the teeth of the subadult horse population suggests that individuals died at the Schöningen lakeshore at a relative consistent rate throughout the seasonal cycle (assuming a constant rate of tooth wear among different individuals). This age distribution suggests a year-round presence of horses in the vicinity of the lake. Additional $^{87}Sr/^{86}Sr$ isotope studies are aimed, in part, to determine if segments of the horse population were resident or migratory. This has important implications for inferring Middle Pleistocene hominin mobility. If the horse assemblage was drawn from an entirely resident, non-migratory population, it can be reasoned that there was also a consistent, perhaps year-round, presence of hominins in the vicinity of the Schöningen lakeshore during the Middle Pleistocene.

Forthcoming studies

In the future, we will further evaluate these and other patterns once the complete faunal assemblage is analysed. Our immediate objectives are to finish the zooarchaeological and taphonomic documentation of the eastern portion of the site. Numerous multidisciplinary studies will help to further define the local depositional environment. Stable isotope and 3D-micro-texture analyses of horse teeth will provide additional data on the paleoecology of the main prey species. Additionally, these studies will also be useful in identifying different horse populations within the accumulation, providing a possible route to distinguish between multiple death events. Micromorphology thin sections and palynological samples taken from sediment blocks stored under deep freeze since the original excavations are currently being analysed to provide precise depositional contexts immediately preceding and following burial. A comprehensive bone refitting programme is also underway to identify potentially distinct activity loci within the main bone concentration and other areas across the site. With an in-depth spatial analysis that incorporates all of these various analyses, we can reconstruct hominin activities at the site on a fine scale. This holistic approach aims to highlight the "human component" to the Schöningen 13II-4 "Spear Horizon".

Discussion

These preliminary findings offer a view into the complex archaeological record of the Schöningen 13II-4 "Spear Horizon". Although our analysis is ongoing and the data presented here are only a portion of what is planned for the overall project, we are beginning to assemble a more clear understanding of hominin behaviour preserved within the Schöningen 13II-4 deposit. While we reserve our final interpretations of the site until the full analysis is complete, we can evaluate several existing hypotheses regarding the events leading to accumulation of the site: a single mass kill (Thieme 2005); multiple kill/butchery episodes (Julien et al. 2015b; Voormolen 2008); and, a mass kill event among a natural background accumulation of bones (van Kolfschoten 2014).

Alone, the quantity of butchered horse individuals all but excludes a single mass kill event. Add to that the butchered remains of bovids and cervids and the different spatial arrangements among these main prey species, the notion of a single hunting and butchery event can no longer be supported. All evidence presented here suggests multiple hunting events over an extended period of time, during all seasons of the year. While we do not deny the possibility exists for one mass kill of 20-25 horses described by van Kolfschoten (2014), we cannot support this hypothesis based on the available taphonomic and spatial evidence. With the horse bones so densely concentrated within a relatively restricted area along the relict shoreline, we make no claims as to being able to distinguish one butchered horse carcass from another. Nor are we currently able to differentiate between horse carcasses (or portions thereof) butchered during a possible single mass kill event from those representing a supposed background accumulation. In fact, we feel the use of the term "background accumulation" should be avoided as it implies little or no active hominin involvement with the faunal accumulation apart from one mass kill event.

Despite strong indications for an extended period of accumulation, there are regularities in the treatment of horse carcasses across these multiple hunting and butchery episodes. The entire butchery

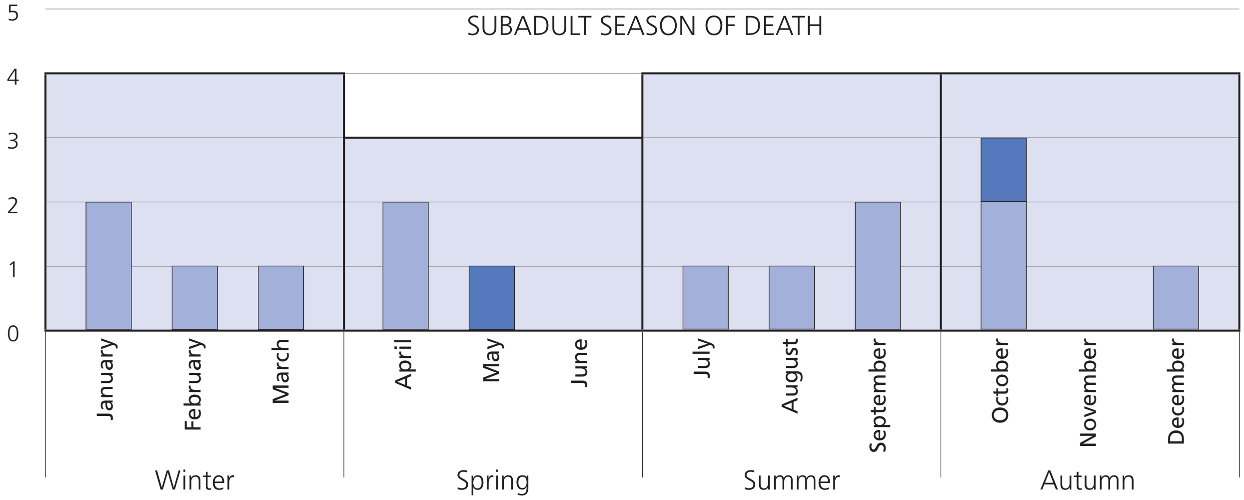


Fig. 12 Seasonality (astronomical) of death among juvenile horses with the birthing season modeled to begin in may. Light blue bars represent young juvenile horses 0-1 years of age; dark blue bars represent juvenile horses 1-2 years of age; shaded blue background represents the total deaths according to season (Winter = 4, Spring = 3, Summer = 4, Autumn = 4). Age in months based on crown height measurements of Bignon (2006).

sequence is preserved, from filleting, disarticulation, marrow processing, and perhaps skinning. Butchery was focused toward the removal of meat from the appendicular skeleton and processing of limb bones for marrow. Impact damage to the same locations on limb bone elements suggests an efficient and systematic approach to obtaining marrow. Overall, elements of the axial skeleton were only minimally processed by hominins, but have been more frequently damaged by carnivores. In all instances of hominin butchery traces coinciding with carnivore damage to bones, hominins had early access to the carcasses, followed by carnivore scavenging. However, that does not preclude the possibility that some animals were killed by carnivores or died naturally along the Schöningen palaeo-lakeshore.

The use of bone as a raw material to manufacture and maintain lithic tools at the site is clearly evident in the numerous bone retouchers identified in the assemblage. Indications for the fashioning of these implements from both fresh and dry bones suggest some previous knowledge of available raw materials at the site, further reinforcing the possible connections between the multiple hunting events. Bone retouchers were an important complement to the Middle Pleistocene hominin tool-kit at Schöningen, especially considering the very small and rather expedient lithic assemblage. Damage to the proximal and distal ends of metapodials in the assemblage implies their use as soft hammers, likely for more heavy-duty purposes. The scarcity of metapodials relative to other limb bones underscores their utility, some of which may have been transported away from the "Spear Horizon" for use at other locations across the landscape.

The Schöningen lakeshore was undoubtedly an attractive location on the landscape for horses both as a source of water and for feeding. Likewise, the Schöningen lakeshore was the focus of hominin hunting activities. The abundance of horses, together with the presence of other large mammals, birds, fish, and a variety of plants, certainly could have supported a modest population of resident hominins throughout all seasons of the year, as implied by the timing of individual deaths among the subadult horse population.

Particularly intriguing is how the Schöningen hominins were able to cope with the challenges of living at northern latitudes during the winter. Even during interglacial periods, low temperatures, snow cover, and reduced resource availability during winter would have posed serious threats to survival. These problems could be eased by a variety of technological buffers, cultural insulators, and other adaptive strategies (Gamble 1987; Hosfield 2016; White 2006). The spears certainly attest to the technological prowess of the Schöningen hominins; add to that the use of bone tools, and it is clear that they possessed a broad knowledge of useful raw materials beyond stone. Based on the quantity and dense concentration of butchered horse bones, it is probable that multiple horse individuals were killed during each hunting episode. Such large quantities of meat may imply some level of food sharing and storage, which would have been a beneficial strategy during times of resource scarcity. Despite the excellent preservation at the site, various forms of cultural insulation, including fire, shelter, clothing, etc., are absent. Evidence of hearths in the "Spear Horizon", once heralded as among the earliest indications of the controlled use of fire in Europe, has since been rejected (Stahlschmidt et al. 2015b). Indications for shelters and clothing are rare, if not entirely absent, at Middle Pleistocene archaeological sites, including the "Spear Horizon". This could simply reflect the limited range of activities performed at the site and its lakeshore location. The Schöningen 13II-4 "Spear Horizon" likely represents a hunting and butchery site, thus providing only a glimpse of Middle Pleistocene hominin activities on the landscape. The prospect of a resident hominin population holds potential for identifying a variety of different activities and types of sites among the various Schöningen lakeshore localities.

Conclusion

The Schöningen 13II-4 "Spear Horizon" discoveries reframed how archaeologists and paleoanthropologists viewed the physical and cognitive capabilities of Middle Pleistocene hominins, and hopefully informed the perceptions of pre-modern humans among the general public. As it stands, the "Spear Horizon" is anything but a simple Palaeolithic hunting and butchery site; rather, Schöningen preserves a very rich and complex record of Middle Pleistocene hominin adaptive behaviours. The Schöningen lakeshore was undoubtedly a dominant feature on the interglacial landscape, a location with predictable resources that were exploited throughout the year by a variety of animal species, including hominins. Yet, like any other, the site only reflects a particular suite of behaviours at one point in space and time. Combined with the other high-resolution archives of hominin behaviour contained in this volume, a clear focus toward lakeshore environments is evident across much of Europe during Pleistocene interglacial periods and into the Holocene (Gaudzinski-Windheuser / Roebroeks 2010). Particularly intriguing are comparisons between Schöningen and the Eemian interglacial lakeshore site at Neumark Nord 2. The sites are analogous in their topographical lakeshore settings and associated interglacial fauna, but the level of carcass processing by hominins and subsequent carnivore activity is strikingly different. At Neumark Nord 2, the bones from all portions of mammal skeletons are more thoroughly processed than at Schöningen, and carnivore involvement with the faunal assemblage is minimal (Kindler / Smith / Wagner 2014). Despite broad environmental similarities between the sites, carcass processing strategies of Middle Pleistocene hominins, i. e., the time and energy expended to satisfy their nutritional needs, was clearly different. From such comparative studies of lakeshore sites, we can begin to appreciate the various ways in which our hominin ancestors viewed and adapted to similar interglacial environments over time.

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THE LAST INTERGLACIAL (EEMIAN) LAKELAND OF NEUMARK-NORD (SAXONY-ANHALT, GERMANY). SEQUENCING NEANDERTHAL OCCUPATIONS, ASSESSING SUBSISTENCE OPPORTUNITIES AND PREY SELECTION BASED ON ESTIMATIONS OF UNGULATE CARRYING CAPACITIES, BIOMASS PRODUCTION AND ENERGY VALUES

Abstract

The high-resolution palaeoenvironmental record from the last interglacial (Eemian) lakeland at Neumark-Nord (Saxony-Anhalt, Germany) holds the rare potential to study Neanderthal subsistence ca. 125,000 years ago in remarkable detail. Using the palynological record from the large lake Neumark-Nord 1 (NN1) and the adjacent small "pool" Neumark-Nord 2 (NN2) a sequence of lithic and faunal assemblages has been established, indicating Neanderthal presence in the lakeland throughout the Eemian. Calculations of the herbivore carrying capacity for the Neumark area during the Eemian reveal high biomass estimates. Using these estimates it was possible to calculate the structure of the source population, based on the faunal record rich in species and individuals, from littoral deposits assigned to the first mesocratic phase of the Eemian. The results can be used as a frame of reference for making inferences on subsistence opportunities and prey selection based on taphonomical and zooarchaeological studies of the Neumark-Nord faunal assemblages. In a broader perspective our study demonstrates the benefits from inferring energy values (kcal) and body mass (kg) as ancillary parameters to zooarchaeological analyses to understand the relationships between death assemblage and their habitats from which they originate.

Keywords

Last Interglacial, Eemian, zooarchaeology, taphonomy, thanatocoenosis, biocoenosis, carrying capacity, biomass, herbivore community structure, subsistence, prey selection, Neanderthals

Introduction

Palaeolithic Archaeology holds the potential to trace the roots of our behaviour far back in time through a diachronic perspective. With first attempts of placing the human "hunting way of life" in an evolutionary framework (Lee / De Vore 1968), reconstructing human subsistence in the Pleistocene became a major research agenda for Palaeolithic Archaeology. In the broadest sense subsistence comprises all the

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Fig. 1 The Great European Plain is one of the major topographical features of Europe characterized by an almost mountain-free landform. Today most of the Plain belongs to a temperate mixed and broadleaf forest biome. The area generally referred to as the North European Plain is roughly outlined with the black rectangle. – (Source: CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=1607793).

efforts undertaken to fulfil and maintain durably the basic demands of humans, most prominently and essential the appropriation and preparation of food (Sahlins 1972). Subsistence is constrained by the availability and distribution of resources in the environment. Thus, subsistence strategies, tactics or patterns decoded from the archaeological record can only be assessed with reference to the framing ecological conditions.

For most of the time in human history climate oscillations were more extreme than what we have experienced in the more recent past, i. e. the odd thousands of years of the Holocene. As a result, we witness landscapes and environments with no modern analogues to the ones in which earlier humans operated and evolved. This constitutes a challenge when connecting human behaviour and ecology in the archaeological context. However, on the North European Plain, relatively short interglacial climatic stages led to comparable environmental conditions, in which we can study the evolution of human ecology and the human niche, through time up to our present interglacial, the Holocene. Thus, the lakeland of Neumark-Nord is a rare high-resolution ecological and archaeological archive from the last interglacial (Eemian) offering ideal conditions to study Neanderthal adaptations to forested environments on the North European Plain (Gaudzinski-Windheuser / Roebroeks, 2014; Gaudzinski-Windheuser et al. 2014).

The earliest occupation of the North European Plain

The North European Plain covers parts of northern France, southeastern England, Belgium, the Netherlands, Germany, southern Scandinavia and Poland. Its limits and extent are defined more by the common use of the term than by strict geographical features. This region is part of the Great European Plain, which stretches from the northwestern foot of the Pyrenees in a long crescent through the North of Europe to the western foot of the Ural in the East (**fig. 1**). Its basic feature is the regular relief in an almost mountain-free landscape. Today this vast region belongs to the temperate mixed and broadleaf forest biome and, far to the southeast, the forest steppe zone.

During the Pleistocene the rather remote position of the North European Plain in the Old World constituted the terminal end of many human and other animal dispersals in Western Eurasia. The climatic oscillations of the Pleistocene, e. g. represented in Marine Isotope Stages (MIS), had enormous effects on the extant of land mass, geomorphology, hydrology and environments. During the pleniglacials of the cold stages large parts of the North European Plain were overthrust by glaciers several times. In contrast, during the full-interglacial warm phases sea levels were rising and mixed and broadleaf forest dispersed over the Plain. Nevertheless, with the onset of the 100 kya glacial-interglacial cycle about 1 mya ago, grassland-types of environments and steppe-tundras covered the European Plain most of the time. The drastic environmental, faunal, botanical and sedimentological responses to global climate change at these latitudes allows for a comparably fine subdivision of the terrestrial Pleistocene stratigraphy on the North European Plain (Litt et al. 2007). This constitutes an ideal framework for the study of hominin environmental responses, including the development of cultural and biological adaptation as well as expansion and contraction of the geographic range of human populations.

Depending on climate and environmental conditions, the North European Plain formed part of the biogeographic range of cold adapted faunal communities with core dispersal areas in the East or warm adapted faunal communities with core dispersal areas in the South (von Koenigswald 2003). When exactly humans became a part of these faunal communities on the North European Plain is still an issue. After phases of short-lived "Pioneer dispersals" around the Lower to Middle Pleistocene transition (exemplified by the evidence from Happisburgh, UK, Parfitt et al. 2005; 2010; Ashton et al. 2014), we can assume that from 600 kya onwards humans became frequent occupants of Central Europe, in the first instance during phases of favourable environmental conditions (Roebroeks 2006; Jöris 2014). From the middle part of the Middle Pleistocene onwards, humans seem to be present in significantly more challenging – cold dry – conditions, with sites no longer limited to the western (Atlantic) and southern (Mediterranean) parts of Europe, but also located in its more continental parts, east of the river Rhine (Haidle / Pawlik 2010; Kahlke et al. 2011; Cohen et al. 2012). Such a range expansion into more challenging environments might be related to the development of new strategies for survival (Hosfield 2016), including the introduction of fire as a fixed part of the human technological repertoire (Roebroeks / Villa 2011; Shimelmitz et al. 2014; MacDonald 2017). Establishing the exact spatiotemporal patterns of presence and absence and the factors determining these, including adaptations and alterations in subsistence and the process of "Neanderthalisation" (Hublin 2009), is still a big challenge.

For obvious reasons Northern Europe was depopulated during the pleniglacials, when glaciers expanded, and the remaining parts of the Plain became a hostile periglacial terrain. For most time segments of the Pleistocene the climate was cool and cool-temperate, and in particular drier, with dispersal of grassland and tundra steppe cover on the North European Plain as well as in the southerly adjacent low mountain range. Most of what we know about human subsistence stems from these environments. It seems that Neanderthals adapted their survival strategies well to these environments and focused on high nutritional resources which were predominantly stored in large herbivores (Gaudzinski-Windheuser/Kindler 2012). The low plant biomass production during most of the Pleistocene in these northern latitudes and the inferred high daily energy requirements of these humans (but see: Heyes/MacDonald 2015) may have enforced a "hunting way of live", which is so characteristic for the late Neanderthals. In addition, many anthropologists identify certain anatomical traits in Neanderthals as special adaptations to these cool climates in Europe (Churchill 1998; Aiello/Wheeler 2003; Weaver 2003). In this perspective, the process of "Neanderthalisation" can be perceived as an adaptation of a Middle Pleistocene European population to cool-dry to cool-temperate environments.

However, the earliest evidence for human presence in the northern parts of Europe, as well as on the North European Plain, derive from sedimentary contexts indicative of warmer interglacial climates with forested environments (Parfitt et al. 2005; Roebroeks 2005). At Happisburgh 3 (Parfitt et al. 2010; Ashton et al. 2014), humans seem to have remained in the area at the end of an interglacial about 800,000 years ago, when mainly deciduous forest became replaced by coniferous trees.

In the course of the Pleistocene these interglacials constituted the relatively short climatic optimum of a glacial cycle with climates and environmental conditions similar to today. Human presence on the North European Plain is also well attested for several interglacials. But, occupation pre-dating the Elsterian/Anglian glaciation (MIS 10 or 12) might have been restricted to the western part of the Plain, influenced by oceanic climate, while during the Holsteinian interglacial (MIS 9 or 11) areas which are more under continental climate influence, were also occupied (Haidle/Pawlik 2010; Kahlke et al. 2011; Cohen et al. 2012; Jöris 2014 following a MIS 12-11 correlation for this glacial-interglacial cycle, but see Geyh/Müller 2005; 2007; Litt et al. 2007; Bittmann 2012 supporting a MIS 10-9 correlation for the Elsterian-Holsteinian succession). However, due to the spread of forests during these interglacials in Europe, these environments are often considered as rather challenging environments for Neanderthals, based on reconstructions of the production and distribution of edible resources. Like modern-day temperate and tropical forests, Pleistocene interglacial deciduous forests within the Neanderthal range would have been characterized by a high primary biomass and a high primary production. Most of this richness would have consisted of trees and vegetational resources relatively expensive to process and only available over short periods of time. Meat must have been a critical food source. In contrast to the open mammoth steppe environments, herbivore mass in forested environments would have been significantly lower, while medium sized and larger mammals would have dispersed in forested environments. Thus, subsisting in these environments would have come with enormous risks and required high mobility (Gamble 1986; Kelly 1995; Binford 2001). Since the introduction of Gamble's (1986) model, which suggests that for most of the Pleistocene changing regional settlement histories are driven by environmental pressures, special attention has been devoted to the interglacials and particularly the last Interglacial, the Eemian (MIS 5e-5d, see Shackleton et al. 2003; Sier et al. 2011), to characterize Neanderthal ecology and ecological tolerance (e.g. Roebroeks/Conard/van Kolfschoten 1992; Speelers 2000; Gaudzinski 2004; Wenzel 2007; Gaudzinski-Windheueser/Roebroeks 2011). In recent modellings of abiotic factors shaping the Neanderthal range during the last interglacial, the North European Plain appears to be a rather unsuitable habitat, based on climate and terrain. Thus, the archaeological evidence in that region should be considered as representations of the tail of Neanderthal distribution during the Eemian (Benito et al. 2017). These results, although only based on abiotic parameters, emphasise again the importance of studying these "interglacial/warm/forest" Neanderthals on the North European Plain. This has the potential to provide a better understanding of their ecological tolerance as well as their flexibility, and plasticity in response to different ecological conditions.

The Eemian occupation of the North European Plain

For several reasons, the last interglacial, the Eemian, offers the best potential to reconstruct Neanderthal adaptations to forested environments on the North European Plain. Eemian terrestrial deposits are mainly found in regions which were previously covered by the Saalian ice sheet on the North European Plain. The retreat of the ice at the end of the Saalian glacification (MIS 6) released large amounts of water in the landscape and sub-surface, much of which was captured in a wide diversity of sediment traps on the North European Plain, such as kettle holes, meltwater channels and basins carved out at the end of the Saalian and beginning of the subsequent interglacial, due to isostatic movements and other geomorphological dynamics. Consequently, lakelands developed on the North European Plain and these lake basins filled up during the Eemian. The ice advance during the following Weichselian cold stage (MIS 4-2) did not penetrate as far south on the North European Plain as the Saalian ice did, so that Eemian basin deposits could survive unaltered in the underground in high numbers until today (Turner 2000). These Eemian basin deposits have a good chance to contain rather undisturbed high-resolution palaeoenvironmental and archaeological archives. But unfortunately, most of these basins are covered and protected by thick Weichselian deposits, mostly loess, preventing archaeological excavations and are only accessible by drilling.

The Eemian interglacial was defined by the palynological record in the region of Amersfoort (NL) (Bosch/Cleveringa/Meijer 2000). Today, the evidence from numerous Eemian deposits draws a very detailed and coherent picture about the plant succession during the Eemian reforestation on the European Plain (Turner 2000), which bears similarities to the recent Holocene and the penultimate interglacial, the Holsteinian, in terms of the dynamic sequence of the protocratic, mesocratic and teleocratic forest development phase during the interglacial cycle (Lang 1994). However, each interglacial has its own individual characteristics and progressions. In general, the Eemian is considered to have been as stable as the present Holocene, but warmer and wetter than today (Kaspar et al. 2005) and with higher sea levels than at present (Dutton/Lambeck 2012; Kopp et al. 2013). Thus, gradients of temperature and precipitation on the North European Plain might have been quite different from our recent interglacial, and thus, the mode of the reforestation and the spread of dense woodland during the Eemian might also have had its own unique dynamics. A rapid and uniform expansion of closed forests over the North European Plain is reconstructed from palaeobotanical evidence (Litt 2000; Turner 2000). For the virgin vegetation of the Holocene on the North European Plain the dominance of closed-canopy primeval forest or alternatively a mosaic of forests, open grassland, scrubs and groves maintained by large herbivores are proposed (Vera 2000; Birks 2005; Mitchell 2005). The large herbivore guild during the Eemian was more diverse than in the Holocene in Europe and contained several megaherbivores and a mix of browsers, grazers as well as mixed feeders indicative of mosaic environments (van Kolfschoten 1995; 1999; 2000). The potential of herbivores and other agents to create and maintain open habitats in interglacial forests are discussed by Svenning (2002). More recent studies also highlight the impact of herbivores on vegetation openness in past interglacials (Sandom et al. 2014; Bakker et al. 2016; and for a case study from Neumark-Nord 2: Pop/Bakels 2015). Thus, environmental reconstruction on a regional or even local scale is of particular importance from an archaeological point of view, when referring to Eemian environments as rather "uncomfortable" for Neanderthals to inhabit.

Eemian deposits on the North European Plain constitute high-resolution temporal and environmental archives compared to other Pleistocene periods. The temporal resolution is based on varve counting of Eemian sediments, which has allowed calculation of the durations of individual pollen stages (Erd 1973; Menke/Tynni 1984), and yielded solid data, which with ca. 11,000 years is relatively short (Müller 1974) (**tab. 1**).

Tab. 1 Interglacial forest development (Lang 1994), the subdivision of the Eemian based on Pollen Zones (Erd 1973; Menke/Tynni 1984) and their estimated durations (Müller 1974).

Interglacial Cycle (Lang 1994)	Forest phase	Eemian Pollen Zones		Duration (Müller 1974)
		Menke/Tynni 1984	Erd 1973	
Phase D (teleocratic phase)	*Pinus* phase	VII	9	~ 2,000 years
	Pinus-Picea-Abies phase	VI	8	~ 2,000 years
Phase C (mesocratic phase, 2. part)	*Carpinus-Picea* phase	Vb	7	~ 4,000 years
	Carpinus phase	Va	6	
Phase B (mesocratic phase, 1. part)	*Corylus-Taxus-Tilia* phase	IVb	5	~ 1,200 years
	Quercetum mixtum-Corylus phase	IVa	4	~ 1,200 years
Phase A (protocratic phase)	*Pinus-Quercetum mixtum* phase	III	3	~ 450 years
	Pinus-Betula phase	II	2	~ 200 years
	Pinus phase	I	1	~ 100 years

Neanderthal occupation during the Eemian is well attested at least for the German part of the North European Plain (Gaudzinski 2004; Gaudzinski-Windheuser/Roebroeks 2011). In contrast, in other parts of the Plain evidence of Neanderthal presence is still lacking, except for its southwestern tip in northwestern France where the fluvial tufa site of Caours close to the current mouth of the Somme river (Locht et al. 2014) and Waziers (Hérrison et al. 2015) are located. The last interglacial sea level rise and subsequent flooding of the channel separated Great Britain from the European main land, which may have prohibited a recolonisation immediately after the Saalian (Sier et al. 2015). The higher water levels during the Eemian also separated Denmark from northern Germany. Here, there is a complete lack of unambiguous evidence for Neanderthal presence during the Eemian as well as prior to or postdating the last interglacial (Egeland et al. 2014; Kellberg Nielsen 2017).

A number of Eemian archaeological sites deposited in basin sediments or travertine are known from the North European Plain (Gaudzinski 2004; Gaudzinski-Windheuser/Roebroeks 2011). Unfortunately, most of these sites were excavated a long time ago, and most of the archaeological and, in particular, zooarchaeological material must be considered extremely biased rather than thoroughly excavated (Gaudzinski 2004). It is a precarious task to draw conclusions about Neanderthal subsistence strategies from faunal analysis of these collections. Evidence from single-carcass elephant sites like Lehringen (Lower Saxony, Germany), including the recovery of a wooden lance and artefacts (Thieme/Veil 1985) and Gröbern (Saxony-Anhalt, Germany) may indicate that weak and isolated elephant individuals wading in shallow water – possibly using water to support their heavy weight – became an easy target of Neanderthals (Gaudzinski 2004). The species rich fauna from the travertine of Taubach (Thuringia, Germany) points to a similar strategy. The fauna of this collection is dominated by forest rhino (*Stephanorhinus kirchbergensis*, MNI = 76) and brown bear (*Ursus arctos*, MNI = 51) (Bratlund 2000). Neanderthals occupied the travertine area repeatedly during the early phases of the Eemian. Mainly young and subadult rhinos and brown bears of all age classes were hunted (Bratlund 2000). Lehringen, Gröbern and Taubach point to a subsistence strategy during the Eemian, which was different to the preferred game repertoire of Neanderthal in cool to cool-temperate environments (Gaudzinski 2004). Large pachyderms, such as elephants and rhino, seem to have become more important in the nutrition of Eemian Neanderthals (but see Smith 2015). To avoid risky and dangerous manoeuvres, weaker individuals were targeted, both older and young ones. Regarding the brown bear, one may conclude that in the search for high nutritional resources in the Eemian environments the hunting focus of Neanderthals diversified to include defensive and/or solitary large mammals, such as elephants, rhinos and bears for the benefit of lower handling cost and higher return rates (Gaudzinski-Windheuser/Roebroeks 2011; Smith 2015). In contrast, evidence from the recently excavated Somme River valley site of Caours in northern France suggests that the environmental change of the last interglacial had limited influence on Neanderthal subsistence strategies. During the Eemian as well as the Weichselian Pleniglacial in northern France hunting preferentially focussed on medium sized herbivores (fallow deer, reindeer, red deer) and subsistence varied in terms of the main prey taxa present in different environments (Locht et al. 2014).

However, we should keep in mind that hunting is more than just killing an animal. Ideally, prey choice, subsistence strategies and the ecological niche humans occupied should be considered in the frame of faunal community structure and prey abundance at a given time, as well as the specific ethology of individual species. Killing reindeer and red deer in an open grassland environment might involve completely different hunting tactics and might be embedded in completely different systems of land-use and organisation than killing fallow deer and red deer in forested environments.

Analysis of the material from our recently excavated small Eemian basin Neumark-Nord 2 and the adjacent large lake Neumark-Nord 1 enables us to study in some detail subsistence opportunities and

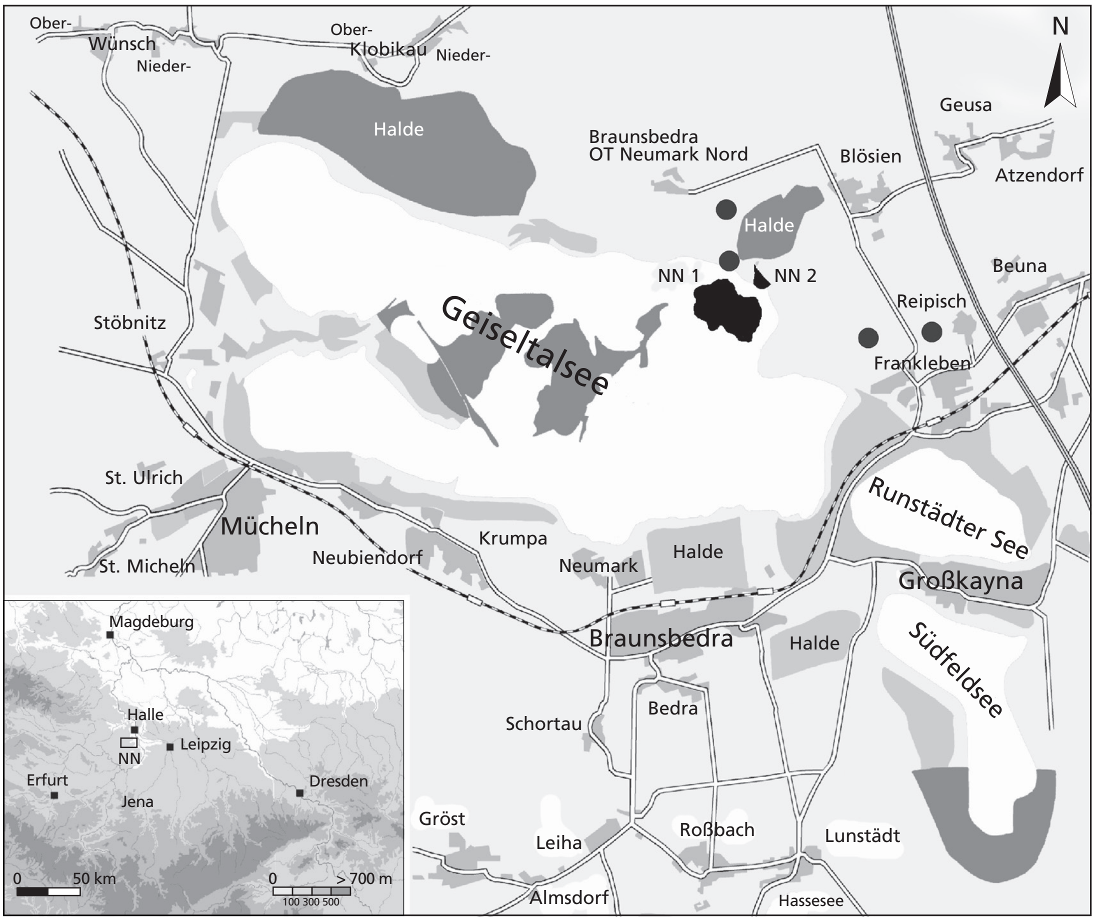

Fig. 2 Location of the Eemian lake basin Neumark-Nord 1 (NN1) and the small pond Neumark-Nord 2 (NN2) within and along the recent Geiseltalsee, Saxony-Anhalt, Germany. The black dots indicate potential basin structures documented by field surveys. The box inset indicates the position of the Neumark-Nord lakeland on a larger regional scale.

Neanderthal behavioural adaptations in forested environments during the Eemian on the North European Plain.

The Eemian lakeland of Neumark-Nord

The Eemian site of Neumark-Nord 2, as well as the adjacent synchronous basin Neumark-Nord 1, are located approximately 10 km south of Halle and 35 km west of Leipzig in Saxony-Anhalt, Germany (51°19′28″N, 11°53′56″E; **fig. 2**). The first Eemian basin, Neumark-Nord 1 (NN1) was uncovered in 1985 in the former lignite open cast mine Mücheln. Thanks to the perseverance and motivation of the research group "Bilzingsleben/Neumark-Nord", founded by and around Dietrich Mania, this basin was investigated and excavated in a continuous marathon against the machines, large-scale bucket-wheel excavators, until the end of mining activities in the mid-90s. NN1 became famous through its unique thanatocoenosis, consisting of numerous (almost) complete large mammal skeletons within the lake basin (Mania et al. 1990; 2010a; Meller 2010). These skeletons were uncovered and in parts damaged by bucket-wheel excavators, and an unknown but probably high number of these skeletons were most likely destroyed without being noticed in the course of quarrying at NN1 (Mania 2010a; Mania/Thomae/Altermann 2010; Mania et al. 2010b). During subsequent reclamation works of the mine to create the Geiseltalsee, which is completely flooded today covering an area of approx. 18 km², Mania also discovered the second basin, Neumark-Nord 2 (NN2), about 100 m northeast of NN1. NN2 was completely uncovered on a wedge like terrace during levelling of the northeastern embankment of the Geiseltalsee at the end of the 1990s. Thorough multidisciplinary investigations and archaeological excavations began in 2004 by the Landesamt für Denkmalpflege und Archäologie Sachsen Anhalt, and continued from 2006 to 2009 in collaboration with the Faculty of Archaeology, Leiden University and MONREPOS Archaeological Research Center and Museum for Human Behavioural Evolution (Gaudzinski-Windheuser/Roebroeks 2014).

Lake basin NN1 covered an area of about 24 ha, while basin NN2 represents a small and shallow pond, of about 1.6 ha in size. The north-south extent and the western margins of NN2 were fully recovered, while former mining activities had already destroyed the easternmost limits of the basin (Hesse/Kindler 2014). Prior to the large-scale excavations of NN2 there had been some debate about the chronostratigraphic position of the interglacial deposits of basin NN2. Multidisciplinary analyses at NN2 and correlations with the record of NN1 however established beyond any doubt a synchronic filling during the Eemian (Strahl et al. 2011; Gaudzinski-Windheuser/Roebroeks 2014). In the area of the Geiseltalsee more basin structures below Weichselian loess deposits are known, which may be part of the extended Neumark lakeland (Hesse/Kindler 2014).

The archaeological record of the recently investigated basin NN2 is an ideal starting point to study Neanderthal occupation and subsistence in the Eemian lakeland area around the current Geiseltalsee.

NN2 – Stratigraphy, basin dynamics, and correlations with NN1

Multidisciplinary studies and excavations at NN2 provide a high-resolution coverage of dynamic processes in the development and filling of the basin, as well as environmental changes during the Eemian (Strahl et al. 2011; Gaudzinski-Windheuser/Roebroeks 2014; Pop/Bakels 2015; Pop et al. 2015). Results of these investigations, including sedimentology, micromorphology, pollen analyses and palaeomagnetism, establish the temporal and spatial context for all archaeological studies at NN2.

The largest extent of basin NN2 is 90 m NE-SW and 60 m NW-SE, with asymmetrical inclinations of the slopes on the northern and southern margins (**fig. 3**, Hesse/Kindler 2014). At the steeper southern part of the basin the sediments build a

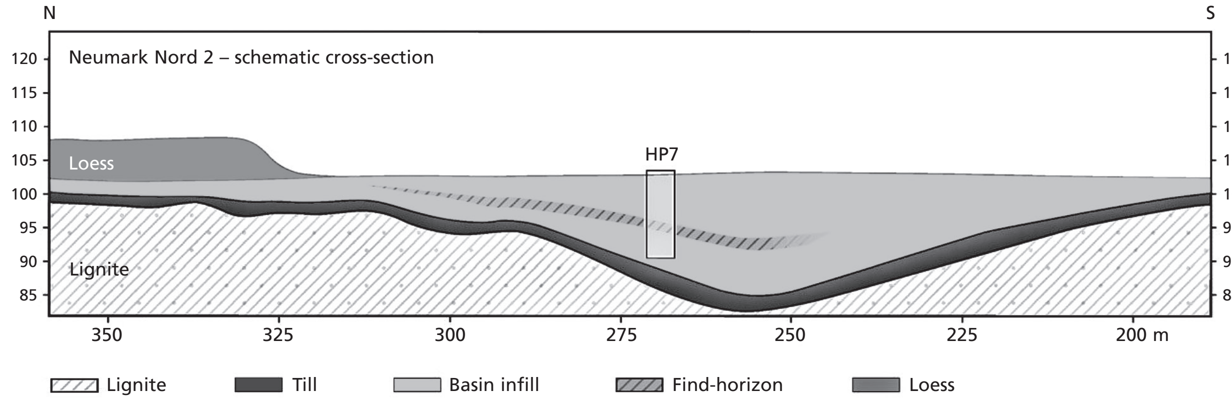

Fig. 3 Schematic north-south cross section of the Neumark-Nord 2 basin and its infill including the stratigraphic position of the archaeological find horizon NN2/2. The box inset refers to the main profile HP7 section. Vertical axis: height in meters above sea level. Horizontal axis: position of the NN2 basin in the excavation grid (in meters).

homogenous almost unstratified infill. In contrast, at the more gently sloping northern part sediments are partly fine laminated and fine sandy layers on the northern margin develop continuously into finer silty deposits towards the centre. The aim of the various multidisciplinary studies was a profile section near the centre of the basin, with the complete succession of the basin infill (main profile 7 = Hauptprofil 7 = HP7) (**fig. 3**) (Strahl et al. 2011; Hesse/Kindler 2014). Eemian archaeological deposits were exclusively restricted to the areas north of HP7. Excavations in these areas were connected by an additional trench to HP7. This provided the opportunity to place the archaeological deposits within the stratigraphy at the basin centre and the Eemian pollen succession. (Sier et al. 2011; Strahl et al. 2011; Bakels 2014; Hesse/Kindler 2014; Pop/Bakels 2015).

NN2 is separated from NN1 by a lignite diapir, that swelled on the western extensions of basin NN2 (Thomae 2003; Thomae/Rappsilber 2010; Wansa/Strahl/Rappsilber 2014). Although NN1 was a large lake and NN2 only a small pond, the infill of basin NN1 is much thicker, but their sedimentology and palynology are highly comparable (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). Both basins developed on a Saalian till. The lowermost layers belong to the Saalian Pleni- and Late Glacial. The infill of NN2 consists of clastic lake silt sediments, at NN1 various types of gyttjas were originally described (Mania 2010a; Mania et al. 1990; 2010a; 2010b; Mania/Thomae/Altermann 2010), but only in the upper part of the sequence, as well as at NN2, the proportion of organic detritus is significantly high (Wansa/Strahl/Rappsilber 2014). The water table in both basins was fluctuating, with several transgressions and regressions (Mania/Mai 2010; Mania/Thomae/Altermann 2010; Mücher 2014; Pop/Bakels 2015; Pop et al. 2015). Thus, different sandy margin deposits with archaeological layers were buried. For the correlation of the NN1 and NN2 deposits (Wansa/Strahl/Rappsilber 2014) Jaqueline Strahl refers in her pollen analyses to a regional standard classification for Eastern Germany for the late Saalian (Strahl/Hermsdorf 2008) and the Eemian (Erd 1973). In the pollen profile established by Corrie Bakels the terminology of Menke and Tynni (1984) was used (e.g. Sier et al. 2011; Bakels 2014; Pop/Bakels 2015). Both pollen profiles at NN2 and the conclusions drawn from them are in good agreement with each other. Only the location of boundaries between certain pollen stages at NN2 may differ. Based on the palynological synchronisation the archaeological and faunal record at NN1 and NN2 can be linked and Neanderthal occupations in the lake landscape of Neumark-Nord can be attributed to different pollen zones (**fig. 4**).

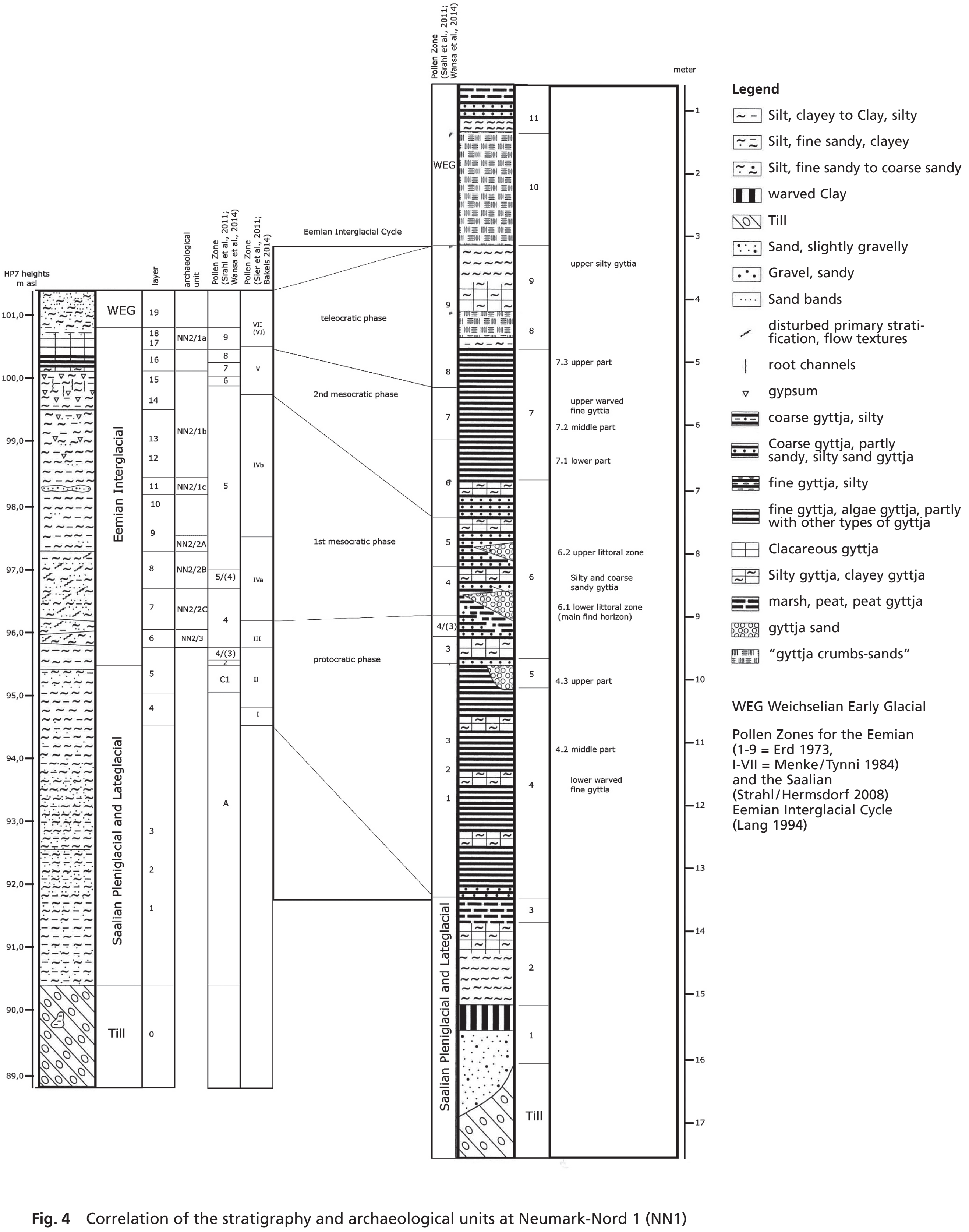

Fig. 4 Correlation of the stratigraphy and archaeological units at Neumark-Nord 1 (NN1) and Neumark-Nord 2 (NN2) based on the palynological sequences in both basins (according to Sier et al. 2011; Strahl et al. 2011; Bakels 2014; Hesse/Kindler 2014; Wansa/Strahl/Rappsilber 2014; Gaudzinski-Windheuser et al. 2018). The record of the individual archaeological units and their chrono-stratigraphic relations are discussed in the text.

The archaeological and faunal record from NN1 and NN2

Investigation and excavation at NN1 and NN2 followed completely different schedules. NN2 was investigated after reclamation works in the lignite mine, extensive and thorough year-round excavation of the northern part of the basin was possible. At NN1 during active mining the constant cutting of bucket-wheel excavators opened large surfaces but only for short periods of time, permitting only rescue excavations and the collection of uncovered complete and partially compete skeletons. An overview of excavation areas, the location of skeletons within basin NN1, and results of faunal analyses at major archaeological littoral zones at NN1 (layers 6.1 and 6.2) and NN2 (NN2/2B) are given in **figure 5**. The fauna from NN2 and NN1 represents the typical Eemian-fauna. Ungulate species include: straight-tusked European forest elephant (*Palaeloxodon antiquus*), three species of rhinoceros (*Stephanorhinus kirchbergensis, Stephanorinus hemitoechus* and *Coelodonta antiquitatis*), wild boar (*Sus scrofa*), horse (*Equus* sp.), aurochs (*Bos primigenius*), potentially steppe bison (*Bison priscus*) (identified by a horn fragment from NN1), potentially elk (*Alces* sp.) (identified by a complete distal metapodial from NN2/2), giant deer (*Megaloceros giganteus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama geiselana*) and roe deer (*Capreolus capreolus*). Car-

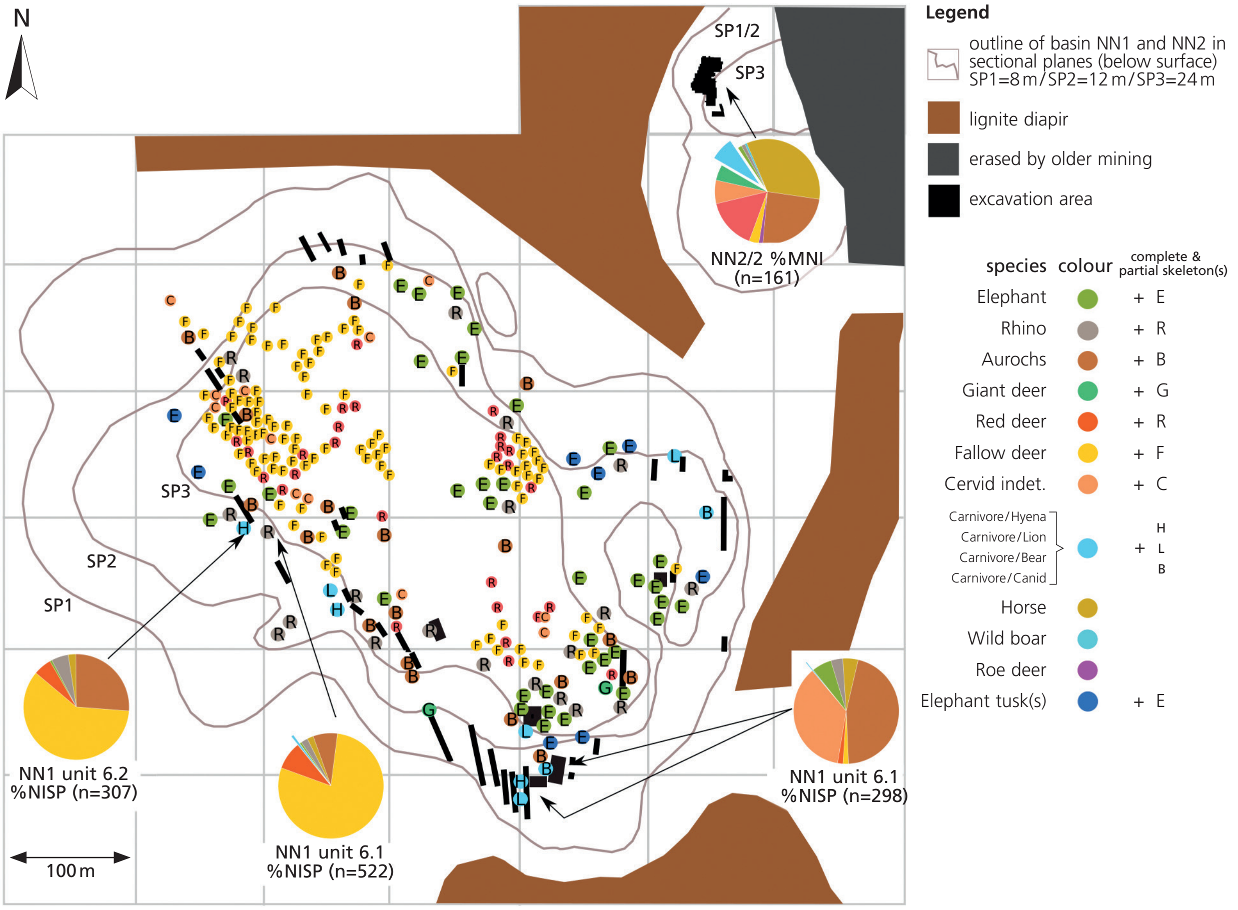

Fig. 5 Topographic map of the large lake basin Neumark-Nord 1 (NN1) in the center and the small "pool" Neumark-Nord 2 (NN2) in the upper right corner, with spatial distribution of (partial) mammal skeletons in basin NN1 (colored dots) and archaeological excavation areas (black rectangles). The pie charts indicate species distribution in selected excavation areas, at NN2 for the main find horizon NN2/2B (expressed as %MNI = minimum number of individuals), at NN1 for the lower littoral zone (unit 6.1) and upper littoral zone (unit 6.2) (expressed as %NISP = number of identified specimens per taxon). – (The synopsis is based principally on figures and data presented in Mania et al. 2010a; Meller 2010.).

Tab. 2 Estimated MNI of carnivores and ungulates in the different archaeological units in basin Neumark Nord 1 (NN1) and Neumark-Nord N2 (NN2) (Sources: Mania et al. 2010a; Meller 2010; own data) (Pollen zones see table 1.)

Basin	NN1											NN2					
Archaeological Unit	unstratified	**4.2** middle part lower warved fine gyttja	**4.3** upper part lower warved fine gyttja	**6** silty and coarse sandy gyttja	**6.1** lower littoral zone (main find horizon)	**6.2** upper littoral zone	**7.1** lower part upper warved fine gyttja	**7.2** lower to middle part upper fine warved gyttja	**7.3** upper part upper fine warved gyttja	**9** upper silty gyttja		NN2/3	NN2/2B	NN2/1c	NN2/1b	NN2/1a	
Pollen Zone	indet	1,2,3	1,2,3	(3),4,(5)	4	5	6	7	8	9		3	4	5	5 (6)	8,9	
Bones present	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	sum	yes	yes	yes	yes	yes	sum
Taxon/MNI																	0
Lion				1	2						3		1				1
large Felid											0		1				1
Hyena					1	1					2			1			1
Bear					1						1		8				8
Wolf					1						1		1				1
Fox	1										1		1				1
											0						0
Elephant		1	3	9	52		4	3			72		2	1			3
Rhino				2	9	2					13		2				2
Wild boar											0		1				1
Horse					>3						3	1	56	2			59
large Bovid				2	8	1	2			1	14		40	2			42
Cervid (*Capreolus* size)											0		2				2
Cervid (*Capreolus-Dama* size)											0		3				3
Cervid (*Dama* size)	26		1	26	>3		94	2	2		154		5	2			7
Cervid (*Dama-Cervus* size)	5						8				13		9	1			10
Cervid (*Cervus* size)	9		2	6	>3		24		1	1	46		26	2			28
Cervid (*Cervid-Alces-Megaloceros* size)											0	1	3				4
Cervid (*Alces-Megaloceros* size)					1	1					2		5				5
Sum	**41**	**1**	**6**	**46**	**84**	**5**	**132**	**5**	**3**	**2**	**325**	**2**	**166**	**11**	**0**	**0**	**179**

nivore species include: lion (*Panthera leo spelaea*), hyena (*Crocuta crocuta spelaea*), cave bear (*Ursus spelaeus*), brown bear (*Ursus arctos*), wolf (*Canis lupus*) and fox (*Vulpes Vulpes*). An estimation of the Minimal Number of Individuals (MNI) during each Eemian Pollen phase based on our analyses and data reported in Meller (2010) and Mania et al. (2010a) is presented in **table 2**. The diversity of species present at Neumark-Nord, especially during the *Corylus*-phase of the Eemian, may reflect high primary production and high degrees of resource partitioning (Fritz/Duncan 1994; Britton et al. 2012; 2014).

From the Saalian sequence at NN1 no remains of larger mammals are reported, also at NN2 no larger mammal bones were recovered from Saalian deposits. The transition from the Saalian to the Eemian at NN2 is only sparsely attested by sediments according to Strahl (Strahl et al. 2011). In contrast, Bakels (2014) has described a thicker and finer subdivision for the protocratic phase, probably by incorporating additional samples from a section (HP10) 8 m away from HP7. Here, a sandy littoral zone was deposited near the centre of the basin (layer 6) and an area of 4 m² was excavated (NN2/3), yielding 71 lithic artefacts and 170 bones, belonging to at least one horse and one large cervid, a robust red deer or larger sized species. The beginning of the Eemian at NN1 is located in the lowermost parts of the lower varved fine gyttja (layer 4). In the middle and upper part of this gyttja remains of at least four forest elephants, one fallow deer and two red deer were uncovered. At the end of the protocratic phase of the Eemian (Pollen Zone 3) fluvial sandy deposits (layer 5) cut into the lower varved gyttja (Mania/Thomae/Altermann 2010) at NN1. There is also evidence for changes in the flow regime from malaocological evidence (Strahl et al. 2011).

The transition to the first part of the mesocratic stage (Pollen Zone 4) is documented at NN2 in the top of lake silts of layer 5 according to Strahl (Strahl et al. 2011), or in layer 7 by Bakels (2014) and at NN1 on the bottom of the silty and coarse sandy gyttja (layer 6). From the lake deposits at NN1 attributed to Pollen Zone 4 complete and partially preserved skeletons of 46 mammals were found, 26 fallow deer, 9 elephants, 6 red deer, and 2 aurochs and rhinos. Intersected in the gyttja is a first littoral deposit, spreading horizontally up to 150 m (layer 6.1, lower littoral zone). The lower littoral zone is the main archaeological horizon at NN1, where most of the archaeological excavations took place and most of lithic artefacts were found. Complete and partially complete skeletons are dominated by elephants, with an MNI (minimal number of individuals) of 52. Detailed zooarchaeological information from the faunal record is pending. NISP-data are available from two excavation sites, where bones of different sized cervids and aurochs dominate. Also, horse is attested, which is absent from the record of complete and partially complete skeletons at NN1. At NN2 the deposits of alternating sand and silts contain scattered lithics and bones (NN2/2C).

Habitat settings and preservation conditions hamper the detection of a clear-cut boundary between Pollen Zone 4 and 5 at NN2 (Strahl et al. 2011). Thus, in the lower 30 cm of layer 8 at HP7 a transitional phase between both Pollen Zones is placed and the upper parts are attributed to PZ 5. This result differs from Bakels (2014) interpretation of the NN2 pollen record, in which the boundary between Pollen Zone 4 and 5 is located higher in the profile. In the northern part of the basin, layer 8 contains the archaeological main find horizon NN2/2B (see **fig. 3**). Along the margin, layer 8 forms a 20 cm thick sandy deposit, which becomes complex and thicker downslope, with laminated substrata up to 1 m in depth. The upper part of this find horizon dissolves downslope towards the center of the basin. In the area of HP 7 the remaining sediments are disturbed and finger out, leaving a ca. 50 cm thick silt loam deposit with isolated sandy lenses. The archaeological record from NN2/2B comprises almost 20,000 lithic artefacts and tools (Pop 2014; Pop et al. 2018) as well as and more than 118,000 faunal remains. From detailed faunal analyses a MNI of 166 large mammals are calculated (Kindler et al. in prep.), mostly horses, aurochs and red deer. Archaeological material from the basal part of the subsequent layer 9, which could be reworked in a slightly upwards position, are attributed to archaeological unit NN2/2A.

Tab. 3 Overview of the position of different archaeological units at Neumark-Nord 1 (NN1) and Neumark-Nord 2 (NN2) in the Eemian Interglacial Cycle.

Interglacial Cycle (Lang 1994)	Forest phase	Archaeological Deposits		Duration (Müller 1974)
		NN1	NN2	
Phase D (teleocratic phase)	*Pinus* phase	NN1.9 (upper gyttja)	NN2/1a	~ 2,000 years
	Pinus-Picea-Abies phase	NN1.7 (upper gyttja		~ 2,000 years
Phase C (mesocratic phase, 2. part)	*Carpinus-Picea* phase	NN1.7 (upper gyttja)		~ 4,000 years
	Carpinus phase		NN2/1b NN2/1c	
Phase B (mesocratic phase, 1. part)	*Corylus-Taxus-Tilia* phase	NN1.6.2 (upper littoral)		~ 1,200 years
	Quercetum mixtum-*Corylus* phase	NN1.6.1 (upper littoral)	NN2/2B	~ 1,200 years
Phase A (protocratic phase)	*Pinus-Quercetum mixtum* phase	NN1.4 (lower gyttja)	NN2/3	~ 450 years
	Pinus-Betula phase			~ 200 years
	Pinus phase			~ 100 years

In the stratigraphy of HP7 at NN2 Pollen Zone 5 extends through the sequence to Layer 14 (Bakels 2014; Strahl et al. 2014). An additional archaeological unit was excavated (NN2/1c). Apart from lithic artefacts 4,724 highly fragmented, intensively weathered and abraded bones were uncovered. At least a part of the assemblage might consist of material reworked from earlier find scatters. From the few larger bones which could be determined to species during excavation a MNI of 8 larger mammals can be estimated. Anthropogenic marks on the bone surfaces are present. Additional small-scale excavations in the area of HP7 above NN2/1c, yielded bone fragments and lithic artefacts summarized as NN2/1b. In sum 752 mostly fragmented bones and teeth are scattered through the sequence of archaeological unit NN2/1b.

Pollen Zone 5 in basin NN1 comprises the middle part of the silty and coarse sandy gyttja (layer 6). Here, a second littoral deposit is intersected (upper littoral zone, layer 6.2.). One rhino skeleton associated with lithic artefacts and a partially destroyed skeleton of a large bovid were found here. Additional bones belong to a second rhino, a giant deer and hyena. From an excavation in the southwestern part of the upper littoral zone 309 bone specimens are reported, with 60 % of the NISP belonging to fallow deer (see **fig. 5**).

The second part of the mesocratic phase (Pollen Zones 6 and 7) is documented in thick deposits at NN1, beginning in the upper part of layer 6 and covering most parts of the following upper fine varved gyttja (layer 7). In HP7 at NN2, both Pollen Zones are much thinner and the deposits are characterized by a transition from clastic lake silts to more organic sediments. Bones and lithics from the uppermost parts of archaeological unit NN2/1b may belong to PZ6. At NN1 the lower part of layer 7 has yielded the most impressive record of complete and partially complete skeletons. Cervids are dominating with more than 100 individuals, mostly fallow deer, compared to only 4 elephants and 2 large bovids. In the middle part of layer 7, attributed to PZ7, additional skeletons of 3 elephants and 2 partial preserved cervids were unearthed.

The teleocratic phase characterising the end of the Eemian (Pollen Zones 8 and 9) begins at NN2 after the deposition of organic material (Bakels 2014), while Strahl detected the boundary within the organic layer (Strahl et al. 2011). Four lithic artefacts and a few bone fragments can be attributed to Pollen Zone 9 and are summarised as archaeological unit 2/1a. At NN1, PZ8 and 9 again cover thick sediment deposits. Two (partial) skeletons of fallow deer and one of red deer belong to PZ8. A destroyed skeleton of a red deer, a skull and other remains of an aurochs were found in the uppermost Eemian deposits in PZ9.

In summary, there is ample archaeological evidence for Neanderthal presence in the lakeland of Neumark-Nord as shown by lithic artefacts from different layers and Pollen phases during the Eemian interglacial cycle at NN1 and NN2 (**tab. 3**). Combining the current faunal records from NN1 and NN2, different compositions of the ungulate thanatocoenoses for the main phases of the Eemian interglacial cycle are evident (**fig. 6**). The highest diversity in ungulate taxa is recorded during the first mesocratic phase during which the main archaeological units at NN1 and NN2 accumulated. In addition, a larger carnivore assemblage is preserved only during the first mesocratic phase (**fig. 7**). To assess the characteristics and "quality" of these thanatocoenoses, to establish a finer temporal sequence, and to derive information on Neanderthal occupations at Neumark during the Eemian, the environmental settings and specific locations within the basins in which the different faunal assemblages were deposited are essential.

Establishing a palyno-stratigraphic sequence of thanatocoenoses at NN1 and NN2

Lake NN1 and the pond NN2 are characterized by fluctuating water tables during the Eemian. These regressions and transgressions formed and preserved littoral zones within the basins. Due to the close proximity of the basins, identical environmental conditions during sedimentation can be expected. However, due to their different morphologies and their specific depositional background, changes in the water table were not inevitably synchronous. In terms of different hydrological situations, the elevation of both basins also has to be considered.

NN2 and also NN1 originate presumably from kettle holes (Wansa/Strahl/Rappsilber 2014). The melting ice activated the diapiris of the lignite in the underground flanking the basins. Basin NN1 is much deeper, the elevation of the Saalian till at the base of both basins is not less than about 4 m higher in NN2. In addition, late Saalian deposits at NN2 are about 1.5 m thicker than in NN1 (Wansa/Strahl/Rappsilber 2014). At the beginning of the Eemian we have to assume that basin NN1 was located about 5 m deeper in the landscape than NN2. Not surprisingly, the interglacial deposits are much thicker at NN1 and the final infilling of the basin occurred earlier at NN2, considering the comparably thin deposits during PZ6-9 at NN2.

Due to its size and elevation the catchment area of water must have been much larger in the lake NN1. If the basins were influenced by changing ground water tables, NN2 should have been more prone to drying out than NN1. Also seepage water from the higher elevated NN2 could have drained down to NN1. In addition, there is a zone of low elevation between the diapirs separating NN1 and NN2 (see **fig. 5**). Here, the outermost extensions of NN2 were truncated during mining and subsequent reclamation works (Thomae/Rappsilber 2010; Wansa/Strahl/Rappsilber 2014). At least intermittent connections of both basins via this breach can't be excluded.

Transgressions and regressions in basin NN1 and NN2 had a major influence on the preservation of the archaeological and faunal records. Their origin, composition and genesis must be linked to specific lake phases. Neanderthal activities should principally be attributed to dry areas within the basins, while subsequent submergence preserved the archaeological record of these activities. Four characteristics of major find contexts throughout the stratigraphy of the basins can be summarized: (1) In littoral zones, associations of lithics and highly fragmented bones are distributed over comparable larger areas. (2) In littoral zones, disarticulated bones from single individuals, partially associated with lithics are also distributed over small areas. (3) Articulated skeletons, partially preserved skeletons of single individuals, and skeletal remains from multiple individuals are found in gyttja deposits at NN1. Articulated cervid skeletons undisturbed by rotary excavators typically display overflexion of head and neck, convex bending of the thorax and parallel leg posture. (4) Finally, bones and lithics are scattered

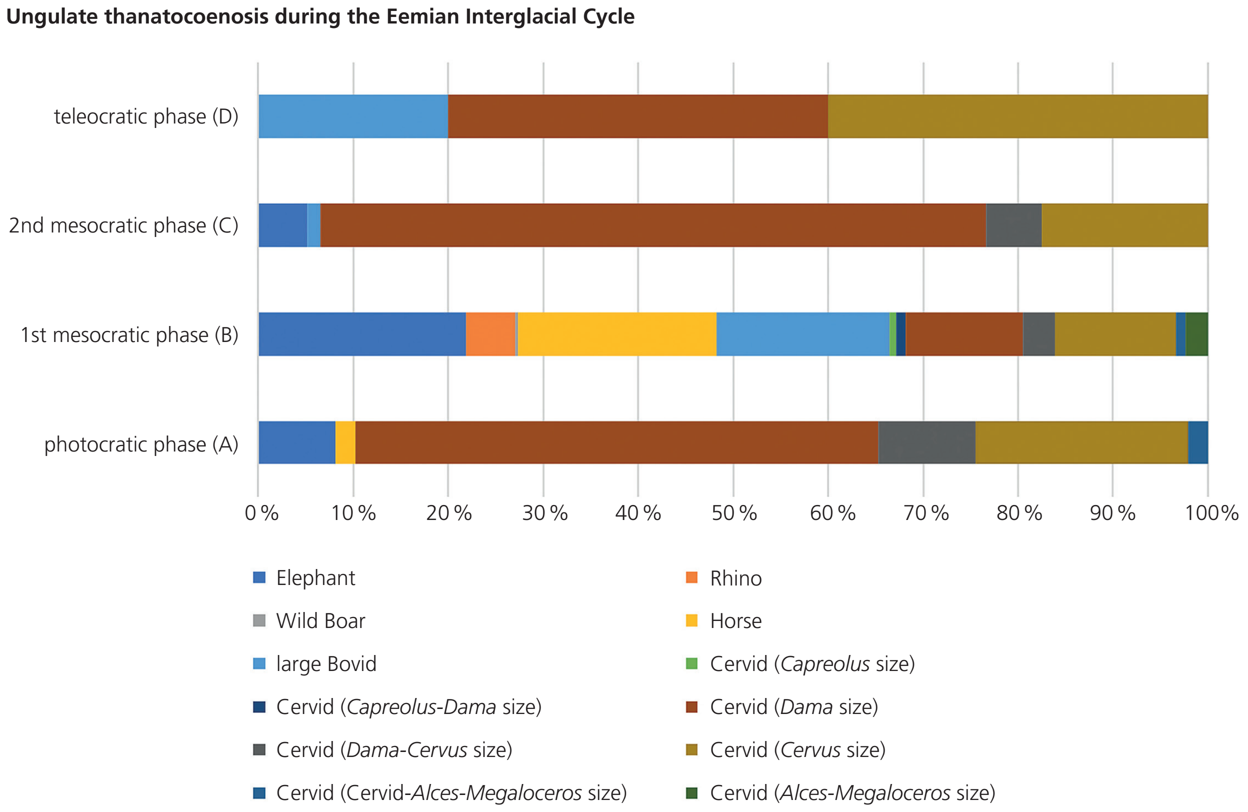

Fig. 6 Composition of the ungulate thanatocoenoses (based on estimates of MNI = minimum number of individuals) in the Neumark lakeland during the Eemian Interglacial Cycle.

in comparatively low numbers through the Eemian sequence.

At the transition to the Eemian protocratic phase, marshland developed in the NN1 basin. The faunal record at Neumark-Nord starts in PZ3 with the thanatocoenosis comprising the few individuals from layer 4 at NN1 during a first Eemian lake phase (Mania 2010a). The fauna is deposited in the gyttja within the basin or near the margins of the former lake. Lithic artefacts are not reported from these deposits. The regression during PZ3 dried out the basin completely. Even so, fluvial sediments accumulated (layer 5) during PZ 3 and subsequently transgression of a second lake phase began (base of layer 6). At NN2 in similar stratigraphic position fluvial depositions are supposed (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). According to Strahl (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014) the early phases of the Eemian in NN2 are represented in thin horizons with evidence of hiatuses. In contrast, Bakels (2014) has described a thicker and finer subdivision for the protocratic phase beginning with marshland development and a first sandy find horizon (find layer NN2/3) close to the center of the basin. For NN2/3 deposition during transgression is reconstructed (Pop/Bakels 2015). In Bakels palynostratigraphy, NN2/3 is attributed to PZ3. Thus, the first sandy littoral horizon at NN2 could correspond to the second lake phase at NN1, with maximum expansion of the water body in NN1.

At NN1, the second Eemian lake phase continues into the first part of the mesocratic phase (PZ4). During a major regression the lower littoral zone and major archaeological horizon (layer 6.1) formed around a waterbody in the centre of the basin. The last occurrence of terrestrial molluscs is recorded (Strahl et al. 2011) in the lower part of the stratigraphy in HP7 at NN2 and above NN2/3. The deposits are characterized by disturbance within the sediments (Wansa/Strahl/Rappsilber 2014; Mücher

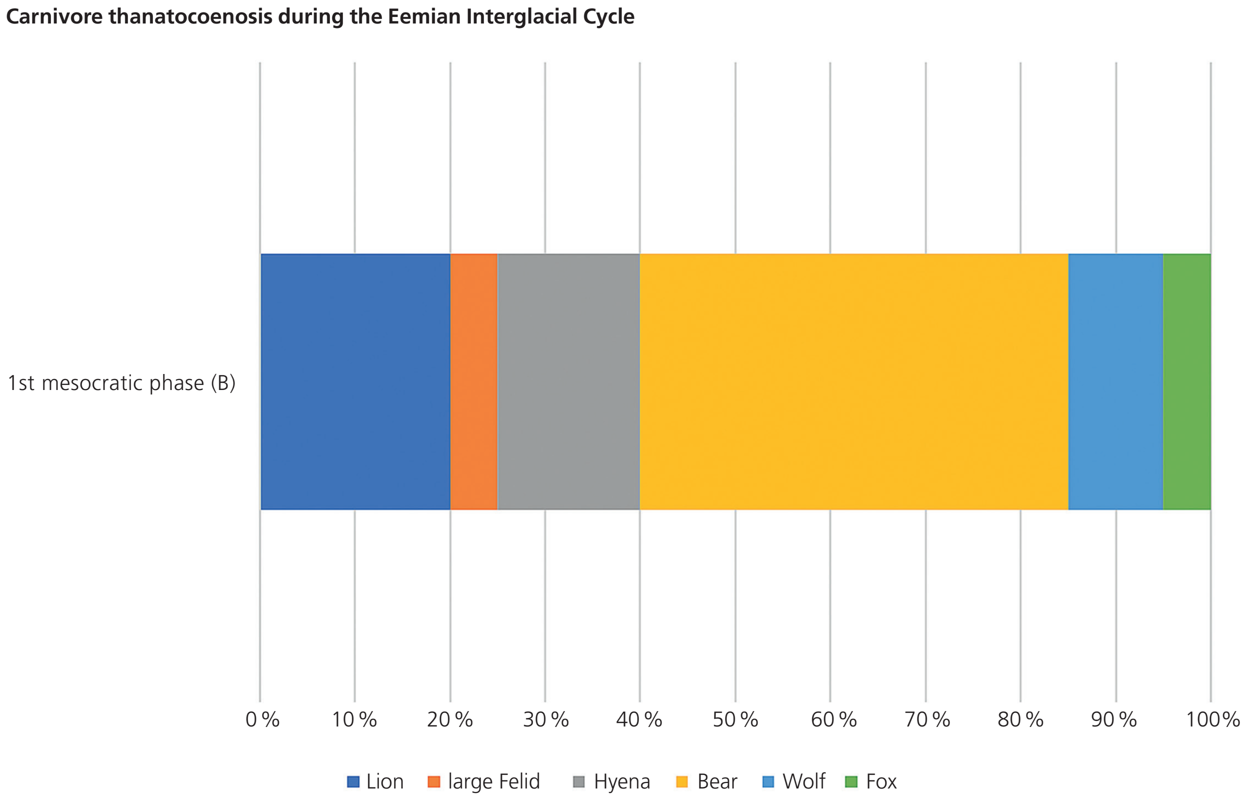

Fig. 7 Composition of the carnivore thanatocoenosis (based on estimates of MNI = minimum number of individuals) in the Neumark lakeland during the first mesocratic phase of the Eemian Interglacial Cycle.

2014) and alternations of transgressing and regressing water (Pop/Bakels 2015). At the top of these deposits the basin had dried out completely (Mücher 2014). Thus, within layer 7 in NN2 an equivalent to the lower littoral zone of NN1 could be deposited. During the subsequent transgression at NN1, the third Eemian lake phase, the water body reached maximum expansion, once again. Higher up in the stratigraphical succession at NN2 transgression is also reconstructed for the archaeological main find horizon NN2/2B (Wansa/Strahl/Rappsilber 2014; Pop/Bakels 2015). In Bakels (2014) pollen zoning NN2/2B still belongs to PZ4, but according to Strahl's reading of the pollen profile (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014) the transition to PZ5 is already present in the lower part of NN2/2B.

Pollen Zone 5 is represented in thick sediment deposits at NN2 in Strahl's pollen zoning as well as in Bakels'. In the lower parts of PZ5 there is a steady and continuous sedimentation of finer grain sizes and the disappearance of the disturbances within the sediments are related to higher water tables than those reconstructed in the lower parts of the stratigraphy (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). Starting in layer 10 there is recurrent evidence of desiccation of the basin NN2 and pedogenesis occurs (Bakels 2014; Mücher 2014; Wansa/Strahl/Rappsilber 2014). At NN1, during PZ5, another major regression reduced the level of the lake and the upper littoral zone (6.2) formed around the water body at the centre of the basin. Thus, the sandy find horizon NN2/1c, scattered finds from archaeological unit NN2/1b at NN2 as well as the finds from the upper littoral zone from NN1 could have been deposited in temporal proximity (Wansa/Strahl/Rappsilber 2014).

The second part of the mesocratic phase and the teleocratic phase is compressed at NN2 but comprises thicker deposits at NN1. At the beginning of this phase a change to more organic components within the sediments is recorded in both basins. Basin NN2 seems to be filled up to its greatest extent, with evidence of extreme shallow water and development of marshland. Extreme shallow waters and eutrophication is reconstructed at NN1 for layer 7 (PZ6, 7, and 8). The lake spreads again to its maximum expansion. The largest accumulation of cervid skeletons is from PZ6. During the second half of the Eemian no littoral zones have been formed and preserved within the basins. According to Bakels, PZ 6 begins slightly lower down in the profile of HP7 at NN2, in contrast to Strahl's observations. Thus, isolated finds from the uppermost part of NN2/1b may already belong to PZ6. Finally, archaeological unit NN2/1a covers the teleocratic phase at the end of the Eemian.

Discussing Neanderthal occupations at NN1 and NN2

In the deeper parts of the Eemian deposits, the lake at NN1 reached maximum expansion during the protocratic phase. Within the lake almost intact skeletons of four elephants, one fallow deer and two red deer were uncovered. At NN2 a first lake transgression followed a phase of marshland in the basin. Near the centre of the basin, remnants of a littoral zone were excavated. The 4 m² site yielded artefacts and cut marked bones of at least one horse and one very large cervid, either a large male red deer, a giant deer or an elk.

The first part of the mesocratic phase is characterized by alternating more open and more closed environments. In addition, several regressions and transgressions were filling up the basins and also almost drying them out occasionally. Due to these changes, littoral horizons in both basins formed and persevered, like the lower littoral zone (6.1) and the upper littoral zone (6.2) at NN1 and NN2/2B in basin NN2. At NN1, the skeleton remains from the littoral zones are mainly from elephant, rhino and aurochs. According to Mania (2010a) and Mania et al. (2010a) at least one aurochs and one rhino were butchered at the spot. In contrast, from the evidence inside the basin, fallow deer skeletons dominate. Analyses of the cervids show that at least two of them show cut marks. At NN2, during this phase, the main archaeological unit NN2/2B formed. The fauna is purely anthropogenic in origin without any significant involvement of other biotic agents. The carnivore bones present in the accumulation also show butchery marks. Our analyses have demonstrated that Neanderthals were active here during all four seasons (Kindler et al. in prep.). The MNI of all taxa in the death assemblage is 166, amongst them 56 horses, 40 aurochs and 53 individuals of different sized cervid taxa (Kindler et al. in prep.). Although we lack substantial faunal data from the excavation areas at NN1, the NISP composition at three sites in the upper and lower littoral zones also indicates high numbers of horses, aurochs and cervids, in the size range of red deer and fallow deer (see **fig. 5**). For the two littoral zones at NN1 more open vegetation is reconstructed, for NN2/2B more closed vegetation (Mania et al. 2010a; 2010b; Pop/Bakels 2015). Thus from palyno-stratigraphical comparisons, the littoral zones at NN1 and NN2 are most likely not contemporaneous and they formed during several relatively short time intervals of a few hundred years during the mesocratic phase (Mania et al. 2010a; 2010b; Sier et al. 2011; Kindler/Smith/Wagner 2014; Wansa/Strahl/Rappsilber 2014). Higher in the profile at NN2, is a smaller and less well preserved lithic and faunal assemblage, with anthropogenic modifications, NN2/1c, whose genesis hasn't been fully assessed yet. But after the formation of NN2/1c the basin was almost filled and had a tendency to dry out completely. Artefacts and bones still occur sporadically in these deposits and are assigned to NN2/1b. The uppermost level of NN2/1b reaches into the second part of the mesocratic phase, also often referred to as the Eemian maximum, characterised by the spread of the most thermophilus plant species. From here to the end of the teleocratic phase at NN2 the sediments are compressed, marshland developed and finally a last shallow water pool. During profile trenching tiny splinters of bone and four artefacts were found in deposits dating to the teleocratic phase, labelled NN2/1a. Extreme shallow waters and phases of eutrophication are reconstructed at NN1 for the second part of the mesocratic phase. The lake spreads again to maximum expansion. The largest accumulation of cervid skeletons, 128 individuals, were deposited in a fine varved gyttja within the lake during the second mesocratic stage. Eight of these skeletons show cut marks and two individuals display hunting lesions (Gaudzinski-Windheuser et al. 2018). The final deposition of elephant skeletons occurs during this phase, in the succeeding teleocratic phase only one bovid and four cervid skeletons were deposited.

Neanderthal presence in the Neumark lakeland is attested by lithic artefacts and anthropogenic bone modifications for all four phases of the interglacial cycle and during phases of more open and more closed environments. However, the characteristics, quantities and "qualities" of lithic and faunal assemblages at NN1 and NN2 vary tremendously. These differences can be linked to spatial and temporal changes in sedimentation, dependent on environment, topography and basin morphologies. The littoral horizons at NN1 and NN2 were deposited during relatively short periods of time with high sedimentation rates (Sier et al. 2011; Wansa/Strahl/Rappsilber 2014) within the basins. Analyses of orientation of lithics and bones at NN2/2B revealed deposition with low-energy and no significant re-distribution of finds by hydrodynamic flows (Pop et al. 2015; García-Moreno et al. 2016). At NN1 the presence of complete skeletons and the distribution of skeletal parts from single individuals over small areas also indicate, that dislocation of finds during or after deposition played a minor role here. The same accounts for complete and partially complete skeletons deposited in the inner part of the lake NN1. High sedimentation rates, but low energy flows allowed the preservation of these unique thanatocoenoses and archaeological units, that reflect occupation and activities of Neanderthals in dry areas inside the depressions of the basins. In contrast, when the basins were completely filled with water or covered by marshland, Neanderthals were forced to operate outside the basins in the Neumark lakeland. The erosional deposits forming the infill of NN1 and NN2 derive from these areas. Sporadic finds of lithics and/or modified bones scattered in the basins infills – especially during the second part of the mesocratic and teleocratic phases – indicate Neanderthal presence in the lakeland, but the evidence doesn't provide any spatial and temporal resolution for littoral deposits.

The preservation of complete and partially complete skeletons from gyttja deposits inside basin NN1 is still puzzling. An interpretation of this unique faunal record based on a comprehensive taphonomical and zooarchaeological analyses is still missing. Most of the specimens belong to fallow deer (*Dama dama geiselana*). For the origin of this *Dama*-record different scenarios were postulated. In the "hunting accidents" scenario the cervids were driven into the lake basin and died there (Mania et al. 1990). In the "natural die off" scenario, an accumulation over several thousands of years was reconstructed culminating in an assemblage which should represent a mix of different natural and anthropic processes (Mania 2010b; Mania et al. 2010b). The "poison scenario" builds on the evidence of cyanobacteria present in NN1 sediments. Animals in the Neumark lakeland, especially young fallow and red deer bulls during the rut, died by poisonous water caused by the cyanobacteria (Pfeiffer 1999; Braun/Pfeifer 2002; Pfeiffer-Demel 2010a; 2010b). This scenario appears attractive at first glance, since it exerts particular events for the origin of a unique thanatocoenosis. Deadly cocktails produced by cyanobacteria can kill a substantial amount of animals in short amounts of time (de Boer et al. 2015; Bengis et al. 2016). However, there is additional evidence challenging the "poison scenario" at Neumark. Pfeiffer-Demel (2010a) thinks that the cervids died soon after drinking at the shore line. With rising water tables the bloated cadavers drifted in the lake, sank to the bottom and became deposited there. This process must occur within days during early stages of decomposition. In contrast, the posture of undisturbed skeletons is typical for desiccation during decomposition (Mania et al. 1990). The occasional presence of cut marks, rodent gnawing and root etching on bones of some cervid skeletons also indicates decomposition and subsequent deposition of the carcasses on dry land and not in water (Gaudzinski-Windheuser 2010; Gaudzinski-Windheuser et al. 2014). In addition, the liability to drink high amounts of polluted water varies between different mammal species. Cyanobacterial blooms usually become deadly cocktails, when wind drift accumulates high amounts of these bacteria at the shores of a waterbody. In a recent study of mortality due to repetitive cyanobacterial blooms in South Africa, it was mainly zebra, wildebeest and white rhino, that died (Bengis et al. 2016). Amongst the Eemian larger ungulates at Neumark, both horse and aurochs need substantial amounts of fresh water, while cervids can meet their water requirements from water stored in the plants they consume. However, remains of horses didn't contribute to the skeleton thanatocoenosis at all and remains of aurochs appear in comparable low numbers. Frequent are elephants in the Neumark thanatocoenosis, while in the recent South African study not a single elephant was poisoned. Elephants wade deeper into water bodies to drink and therefore don't consume the cyanobacteria floating at the shores (Bengis et al. 2016). Thus, it becomes complicated to incorporate the cervid taphonomical data into the structure of the skeleton thanatocoenosis in the "poison scenario". But also for the "hunting scenario" and "natural die-off scenario" we still lack supporting zooarchaeological and taphonomical data for coherent contextualisations. Hunting lesions recently detected on a cervical vertebra and a pelvis of two fallow deers clearly demonstrate close range hunting of these individuals during the 2nd mesocratic phase (layer 7) (Gaudzinski-Windheuser et al. 2018). However, data on cut marks from the thanatocoenosis show that the carcasses were only marginally exploited. Given that the cadavers were decomposing and depositing on dry land it is also surprising that evidence of carnivore involvement and scavenging is almost non-existent. Although Neanderthal involvement becomes more and more visible, the exact origin(s) and processes shaping the skeleton thanatocoenosis at NN1 still remain enigmatic. Work on the thanatocoenoses of the skeleton is still in progress and it will take some more time to analyse the material of other taxa present at NN1.

Nevertheless, the NN1 and NN2 evidence provides a uniquely large and clear window into the faunal community of the lakeland about 125,000 years ago, as well as the activities of Neanderthals in an early last Interglacial setting, including anthropogenic fires (Roebroeks/Bakels 2015; Pop et al. 2016). In the current state of research at Neumark and referring to the record of NN2/2B, the high-resolution palaeoenvironmental data, the rich and generally well-preserved fauna heavily exploited by humans, and the virtual absence of carnivore marks suggest a Neanderthal "permanence" or at least "dominance" in the Neumark-Nord lakeland, and the distinct possibility to document spatial variability in faunal exploitation over a large area. This variability is well attested when comparing the number of individuals encountered at NN1 and NN2/2B. Horse, aurochs and red deer dominate in the assemblage of NN2/2B, while at NN1 it is elephant and fallow deer. This may point to specific prey preference, even when assuming that Neanderthals are responsible for the thanatocoenosis from NN1, they took little benefit from their efforts and left the carcasses and remains almost untouched.

Crucial for an assessment of subsistence strategies are the opportunities an ecosystem or biotope offers, i. e. community structure, prey abundance and distribution. Reconstructions of these variables from death assemblages are challenging due to biases by taphonomic processes and other factors, such as differences in mortality rates in individual taxa and temporal resolution (e. g. Behrensmeyer/Western/Boaz 1979; Behrensmeyer/Dechant Boaz 1980; Western 1980; Lyman 1994; 2008; Kidwell/Rothfus 2010; Kidwell/Tomasovych 2013). As an additional frame of reference to discuss subsistence opportunities the carrying capacity (CC) for the Eemian in the Neumark lakeland and the biomass deposited in the thanatocoenosis are calculated.

Deducing subsistence opportunities in the Neumark lakeland from ungulate carrying capacity and biomass

From an ecological perspective human subsistence must meet the energetic and dietary demands of individuals. Based on isotopic studies, Neanderthals are characterised as humans relying heavily on animal resources (e. g. Richards et al. 2008; Wissing et al. 2016; but see also Smith 2015), but regional variation in diet composition may have existed. Recent studies of ancient DNA present in dental calculus on Neanderthal teeth supports the notion of a meat-based diet for the higher latitudes of the Neanderthal range, while two individuals from Spain appeared to have had a quite vegetarian lifestyle (Weyrich et al. 2017). Prey abundance must have been a crucial variable in Neanderthal subsistence. Energy production and energy flow in ecology is in general expressed in weight (e. g. kg) or calories (e. g. kcal) in a certain area (e. g. km²). Deducing biomass and energy values from archaeofaunas can contribute to better understanding of Neanderthal subsistence and ecology. In a zooarchaeological perspective these calculations can be used as ancillary key figures, when comparing and interpreting minimal numbers of individuals (MNI) in faunal assemblages (see Lyman 2008).

For estimations of body weight the catalogue of data compiled by Smith et al. (2003) for late Quaternary mammals can be used. In addition, Thompson and Henshilwood (2014) have collected data on edible calorie values for different sized African ungulates. Combining their data for different species an approximately 600 kcal per kg ungulate body weight can be derived, which is used to transform the body weight of a species into its calorie content.

Prey abundance is controlled by primary production, which is influenced by a variety of factors like soil substrate, precipitation, temperature and insolation (Churkina / Running 1988; Nemani et al. 2003). Based on these variables a theoretical estimation of the carrying capacity, i. e. the maximum amount of biomass, for an ecosystem can be calculated. From a comparative data set of 95 recent faunal communities Rodriguez et al. (2014) developed an equation to calculate large herbivore biomass production expressed in kg / km² based on temperature and rainfall. Calculation of large herbivore biomass (Rodriguez et al. 2014) based on rainfall follows the equation:

$$\text{maxB}(P) = 18.3\ P - 3993 \qquad (1)$$

Calculation of large herbivore biomass based on temperature follows the equation:

$$\text{maxB}(T) = 1634\ \text{MAT} - 12502 \qquad (2)$$

where maxB(T) is maximum ungulate biomass as limited by mean annual temperature. The equation doesn't fit for mean annual temperatures below 8° C. Estimating large herbivore carrying capacity (CC) at a certain locality should be based on the minimum value obtained in both equations:

$$\text{CC} = \text{Min}\ (\text{maxB}(P);\ \text{max}(\text{BT})) \qquad (3)$$

For the Eemian on the North European Plain and in Central Europe estimations of temperature and precipitation are based on palaeobotanical data, including data from Neumark-Nord and / or data obtained in the larger region around Neumark-Nord (Zagwijn 1996; Aalbersberg / Litt 1998; Kaspar et al. 2005; Kühl et al. 2007). Results from climate simulation models for that region are in overall concordance with the botanical results (Kaspar / Cubasch 2006). For the first half of the Eemian the region of Neumark-Nord was influenced by (sub)continental conditions. Summer mean temperatures were higher, but winter mean temperatures lower than today. For the second half of the Eemian a change to (sub)oceanic conditions is reconstructed, with a lower amplitude between summer and winter temperatures, i. e. lower mean temperatures in summer and higher mean temperatures in winter. An increase in precipitation in both parts of the Eemian is reconstructed, for the first half above 600 mm and below 700 mm, for the second half probably above 700 mm.

The results of CC calculations for Neumark-Nord are given in **table 4** using the range of mean annual temperature and rainfall today and different values for reconstructed Eemian climate conditions in the region. The results suggest, that ungulate biomass during the Eemian was limited by mean annual temperature at Neumark-Nord. The number of herbivores in recent ecosystems is usually below the estimated CC. The same may account for Pleistocene ecosystems. However, CC values give an indication of the highest biomass values, which may serve as a very first reference to characterise and compare recent and past ecosystems. Comparing the recent and the past is always prone to faulty and misleading conclusions. In particular, past interglacials are in many ways different from our recent interglacial. On the other hand, in recent settings we can observe mechanisms shaping biocoenoses, in past settings we observe mechanisms shaping thanatocoenoses, which usually reflect a biased extract of the living community. Nevertheless, death assemblages originate from processes operating in biocoenoses. Especially, when reconstructing human subsistence from death assemblages reference to past biocoenoses is needed. Thus, and at best, observations in both settings should complement each other and broaden perspectives.

Given a wetter and warmer climate during the Eemian at Neumark-Nord, CC could have been considerably higher than today. The ungulate biomass could have been about three times higher compared to recent climatic conditions in the Neumark area (**tab. 4**). Thus, diversity of species and the high numbers of individuals in the Neumark thanatocoenoses can be linked to high ungulate biomass production. However, observed biomass usually oscillates below calculated CC, especially in forested environments, in which primary plant biomass production is vertically structured and thus limits food availability for ungulate species (Rodriguez et al. 2014).

For comparison, there is limited data on recent ungulate biomass production on the North European Plain, simply because native environments with free roaming ungulates are almost absent in Europe today. About 900 km east of Neumark-Nord one of the last refugia for European ungulates was established in 1932, the Biolawieza Primeval Forest (BPF). The park covers about 1,450 km^2 in eastern Poland and western Belarus today, but doesn't represent a virgin interglacial forest (Mitchell/Cole 1998). In BPF five ungulate species, European bison, elk, red deer, roe deer and wild boar can live undisturbed and coexist with their predators, wolf and lynx. Fallow deer was introduced to the Biolawieza forest in the 19th century, eradicated during the first world war and never re-introduced since then. At Bialowieza an almost complete, historical annual animal census from 1830 up to 1993 is documented (Jedrzejewska et al. 1997). In BPF ungulate biomass is controlled by temperature, the number of predators and the effects of changing political situations in the 20th century, which led to severe poaching and repression of wild game by increasing numbers of livestock in the forest. Highest mean annual temperature during that times was 8.5 degrees giving an estimated ungulate CC of 1,180 kg/km^2. The highest observed ungulate CC in the historical census, with more than 10,000 individuals of different species in the final year (1992/93), is 1,307 kg/km^2 and 7.4 individuals per km^2 using the compilation of body mass in late Quaternary mammals (Smith et al. 2003). This means more than 4 million calories per km^2 (600 kcal per 1 kg ungulate body weight) including almost 600 cattle individuals still roaming in the park (**tab. 5**).

These results suggest that calculated CCs in forested environments on the Northern European Plain can be reached, especially when acknowledging that at Bialowieza only an impoverished interglacial fauna has survived and domesticates still reduce the biomass of the wild game.

Tab. 4 Ungulate carrying capacity (kg/km^2) using the range of different temperature and precipitation estimates for the region of Neumark-Nord during the Eemian.

Temperature (°C) maxB(T)	CC	Precipitation (mm) maxB(P)	CC
9.1 (recent)	2,367		
10	3,838		
		453 (recent)	4,297
		500	5,157
11	5,472		
		550	6,072
		600	6,987
		700	7,902

The thanatocoenoses at Neumark-Nord reflect mortality in a lakeland during the course of the Eemian. Waterholes are essential for most larger mammals and should be considered as magnets for herbivores and their accompanying predators. Much hunting and killing occurs around waterholes. The role of surface water for the structure and dynamics of herbivore communities is addressed in recent studies in African settings from different ecological perspectives, including biomass production and its spatial distribution around and in the near vicinity of water holes, drinking behavior, competition and niche portioning, as well as hunting and predation (Western 1975; Valeix/Chamaillé-Jammes/Fritz 2007; Valeix et al. 2007; 2009a; 2009b; Crosmary et al. 2012; Hayward/Hayward 2012). From this perspective, the Neumark depositional environment, high biomass production and high numbers of individuals in a diverse herbivore fauna provide ideal references to inspect the structure of the Eemian herbivore community and potential Neanderthal subsistence and hunting behaviour in more detail.

For the ungulate species present in the Neumark thanatocoenoses weight estimations are based on data compiled by Smith et al. (2003) (**tab. 6**). Inferring a 600 kcal per 1 kg ungulate (Thompson/Henshilwood 2014) the calorie value for each taxon can be derived. Against the background of the overall larger size of ungulate species at Neumark compared to their Holocene counterparts (Döhle 2010; Palombo/Albayrak/Marano 2010; van der Made 2010), the values were slightly adjusted for some species, but the values are still based on conservative estimations. Because of high fragmentation of bones and size overlap between cervid species (Pfeiffer 1999), unambiguous taxonomic identification in the thanatocoenosis of NN2/2B is mostly impossible, so the cervids were subdivided into different body size and weight classes (Kindler et al. in prep.). The cervids and all other taxa are lumped in six size classes, from taxa less than 100 kg up to the size of elephants with 6,000 kg.

Species diversity and quantity of individuals is poor in the protocratic and teleocratic phase of the Eemian at Neumark. In the second mesocratic phase many individuals were deposited, but species diversity is limited (see **tab. 2** and **fig. 6**). In contrast, the record of the first mesocratic phase is rich in species and individuals and comprises different death assemblages, with different taphonomic histories. The records from the littoral zones at NN1 and NN2/2B, although most likely consecutive in their temporal formation, should permit a synthetical view on the community structure during the first 2,400 years of the mesocratic phase of the Eemian, because evident biases in the individual thanatocoenoses can be off set against and complement each other. The different death assemblages at NN1 and NN2 formed

Tab. 5 Weight (kg) and calorie (kcal) values for the Bialowieza ungulate population. Census data are taken from Jedrzejewska et al. (1997), body weight estimates are taken from Smith et al. (2003).

Bialowieza Primeval Forest/Bialowieza National Park (BNP), Poland/Belarus (size: 1,450 km²)					
Taxon	Census 1992/93	Weight (Individuum)	Weight (Population)	Kcal (Individuum)	Kcal (Population)
Wisent	554	500	277,000	300,000	569,400,000
Elk	200	355	71,000	213,000	155,490,000
Red deer	4,177	156	652,656	93,750	637,500,000
Roe deer	2,630	23	59,175	13,500	82,620,000
Wild boar	2,571	117	300,807	70,200	381,747,600
Dom. cattle	594	900	534,600	540,000	4,504,680,000
sum	**10,726**		**1,895,238**		**6,331,437,600**
per km²	**7.40**		**1,307**		**4,366,509**

Tab. 6 Body weights estimates for ungulate taxa from Neumark-Nord using data for late quaternary mammals as a reference (Smith et al. 2003).

Smith et al. 2003			Neumark-Nord (NN)	
Taxon	Species	Weight (kg)	Taxon	size class
Elephantidae	*M. imperator*	10,000		
Elephantidae	*M. columbi*	8,000		
Elephantidae		6,000	Elephant (*P. antiquus*)	size 7 (>2,500 kg)
Elephantidae	*M. primigenius*	5,500		
Elephantidae	*L. africana*	3,940		
Rhinocerotidae	*C. sinum*	2,949		
Elephantidae	*E. maximus*	2,720		
Rhinocerotidae	*S. kirchbergensis*	2,000	Rhino (*S. kirchbergensis, S. hemitoechus, C. antiquitatis*)	size 6 (<2,500 kg)
Rhinocerotidae	*R. sondiacus*	1,750		
Rhinocerotidae	*R. unicornis*	1,602		
Rhinocerotidae	*D. sumatrensis*	1,266		
Rhinocerotidae	*D. bicornis*	1,180		
Bovidae		1,000	large Bovid (*B. primigenius, B. priscus*)	size 5 (<1,000 kg)
Bovidae	*B. priscus*	900		
Bovidae	*B. taurus*	900		
Cervidae	*A. latifrons*	850		
Cervidae	*M. algericus*	800		
Cervidae		800	Cervid (*Alces-Megaloceros* size) (large specimens: *Alces* sp., *Megaloceros* sp.)	size 5 (<1,000 kg)
Bovidae	*B. bison*	579		
Bovidae	*B. bonasus*	500		
Cervidae		500	Cervid (*Cervus-Alces-Megaloceros* size) (very large specimens: *Cervus elaphus,* small specimens: *Alces* sp., *Megaloceros* sp.)	size 4 (<600 kg)
Equidae	*E. grevyi*	409		
Equidae	*E. quagga*	400	Horse (*Equus* sp.) Horse (*Equus* sp.)	size 4 (<600 kg)
Cervidae	*A. alces*	359		
Equidae	*E. zebra*	287		
Equidae	*E. burchelli*	276		
Equidae	*E. caballus*	250		
Cervidae	*C. elaphus*	218		
Cervidae		180	Cervid (*Cervus* size) (*C. elaphus*)	size 3 (<300 kg)
Cervidae	*C. elaphus*	167		
Cervidae	*C. elaphus*	157		
Cervidae	*C. elaphus*	120		
Suidae		120	Wild Boar (*S. scrofa*)	size 3 (<300 kg)
Suidae	*S. scrofa*	117		
Cervidae		100	Cervid (*Dama-Cervus* size) (small speciemens: *C. elaphus,* large specimens: *D. d. geiselana*)	size 2 (<100 kg)
Cervidae		80	Cervid (*Dama* size) (*D. d. geiselana*)	size 2 (<100 kg)
Cervidae	*D. dama*	56		
Cervidae	*D. dama*	49		
Cervidae		45	Cervid (*Capreolus-Dama* size) (small speciemens: *D. d. geiselana*, large specimens: *C. capreolus*)	size 2 (<100 kg)
Cervidae	*C. capreolus*	22.5	Cervid (*Capreolus* size) (*C. capreolus*)	size 2 (<100 kg)

Tab. 7 MNI for ungulate taxa at NN2/2, weight estimates (kg) and energy values (kcal).

Species	size class	MNI	Weight (Ind) kg	Weight (Pop) kg	kcal (Ind) × 10^6	kcal (Pop) × 10^6	kcal sum size class (Pop) × 10^6	species per size class
Elephant	size 7 (>2,500 kg)	2	6,000	12,000	3.6	7.2	7.2	1
Rhino	size 6 (<2,500 kg)	2	2,000	4,000	1.2	2.4	2.4	1
large Bovid	size 5 (<1,000 kg)	40	1,000	40,000	0.6	24	26.4	2
Cervid (*Alces-Megaloceros* size)		5	800	4,000	0.48	2.4		
Cervid (*Cervus-Alces-Megaloceros* size)	size 4 (<600 kg)	3	500	1,500	0.3	0.9	14.34	2
Horse		56	400	22,400	0.24	13.44		
Cervid (*Cervus* size)	size 3 (<300 kg)	26	180	4,680	0.108	2.808	2.88	2
Boar		1	120	120	0.072	0.072		
Cervid (*Dama-Cervus* size)	size 2 (<100 kg)	9	100	900	0.06	0.54	0.888	4
Cervid (*Dama* size)		5	80	400	0.048	0.24		
Cervid (*Capreolus-Dama* size)		3	45	135	0.027	0.081		
Cervid (*Capreolus* size)		2	23	45	0.0135	0.027		
sum		**154**		**90,180**		**54.108**		
					without Elephants	**46.908**		

most likely within time windows of only a few hundred years, based on estimation of sedimentation rates (Mania et al. 2010a; 2010b; Sier et al. 2011; Kindler/Smith/Wagner 2014; Wansa/Strahl/Rappsilber 2014) and thus provide insights into mortality in a biocoenosis due to Neanderthal hunting and other processes during relatively short time intervals. During that time more than 280 individuals of different ungulate taxa identified so far, were deposited in an area covering approx. 0.4 km² (**tab. 2** and **fig. 5**). An additional frame around the question of the duration of accumulation can be established for NN2/2B with reference to the energy flow between prey and Neanderthals. An exclusively anthropogenic origin of this faunal assemblage is reconstructed. Except elephants all species identified bear traces of exploitation by Neanderthals. The minimum number of 152 identified ungulate individuals of different species bearing butchery marks represents 78,180 kg and 46,908,000 kcal (**tab. 7**). A considerably higher daily energetic expenditure for Neanderthals compared to modern humans is debated (e.g. Heyes/MacDonald 2015). For modern hunter-gatherers a total daily energy intake of 3,000 kcal per individual is assumed (Sebastian et al. 2002). In **figure 8** calculations for a daily intake of 3,000 kcal and 5,000 kcal and different proportions of meat in daily diets are used to calculate for how long groups of different sizes can subsist on the calories deposited at NN2/2B. Although Neanderthal group size in the Neumark lakeland is unknown, both tables show, that the calories deposited at NN2/2B can reflect ungulate meat consumption within a maximum of a few decades or a generation. This illustrates, that a predator, in this case Neanderthals, active in habitats with high herbivore biomass can produce large bone assemblages in areas of prey aggregation, like water holes, in rather short amounts of time. Given high mortality at Neumark because of herbivore aggregation at

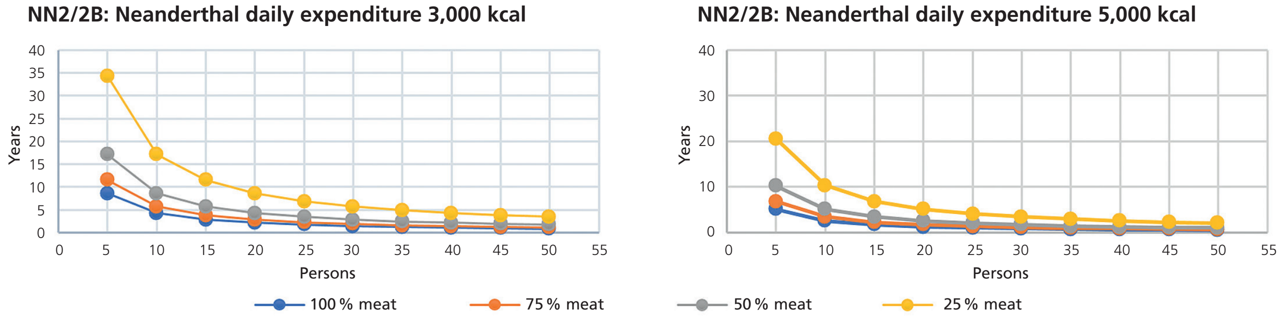

Fig. 8 Estimates of the number of years different-sized groups could subsist on the calories deposited at NN2/2B, based on a daily energetic expenditure of 3,000 kcal (left) and 5,000 kcal (right) and varying proportions of meat in daily foods.

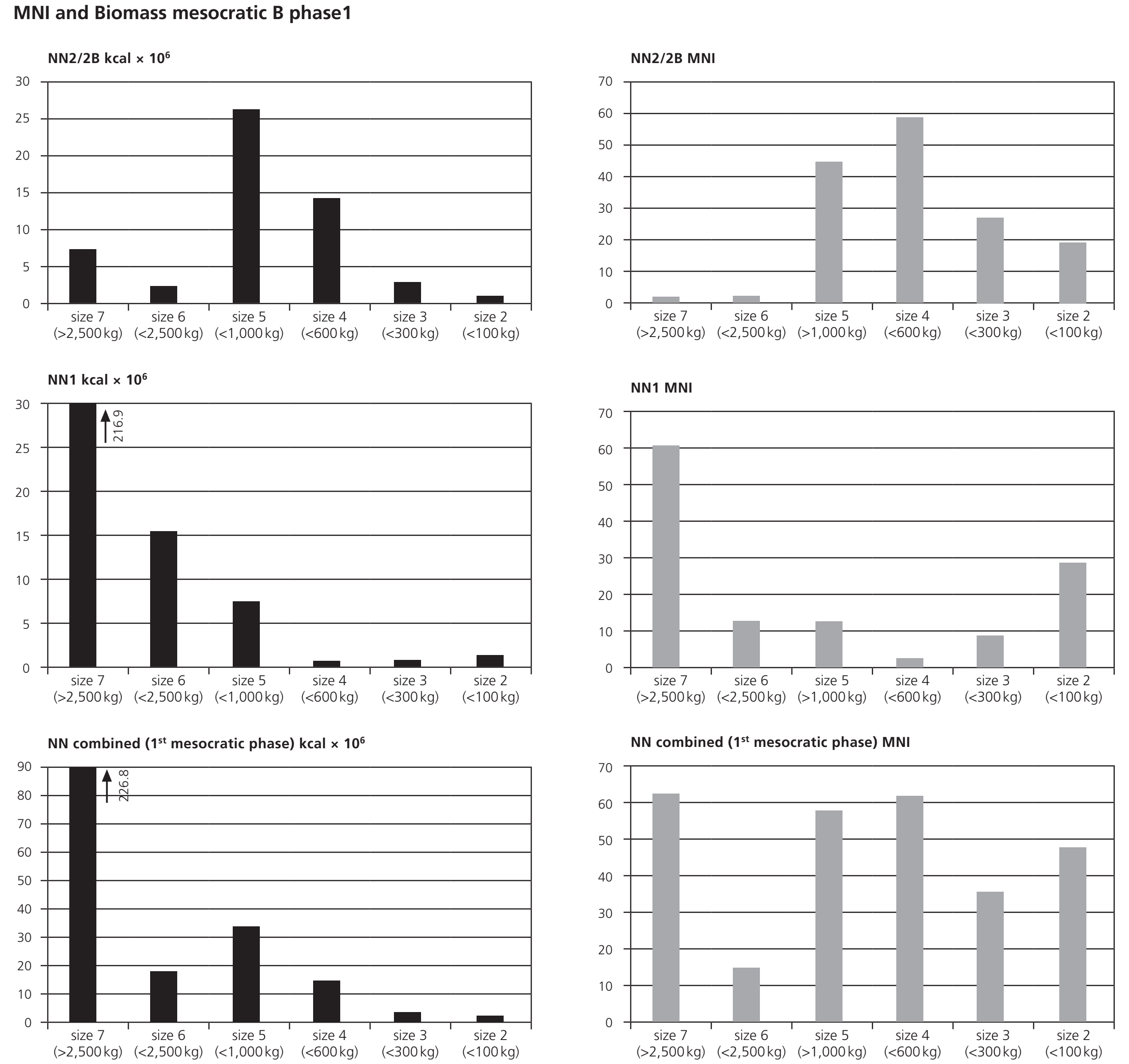

Fig. 9 Thanatocoenoses of the first mesocratic phase of the Eemian at Neumark-Nord. Top row: NN2/2B. Middle row: NN1, unit 6. Bottom row: NN2/2B and NN1, unit 6 combined. Left column: Calories (kcal). Right column: Minimal number of individuals (MNI). Species represented by size class are listed in table 6.

Tab. 8 Reconstruction of the living ungulate community during the first mesocratic phase at Neumark-Nord (MNI dead × Birth/Death rate × Correcting factor). Birth/Death rates are taken from Western (1980) and adjusted for the species and their estimated weight at Neumark. The correcting factor expresses the susceptibility for taphonomic destruction per size class and is calculated from ratios of observed and expected carcasses presented by Western (1980). Species represented by size class are listed in table 6.

Weight	MNI dead	Birth/Death rate	Correcting factor	Population (N)	proportion population (N)	kcal × 10^6 per size class (geo. mean)	kcal × 10^6 in stable population	proportion population (kcal)
size 7 (>2,500 kg)	63	8	0.167	968	0.104	3.60	3,484.56	0.696
size 6 (<2,500 kg)	15	9	0.167	228	0.025	1.20	273.55	0.055
size 5 (<1,000 kg)	58	12.5	0.181	919	0.099	0.54	492.96	0.098
size 4 (<600 kg)	62	22.5	0.33	1,586	0.171	0.27	425.47	0.085
size 3 (<300 kg)	36	25	1	2,700	0.291	0.09	238.09	0.048
size 2 (<100 kg)	48	30	2	2,880	0.310	0.03	92.19	0.018
				9,280	1	5.73	5,006.81	1

water holes, Neanderthal hunting, and the actions of other predators, the individual thanatocoenoses during the first mesocratic phase could have formed during much shorter time intervals as expressed by calculations of sedimentation rates of the burying deposits. Apart from the question of the exact temporal frame for a thanatocoenosis – something that we will most probably never achieve in a Palaeolithic context –, the species and individual rich faunal assemblages from the littoral horizons are in concordance with time restricted accumulations of mortality within the biocoenosis during the first mesocratic phase. Thus, estimations of the structure of the living community should at best incorporate all death assemblages of the first mesocratic phase.

The combined thanatocoenosis summarizes the minimal number of individuals (MNI) and energy (kcal) per size class from the NN2/2B and unit 6 from NN1 (**fig. 9**). The record from NN2/1c and NN2/1b are not taken into consideration, because their depositional contexts are still not fully assessed. Most individuals belong to elephant (size class 7) and horse (size class 4) followed by aurochs (size class 5), fallow deer (size class 2), red deer (size class 3) and considerable fewer individuals from rhino (size class 6). Considering biomass, elephants exceeds by far over all other taxa, followed by aurochs, rhino and horse. The deer species contribute only a minor portion to the biomass deposited in the death assemblage.

Neotaphonomic studies in eastern and southern Africa have clearly demonstrated the relationships between living community and death assemblage (Western 1980; Western/Behrensmeyer 2009; Hutson 2012; 2016; Miller et al. 2014). The proportions of individuals per species in a death assemblage are influenced by differences in birth and mortality rates as well as in differences in the susceptibility for taphonomic destruction. Both variables are dependent on body size of a species (Western 1980; Western/Behrensmeyer 2009). In general, species with lower body weight have higher birth rates and vice-versa. In a stable population the birth rate must correspond to the mortality rate. In contrast, bones of larger species are more robust against taphonomic loss than bones of smaller species. Western (1980) provides data on birth rates for different sized mammals and ratios for observed and expected individuals per species in the Amboseli National Park, Kenya. For the neotaphonomic study in Amboseli the living community from which a death assemblage originates is known, while the structure of the biocoenosis during the first mesocratic phase at Neumark can only be derived from the thanatocoenosis alone. But from the data provided by Western (1980) the observed mean birth rates per size class present at Neumark can be used to account for different mortality rates and the mean differences between observed and expected individu-

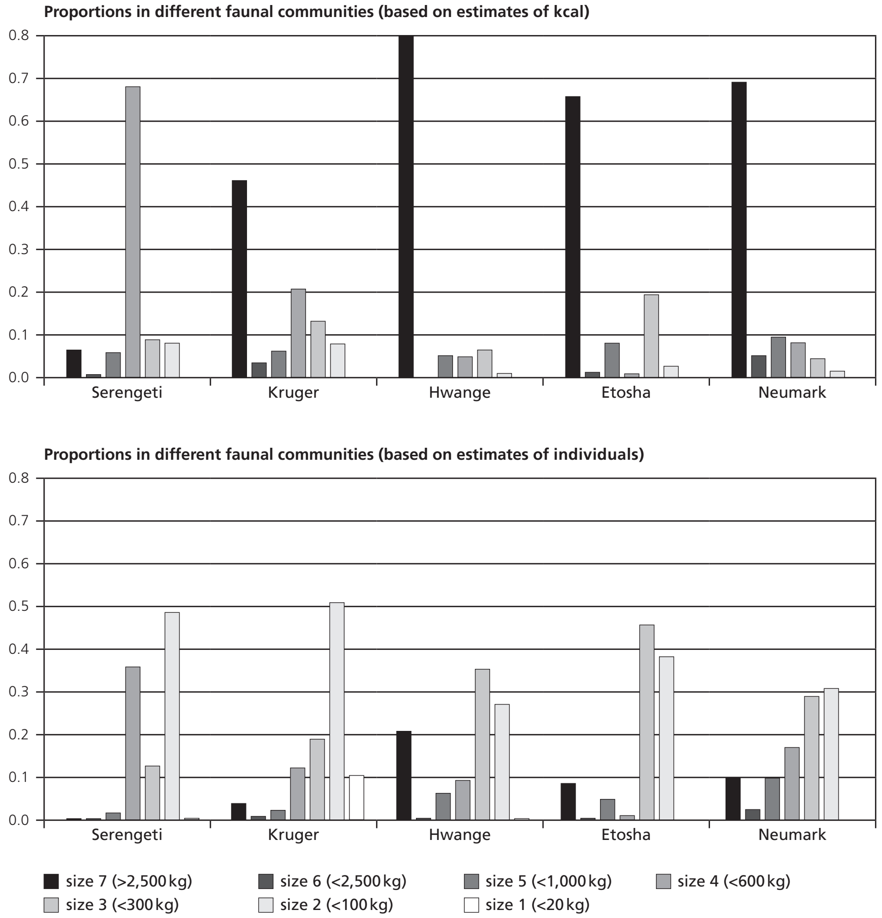

Fig. 10 Proportions of species of different size classes as calculated for the living community of the first mesocratic phase at Neumark compared with census data from African National Parks. Above: proportions based on estimates of calories (kcal). Below: Proportions based on estimates of individuals. – (Sources: Serengeti ecosystem, residential individuals only: TAWIRI 2010; Kruger National Park: SANParks 2012; Hwange National Park: Chamaillé-Jammes et al. 2009; Etosha National Park: Lindique and Lindique 1997).

als per body size class can be used as a correcting factor to account for different survivorship due to taphonomic processes. With these two variables a source population for the thanatocoenosis can be calculated (**tab. 8**). The number of individuals in the calculated source population is not necessary identical to the factual number of individuals in the past living community, because the number of individuals in the death assemblage should in the long run increase in time, although the number of individuals in the living community will remain stable. But the proportions of taxa in the calculated source population should reflect the past community structure more accurately as the proportions of biomass and individuals in the thanatocoenosis. The proportions of body size groups in the reconstructed source population for Neumark are in good agreement with the distribution of taxa in recent African ungulate communities with elephants as the heaviest species (**fig. 10**). In the reconstructed Neumark living population most individuals represent red and fallow deer, followed by horse, elephant, aurochs and finally rhino (**fig. 11**). Elephant is the dominant species in this community, storing approximately 70 % of the biomass, while the other taxa contribute less than 10 % of biomass to the reconstructed living community respectively (**fig. 11**). Mortality at Neumark is not evenly distributed across taxa, when considering their proportions in the death assemblage and their proportions in the reconstructed community. Mortality among the large taxa, elephants, rhino, and aurochs is around 6 %, among the deer less than 2 % and among horses around 4 %. This pattern may be related to different drinking behaviours between the taxa. Elephants, rhino and horses and most likely the aurochs need fresh water. Red and fallow deer can satisfy their water needs by extracting fluids from consumed plants, but at least red deer are known to wallow in water bodies. Thus, differences in mortality between taxa could be related to differences in the spatial diffusion and frequencies of taxa approaching the lake margins and thus different probabilities to die at the spot as well as to prey selection of specific predators, including Neanderthals. It is only during the first mesocratic phase of the Eemian, that carnivore bones contributed to the thanatocoenosis, but there is only ample evidence for butchery by Neanderthals (Gaudzinski-Windheuser et al. 2014). Thus, while the reconstructed source population of the

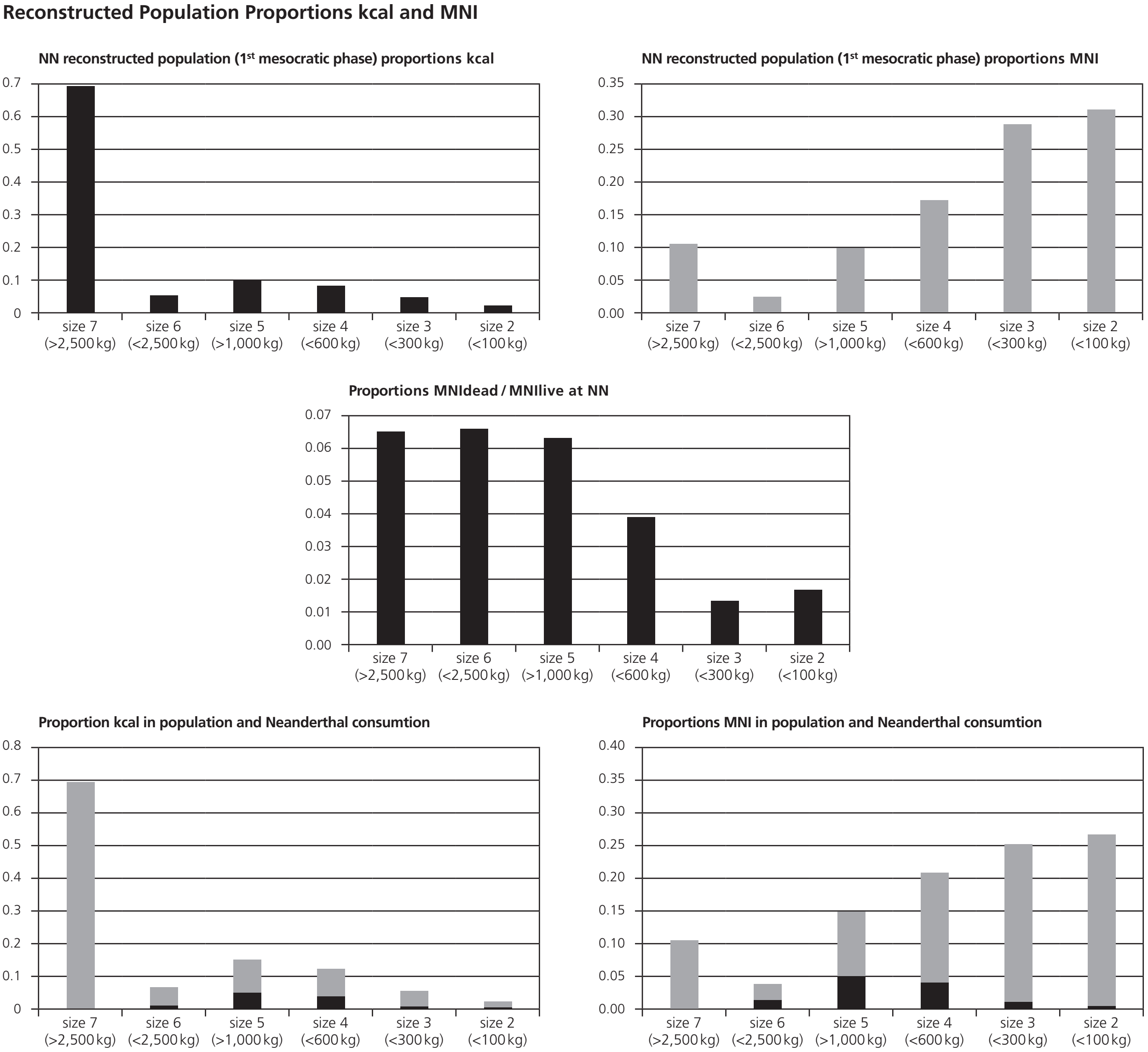

Fig. 11 Top row: Proportions of size classes in the reconstructed living community during the first mesocratic phase of the Eemian at Neumark. Top left: Calories (kcal). Top right: Minimum number of individuals (MNI). Center: Proportion of the observed dead individuals and the calculated living individuals at Neumark. Bottom row: Proportions of taxa consumed by Neanderthals plotted against the proportions of size classes in the reconstructed living population: Bottom left: Calories (kcal). Bottom right: Minimum number of individuals (MNI). Species represented by size class are listed in table 6.

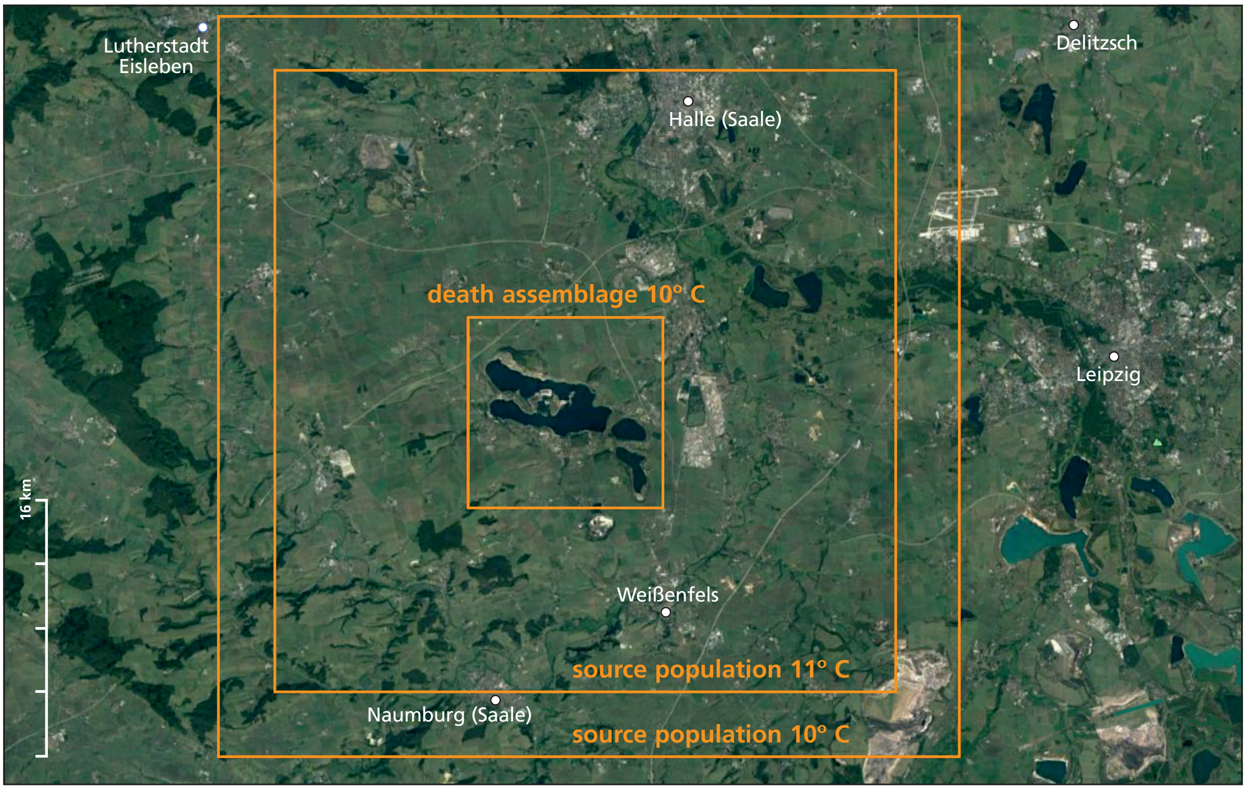

Fig. 12 The region of the Neumark lakeland today, with the Geiseltalsee in the center (snapshot from Google Earth) and the minimal catchment areas of the combined thanatocoenosis of the first mesocratic phase of the Eemian at Neumark and of the reconstructed source population based on the carrying capacity at 10° C and 11° C mean annual temperature.

first mesocratic phase can serve as a frame of reference to highlight subsistence opportunities in terms of ungulate resources, a closer look at the evidence of herbivore exploitation we have so far, can illuminate potential Neanderthal prey selection.

For an estimation of spatial diffusion, the area occupied by the reconstructed source population of the Neumark thanatocoenosis can be calculated by dividing the biomass by the carrying capacity. The results should be considered as the minimum catchment area of the source population and the individuals of the death assemblage (**fig. 12**). Based on CC for 10° C for Neumark the source population must have occupied an area of approx. 2,200 km² and for the combined thanatocoenosis of the first mesocratic phase of the Eemian an area of approx. 130 km² is required. The results illustrate again the high biomass distribution in the surroundings of the Neumark lakeland and point to opportunities for Neanderthals to subsist on a diverse ungulate community rich in individuals on a rather local scale and with low residential mobility.

How Neanderthal worked with these opportunities may become visible by putting the proportions of biomass and individuals in the source population in relation to their proportions in the Neumark thanatocoenosis with traces of human interference, these being the individuals from NN2/2B and individuals from the NN1 thanatocoenosis for which butchery is proposed and those bearing clear cut marks on bones (**tab. 9** and **fig. 11**). Evidence of human interference is lacking for elephants. Nevertheless, the proportions of anthropogenic modification per size class sum up to 12 % of the entire size and biomass of the source population. Anthropogenic modification correlates with biomass and not with the proportions of individuals in the source population. Highest proportions are documented in size class 5 (aurochs) and size class 4 (horse). This focus can be a result of a trade-off between risk, handling costs and return rates. Ungulate species react differently in their behavioural adjustments to hunting and predation risks at water holes (e.g. Valeix et al. 2009a; Crosmary et al. 2012). Permanent Neanderthal presence and intense hunting of a single species at Neumark could have lead ultimately to the species' avoidance of the water bodies. Although a strong focus on prey of 300 to 1,000 kg can be reconstructed for Neanderthals at Neumark, additional harvesting in other size classes could compensate for the risk of chasing away preferred prey from the Neumark lakeland. Thus, the limiting factor influencing Neanderthal occupation of the Neumark lakeland would have been the responses of prey to their presence and hunting pressure. Shifting hunting grounds and habitation areas could have been an additional strategy to avert the risk to deter prey from approaching the Neumark water bodies.

Conclusions and Prospects

The high-resolution palaeoenvironmental archive of the Neumark-Nord lakeland has preserved evidence of Neanderthal presence during all Eemian substages. In the first instance the "quality" of the archaeological record can be related to the specific taphonomical conditions of the depositional environments. Nevertheless, changes in structure and composition of vegetation and with that faunal communities during the Eemian may have affected Neanderthal land-use, mobility and subsistence, which must be considered when analysing patterns in the archaeological record.

The record from Neumark-Nord gives a rare opportunity to integrate ecological factors from the faunal evidence, when reconstructing Neanderthal subsistence strategies during the Eemian interglacial. Calculations of carrying capacities demonstrate high ungulate biomass production limited by mean annual temperatures during the Eemian. Species richness and niche partitioning between taxa observed during the first mesocratic phase at Neumark is a direct outcome linked to high primary production. During this phase large mammal community structure was most probably analogous to recent African faunas rich in or dominated by elephants, i.e. taxa with high body weight contribute most of the biomass and taxa with low body weight contribute more individuals to the community. Species richness, the distribution of biomass and individuals in the community gives a wide array of subsistence opportunities. In this context, the current zooarchaeological data from the first mesocratic phase shows a clear focus on aurochs, horse and large cervids, subsidized in descending order by rhino, size class 3 cervids, and size class 2 cervids. Subsistence on ungulates is biomass oriented and to a lesser degree determined by the abundance of individual taxa in the community. Trade offs between risk, handling cost and return rates are certainly major variables influencing this subsistence strategy and prey choice. Putting the number and biomass of ungulate individuals in a spatial context it becomes apparent, that Neanderthals in the Neumark area could subsist on a local scale, i.e. with a low residential mobility, with the presence of waterholes attracting animals and guaranteeing an almost continuous presence of prey.

Currently, we can qualify aspects of subsistence just for the archaeological record of NN2/2B. Narrowing down the temporal resolution of the archaeological levels is fundamental for a detailed assessment. For the littoral zones at NN1 and NN2 during

Tab. 9 Minimal number of individuals (MNI) and calories (kcal) per size class with evident modifications from butchery in the combined thanatocoenosis of the first mesocratic phase of the Eemian and their proportions in the reconstructed source population.

Neanderthal consumption: first mesocratic phase/size class	MNI	kcal × 10^6	proportion in source population
size 7 (>2,500 kg)	0	0.00	0.000
size 6 (<2,500 kg)	3	3.60	0.013
size 5 (<1,000 kg)	46	24.69	0.050
size 4 (<600 kg)	62	16.64	0.039
size 3 (<300 kg)	30	2.65	0.011
size 2 (<100 kg)	20	0.64	0.007
sum	**161**	**48.21**	**0.120**

the first mesocratic phase accumulation within few centuries are reconstructed. Biomass and energy values contribute to a better understanding of the duration of occupation. The fauna from NN2/2B is rich in species and individuals. The respective data derived from the MNI and biomass indicate a much shorter "chronology of occupation(s)" during which a larger group of Neanderthals could have been supplied. Qualifying the origin of NN1 can expand our knowledge. Here, the composition of the thanatocoenoses from the so-called butchery areas and the causes of death for the skeleton thanatocoenosis are of major interest. The differences are striking. Due to the preservation of (partly) complete skeletons elephants are dominating in the first mesocratic phase, but are, at the current state of knowledge, almost absent from the butchery areas. In contrast, not a single horse is among these skeletons, but horse constitute most of the MNI from NN2/2B. Independent from the causes of death, one must ask, why these skeletons haven't been scavenged and dismembered by humans and carnivores, beside a few cut and gnaw marks. Carnivores were present in the Neumark lakeland and were also exploited at NN2/2B, but it has to be established, which role carnivores played in the Neumark faunal community. It is unclear in which ungulate size classes the different predators mainly operated and how this interrelates with Neanderthal subsistence and prey selection. At present, it seems that the whole lakeland was under "Neanderthal control" during the first mesocratic phase. Prudence must be exercised, when comparing the records from different Eemian substages at Neumark-Nord, especially with the record from the second mesocratic phase rich in cervid skeletons. Although some aspects of the thanatocoenoses share similar general taphonomical patterns, species diversity is considerably lower and the number of individuals per species different in the second mesocratic phase, specifically the high numbers of fallow deer. With changes in vegetation during both phases, and potentially denser forest canopy cover in the second mesocratic phase, the structure of the living ungulate community must have also changed and thus, the source population for both thanatocoenoses might be quite different. Against this background, we also have to assume shifts in Neanderthal subsistence in response to environmental change.

Nevertheless, in a broader perspective the record from Neumark-Nord reveals new aspects of Neanderthal subsistence and challenges concepts of Neanderthal adaptations in forested environments in North and Central Europe (e.g. summarised in Gaudzinski-Windheuser/Roebroeks 2011). Compared to well-known Neanderthal subsistence habits on the North European Plain during cool and cool-temperate climatic conditions, we may conclude that during interglacials Neanderthals still focussed on the exploitation of large mammal resources, but strategies of land-use and the patterns of settlement have differed. When temperature and precipitation is the crucial variable for ungulate biomass production, at least for the early part of the Eemian, with alternating patches of vegetation openness, we can conclude higher ungulate biomass compared to cool- and cool-temperate climate phases. Thus, prey is more abundant, less dispersed in the landscape and migration distances are shorter. Neanderthals could subsist on a more local basis, indicated e.g. by the catchment area of the ungulate population during the first mesocratic phase of the Eemian at Neumark. Following standard models of predator-prey relationships (e.g. Begon/Mortimer/Thompson 1996), higher production in prey biomass might also affect Neanderthal populations, causing them to increase at a local scale.

The vast and almost inexhaustible paleoenvironmental and archaeological record from Neumark-Nord teaches us that analysing Neanderthal subsistence strategies must be framed in the habitat, in which subsistence was exercised. Carrying capacities, calculations of biomass and calorie values are good auxiliary proxies to build bridges between thanatocoenoses and biocoenoses. When we succeed in placing Neanderthals in different and changing past living communities, we will reach a new level of detail and accuracy in the reconstruction of their subsistence, ecological tolerance and variability at Neumark and elsewhere in the Neanderthal world.

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BRITT M. STARKOVICH · NICHOLAS J. CONARD

WHAT WERE THEY UP AGAINST? LOWER PALEOLITHIC HOMININ MEAT ACQUISITION AND COMPETITION WITH PLIO-PLEISTOCENE CARNIVORES

Abstract

The habitual inclusion of meat into the diet was one of the most significant developments in hominin evolution. In addition to the nutritional benefits, competition with carnivores for animal resources was most likely a significant selective force in the Lower Paleolithic. In this paper, we provide a literature review of the origins of hominin meat acquisition. We address major debates that have shaped archaeologists' understanding of this topic (i. e., hunting versus scavenging, primary versus secondary acquisition) and synthesize the current state of the discussion. In addition to taphonomic data from zooarchaeological assemblages, we discuss evolutionary processes that were occurring in the carnivore guild during the Plio-Pleistocene, when we see the earliest evidence for meat acquisition by hominins. From the data currently available, we draw two main conclusions regarding meat procurement by hominins. The first is that, though scientists have documented earlier cases, there seems to be a marked increase in evidence for meat acquisition between 1.8 and 1.5 Ma in both Africa and Eurasia. It is possible that early hominins used a combination of passive and confrontational scavenging to access meat during this period, and we do not exclude the possibility that they also occasionally hunted. The second conclusion is that after 500,000 BP, we see extremely strong evidence for hominin hunting. This also might have occurred before this time, but there are more examples after this time period over a wide geographic range. We do not see these shifts as a strict linear progression, but rather as a mosaic of different strategies that began at different times in multiple locations. Based on the meat acquisition strategies of many carnivore species, in addition to modern hunter-gatherers, we, like many authors, do not see hunting and scavenging as an all-or-nothing-prospect, but rather as a continuum that shifts depending on the circumstances. We also discuss some differences in interpretations made by zooarchaeologists that seem to be more closely related to the time period (pre- or post-1.0 Ma) or geographical region (Eurasia or Africa) in which scientists are working, as opposed to the actual archaeological record.

Keywords

Lower Paleolithic/Early Stone Age, zooarchaeology, taphonomy, mortality profiles, carnivore guild

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Introduction

The inspiration for this paper came from the session "A diachronic perspective of human behavioural adaptations to interglacial lakeshore environments during the European Pleistocene to early Holocene" at the 2014 UISPP conference held in Burgos, Spain. The session focused on the importance of lakeshore environments as critical ecosystems for hominins and as favorable preservation settings of archaeological sites. As we listened to the different presentations, particularly those on the Lower Paleolithic sites of Miesenheim I and Schöningen, we thought about the many other important Eurasian interglacial lakeshore sites from this period (e. g. Gesher Benot Ya'aqov, Israel; Hoxne, England; Torralba, Spain). Part of our ongoing work at Schöningen highlights the importance of lakeshore environments, not only for hominins, but also for carnivores that exploit such ecosystems for water and prey (e. g. Serangeli et al. 2015; Starkovich / Conard 2015), meaning that lakeshores are prime areas for competition between hominins and carnivores. We are certainly not the first to make this connection; a particularly large body of Lower Paleolithic research addressing this topic (at least implicitly) comes from the east African sites of Olduvai Gorge (Tanzania) and Koobi Fora (Kenya) (see below). So we began to review the literature in order to understand the current ideas surrounding hominin meat acquisition, and the role that hominin-carnivore interactions played in the origins of meat-eating for the genus *Homo*. We quickly realized 1) that it had been some time since archaeologists had presented a review on this topic for Africa or Eurasia (e. g. Gifford-Gonzalez 1999; Domínguez-Rodrigo 2002; Stiner 2002; Domínguez-Rodrigo / Pickering 2003), and 2) it would be remiss of us to exclude iconic cave and rock shelter sites such as those in the Sierra de Atapuerca (Spain) or Dmanisi (Georgia), simply because they are not on a lakeshore, or Boxgrove (England) and Ambrona (Spain) because they preserved glacial deposits.

Therefore, we decided to expand our initial focus on carnivore-hominin competition at lakeshore localities to explore the larger picture of hominins entering the carnivore guild during the Plio-Pleistocene, though lakeshore sites still hold a prominent place in this discussion. We provide an in-depth review of Lower Paleolithic sites in Africa and Eurasia that yield evidence of meat eating to evaluate the extent to which hominins had access to animal tissues and to test whether or not there are any clear chronological shifts that might signal the origins of hunting. We consider these behaviors in the context of other large-bodied carnivores on the landscape with which hominins had competitive and co-evolutionary relationships. We end the review around 300,000 BP. This date is semi-arbitrary; we chose it because it is the date of the Spear Horizon at Schöningen, one of the late interglacial lakeshore sites that sparked this paper, and a site that we are both intimately familiar with (see papers in Conard et al. 2015a). It is also a logical endpoint because Schöningen is among the oldest sites with unequivocal evidence for hominin hunting (Thieme 1997; Voormolen 2008; Conard et al. 2015b). Though the site has a strong anthropogenic signature, there is also ample evidence for large-bodied carnivores such as wolves (*Canis lupus*) and sabertooth cat (*Homotherium latidens*) modifying the bones. This is a strong reminder that even by the time hominins had clearly entered the predatory guild, they were still competing with carnivores, particularly when it came to issues such as settlement patterns and carcass butchery.

As we know well, modern humans have the ability to control and manipulate their environments to an extent that is unprecedented in the animal kingdom. This ranges from large-scale processes such as deforestation, coastline maintenance with levees and dykes, industrial agriculture, and the rerouting of major rivers through irrigation, to smaller, more local processes. A modern example of the latter is the ongoing conflict between humans and predators over livestock or game animals, which has resulted in myriad responses: predator suppression, the release of farm-raised game, translocation, or even diversionary feeding (see review in Graham / Beckerman / Thirgood 2005). This treatment of predators is actually a fairly recent phenomenon that has its roots in the domestication of ungulates, when the very livelihood of pastoral groups was suddenly threatened by large carnivores such as wolves, tigers, lions, and hyenas (e. g. Diamond 1989). And while the relationship between large carnivores and humans was not always so unbalanced in favor of human control, tension between the groups has existed for millennia. The connection between large-bodied carnivores and humans is unique because it transcended boundaries from a time when hominins fell victim to carnivores, to direct and indirect competition for meat resources as part of the predator guild, to the eventual domestication of dogs. The next phase of this transition, the point at which hominins started incorporating a significant amount of meat in their diets and entered the predator guild, is at the heart of this paper. When this occurred is not known, but has evolutionary importance for our development as a species. By the Upper Paleolithic, it is clear that modern humans were successful hunters of a range of prey types. Even by the Middle Paleolithic of Eurasia and Middle Stone Age of Africa, hominins were at the top of the food chain. Evidence for this comes from increasingly complex toolkits, and an abundance of sites featuring a range of large ungulate prey species hunted in the prime of their lives (e. g. Gaudzinski 1995; Speth / Tchernov 1998; Gaudzinski / Roebroeks 2000; Stiner 2005; 2009; Adler et al. 2006; Costamagno et al. 2006; Speth / Clark 2006; Shea / Sisk 2010; Starkovich 2014; Niven et al. 2012; Rendu et al. 2012; Starkovich 2012a). The implications of this are that hominins entered the predator guild as competent hunters sometime during the Lower Paleolithic.

In Africa, early members of the genus *Homo* and late australopithecines incorporated meat into their diets as early as 2.6 million years ago (Ma), or possibly even 3.39 Ma (de Heinzelin et al. 1999; McPherron et al. 2010; Thompson et al. 2015). There were many paths to meat acquisition, and whether or not it initially involved hunting, passive scavenging, confrontational scavenging, or a combination of these strategies, early hominins had to contend with a complex and well-established predator guild. Interactions with carnivores would have followed multiple pathways, starting with hominin ancestors attempting not to fall victim to predators and behavioral modifications to maximize avoidance (i. e., diurnal activities as opposed to those at dusk or dawn when carnivores are most active), which developed into day-to-day competition for individual carcasses and predation of the same prey populations. Eventually, the position of hominins in the predator guild crystalized to the extent that by the Middle Paleolithic, hominins were successful hunters of large game on multiple continents. The route to this adaptation is of special interest to archaeologists and paleoanthropologists alike, as it was eventually accompanied by increases in cranial capacity, more advanced tool technologies, the adoption of fire, the origins of language, and widespread colonization.

Origins of Hominin Meat Eating

There are many questions surrounding the earliest use of meat by hominins. At the most basic level, there is the issue of when meat-eating began, and who started it. Based on our current knowledge, the earliest widely-recognized stone tools are found at Gona (Ethiopia) and date to 2.6-2.5 Ma, and the earliest accepted evidence for cut marks on bones come from the 2.5 Ma site of Bouri (Ethiopia) (de Heinzelin et al. 1999). A few scholars have questioned this paradigm in recent years, with the 3.3 Ma industry found at Lomekwi 3 (Kenya) (Harmand et al. 2015), and seemingly cut bones at Dikika (Ethiopia) which date to 3.39 Ma (McPherron et al. 2010; Thompson et al. 2015), though more work is needed in this early period. It is possible, and even likely, that the earliest stone tools were used for cutting materials other than meat, for example plants; though based on the roughly contemporaneous appearance of stone tools and cut bones, early stone tools probably served multiple functions. The question of who used the earliest tools is not entirely clear; scholars have implicated species of both *Homo* and *Australo-*

pithecus as the first manufacturers of stone tools (Semaw et al. 1997; de Heinzelin et al. 1999; McPherron et al. 2010; Harmand et al. 2015; Thompson et al. 2015), though this debate is beyond the scope of our paper. Moving into more advanced questions involving meat procurement and early hominins, there is the issue of how significant meat was to the diet of past hominins. Based on the current body of data, this is largely unknowable and we will not pursue the question further here. Central to our interests, is how did early hominins acquire meat (i. e., hunting or scavenging), and how did they interact with Plio-Pleistocene predators in Africa, and later in Eurasia. We would like to stress, however, that while the hunting / scavenging debate is important to our understanding of the past, these strategies certainly existed along a continuum, with shifting proportions of hunting and scavenging depending on the circumstances. While the introduction of meat into the diet had evolutionary significance from a nutritional standpoint, in the sense that easier digestion and the consumption of long fatty acid chains facilitated brain growth (Hayden 1981; Speth 1989; Eaton / Eaton III / Cordain 2002), we would argue that the entrance into the carnivore guild and competition with large predators was equally significant in terms of the social, technological, and cultural adaptations it required (see also Stiner 2002). As such, hominin-carnivore interactions at Plio-Pleistocene sites and order of access to meat is a key area of research at early Lower Paleolithic sites. In this section, we outline the state of research on early hominin meat acquisition, and discuss the African and Eurasian carnivores that helped shape the evolution of our hominin ancestors.

Small game and aquatic resources

Though we will devote most of this discussion to the consumption of large game, it is increasingly apparent that early hominins exploited a range of prey types. A significant initial source of protein and fat might have come from aquatic resources, as researchers have documented in the Omo (Ethiopia) as early as 2.4 Ma, at Koobi Fora (Kenya) between 1.95 and 1.5 Ma, and at Olduvai Gorge (Tanzania) between 1.85 and 1.2 Ma (Chavaillon 1976; Stewart 1994; 2010; Pobiner 2007; Braun et al. 2010; Archer et al. 2014). All of these sites contain disproportionately high numbers of taxa such as turtles and especially catfish, some of which preserve evidence of cut marks (Stewart 1994; 2010; Pobiner 2007; Braun et al. 2010; Archer et al. 2014). The authors argue that at certain times of year, these taxa become sessile prey that are easily collected without any specialized hunting technologies. Specifically, catfish spawn in shallow pools during the dry season, and are vulnerable to becoming stranded. Because they have primitive lungs, they can live out of water for multiple days, providing an easily collected fresh aquatic food source for hominins and other animals (Stewart 2010; Archer et al. 2014). Access to this type of prey is important for two reasons. First, catfish are available in the late dry season, when ungulate fat stores are depleted. Second, aquatic resources provide docosahexaenoic acid and long-chain polyunsaturated fatty acids that are linked to brain growth in hominins (Broadhurst / Cunnane / Crawford 1998; Braun et al. 2010; Stewart 2010; Archer et al. 2014). Approaching this question from a theoretical standpoint, Joordens et al. (2009) introduced a model based on the ecological parameters of Trinil (Java) to predict that hominins should have exploited aquatic resources in that particular environment around 1.5 Ma. While they did not find direct evidence of hominin exploitation of marine resources at the site, though the shells are still under study, the authors point out that omnivorous mammals living in a coastal environment that have access to nutritious and catchable prey, such as shellfish or stranded catfish, inevitably exploit these resources (Joordens et al. 2009).

Evidence for the consumption of aquatic resources by early Lower Paleolithic hominins should come as no surprise to archaeologists; there is ample evidence of the exploitation of marine resources by modern primates including tarsiers, monkeys, macaques, baboons, orangutans, and bonobos (see reviews in Stewart et al. 2008; Kempf 2009; Stewart 2010; Russon et al. 2014). These authors, however, are quick to point out that the use of aquatic animals by modern primates is unusual, and fishing is even rarer. While there are a few documented cases of tool use for fishing (i. e., stick tools and food bait), most marine resources eaten by primates are easily gathered, including sessile catfish (Russon et al. 2014).

In terms of terrestrial small game, some of the earliest evidence of hominin exploitation of this prey type comes from cut hedgehog bones recovered from the 1.76 Ma layers at Olduvai Gorge Bed I (Tanzania) (Fernandez-Jalvo / Andrews / Denys 1999). Moving to the late Lower Paleolithic, Blasco et al. (2011) document the consumption of tortoises at Sima del Elefante (Atapuerca, Spain) between 1.2 and 0.78 Ma, along with cut marks on one bird and two leporid bones. Subsequent evidence of terrestrial small game use is rare until the Middle Paleolithic and Middle Stone Age, when tortoises became common in archaeological assemblages (e. g. Stiner / Munro / Surovell 2000; Speth / Tchernov 2002; Steele / Klein 2009; n. d.; Starkovich 2012b). An exception to this is at Gran Dolina (Atapuerca, Spain) and Bolmor Cave (Spain), where there is evidence for the exploitation of rabbits and birds in marine oxygen isotope stage (MIS) 9. The authors note multiple specimens with cut marks, and what they interpret as human gnaw marks (Blasco / Peris 2009; Blasco / Peris 2012; Blasco et al. 2013), though these kinds of observations are unusual at Middle Pleistocene sites.

As with other subsistence evidence from the Lower Paleolithic, it is unclear exactly what proportion of the diet aquatic resources and small terrestrial game comprised, though they undoubtedly contributed important nutrients to hominins with increasingly larger and more complex brains. Indeed, Stewart (2010) proposes that aquatic foods led to brain growth and tool use even before hominins exploited large, terrestrial mammals on a regular basis. The difficulties with testing this hypothesis, and with understanding the extent of small game use in general, is that sites yielding unambiguous evidence for small game exploitation from this time are still rare. New studies, as well as re-evaluations of old assemblages using new experimental data that specifically address the taphonomy of small animals (e. g. Archer / Braun 2013) are critical. For this reason, and because the major focus of this paper is the evolutionary pressure exerted by competition between carnivores and hominins (see Stewart 1994 for a discussion of expected low-levels of competition when it comes to aquatic resources), we now shift our focus to large-bodied game.

Megafauna

A particularly difficult to interpret aspect of the Lower Paleolithic faunal record is the use of megafauna, such as elephants, rhinoceros, and hippopotamus, by hominins. There are many instances of stone tools being found in association with proboscidean remains (e. g. Olduvai FLK North, Tanzania; Barogali, Djibouti; Southfleet Road, England; Notarchirico, Italy; Gesher Benot Ya-aqov, Israel; Kärlich-Seeufer, Germany) (Leakey 1971; Chavaillon et al. 1987; Goren-Inbar et al. 1994; Gaudzinski et al. 1996; Cassoli et al. 1999; Berthelet / Chavaillon 2001; Piperno / Tagliacozzo 2001; Wenban-Smith 2013), though few sites provide evidence for cut marks on bone (e. g. Olduvai SHK Main and BK, Tanzania; Buia, Eritrea; Revadim Quarry, Israel; Fuente Nueva-3, Torralba, Ambrona, and Áridos 2, Spain; La Polledrara di Cecanibbio and Castel di Guido, Italy) (Anzidei / Cerilli 2001; Fiore et al. 2004; Yravedra et al. 2010; Boschian / Saccà 2010; Domínguez-Rodrigo et al. 2010; 2014a; 2014b; Anzidei et al. 2012; Rabinovich et al. 2012; Saccà 2012; Espigares et al. 2013). Looking only at the latter set of sites, there is also the question of whether, or to what degree, Lower Paleolithic hominins hunted or scavenged megafauna.

This debate played out over nearly a decade between Lewis Binford on the one hand and Clark Howell and Leslie Freeman on the other. After excavating Torralba and Ambrona, Howell and Freeman suggested that early hominins were successful hunters of large game including megafauna (Howell 1963; 1966; Freeman Jr. / Butzer 1966; Freeman / Freeman 1975; Freeman Jr. 1978). Binford subsequently analyzed the data from Torralba and concluded that the remains mostly represented hominin scavenging from large carnivore kills (Binford 1987). In the meantime, Shipman and Rose (1983) used scanning electron microscopy to analyze the surfaces of the Torralba and Ambrona faunal remains, and only found a total of 16 cuts in both assemblages. Klein (1988) added to the debate with his own analysis, in which he argued that the mortality profiles of elephants at the two sites correspond more closely with attritional mortality, indicative of natural or accidental deaths, as opposed to a catastrophic profile expected by hominin hunting or game drives. The idea of examining mortality profiles turns out to be critical to our understanding of meat acquisition in the past and we will expand upon it further below. Based on additional excavations and data analysis at the sites, Howell and Freeman continued to argue that hominin hunters were responsible for the deaths of the elephants at Torralba and Ambrona. Further, they re-calculated Klein's mortality profiles and determined that the age representation was both catastrophic and attritional, lending further support to their original hunting scenario (Freeman 1994; Howell et al. 1995). In the most recent contribution to the debate, Villa et al. (2005) provide the results of a re-excavation at Ambrona. They find additional elephant remains with occasional traces of hominin activities in the form of cuts and spiral fractures. Carnivore gnawing is rare on the assemblage, and significantly, bone surface preservation is better than in the earlier studies (e.g. Shipman/Rose 1983). The authors conclude that due to the complexities of site stratigraphy and palimpsest nature of the deposits, Ambrona does not provide adequate evidence to support the scavenging hypothesis advocated by Binford, nor the hunting hypothesis supported by Howell and Freeman (Villa et al. 2005).

The back-and-forth nature of this debate is fairly typical for many important Lower Paleolithic sites, and is largely a product of the small number of well-preserved assemblages. This was particularly a problem in the 1980s and 90s, when the arguments were the most contentious. However, additional complicating issues are the fact that many sites occur near bodies of water (e.g. Gesher Benot Yaaqov, Torralba, Ambrona, FLK North, etc.). Such environments may contain a disproportionate number of mega-herbivores, as stressed elephants and rhinoceros seek out water in times of drought, or semi-aquatic hippopotamus die in their natural habitats. Another problem is the lack of direct evidence of hominin exploitation of carcasses from cuts or other butchery marks. Finally, many sites contain only one or a few animals, so it is difficult to establish meaningful mortality profiles for megafauna at Lower Paleolithic sites, and these profiles could indicate the likelihood that animals were hunted or scavenged. With the small amount of data currently available, some authors argue that mostly prime-aged adults are typically represented, which indicates hominin hunting (e.g. Wenban-Smith 2013), while others contend that the vulnerable old and young are typically found (e.g. Gaudzinski et al. 2005). At this stage, until a synthesis of a large number of stratigraphically intact, well-studied sites is available, the most meaningful conclusion that we can draw is that Lower Paleolithic hominins occasionally consumed the meat of megafauna. Whether this was through coordinated hunting efforts, the scavenging of carcasses that then had to be protected from carnivores, or some combination of both, is behaviorally important. However, the available data are insufficient to address this question conclusively. Data from smaller-bodied herbivores currently provide the greatest potential to address the origins of meat procurement and consumption.

Hunting among non-human primates

Before we turn our discussion to early evidence for hominin meat acquisition, it is useful to address the meat eating behaviors of non-human primates. Of course, modern primates are not an analog for past hominins, but they are important to provide a frame of reference for understanding the evolution of modern human hunting behaviors, which are far from the norm compared to our primate relatives. As we have touched on above, primates are known to consume animal protein in the form of marine or terrestrial resources. Scientists have also documented hunting behaviors among baboons, chimpanzees, and bonobos, which exploit taxa such as monkeys, young gazelles, bushpigs, bushbucks, forest antelope, hares, squirrels, and rodents (e. g. Harding 1973; 1974; Harding/Strum 1976; Hausfater 1976; Wrangham 1977; Morris/Goodall 1977; Hamilton/Bussne 1978; Strum 1981; Stanford et al. 1994; Stanford 1995; Watts/Mitani 2002; Surbeck/Hohmann 2008). However, hunting is uncommon among primates (and scavenging is even more unusual), and no taxa even approach the amount of meat eating we see among modern humans (C. Boesch/H. Boesch 1989; Stanford et al. 1994). Another relevant point concerning primate hunting is that primates rarely engage with prey that are larger or have similar body sizes to their own (McGrew 2001; Rose 2001; Stanford 2001). So while at least three other species of primate incorporate meat into their diets, it is at a very different scale than what we see with modern humans. It is unclear how the quantity of meat compares to that eaten by earlier hominins, but at least in terms of the body sizes of prey it is quite different, as we will now discuss.

Evidence pre-1.0 Ma

Most of the data we have regarding hominin subsistence strategies from the early part of the Lower Paleolithic come from a small number of Early Stone Age fossil accumulations from East Africa, namely Olduvai Gorge and Koobi Fora. Numerous scholars have analyzed, reanalyzed, and debated the meaning of these assemblages for nearly half a century. A central question in these studies is whether hominins or carnivores had primary access to large mammal remains at a small number of preserved sites that are more than a million years old. This is particularly the case at FLK Zinj (1.75 Ma, Olduvai Gorge), where zooarchaeologists and taphonomists have tried to understand the nature of the remains since the early 1980s. Before this, the dominant paradigm was that many Oldowan sites represented a "home base" on the landscape, where male hominins brought meat that was provisioned to females and other members of the group (Isaac 1971; 1978; 1984). Similar to the discussion surrounding Torralba and Ambrona, this view was criticized by Binford, who argued that early hominins at FLK Zinj were marginal scavengers who passively accessed bone marrow from carnivore kills, only after the carcasses were already stripped of meat (Binford 1981; 1985; 1988; Binford/Blumenschine 1986). Initially analysts attempted to use the anatomical representation of ungulates present at sites to determine if the faunas were accumulated by hominins, and therefore if they had primary or secondary access to carcasses. This is problematic, however; while the majority of early Lower Paleolithic faunal assemblages are dominated by head and limb elements (Bunn/Kroll 1986; Bunn 1997), archaeologists have documented both humans and carnivores transporting limb bones away from kill sites (Binford 1981; Bunn 1983; 1991; Bunn/Kroll 1986), which can be used to support either side of the argument. Another complication is the fact that most of the early assemblages are heavily biased by taphonomic factors, including mechanical processes, chemical weathering, carnivore damage, and hominin butchery. These processes destroy structurally weak portions of bone, and render interpretations of the original composition of the assemblages and subsequent movement of elements to or from the site difficult or nearly impossible (Binford/Bertram 1977; Lyman 1984; 1994; Grayson 1989; Kreutzer 1992; Lam/Chen/Pearson 1999).

In the meantime, taphonomists conducted a range of actualistic studies and developed new quantification techniques and models in order to examine hominin and carnivore modifications on bones. This work, combined with bone surface damage and skeletal part ratios from Plio-Pleistocene sites, led Robert Blumenschine and colleagues to postulate that early Lower Paleolithic hominins primarily scavenged bone marrow from carnivore kills (Binford/Blumenschine 1986; Blumenschine 1986; 1988; 1991; 1995; Blumenschine/Marean 1993). In doing so, they created a formation model for the FLK Zinj faunas. First, leopards killed or scavenged ungulates. After feeding, the cats abandoned the meatless bones, which were then collected by hominins who transported the remains to the site and broke them open for marrow. Once the hominins were done, hyenas gnawed the greasy cancellous bone ignored by hominins, extracting the last nutrients from the remains. Blumenschine and colleagues based these conclusions on a large number of bite marks on midshafts, ample hammerstone fractures, and extensive gnawing on longbone epiphyses, which were consistent with marks these authors recorded during feeding experiments with carnivores (Binford / Blumenschine 1986; Blumenschine 1986; 1988; 1991; 1995; Blumenschine / Marean 1993; Selvaggio 1994; Capaldo 1997; 1998a; 1998b; Selvaggio / Wilder 2001; Pante et al. 2012). Due to the often ambiguous nature of cut mark damage, these butchery indicators were typically excluded from the formation models.

From the beginning, Henry Bunn argued that hominins had early access to ungulate carcasses, based on his analysis of the FLK Zinj and FxJj 50 (1.6 Ma, Koobi Fora) assemblages (Bunn et al. 1980; Bunn 1983; 1991; 1997; 2007; Bunn / Kroll 1986; Bunn / Ezzo 1993). Over the years, several authors have challenged him on this point, most notably Binford and later Blumenschine and colleagues, both of whom we discussed previously. In his work on the FLK Zinj and FxJj 50 faunas, Bunn's arguments supporting early hominin access to carcasses hinges on the kinds of taxa found at the sites and their respective skeletal portions, as well as the number and location of cut marks on the bones (Bunn et al. 1980; Bunn / Bartram / Kroll 1988; Bunn 1983; 1991; 1997; 2001; 2007; Bunn / Kroll 1986; Bunn / Ezzo 1993). For the first point, he notes that there are cut marks on animals of all sizes at the sites, including elephants and hippos. The lack of axial elements in the assemblages leads him to interpret the localities as central places where hominins brought meat-bearing bones, probably to share with other members of the group. Bunn also notes the presence of gazelle-sized ungulates in the assemblages, and argues that large-bodied carnivores tend to completely consume animals in this size class, increasing the likelihood that hominins accumulated these taxa.

Regarding butchery, Bunn highlighted both the number and location of cut marks, particularly at FLK Zinj, which tend to cluster near the major muscle attachments of long bones. Taking this analysis a step further, he compared the taphonomic signatures of these archaeological assemblages with modern butchery practices of the Hadza, and found the location of cut marks to be similar (Bunn / Bartram / Kroll 1988; Bunn 2001). Noting that the Hadza scavenge approximately 20 % of their meat, he proposed that similar to modern foragers, Plio-Pleistocene hominins might have engaged in a kind of "power scavenging", which involves confronting carnivores such as jackals, cheetahs, leopards, and lions, and chasing them from their kills. Bunn (2007) interprets the FLK Zinj and FxJj 50 assemblages as forming when hominins accessed prey, either through power scavenging in the case of large carcasses or hunting smaller-bodied ungulates, during the day, then carnivores had uninterrupted access to the same carcasses at night.

Additional data from other early Lower Paleolithic sites and subsequent work by Manuel Domínguez-Rodrigo and Travis Pickering has supported Bunn's earlier claims. Domínguez-Rodrigo, in particular, conducted complementary actualistic studies to those done by Blumenschine and colleagues, and found that large felids such as lions tend to deflesh ungulate carcasses when they have primary access to the point that no meat remains on the midshafts of long bones for hominins to remove (Domínguez-Rodrigo 1999a). Therefore, the very presence of cut marks on long bone shafts, particularly of the upper limbs, indicate that meat was present, and hominins had access to carcasses before felids (Domínguez-Rodrigo 1997; 1999b; 2002; Domínguez-Rodrigo / Bunn / Yravedra 2014). Furthermore, his work shows that when provided early access to a complete carcass, human butchery concentrates cut marks on the midshafts of the upper limb bones where the bulk of the muscle tissue is found. Conversely, in situations where carcasses are already largely defleshed, human cut marks focus on lower limb bones and the ends of long bone shafts. These experimental data support Bunn's observations of the FLK Zinj faunas.

Other recent studies that apply the actualistic observations developed over the last few decades seem to agree with Bunn's original hypothesis, that hominins started gaining early access to meat between about 2.0 and 1.5 Ma, and it became increasingly important after this time. Excavators interpret this to be the case at El-Kherba (Ain Hanech, Algeria), which dates to 1.8 Ma (Sahnouni et al. 2013), the 1.5 Ma Okote Member (Koobi Fora, Kenya) (Pobiner et al. 2008), and the ST Site Complex at Peninj (West Lake Natron, Tanzania), which also dates to 1.5 Ma (Domínguez-Rodrigo et al. 2002). All three of these sites preserve cut marks at locations on bones that are unexpected if the carcasses were already defleshed by carnivores. Pickering and colleagues (Pickering et al. 2004; 2007; 2008) have observed a similar pattern at Members 1 through 3 at Swartkrans (South Africa). The precise dating of these layers is problematic, but they all formed between 1.8 and 1.0 Ma. Multiple researchers working on Upper Bed II (Olduvai Gorge, Tanzania) have made similar arguments based on the location of percussion marks, cuts, and bites on bones in the 1.70-1.34 Ma layers (Monahan 1996; Egeland/Domínguez-Rodrigo 2008; Domínguez-Rodrigo et al. 2009; 2014a; 2014b); JK2, Upper Bed III (1.15-0.8 Ma) at the site also contains evidence of early meat access by hominins, from either hunting or confrontational scavenging (Pante 2013).

In moving past studies of anatomical representations and taphonomic data, Bunn and colleagues (Bunn/Pickering 2010; Bunn/Gurtov 2014) use mortality profiles based on ungulate teeth in order to determine if hominins were hunting at FLK Zinj. The earlier of these two papers is in response to the long-standing hunting versus scavenging debate, and a recent discussion between Bunn and colleagues (Pickering/Bunn 2007; Bunn/Pickering 2010) and Bramble, Lieberman and colleagues (Bramble/Lieberman 2004; Lieberman et al. 2007) regarding the possibility that the ability to run prey to the point of hyperthermic shock was an important selective advantage for early *Homo*. Initially, Bramble and Lieberman (2004) proposed that endurance running would allow hominins to acquire meat through persistence hunting or competitive scavenging. This was met with stark criticism by Pickering and Bunn (2007), who contend that the mixed savanna-woodlands in which early *Homo* evolved are not ideal for endurance running or tracking, and point out that the majority of modern groups that utilize this strategy are found in hot, dry, environments. In our opinion, one important outcome of this study is the way in which the authors investigate the possibility of hominin hunting in the Plio-Pleistocene, and more significantly, the presentation of bovid mortality profiles using updated methodology and data not available in earlier papers.

Bunn and Pickering (2010) compare mortality data from the FLK Zinj assemblage to accumulations from several modern carnivore taxa, and natural background faunas from Bed I at Olduvai Gorge as well as three South African sites (Swartkrans, Komdraai A, and Gondolin). Bunn and Gurtov (2014) expand the sample to include more Plio-Pleistocene archaeological assemblages, ethnographic data from the Hadza, and natural catastrophic wildebeest drowning events. The authors use tripolar graphs to compare the faunas by plotting the proportion of juvenile, prime-aged, and old adults in the assemblages, following Stiner (1990) and Steele and Weaver (2002). Previous authors have found that prime-aged adult or mixed prime-aged/juvenile assemblages tend to characterize hominin hunting patterns in the Middle Paleolithic through Holocene, which are significantly different from assemblages formed by carnivores (Stiner 1990; 1994; 2002; 2005). In the initial study, Bunn and Pickering (2010) find that the remains overlap with what is expected for a living structure or prime-aged adult mortality profiles. Based on this, along with fetal or neonate individuals and sex data for waterbucks, the authors conclude that hominins practiced a mixed strategy of power scavenging from felid kills along with the successful hunting of older male and pregnant or recently pregnant female waterbucks. In the updated study, Bunn and Gurtov (2014) contend that early *Homo* was a successful ambush hunter of large bovids. They find a similar pattern for gazelle- and antelope-sized bovids at FLK Zinj, though there is a slightly stronger old adult bias (Bunn/Pickering 2010).

Archaeologists have found far fewer sites that preserve fauna and predate 1.0 Ma outside of Africa. Exceptions to this are Dmanisi (1.77 Ma, Republic of Georgia) (Lordkipanidze et al. 2007), 'Ubeidiya (1.4 Ma, Israel) (Gaudzinski 2004), Sima del Elefante (1.22 Ma, Atapuerca, Spain) (Rodríguez et al. 2011; Huguet et al. 2013), and Vallonnet Cave (1.07-0.99 Ma, Alpes-Maritimes, France) (Echassoux 2004). At all of these sites, cut marks on ungulate long bones lead the authors to conclude that hominins had early access to meat. Some take their interpretations further and suggest that the remains represent evidence of hominin hunting. Huguet et al. (2013) postulate that hominins occupying Sima del Elefante employed a mixed strategy of hunting or confrontational scavenging, along with occasional passive scavenging, based on cut and impact marks on bones; Echassoux (2004) draws a similar conclusion at Vallonnet Cave. Gaudzinski (2004) interprets the relatively narrow range of species (i.e., cervids and equids) with cuts found within the context of more diverse background faunas at 'Ubeidiya as evidence of specialized hunting by hominins. In general, the zooarchaeological evidence from Eurasia is similar, though less abundant and less heavily scrutinized, than that from contemporary African sites, but the conclusions are largely similar to those set forth by Bunn and his colleagues.

The contributions that attempt to understand hominin subsistence in the Lower Paleolithic before 1.0 Ma make it clear that sites from this time period are difficult to interpret and probably represent a range of circumstances. Some of the assemblages are primarily carnivore accumulations, while others imply multiple possible modes of access to meat for hominins. The variation found at these sites probably characterizes the nature of hominin meat acquisition strategies in the earlier part of the Lower Paleolithic in fairly realistic terms; instead of an all-or-nothing model pitting hominins versus carnivores for primary access to carcasses, there were likely a number of different methods of meat procurement for millennia when hominins first began to venture into the carnivore niche. And indeed, many more sites must be discovered and analyzed before we can fully grasp the situation surrounding the earliest hominin meat acquisition strategies. Similar to modern hunter-gatherers, Plio-Pleistocene foragers likely adopted a number of tactics for acquiring meat, including passive or confrontational scavenging, and occasional hunting of certain taxa (O'Connell/Hawkes/Jones 1988). Following decades of debate surrounding the location of bite marks, cut marks, and impacts, many of these studies illustrate the fact that interpretations are difficult to make without a full suite of taphonomic data. Further, we suggest that constructing mortality patterns of herbivores, such as those attempted by Bunn and colleagues (Bunn/Pickering 2010; Bunn/Gurtov 2014), are key to making the analytical leap from whether hominins were scavenging carcasses to fairly convincing evidence for hunting.

Evidence post-1.0 Ma

In the late Lower Paleolithic, after 1.0 Ma, there are far fewer well-studied African faunal assemblages, both compared to earlier times, and the same period in Eurasia. One such example is Elandsfontein (Western Cape Province, South Africa). This particular site preserves a hominin skullcap and Acheulean tools, yet it is poorly dated; Klein and colleagues (2007) place its formation between 1.0 Ma and 600,000 BP based on biostratigraphic comparisons. The authors note that the proportion of cut marks is fairly low (0.2 %) so the faunas were probably accumulated and modified by carnivores as opposed to hominins. Further, Klein et al. (2007) explore mortality profiles of zebras and cape buffalo, the two most common taxa at the site. They set up the expectation that carnivore-formed assemblages are roughly attritional (old-dominated) because young animals are thoroughly consumed by carnivores, while hominin assemblages are broadly catastrophic (high percentages of young and prime-aged adults) (Klein et al. 2007, 180-182). They establish that cape buffalo conforms to an attritional mortality profile, which supports their interpretation that carnivores were responsible for the assemblage. The zebra profile is catastrophic, but instead of attributing this to hominin hunting efforts, they propose that it reflects the formation environment of the assemblage along a shallow lakeshore or in marshlands (Klein et al. 2007, 183). It is also worth noting that Gaudzinski (2004) observed an identical (0.2 %) cut mark percentage at 'Ubeidiya, which contributed to her interpretation that certain taxa were probably hunted by hominins 1.4 Ma. This case study highlights the often subjective nature of interpreting the taphonomic record, and that there is still a long way to go before zooarchaeologists agree on the best way to apply mortality data.

In Eurasia, sites are regularly interpreted as providing convincing evidence that hominins had entered the hunting niche after 1.0 Ma. Much of the information we have about this period comes from southern Europe. Martinez et al. (2010) postulate that hominins were predators at 830,000 BP at Vallparadís in southern Spain. This is based on the diversity of taxa found at the site, as well as the represented elements and the mortality data, but the authors provide few details. Sierra de Atapuerca in northern Spain preserves a long sequence of hominin activity and subsistence data. Layer TDW4 at Gran Dolina (Atapuerca) is undated, but lies below 857,000-780,000 year-old deposits. Due to the location and kinds of butchery damage on the faunas, Huguet et al. (2013) concludes that hominins had primary access to the bones, which they interpret as hunting or confrontational scavenging by hominins. Multiple analysts have examined the faunal assemblages from layer TD6.2, also at Gran Dolina, which yields a date of at least 780,000 BP. Saladié et al. (2011) provide the most complete and updated presentation of the faunas (but see Diez et al. 1999 for an earlier version, and Huguet et al. 2013 for an additional summary). The faunal spectrum is fairly diverse, but skews to mammals in the 100-300 kg range. The assemblage is comprised primarily of limb and head elements, which the authors interpret as hominins mostly transporting carcasses to the site complete, then carnivores ravaging the more fragile axial elements (Saladié et al. 2011). Cut marks are common, and in instances where cut marks and carnivore gnaw marks are found on the same specimen, tooth marks are always on top of cuts, indicating hominins had primary access to the remains. Based on taphonomic damage and anatomical profiles, Saladié et al. (2011) postulate that groups of hominins hunted ungulates, then delayed consumption of animal tissues in order to carry meat back to the base camp to share with others in the group. The authors publish mortality profile data, and conclude that immature and adult animals dominate the assemblages. The methods divide ungulate ages into four different groups as opposed to other commonly used schemes that use three divisions (e. g. Stiner 1990; 2005; Steele / Weaver 2002; Weaver / Boyko / Steele 2011; Discamps / Costamagno 2015), and when their data are adjusted and plotted on a tripolar graph, a fairly clear prime-aged adult bias emerges, which many faunal specialists interpret as evidence for hominin hunting behaviors.

Moving to Israel, Gesher Benot Ya'aqov (MIS 20-18, ca. 815,000-710,000 BP) preserves a rich faunal spectrum along the edge of a paleolake (Rabinovich et al. 2008; Rabinovich / Biton 2011). Though the authors have identified a range of cervids, bovids, and megafauna, the most notable remains are those of fallow deer. Rabinovich / Gaudzinski-Windheuser / Goren-Inbar (2008) document repetitive butchery marks on at least ten individuals, which leads them to conclude that hominin hunters at the site understood prey anatomy, and also had the technical and communication skills necessary to process the carcasses in a standardized way.

The next available faunal assemblages date to more than 100,000 years later than Gesher Benot Ya'aqov. Caune de l'Arago Cave (France) contains at least four major archaeological deposits that span from 550,000 to 440,000 BP (Moigne / Barsky 1999; Rivals / Kacimi / Moutoussamy 2004). Depending on the layer, a different ungulate taxon dominates (reindeer, red and fallow deer, musk ox, and argali, from oldest to youngest layers), but in all cases adults are well-represented in the assemblages (Moigne / Barsky 1999; Rivals / Kacimi / Moutoussamy 2004).

Both sets of authors hypothesize that these heavily-butchered faunas were formed by hominin hunting practices, but Rivals/Kacimi/Moutoussamy (2004) present reconstructions of sex ratios and seasonality for all of the layers and conclude that hominins were following a non-selective hunting strategy, exploiting the most commonly available animals of a particular taxa in each time period.

In Great Britain, Boxgrove (MIS 13-12, ca. 490,000 to 425,000 BP) has cut bones in multiple archaeological layers from different ungulate taxa, especially cervids and horse, but also on some megafauna (Smith 2012; 2013). Most notable is a butchered horse (*Equus ferus*) individual with evidence of an impact mark on the scapula, which might have come from a wooden spear similar to those found at Schöningen (Roberts/Parfitt 1999; Smith 2012; 2013). The excavators and analysts interpret the remains as evidence for primary access through hominin hunting or confrontational scavenging, but do not specify which is more likely. Also in Great Britain, fauna found in association with lithics and fossil hominin remains at Swanscombe played an important part in the hunting versus scavenging debate of the 1960s-1980s. On the one hand, the excavator, John d'Arcy Waechter (1968; 1969; 1976), claimed that the site was evidence of a riverside hunting camp, while Binford (1985) argued that it actually represents hominin scavenging behaviors. In a recent reanalysis of the materials, Smith (2012; 2013) concludes that a combination of taphonomic factors and excavation methods actually does not leave enough evidence to support either claim, which is largely similar to the situation with Torralba and Ambrona that we discussed above.

Returning to the later layers at Sierra de Atapuerca in Spain, Galería preserves several archaeological layers, including GII and GIIIa, which date to roughly 500,000-460,000 BP. During this phase, the site was a natural trap for juvenile ungulates, which were subsequently scavenged by both hominins and carnivores (Huguet Pamies et al. 2001; Rodríguez et al. 2011). The authors hypothesize that hominins had access to carcasses before carnivores, and note that long bones were selectively transported away from the cave. Layer TD10.2 at Gran Dolina contains some of the most compelling early evidence for large game hunting we have presented so far. The deposit contains at least 60 individual bison carcasses that were heavily processed by hominins (Rodríguez-Hidalgo et al. n.d.). Rodríguez-Hidalgo et al. (n.d.) note the large number of axial elements in the assemblage, which leads them to conclude that the animals died at the site. Ageing data reflects a catastrophic mortality profile, and microwear analyses of the teeth indicates that the animals died in at least two seasons (late spring and early fall) (Rodríguez-Hidalgo et al. 2016; n.d.). Based on these multiple lines of evidence, the authors make the case that hominins engaged in communal hunting on more than one occasion, by using the contours of the cave as a natural trap for bison. This would have required an advanced level of planning, communication, and technological investment, which shows a fairly high level of cognition for late Lower Paleolithic hominins at Gran Dolina (Rodríguez-Hidalgo et al. n.d.).

Stopp (1993) presents the faunal remains from Hoxne in Great Britain, which was recently dated to MIS 11 (ca. 424,000-374,000 BP) (Ashton et al. 2008). The assemblage is not large, and while the author hypothesizes that hominins preferred horse (*Equus ferus*) and red deer at the site, it is impossible to determine whether hunting or scavenging was the method of meat acquisition (Stopp 1993). The faunal assemblage from Qesem Cave (400,000-200,000 BP) in Israel is much larger and has been studied in greater detail. Stiner and colleagues (2009; Stiner/Barkai/Gopher 2011) present a sample identified from multiple layers in the site. They make a strong case that hominins using the cave were hunting, in particular medium to large bodied ungulates, then were preferentially transporting meat- and marrow-rich elements to the site in order to share with other members of the group. They also use mortality profiles to establish that hominins were intentionally targeting prime-aged adult ungulates, in this case fallow deer, which is consistent with the hunting niche we see later among Middle and Upper Paleolithic hominins (Stiner/Barkai/Gopher 2009; 2011). In a later study, Blasco and colleagues (2014) present a more focused analysis of a single hearth area at Qesem. The fauna from the hearth largely agrees with Stiner's studies, with a dominance of fallow deer and a large number of high-utility elements that were probably shared with a larger group. However, the authors seem to find a slightly wider mortality profile for fallow deer, which they interpret to reflect cooperative hunting, possibly of multiple animals at once. We should note that their age categories conform to those used by Saladié et al. (2011), and are not consistent with those found in earlier studies of Qesem (Stiner/Barkai/Gopher 2009; 2011). If we apply the conventions set forth by Stiner, Steele, and Weaver (Stiner 1990; 2005; Steele/Weaver 2002; Weaver/Boyko/Steele 2011), the hearth area at Qesem does not differ from the larger sample. Despite this difference in analytical techniques, Blasco and colleagues (2014) note the threads of modernity that seem to emerge during this period at Qesem, at least in terms of cooperative hunting and meat sharing, which we also find in common with Late Pleistocene hominins.

We now move to the latest set of sites in this review, which were formed in the warm interglacial of MIS 9. Level 6 at Orgnac 3 (France) dates to about 300,000 BP (Moigne/Barsky 1999; Moncel/Moigne/Combier 2005). The cave contains heavily butchered cervid, bovid, horse, and pig bones, many of which were brought to the site complete. The authors note repetitive fracture patterns, particularly on horse long bones, which they interpret as more organized butchery than what is typically seen at older sites (Moigne/Barsky 1999; Moncel/Moigne/Combier 2005). Blasco and colleagues (2013) present faunal data from the 300,000 year old layer TD10-1 at Gran Dolina and similarly-dated levels at Bolmor Cave (Spain). In addition to highlighting some incidences of small game use (see above), the authors mainly find that hominins exploited a wide range of taxa in these particularly diverse environments. In a more detailed look at the TD10-1 Gran Dolina assemblage, Rodríguez-Hidalgo et al. (2015) make the case that during this period the site was used as a hominin base camp. They note a dominance of red deer, which they attribute to selective hunting. The authors record ample evidence of butchery, and note that carcass transport patterns seem to indicate a preference for marrow-rich elements. Mortality data from the site indicate a preference for prime-aged adult animals, so the authors conclude that occupants of the site had entered into the hominin prey niche (Rodríguez-Hidalgo et al. 2015). We should note that the authors used the tripolar age grouping model, as opposed to dividing animals into four cohorts.

Our final example is Schöningen (Germany, 300,000 BP), which also contains strong evidence for hunting. The site is situated alongside a paleolake and preserves the remains of over fifty horses, in addition to nine wooden spears, which if interpreted correctly, represent the earliest hunting implements recorded to date (Thieme 1997; Voormolen 2008; Conard et al. 2015b). The faunas are overwhelmingly comprised of large-bodied Pleistocene horses (*Equus mosbachensis*) with extensive evidence of meat removal and marrow extraction (Voormolen 2008; Van Kolfschoten 2014; Starkovich/Conard 2015; Van Kolfschoten/Buhrs/Verheijen 2015). Body part profiles are largely complete, indicating that the animals died at or near the site (Voormolen 2008; Starkovich/Conard 2015). Mortality data conform to a catastrophic age profile, with a large number of prime adult and juvenile animals in the death assemblage (Voormolen 2008). Originally, when Schöningen was first excavated, archaeologists interpreted it as a mass kill (e.g. Thieme 2000; 2005; 2007). However, with further analysis of the faunal remains and isotopes, multiple lines of evidence point to a number of kill events of one or many animals at a time, along with the accumulation of a few individuals that died naturally (Musil 2007; Voormolen 2008; Julien et al. 2015; Kuitems et al. 2015, but see Van Kolfschoten 2014 for an argument favoring one large event along with the background accumulation of many animals). Regardless of the exact formation processes of the site, the combination of mortality profiles, a large number of heavily processed horse carcasses, and wooden spears leads to a compelling argument for hominin hunting at Schöningen.

After 1.0 Ma, the evidence for hominin hunting, and certainly primary access to meat during scavenging situations, seems to be more solid. Samples from this period tend to be overall larger and more numerous than before 1.0 Ma, so archaeologists are able to apply a greater range of analytical techniques to available datasets in order to more securely interpret hominin behaviors. In addition, there are a few instances of more direct evidence for hominin hunting: the impact fracture on the horse scapula at Boxgrove (Roberts/Parfitt 1999; Smith 2012; 2013), the apparent communal hunting of bison at Gran Dolina (Rodríguez-Hidalgo et al. 2016; n.d.), and the dozens of horses found associated with wooden spears at Schöningen (Thieme 1997; Voormolen 2008; Conard et al. 2015b). It is worth noting that there seems to be a fundamental difference, not just in the archaeological data, but also the interpretive framework many analysts use when trying to understand their results from this period. With the exception of a few authors (e.g. Huguet Pamies et al. 2001; Echassoux 2004; Gaudzinski 2004; Bunn/Pickering 2010; Bunn/Gurtov 2014), most zooarchaeologists working on sites that date to before 1.0 Ma do not explicitly state that hunting by hominins was a possible route to meat acquisition. Yet after this time, Klein and colleagues (2007) stand out as the lone voices that deny hunting as a possibility. Perhaps the line is more appropriately drawn between Eurasian and African sites regardless of their chronology; analysts working in Europe are much quicker to propose hunting, while those studying African sites hedge on this issue, almost as if it is natural to assume that hominins that are capable of leaving Africa were also advanced enough to hunt large-bodied game. Whatever the explanation, these *a priori* assumptions seem to color the conclusions drawn by faunal analysts. In several cases, which we highlighted above, nearly identical evidence from sites in different regions or times is used to argue completely opposite positions. For this reason, in addition to using multiple lines of consistent evidence for identifying hominin hunting or primary meat acquisition, it would be useful for faunal analysts to at least adopt a consistent null hypothesis when approaching Lower Paleolithic zooarchaeological assemblages. The most prudent starting point for analysts, given the evolutionary history of hominins before the advent of stone tools, is to assume that Lower Paleolithic hominins were *not* actively involved in large game procurement. This should ensure that arguments to the contrary are supported by convincing data, which is certainly the case with many (but not all) examples cited above, and would help us better understand the appearance and importance of early hunting and active scavenging behaviors.

Impacts on carnivore communities

Throughout this paper carnivores have played a consistent, though somewhat periphery, role in our discussion. At the oldest sites, carnivores are important because hominins might have directly competed with them for carcasses, or even capitalized on their hunting efforts through kleptoparasitism (meat theft). It is interesting to consider the effect this might have had on the evolutionary success of top predators. Many authors have investigated this question through studies of carnivore behavior, migrations, and the modelling of carnivore niches (Turner 1988; Marean 1989; Lewis 1997; Werdelin/Lewis 2005; 2013; Croitor/Brugal 2010; Rodríguez et al. 2012), and it seems plausible that hominins had an impact on the predator guild not long after they regularly began to incorporate meat into their diets.

Along these lines, one question that has surfaced in the literature is whether or not hominins targeted specific predators from which to scavenge, for example cheetahs (*Acinonyx pardinensis*) or certain species of sabertooth cat (e.g. *Megantereon*) (Lewis/Werdelin 2010; Hemmer/Kahlke/Vekua 2011). Hemmer/Kahlke/Vekua (2011) present carnivore remains from Dmanisi and point out that a single adult cheetah has about 1,000 kg of meat per year stolen by other carnivores, which might have been a significant food source for early hominins. Similarly, Lewis and Werdelin (2010) explore the hypothesis that East African Plio-Pleistocene hominins specifically targeted the sabertooth *Megantereon* for scavenging opportunities. However, they note that this kind of dynamic would have exerted a negative selective pressure on the sabertooth. Not only is there no evidence for this, but both *Megantereon* and hominins left Africa at roughly the same time and continued to co-exist for many millennia afterwards. They hypothesize that after 1.8 Ma, hominins started to become a significant part of the ecosystem as scavenging meat-eaters. This shift likely destabilized the entire carnivore guild, though it was not extreme enough to cause the extinction of the many carnivore taxa that disappear at this time (Lewis/Werdelin 2010).

In a discussion of changes in the broader African carnivore guild, Werdelin and Lewis (2013) model the functional richness and evenness of the ecosystem between 3.5 and 1.5 Ma. The authors find that there was a depression in both the number of large-bodied carnivores, and a reduction in overall niche width after 2.0 Ma, which is about the same time we start to see multiple examples of hominin meat acquisition. Even more compelling, the first clear decline appears among large African omnivores at 2.0 Ma, which likely would have been the first group of species impacted by largely herbivorous hominins starting to eat meat. This is followed by a decrease in canids and hypercarnivorous felids (i. e., animals whose diets include more than 70 % meat, see Holliday/Steppan 2004) by 1.5 Ma. Werdelin and Lewis (2013) are quick to point out that a climatic explanation might also exist, particularly for the disappearance of omnivorous taxa, though this is probably not the case for hypercarnivores, and concludes that one possible cause of this change to the carnivore guild was the appearance of more meat-reliant hominins after 2.0 Ma.

Egeland (2014) examines this question from a different angle, by looking specifically at carnivore-hominin competition at several localities at Olduvai Gorge Beds I and II. He points out that sites with evidence for exploitation by both carnivores and hominins must have formed fairly quickly since carcasses are only edible for a finite amount of time, particularly in hot climates. This is directly related to competition because it addresses the degree of avoidance between early hominins and carnivores. In the study, Egeland (2014) conducts a multivariate analysis based on lithic densities and butchered bones at some of the Bed I and II sites. He finds no negative correlation between carnivore intensity and hominin behavior, and in fact at Bed II there is an increase in lithic densities when carnivore activities intensify. This leads him to conclude that even by 1.4 Ma, hominins were not intentionally avoiding places on the landscape where carnivores were active, and were instead successfully competing with carnivores for space and resources (Egeland 2014). He proposes some possible reasons for this success, such as changes in body size, group size, or technological factors (e. g. spears, fire, etc.), though he does not speculate as to which factor was the cause. Egeland (2014) also cites work by Werdelin and Lewis (2005), who place the extinction of multiple species of sabertooth hypercarnivores at about the same time.

Croitor and Brugal (2010) explore similar questions regarding carnivore guild dynamics in the Plio-Pleistocene of Eurasia. At 1.8 Ma, several significant taxa including *Homo* entered Eurasia, along with the relatively flexible or social carnivores: jaguar (*Panthera onca*), hunting dog (*Lykaon*), and giant hyena (*Pachycrocuta brevirostris*). After this time, and especially after 1.0 Ma, many of the solitary hypercarnivores (mostly felids) went extinct and social hunters (e. g. lions, striped hyenas, wolves) and omnivores expanded (Croitor/Brugal 2010). The authors compare this to similar changes in East Africa, specifically the decline of specialist carnivores and corresponding expansion of generalist carnivores (canids and *Panthera* sp.) (Werdelin/Lewis 2005). Croiter and Brugal (2010) hypothesize that this benefitted hominins who entered Eurasia into an impoverished predator guild.

Looking at southern Europe, Rodríguez et al. (2012) reconstruct the predator guild between 2.6 and 0.78 Ma. They find relatively low levels of carnivore competition in early and later phases of their study, but an extremely competitive situation shortly before 1.2 Ma, which either coincides with or slightly postdates the earliest arrival of hominins. The authors take the position that hominins probably entered southern Europe early enough that the carnivore guild was still quite competitive. Based on this, Rodríguez et al. (2012) conclude that early hominins in Europe were most likely flexible feeders, a position that supports the model proposed by Ungar / Grine / Teaford (2006) that attributes the overall success of hominins to flexible omnivory. However, Rodríguez et al. (2012) also note that a large number of scholars interpret the decline of carnivores and appearance of hominins in southern Europe as related phenomena (e.g. Turner 1992; Martinez-Navarro / Palmqvist 1996; Arribas / Palmqvist 1999; Palombo 2010).

In general, it is difficult to determine the cause-and-effect nature of the evolutionary pressures between carnivores and hominins in the Plio-Pleistocene because the temporal resolution is so poor. However, the carnivore-based studies we reviewed above indicate that hominins might have begun to impact certain predator communities between 2.0 and 1.5 Ma. This is interesting, as it corresponds well with the earliest relatively widespread evidence for meat eating by hominins. This also suggests that by the time hominins entered Eurasia, they were already engaged in some degree of competition with carnivores. A particularly striking line of evidence regarding carnivore-hominin competition regards situations where cut marks and bite marks overlap on a single faunal specimen. Though this is rare, it occurs at enough sites and typically seems to follow the same pattern that it is important. Starting at sites dating to 1.8 Ma, there are multiple examples of carnivore bite marks overlying cut marks from hominin stone tools. Analysts have observed this at El-Kherba (1.8 Ma; Sahnouni et al. 2013), Dmanisi (1.77 Ma; Lordkipanidze et al. 2007), Gran Dolina (ca. 800,000 BP; Blasco / Rosell 2009; Rodríguez et al. 2011), Boxgrove (490,000-425,000 BP; Smith 2012; 2013), and Schöningen (300,000 BP; Voormolen 2008; Starkovich / Conard 2015, but see Van Kolfschoten 2015 for one or two examples of cut marks on top of bites). We can only explain these observations if 1) carnivores actively chased hominins off of carcasses, or hominins were concerned about this threat, or 2) carnivores had secondary access to animal remains after hominins were done. Based on multiple lines of evidence we have presented in this paper we argue that the latter is the case. Within this discussion it is important to keep in mind that even if hominins on the species- or population-level gained primary access to meat or entered the carnivore guild between 2.0 and 1.5 Ma, encounters between individual hominins and carnivores probably did not always favor the hominin. Furthermore, it is likely that early hominins and carnivores avoided each other, at least in the sense that the two groups did not seek one another out to initiate conflicts.

Discussion and Conclusions

The timing and nature of the origins of meat acquisition by hominins are among the most important and difficult questions in understanding human evolution. Access to a wider range of protein and other nutrients certainly had an effect on the cognitive capabilities of early hominins, but it was also critical from a co-evolutionary point of view in terms of the competitive challenges between hominins and carnivores. Based on the evidence we have reviewed here, it is difficult to pinpoint an exact date for the origins of meat acquisition in general, or hunting behaviors in particular, and in fact such a conclusion would oversimplify the actual situation. One reason for this is that the incorporation of meat into the diet was not a one-time event that catalyzed a universal shift to meat eating. Dietary flexibility is one of the most successful adaptations of the hominin lineage (e.g. Ungar / Grine / Teaford 2006), so there is no reason to believe that once meat-eating began it was adopted uniformly between or even within populations. The second reason is that meat acquisition for many carnivores exist along a continuum between hunting and scavenging, and omnivorous hominins are no different. Since we know that modern hunter-gatherers regularly subsist on some percentage of scavenged meat (e.g.

O'Connell/Hawkes/Jones 1988; Bunn 2001) despite having the tools and skill to shift completely to a hunting-based diet, there is little reason to believe that any past hominin groups acquired meat entirely through hunting. We also cannot forget that some of our closest primate relatives occasionally eat meat without the aid of stone tools, so it is possible that meat-eating actually has its origins in a form unrecognizable in the archaeological record before ape and hominin lineages even split. This hypothesis is difficult to test, though most of the meat-eating we focus on in this paper involves the consumption of large animals (relative to hominin body size), which is not found among monkeys and the great apes, so it is likely that this behavioral pattern appeared later. Despite these many difficulties, we do see some trends in the literature that allow us to draw some conclusions regarding the origins of meat eating by hominins.

First, evidence from Gona, Omo, and Dikika indicate that hominins had occasional access to meat (and fish) before 2.0 Ma. This is important for marking some of the earliest meat eating, though it does not seem to represent a fundamental or universal shift in subsistence strategies to regular carnivory. An increase in evidence for meat eating, including aquatic resource exploitation, scavenging, and possible occasional hunting of large terrestrial mammals, appears in both Africa and Eurasia between 1.8 and 1.5 Ma. This begs the question of whether hominins started exploiting meat on a more regular basis before or after they left Africa, which unfortunately we cannot address with the current state of the data. It is also significant that there was a fairly substantial change in the carnivore guilds of Africa and Eurasia at about the same time. This is reflected in the localized extinction of certain taxa (e.g. sabertooth cats), but also broader behavioral groups of carnivores (e.g. some omnivores and specialized hypercarnivores). Due to the temporal resolution of the sites from this period, it is unclear if the entrance of hominins into the carnivore guild drove some or all of these processes, or if the natural evolution of the guild left a niche open for omnivorous hominins. There is compelling evidence that hominins were able to compete on a fairly high level with other carnivores even at this early stage, for example carnivore bite marks found on top of cut marks at multiple sites starting at 1.8 Ma, or Egeland's (2014) conclusions that intense carnivore competition had little effect on hominin activities at 1.4 Ma at Olduvai Gorge Beds I and II.

The second conclusion we draw is that the evidence for hominin hunting after 500,000 BP is clear. This is particularly the case in Eurasia where most sites dating to this time period are located, but there is no reason to believe that hominin hunting was also not well-developed in Africa at the same time. It is possible, or even likely, that there is earlier evidence for hunting, perhaps at ca. 800,000 BP (e.g. Vallparadís or Gran Dolina TD6.2) or even at 1.75 Ma (FLK Zinj), but after 500,000 BP sites such as Gran Dolina TD10.2, Boxgrove, and Schöningen provide irrefutable evidence.

As a side point that has less to do with the archaeological record, we notice some difficulties in comparing data between the sites, as well as some interesting differences in the null hypotheses and interpretations of faunal analysts working in different time periods and geographic regions. To the first issue, different methods in terms of data collection and interpretation are definitely not unique to Lower Paleolithic zooarchaeology, nor is there an obvious solution to this problem. However, it does seem that the highest profile debates on this topic (i.e., primary meat acquisition at Olduvai Gorge) center around different scholars approaching the exact same assemblages differently by highlighting one or two lines of evidence (e.g. location of cut marks, location of bite marks, species representation, etc.), and authors who take into account as much of these kinds of data as possible are able to support their arguments more convincingly. We agree with many other authors (e.g. Klein 1981; 1982; Klein/Allwarden/Wolf 1983; Klein/Cruz-Uribe 1984; Stiner 1990; 2002; 2005; Bunn/Pickering 2010; Bunn/Gurtov 2014) that establishing mortality profiles for prey taxa in archaeological assemblages is critical to attempting to understand if faunas were formed by carnivores or hominins.

And while the tripolar system established by Stiner (1990; 2005) is extremely popular, revisions by Weaver, Steele, and colleagues (2002; 2011), and more recently Discamps (2015) provide mathematically based updates to the model that highlight the importance of understanding the herd structure of individual taxa (see also Kahlke/Gaudzinski 2005; Stiner 2005 for more examples of this). Therefore, analyses of Lower Paleolithic assemblages should ideally include species abundance, butchery, fragmentation, carnivore, and mortality data whenever possible, as well as isotope and tooth meso- and micro-wear analyses.

To the second issue, it would be beneficial if faunal analysts studying the Lower Paleolithic could at minimum agree on a null hypothesis. Since one of the main goals of this period is to establish the origins of hominin meat acquisition or hunting, it seems that the burden of proof should be on the side arguing that hominins were established hunters. This seems like a pragmatic solution until we have a larger set of data from this time period, and indeed this approach is the already-established pattern, particularly among archaeologists working in Africa or on pre-1.0 Ma sites.

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MARTIN STREET

SUB-AQUATIC DISPOSAL OF BUTCHERING WASTE AT THE EARLY MESOLITHIC SITE OF BEDBURG-KÖNIGSHOVEN

Abstract

The early Mesolithic site of Bedburg-Königshoven was discovered in the Garzweiler open-cast lignite mine (German Lower Rhineland) at the end of the 1980's. A four month salvage operation recorded the 3D location of all identified finds and wet-sieving ensured the contextually secure recovery of smaller material. Pollen analysis and radiocarbon date Mesolithic activities at the site to the initial Preboreal warming. Among the more remarkable finds are two intentionally modified antler frontlets and the skull of a dog. The find-bearing horizon at Bedburg was formed under sub-aquatic conditions in the still or very slow moving water of a palaeochannel of the River Erft. It was not expected that distribution plots of finds deposited underwater would reveal any spatial patterning meaningful for human activity at the site. In fact it was possible to identify clear spatial sorting of well preserved (mainly large mammal) faunal remains which, in combination with zooarchaeological analysis of cut and impact marks, located sites of repetitive processes of butchery and disposal for specific elements of the carcass. Since faunal material deposited upon terrestrial surfaces will generally be preserved only poorly or perhaps not at all, faunal waste deposited in adjacent bodies of water can provide better insights into the details of how an animal carcass was processed.

Keywords

Early Mesolithic, initial Preboreal, sub-aquatic discard, spatial patterning, butchering processes

Introduction

The following presentation examines the context of early Holocene finds recovered by salvage excavations at Bedburg-Königshoven, an early Mesolithic camp discovered at the end of 1987 during quarrying at the Garzweiler open-cast lignite mine. The site was located west of the lowland Cologne Embayment of the Lower Rhine Valley in the valley of a tributary, the River Erft (Street 1989a; 1991; 1995) (**fig. 1**).

The discovery of an early Holocene archaeological site in stratigraphic context and with well preserved faunal remains, both features until then almost unknown for the period in the region, were reason enough to initiate a campaign of salvage excavation. Recognition of an antler frontlet analogous to those from Star Carr (Clark 1954) provided a further incentive for carrying out exhaustive and intensive investigations of the site over just four months in winter before its final destruction at the beginning of 1988. Much of the original site had in fact already been removed by railway construction in the 19th century, long before lignite quarrying began. Con-

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Fig. 1 Location of the Bedburg-Königshoven initial Mesolithic site on the western edge of the Cologne Embayment and at the boundary between the North European Lowland and the Central European upland zone. – (Map created by S. B. Grimm).

fronted with the isolated block of sediment at the centre of the lignite quarry, the prospects for any kind of "landscape archaeology" seemed remote. Fortunately, identification of the precise position of the site and consultation of historical maps together provided a topographical and geomorphological context for the site.

In the field it was quickly recognized that only deeper levels of limnic deposits had survived. Terrestrial areas of the site had been entirely destroyed, ruling out the possibility of locating intact settlement features such as dwelling structures or other zones of dry land activities. It was therefore not expected that plotting material recovered from off-bank limnic deposits would identify any meaningful spatial patterning. Unexpectedly, particularly in the case of faunal remains, spatial plotting did reveal meaningful distributional sorting. In combination with zooarchaeological analyses of the mainly large mammals this allows identification of locations of butchery and disposal for specific elements of the carcass and even recognition of repetitive processes.

The information obtained for the Bedburg site can be viewed at a number of different scales. At a macro-scale of kilometres there is the question of site placement in the geographical and human landscape. At a meso-scale of metres (within the area of the site) there is the information pertinent to behaviourally related activities and taphonomic factors before and during final deposition. Even at a micro-scale of centimetres it is exceptionally possible to identify very short-term or minor events, or indeed absence of secondary contextual modification.

Despite initial difficulties, spatial analyses of the Bedburg site can provide a meaningful contribution for the interpretation of site location, activities and depositional processes in hunter-gatherer waterside contexts.

Site location

Upon discovery of the Bedburg site all that remained at the centre of a huge area already stripped of overburden was an isolated triangular block of late

Pleistocene and Holocene deposits severely truncated in all dimensions by earth-moving activities (**fig. 2**). A first priority was therefore to establish any sort of geographical or chronological context for the encountered situation.

Reconstruction of the original geography of the Bedburg locality using historic maps (**fig. 3**) shows that the site was located at the northern edge of a meander of the River Erft, at the foot of gently sloping land bordering on marshland. It is at the narrowest point of the valley and sheltered from the north by a ridge of higher ground. Valleys draining into the meander from the North and West would have served as useful access routes between the valley bottom wetlands occupied by the site and the higher locations of the hinterland. They also possibly contained streams providing a source of fresh (clean and running) water for the site. The *Pielskamp*, a ridge of higher ground extending out into the valley, may have provided a natural causeway located strategically at a point suitable for hunting expeditions returning from the marshy valley floor. The advantages of the location for the exploitation of a range of resources are obvious.

Chronology

The surviving stratigraphy at the Bedburg site (**fig. 4**) comprised a sequence of deposits formed under initially sub-aquatic conditions in a palaeochannel of the River Erft (Behling 1988; Ikinger 1989; Behling/Street 1999). Basal coarse gravels were succeeded by finer sands grading into silts, all indicative of a process of channel infilling, probably as a result of the meander becoming cut off from the active Erft watercourse. A thin organic band (described as a sapropel formed at the top of the largely mineral deposit) represents a period of very warm temperatures (shown by high pollen values for *Typha latifolia*) and was itself overlain by calcareous and organic limnic deposits (gyttja) formed under still or very slowly moving water. This deposit enclosed the archaeological material. The sub-aquatic limnic sediments were themselves covered by peat formed during overgrowth of the now infilled channel, at the base reed peat followed by birch carr. The nature of the sedimentation process in this fluvial and wetland environment ensured optimal preservation of bone and some other organic materials. Pollen

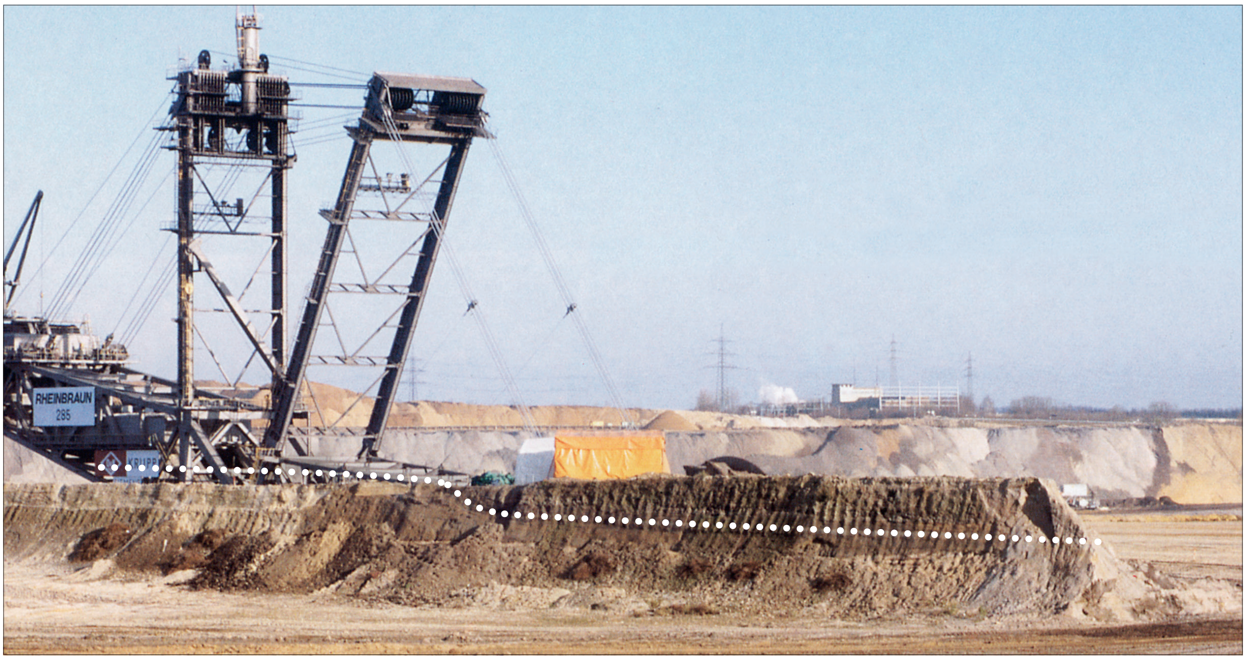

Fig. 2 Block of late Pleistocene and early Holocene sediments left by quarrying at the centre of the Garzweiler open cast lignite mine. The broken white line indicates the find bearing level.

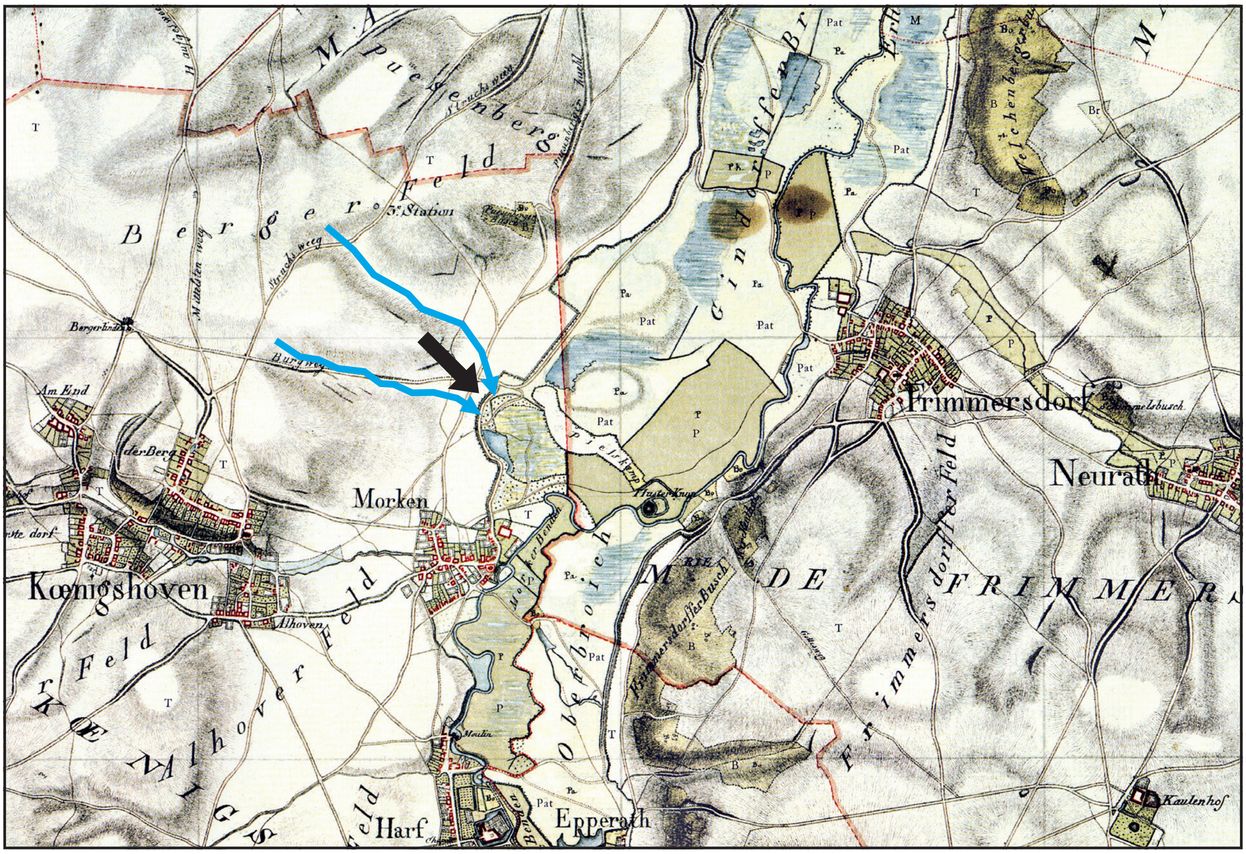

Fig. 3 Location (arrow) of the Bedburg-Königshoven initial Mesolithic site at the northern edge of a palaeo-channel of the River Erft, a tributary of the Rhine. Historic maps show valleys draining into the Erft meander close to the site. These may have served as routes between higher locations and the low-lying wetlands. – (Map taken from Sheet 59, Grevenbroich, of the "Kartenaufnahme der Rheinlande durch Tranchot und v. Müffling 1803-1820", Scale = 1:25,000. Landesvermessungsamt Nordrhein-Westfalen).

analysis and radiocarbon dates taken throughout the stratigraphic sequence provided an early Holocene age for the site (Behling 1988; Behling/Street 1999). The lowermost organic band provided two radiocarbon dates on small wood fragments which fell exactly at the Pleistocene-Holocene boundary. Dates for small wood fragments from the layer containing the archaeological lithic and faunal material gave a mid-Preboreal age, while the lowermost of the overlying peat deposits were dated to the late Preboreal. The date of Mesolithic human activity at the site thus seemed to be very precisely constrained to the middle of the Preboreal pollen zone.

Attempts to date faunal material directly using conventional radiocarbon measurement provided heterogeneous and highly anomalous results extending from the early Younger Dryas until the late Preboreal and younger and were rejected as unreliable, probably as a result of unknown contaminants. Recently obtained AMS results for a series of bones assigned to several distinct aurochs individuals (**tab. 1**; Street et al. in prep.) unequivocally assign the human occupation of the Bedburg site to the very beginning of the Preboreal at the time of the initial Holocene rise in temperature (**fig. 4**). This would make them contemporary with a dated organic band characterized by thermophilous plants, which is located below the gyttja containing the archaeological assemblage. This implies that the gyttja deposit must have formed subsequently to the activities represented by the faunal and lithic material. This represents a logical sequence of events since the gyttja would have been formed by the binding and precipitation of dissolved carbonate by water borne algae during the silting up of the meander. Most of the discarded remains of the Bedburg occupation appear to have been rapidly

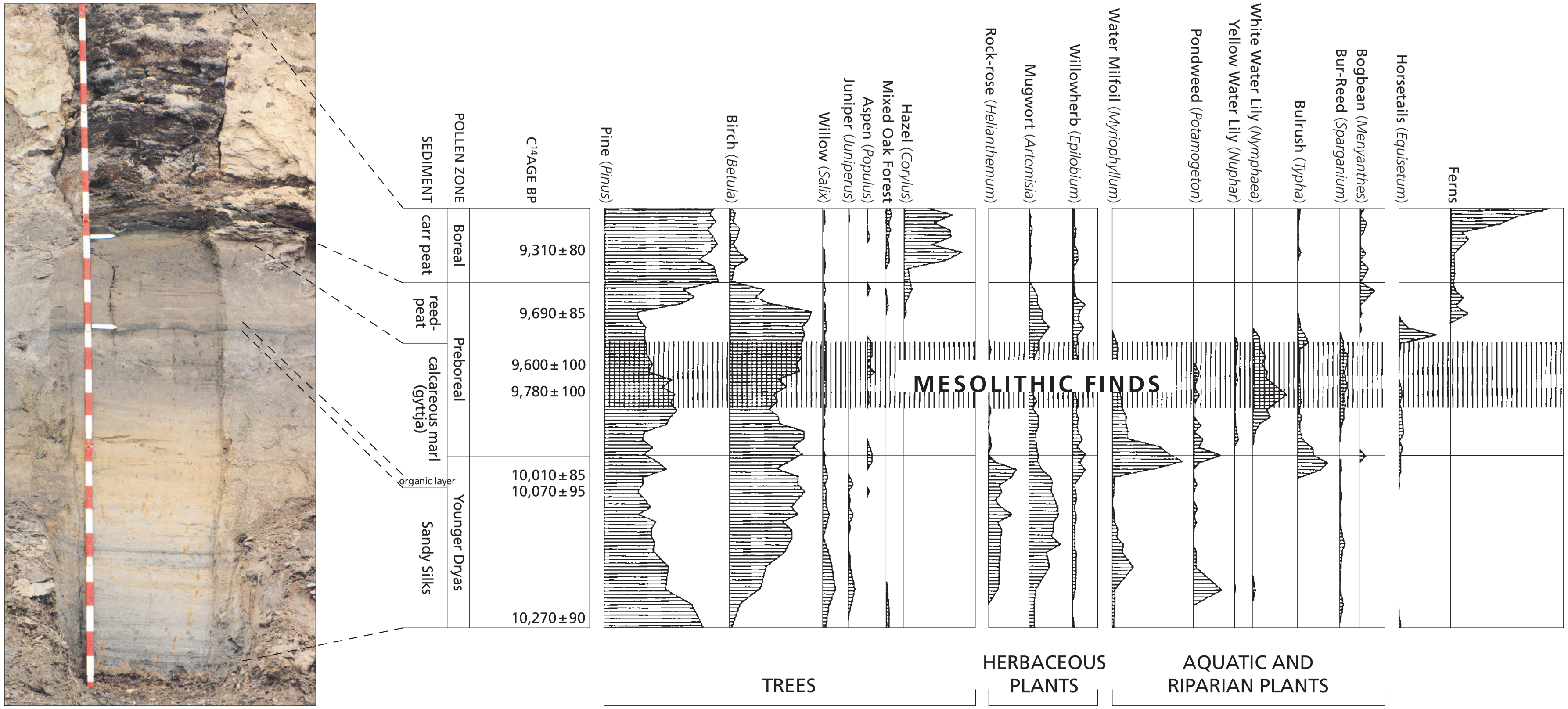

Fig. 4 Section at the Bedburg-Königshoven initial Mesolithic site and summary of palynological analysis (Behling 1988; Street 1989a). The top of the intact section is formed by 15-20 cm of dark brown compact and poorly decomposed late Preboreal reed (*Phragmites*) peat (immediately above the upper white arrow), overlain by strongly decomposed and compressed brown carr peat formations of Boreal age. Yellow deposits to the right are the infill of sub-recent peat-cuttings. Below the upper white arrow is a dark grey-green calcareous and sandy fine detritus mud (gyttja with *Chara oogonia*) which contains the archaeological material. The lower white arrow marks a dark, black-grey calcareous sandy fine detritus mud, which is dated to the initial Preboreal (10,010±85 14C BP and 10,070±95 14C BP) and contemporary with human occupation. This overlies a sequence of grey calcareous sandy mud with yellow sand lenses merging with increasing depth into calcareous yellow fine sand.

Tab. 1 Summary of radiocarbon dating for Bedburg-Königshoven (results calibrated with CalPal and OxCal 2016).
Conventional radiocarbon dates were obtained at the Cologne laboratory on plant remains sampled immediately after discovery of the site and during excavation. The latter were taken through the entire surviving Bedburg sequence (fig. 4) from the contact between terrace gravels and basal sands (Younger Dryas) to peat of Boreal and Atlantic age.
Subsequently five conventional 14C dates were produced for aurochs bone by the Cologne laboratory in the early 1990s. Results scatter widely, extending far back into the Younger Dryas, and this was interpreted as a result of unexplained methodological problems. The dates were and are rejected as unreliable indicators of the true age of the site, although the one plausible result (KN-4136) is reproduced here.
New direct dates on aurochs remains have been produced by the Cologne AMS laboratory. Although a number of results were initially rejected on methodological grounds, the repeat-dating following appropriate and more stringent pre-treatment protocols produced consistent results for all samples. The still unpublished dates (given here only as calibrated values) assign the hunting and butchery of aurochs to the very beginning of the Holocene warming episode.

Lab ID	14C date	SD	Context	Material	cal BC (CalPal)	SD	cal BC (OxCal)	Reference
KN-3883B	9540	120	Level B or C (preliminary sample)	peat	8933	190	9252-8611	Street 1991; 1993: Street/Baales/Weninger 1994
KN-3998	9600	100	101/103 Vt 3/4, level C1 (sample 4)	wood	8998	163	9260-8722	Street 1991; 1993: Street/Baales/Weninger 1994
KN-3883A	9660	120	Level B or C (preliminary sample)	peat	9038	177	9318-8711	Street 1991; 1993: Street/Baales/Weninger 1994
KN-4001	9690	85	93/105, level B (sample 7)	reed peat	9074	156	9290-8820	Street 1991; 1993: Street/Baales/Weninger 1994
KN-3999	9780	100	100/107 Vt4, level C1 (sample 5)	wood	9176	174	9461-8823	Street 1991; 1993: Street/Baales/Weninger 1994
COL 2669.2.1			87/108-4	bone, aurochs 4, *os petrosum*	9560	148	9700-9330	Street et al. in prep.
KN-3997	10010	85	83-85/106-110 (sample 3)	wood from organic band	9598	192	9981-9292	Street 1991; 1993: Street/Baales/Weninger 1994
COL 2674.1.1			85/105-3	bone, aurochs 9, metacarpus	9574	156	9768-9329	Street et al. in prep.
COL 2672.1.1			91/107-1	bone, aurochs 2, humerus, juvenile	9579	158	9772-9339	Street et al. in prep.
KN-4136	10020	100	96/108-1	bone, aurochs rib	9626	213	9892-9292	Street 1991; 1993: Street/Baales/Weninger 1994
COL 2680.2.1			104/102-1 (Streu 33)	bone, aurochs 8, *os petrosum*	9608	151	9805-9385	Street et al. in prep.
COL 2675.1.1			93/110-1	bone, aurochs 10, metacarpus	9617	158	9819-9368	Street et al. in prep.
COL 2948.1.1			93/106-2	bone, aurochs 7, skull, horn core	9641	161	9855-9394	Street et al. in prep.
COL 2673.1.1			97/107-3	bone, aurochs 11, metacarpus	9668	175	9877-9436	Street et al. in prep.
KN-3996	10070	95	83-85/106-110 (sample 2)	wood from organic band	9701	233	10043-9324	Street 1991; 1993: Street/Baales/Weninger 1994
COL 2671.2.1			97/107-4, 7	bone, aurochs 3, *os petrosum*	9758	191	10036-9647	Street et al. in prep.
COL 2974.1.2			93/106-2	bone, aurochs 6, *os petrosum*	9763	204	10045-9455	Street et al. in prep.
KN-3995	10270	90	(sample 1)	wood from basal sandy silts	10134	255	10466-9695	Street 1991; 1993: Street/Baales/Weninger 1994

removed from the influence of terrestrial weathering by intentional discard into water. It now seems very probable that the bed of this body of water was not, as previously concluded, already completely covered by the gyttja deposit (into which the material would have sunk) but will have been heterogeneous in nature depending on distance from the bank and the stage of vegetational development reached at this point in time and space.

The presence of humans merely represents a brief and fixed moment in time during the course of the dynamic process involving the silting up of an open body of water and its subsequent overgrowth by the time-transgressive development (sere) of a sequence of vegetation. This has implications for the interpretation of the site since contemporary finds might be recovered by excavation from quite different depositional units. Parts of the same animal bone would have been overgrown by reeds closer to the shoreline but might have laid initially uncovered among water plants in deeper water only a few metres away and subsequently been covered by gyttja. Indeed this very process is suggested by refitted fragments of bone material with clearly diverging taphonomic histories. Moreover, a spatially intermediate specimen might occupy a stratigraphic position within the body of an already accumulating gyttja deposit. This is perhaps counterintuitive for an archaeologist used to regarding sedimentological units as superposed, static, and perhaps chronologically distinct horizons. In the case of the sedimentary units at Bedburg the chronology of sedimentary units would move not only vertically but horizontally.

Interpretation of the Bedburg lithic (Street 1998) and especially faunal assemblages must therefore recognize that material derived from contemporaneous activities underwent quite complex and potentially divergent processes of dispersal and destruction/preservation over very small distances before and during their final burial within the offshore deposits from which they were recovered.

The overall small size of the Bedburg lithic and faunal assemblages renders many conclusions drawn by the present analysis anecdotal rather than statistically demonstrable. Arguably this is more than compensated by the excellent conditions of preservation of the material and, indeed, by the avoidance of complications often encountered due unquantifiable "palimpsest" effects by analyses of very large assemblages. The paper will present a number of "anecdotes" which may be of help for the recognition of similar anthropogenic or depositional factors or of use in teasing these apart within larger complexes of finds.

Lithic assemblage

Although fewer than 200 artefacts were recovered, the Bedburg lithic assemblage permits a number of conclusions to be drawn. 15 discarded cores and a high proportion of cortex flakes show that knapping took place at the site. The over-representation of cores in the sub-aquatic assemblage probably reflects their active discard into the body of water adjacent to the camp. The absence of micro-debitage is clearly due to the non-survival of the terrestrial areas in which lithics were actually knapped.

The important component of large laminar debitage at Bedburg is unusual for a Rhineland Mesolithic assemblage and might reflect a need for large flint blades for animal butchery. Used at the water's edge, the lithic butchery implements and larger waste faunal elements were subsequently discarded off-bank. The large laminar component might also be explained to some extent by the very early date of the assemblage since, while unusual for the Rhineland, the technology and dimensions of the Bedburg assemblage are typical of the early "Broad Blade" Mesolithic of the British Isles.

The presence of modified (retouched) lithic tools may be accounted for by analogous arguments. Scrapers may also have been used at the water's edge and actively discarded into the water, while the few microlithic points might represent projectile components passively discarded as "riders" together with the butchery waste. The composition and spatial patterning of the lithic assemblage can thus be explained as a result of interplay between intentional off-bank discard of larger and selected elements and

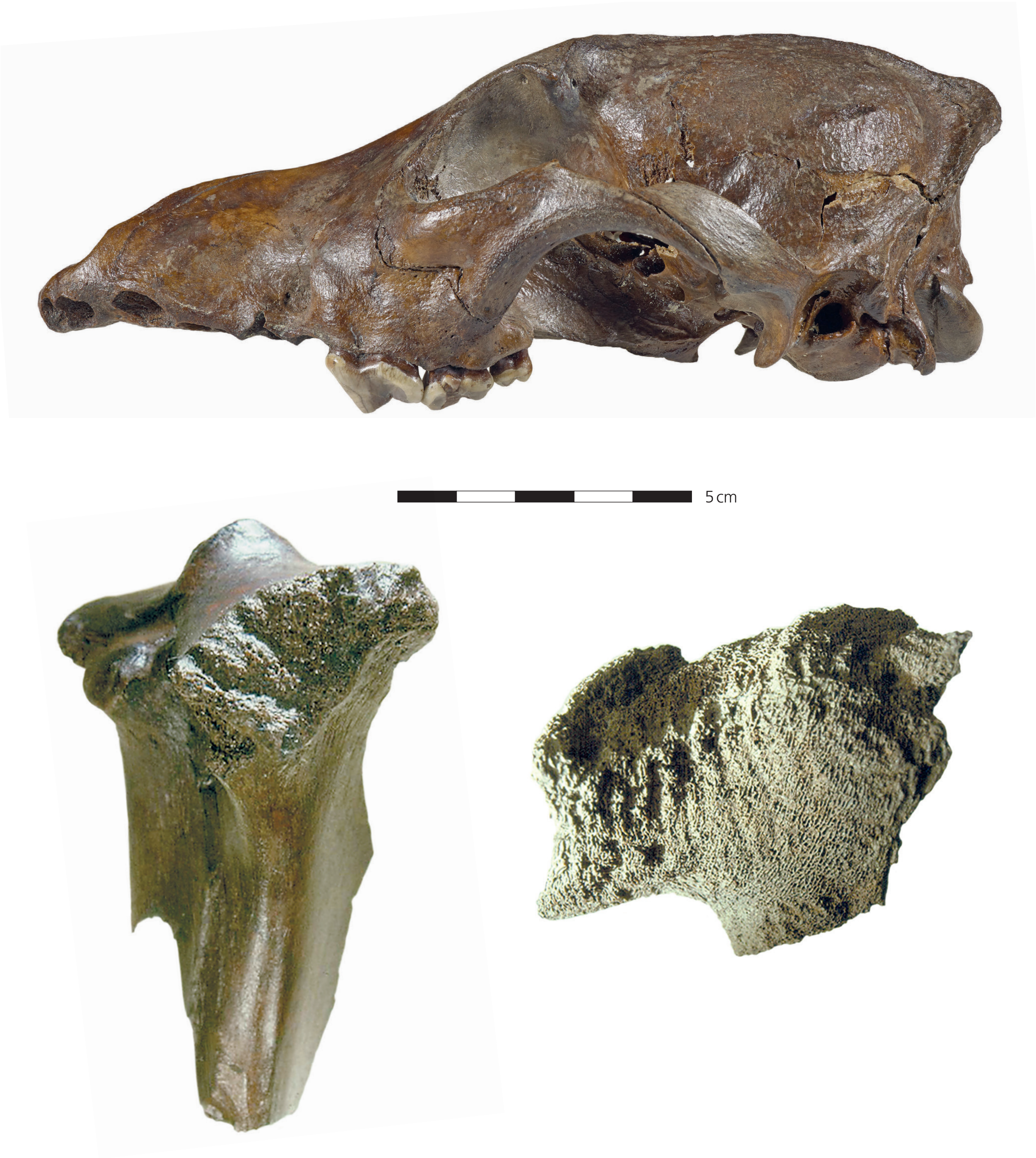

Fig. 5 Many bones in the Bedburg assemblage bear traces of gnawing by medium-sized carnivores: Proximal tibia of red deer (below left); distal femur of aurochs (below right). Dogs present during occupation of the site (above) clearly had extensive access to butchered material and both gnawed and ungnawed remains were subsequently discarded by humans into the adjacent body of water.

contextually determined absence of smaller waste elements. This can be seen as a variation on the classic "toss and drop zone" model of Binford (1983).

Faunal assemblage

The composition of the large mammal fauna reflects the early Holocene context within transition to postglacial woodland (Street 1993; 1997; 1999; Street/Baales 1999). Species typical of the open arctic landscape of Dryas III, such as reindeer (*Rangifer tarandus*), are no longer represented. Large mammal species indicative of a more temperate, forested environment, the cervids red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) and also wild pig (*Sus scrofa*) are already present. The presence of horse (*Equus* sp.) indicates that forest cover was certainly not closed and this might also be true for aurochs (*Bos primigenius*). Medium-sized mammal species are represented in the faunal assemblage by badger (*Meles meles*) and beaver (*Castor fiber*), the latter unsurprisingly in the lowland wetland context. Domestic dog (*Canis familiaris*) is present as an almost complete cranium and some postcranial bones. Indirect evidence for its presence is provided by the ubiquitous traces of gnawing on the bone assemblage (Street 1989b).

Small mammal remains are mainly those of species typical of the immediate wetland biotope (van Kolfschoten 1994) and cannot be linked to human activities. Many bird bones are identified as waterfowl (Street 1993). The ecological evidence of the large mammal fauna is supported by the presence of two bird species, white stork (*Ciconia ciconia*) and crested lark (*Galerida cristata*), which also require open conditions (Street/Peters 1991). The fish remains are mainly of species typical for the conditions of the still (or very slow moving) eutrophic body of water represented by the Preboreal Erft meander (Krey 1990). The bones of birds and fish indicate the availability of these resources at the site, although their exploitation by humans is not demonstrated by bone modification and any human role, if any, in the accumulation of this material is not clear.

Butchery

By contrast, the bone, tooth and antler of large and medium sized mammals recovered at Bedburg-Königshoven overwhelmingly represent material intensively modified by humans, particularly during butchery, and subsequently discarded into a body of water adjacent to the actual settlement area (Street 1990). Butchery was carried out according to a standardised system. Carcasses were exhaustively processed by removal of meat, marrow smashing of long bones, and partial fragmentation of cancellous bone, probably for the extraction of fat and grease.

By far the largest Number of Identified Specimens (NISP) among the large faunal material is assigned to the aurochs and at least 11 individuals are identified by combining the information provided by duplication of elements of the skeleton and ageing and sexing criteria (Street 1999). The representation of parts of the skeleton suggests that animals were hunted close to the site, but that the site itself is not the kill site.

Uniform treatment and spatial patterning of faunal elements, refitting of fragmented bone and artefacts across the site and consistently very close dates for several aurochs individuals suggest that the assemblage represents the accumulation of material from one longer stay, rather than from a series of unconnected events. Bones and teeth of young aurochs and remains of roe deer suggest occupation of the site in late spring or summer. Two red deer antler frontlets, probably not directly related to subsistence, may suggest activities more typical of a diversified longer-term residential site rather than of a sporadically occupied hunting camp.

Bone gnawing by dogs

Many of the Bedburg large mammal bones found throughout the limnic gyttja deposit, especially those of aurochs, show tooth marks left by scavenging animals (**fig. 5**), (Street 1989b; 1993). Both gnawed and ungnawed butchery waste was clearly discarded by humans into the body of water adjacent to their camp. Preservation of the gnawed and the non-chewed bones is identical and not suggestive of different taphonomic histories such as longer surface exposure to weathering and carnivore access.

Ravaging of a faunal assemblage by scavengers can be a major factor affecting the survival of bones. In order to evaluate the importance of this influence in Bedburg all bone fragments were examined for traces of carnivore gnawing following accepted methodologies (Brain 1981; Binford 1981; Legge/Rowley-Conwy 1988).

The development of various types of gnawing damage (e.g. Binford 1981) is very much conditioned by the character of the bone. *Crenellation* affects mainly thinner cancellous bones when the removal of short sections of bone gives the edge of the bone a scalloped appearance. *Furrowing* of cancellous bone, in this case usually the extremities of the limb bones, leaves distinctive irregular edges. *Punctures* on thin and cancellous bone represent perforation of the outer surface by a tooth, usually a canine or carnassial cusp, leaving a depression, often with a central plate of bone. They often occur in opposed pairs. Pitting and striation are also present on denser bone, such as the shafts of limb bones. The types of gnawing recognized at Bedburg on bones of *Bos primigenius* (several of which bear traces of more than one type of alteration) were counted and the proportional representation calculated relative to the total number of identified specimens of each bone element (Street 1989b; 1993). Of 336 identified bones of aurochs, 110 (32.74 %) show carnivore gnawing, an overall proportion well above that observed for the broadly contemporary Star Carr assemblage (Legge/Rowley-Conwy 1988). Nevertheless, gnawing damage was in many cases not severe and never prevented the identification and recording of a specimen.

The formation of a bone assemblage influenced by scavenging dogs (Brain 1981) provides a control for the degree of attrition of archaeological bone assemblages and was referenced in a revision of the Star Carr fauna (Legge/Rowley-Conwy 1988), which demonstrated that this assemblage does not resemble one ravaged by scavengers. This was in accordance with the observed low frequencies of carnivore gnawing on bones. Perhaps unexpectedly in view of the greater presence of carnivore gnawing on much of the Bedburg assemblage, the "Percent Survival" of each bone element is also not that of a ravaged assemblage; in fact certain elements with a low survival potential, such as the sacrum, proximal femur and proximal humerus, are quite conspicuous. The elements of the *Bos primigenius* skeleton recovered from the excavated Bedburg limnic deposit are thus still mainly representative of human influences and not activities of scavenging animals, no doubt because the examined material was removed from their influence before this could dominate the character of the assemblage. Carnivore access to fresh bones was clearly *quasi*-synchronous with settlement activities, which together with the size and morphology of the observed gnaw marks makes scavenging by or deliberate feeding of the medium-size dogs present at the site the most plausible interpretation.

Bjarne Grønnow (1987) describes ethnographically documented examples of the cleaning up of a butchering site involving the disposal of waste material into an adjacent body of water, which would seem to be the most plausible explanation for the presence and distribution of the bone assemblage at Bedburg. On this model at least some cleaning up of the Bedburg site only took place after butchering waste had been accessible to dogs, probably intentionally as the most rational way of feeding them.

Bone distribution patterns, refitting and site dynamics

Approximately 500 m² of surviving sediments at Bedburg were investigated, identifying and excavating the find-bearing horizon and recording the 3D-location of all identified finds within a grid system. This was not oriented exactly to compass north but was aligned to be relevant to the ancient topography of the site, parallel and at right angles to the edge of a palaeo-channel. The excavated surface (**fig. 6**) can

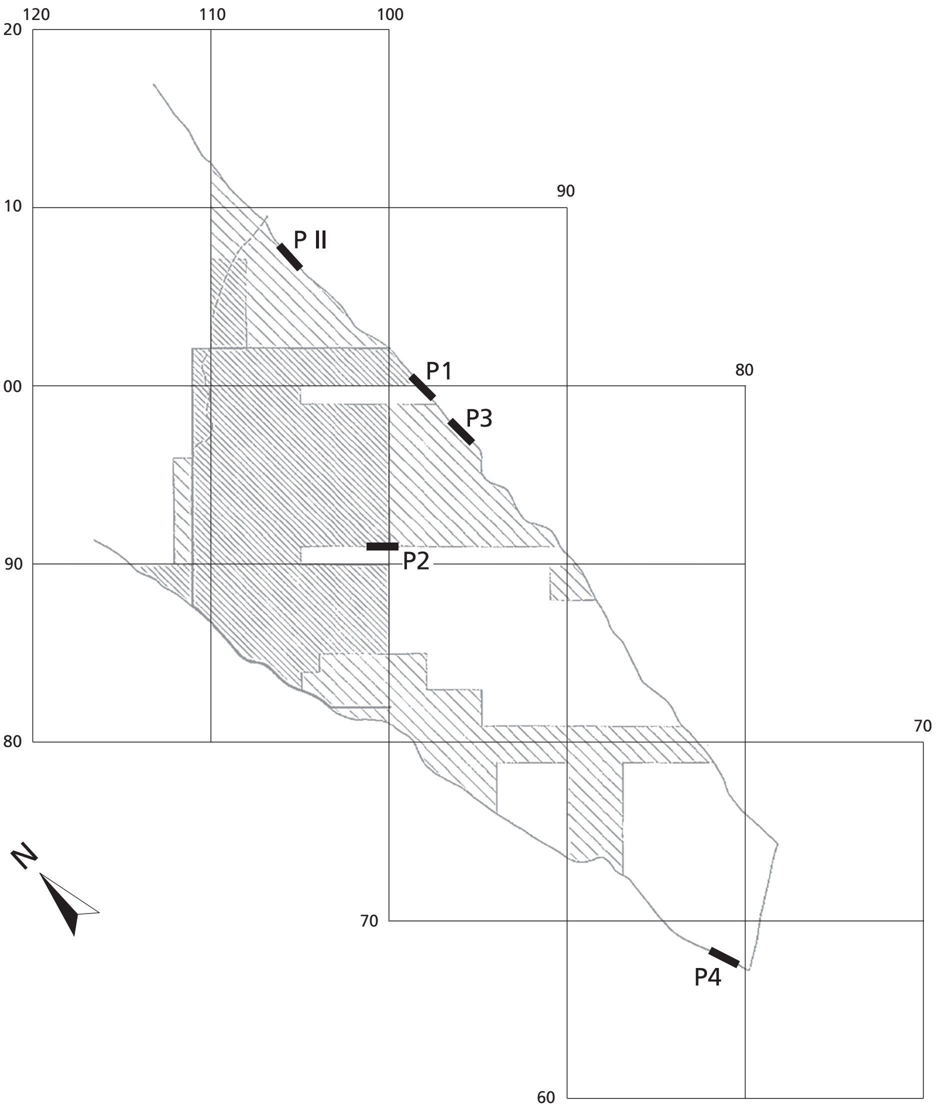

Fig. 6 Bedburg-Königshoven initial Mesolithic site: Plan of the excavation showing the extent of areas excavated using different procedures, and the location of palynological sections. Terrestrial sediments in higher-lying parts of the site (top of the plan) had already been destroyed in the 19th century and there was no hope of finding intact dry-land settlement structures. 190 m² of the immediate littoral area were excavated and finds recorded in 3D, with all sediment wet screened (narrow hatching). 180 m² of the off-bank area poor in material were excavated by test trenches but sediment was not screened (broad hatching). Some 150 m² of mainly sterile sediments could not be investigated (white). What remained of the site was destroyed by quarrying early in 1988.

be broken down logistically as follows: An area of 190 m² covering the immediately littoral area of the site was excavated and all of the removed sediment (a calcareous gyttja deposit underlying reed peat) subsequently wet-sieved, ensuring a contextualized recovery of any smaller material possibly overlooked during excavation. A further 180 m² of the off-bank area were excavated but since test screening showed sediment from this part of the site to be practically devoid of any contained lithic or faunal material the rest of it was not wet-sieved. Finally, some 150 m² of sediments located towards the middle of the palaeo-channel, which proved to be largely devoid of finds during test excavation, could not be excavated during the time available. Two 1 m baulks left standing as witness sections in alignment from bank to deeper water were recorded and sampled, importantly for subsequent site contextual analyses, but could not be fully excavated before what remained of the site was destroyed.

Fig. 7 Bedburg-Königshoven: Bone distribution patterns. Remains of the two “antler frontlets” of red deer (1, 3) and skulls of aurochs (marked green: 4, 5) lie approximately equidistant from the ancient river bank (to left of plan). Two aurochs M3 molar teeth 96/105-1 and 97/106-1 and the skull 96/105-2 (unbroken green lines) were originally discarded into the water as a unit. Anterior M1 and M2 (94/110-2, 4: broken green line) remained at the site of butchering and smashing the skull on drier ground several metres to the northwest. Aurochs ribs (marked blue) were found widely across the excavation and may have been moved by even weak underwater currents and so further disarticulated and displaced into deeper water. Fragments of a left aurochs pelvis (marked red) were dispersed across several metres. Pieces of the ischial blade 89/107-1 and 94/102-1 refit to each other and to the acetabulum 81/100-1, which also refits to the iliac blade 91/106-1.

Plotting the butchering waste discarded by early Holocene humans into the Erft meander shows distribution patterns influenced by a number of criteria. In a few cases the spatial patterning of refitted and rearticulated bone faunal remains provides more detailed insight into the dynamic processes of butchery and waste discard at the site. That the greater part of the assemblage was quickly covered by water and removed from the influence of scavengers and weathering is demonstrated by its good preservation. Subsequent movement of bones, for example by underwater currents potentially winnowing the assemblage, might not leave visible traces and cannot *a priori* be ruled out. This factor can at least be excluded for bones recovered in articulation, but there are in fact few bones which can be placed into this category.

Aurochs skulls and their fragments lay in a zone located between 2 and 5 m from the northern edge of the excavation (**fig. 7**), which equates approximately to the boundary between the surviving limnic deposits and the destroyed terrestrial part of the site. The location of the finds might primarily reflect the distance such heavy material could have been thrown into the water, although subsequent underwater movement would probably have brought the skulls down slope to rest on the flatter bed of the meander.

The relative locations of an aurochs skull and several maxillary teeth reveal both the final resting place of actively discarded waste and the original location of butchery, which involved fracturing of the anterior skull by blows immediately in front of the M3. The same considerations regarding distance from the bank may apply to the two humanly modified red deer antler frontlets, although in this case it should be considered whether they are merely discarded waste or alternatively material stored underwater for potential future use.

Aurochs ribs are found widely across the excavation and some specimens from neighbouring positions in the rib cage remain in broad spatial association, possibly indicating that they were originally discarded as larger or smaller slabs of rib cage rather than as disarticulated bones. However, once disarticulated this relatively light material has a high surface area to weight ratio, and could probably have been moved by even weak underwater currents. Much of it was therefore probably displaced downstream and/or into deeper water, as might be suggested by the quite even spread of ribs at distances of up to 10 m and more from the ancient riverbank.

The refitted fragments of an aurochs pelvis underline that material recovered widely dispersed across the site represents a single assemblage and provide an insight into butchering practises and the disposal of waste, i. e. the dynamics of human activity at the site. In any discussions of spatial interpretation it is important to note that the bank of the meander was at the left of the plan, with deeper water at right, while any flow of current still active enough to transport material underwater would have been from below to above on the plan.

The fragment of the pelvis furthest from the bank and hence in deepest water is also the densest and heaviest, the acetabulum. This refits to a fragment of the iliac blade and to two refitting fragments of the ischium. While the iliac blade might have been moved from the location of the acetabulum by underwater currents, it is improbable that this applies to the fragment of ischium, which would then have needed to be transported to a higher location. Equally improbable is that the acetabulum was moved by currents from the other elements, since this goes against direction of water flow.

It is improbable that the acetabulum should be eroded or washed more than 10 m from the other fragments, while the peripheral elements remained relatively close together. The logical original butchery site would be near to, or on, the drier land at the left of the plan, closer to the position of the ilium and ischium. The latter elements may have been discarded just off bank, with one fragment of ischium later transported down slope in the direction of water flow. Removed from the rest of the pelvis by fracture and possibly in articulation with the femur, the acetabulum was discarded separately "upstream" and came to rest in deeper water.

This distribution pattern was observed on other elements, with smaller fragments remaining close to

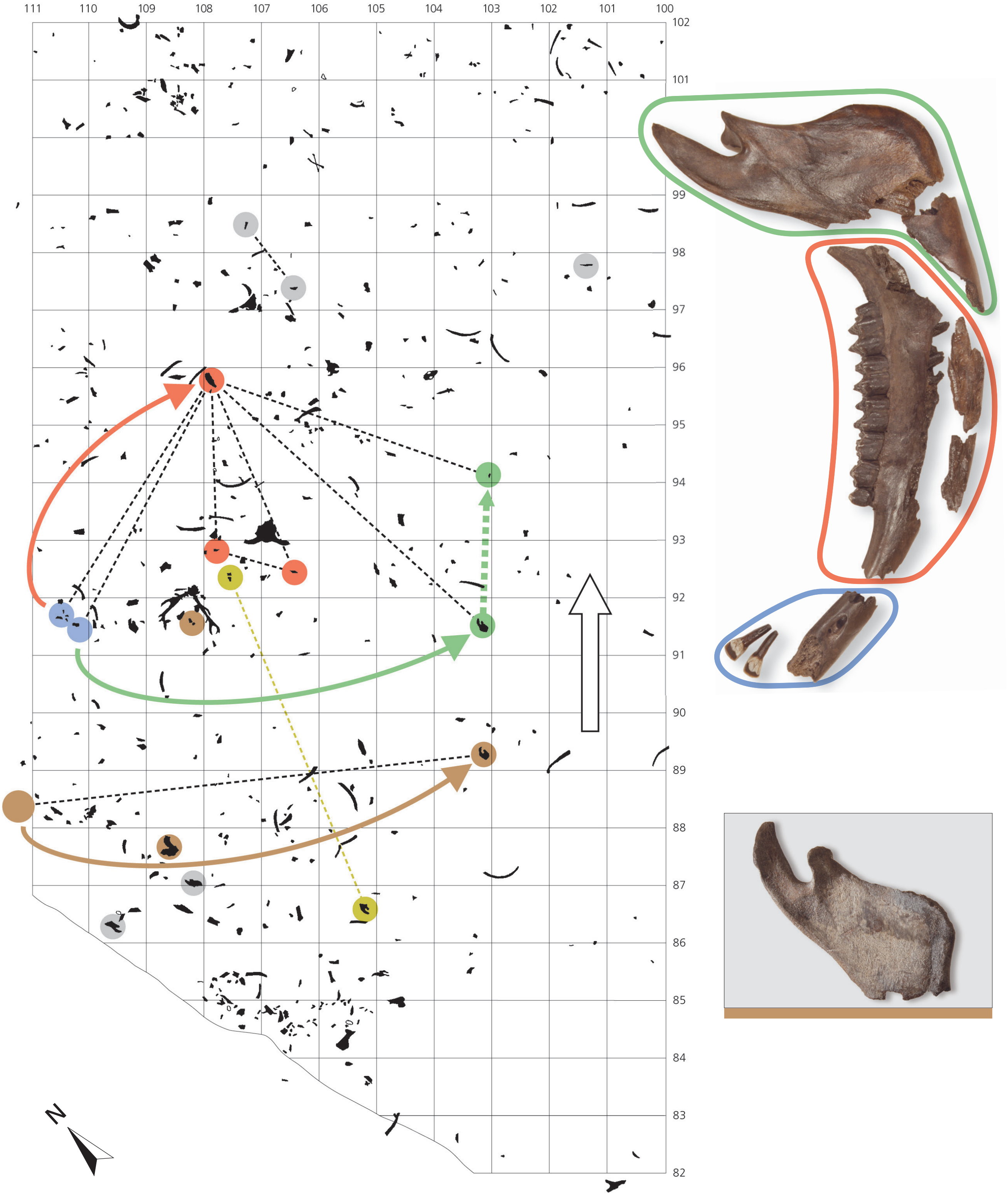

Fig. 8 Bedburg-Königshoven: Processing of aurochs mandibles. Detachment of the distal mandible and rostral teeth (marked pale blue) took place at the ancient river bank (at left). The ascending ramus was fractured off the left hemi-mandible and discarded into the water (unbroken green arrow) as two refitting fragments, the smaller of which may have been moved downstream by current flow (broken green arrow). The inferior margin of the horizontal ramus was removed to access the marrow cavity, producing a cleaned mandible with molar dentition and two detached fragments (marked red) also discarded into the water (red arrow). The positions and orientation relative to potential stream flow of the left adult element are mirrored by fragments of the right hemi-mandible of the same animal (identified by morphology, marked yellow) and of a left hemi-mandible of an immature aurochs (brown, brown arrow) the skull of which lies along the trajectory of proposed disposal.

the original the site of actual butchery while larger "selected" pieces are discarded into deeper water, a pattern which basically conforms to the "drop" and "toss" zone model proposed by Binford (1983).

An identical method of processing was recognized in the case of the deliberate fragmentation of aurochs mandibles, in some cases associated with spatial patterning (**fig. 8**). The exact dynamics of the distribution patterns are not fully clear; slope angle and water action have probably influenced the final position of the fragments which is thus the result of a combination of anthropogenic and subsequent natural processes. Nevertheless, the logical spatial association of sequentially fragmented butchering waste does suggest that the original locations of activity and disposal areas can be identified. Smaller bone pieces created by initial fragmentation of the mandible are generally found close to the water's edge (presumably at, or very close to the site of the bone smashing activity), while larger fragments subjected to further processing are located further from the shore. Were the distribution of refitted material primarily non-anthropogenic it would instead be expected that the smaller and lighter fragments would have been eroded and washed down slope, while the heavier elements remained *in situ*.

A first stage of processing saw the division of the lower jaw into two halves by smashing through the anterior mandible (containing the rostral dentition). The ascending *ramus* of each hemi-mandible was also removed by a blow to the posterior angle of the respective elements leaving the individual left and right horizontal *rami* for easier opening of the marrow cavities. The incisor teeth and small bone fragments from the initial fracturing operations remain where they drop in an upslope location on or close to the ancient river bank. The caudal parts of the mandible were discarded into the water. In some cases the ascending *ramus* was found as much as 8 m from the ancient river bank, either thrown that far by the butchers or due to subsequent movement of the disc-like flat bones by currents into deeper water. The desired element, the horizontal *ramus*, was broken open for the contained marrow by smashing away the lower margin of the bone. The detached fragments and the emptied *rami* were also discarded into the water, ending up some 3 m from the riverbank. Traces of gnawing on some mandible fragments suggest that they were only discarded into the water after first being accessible to the dogs present at the site (deliberate feeding?).

Humanly modified skulls of roe deer and domestic dog were found very close together (**fig. 9**). They are located at a distance of some 7 m from the northern edge of the excavation, which probably equates with the ancient river bank, and it is not clear to what extent their proximity (association?) so far out into the body of water might be a result of deliberate human action.

Similarly, a broken bone point and a chisel or burnisher made on a red deer radius, the only two formal organic tools (discounting the antler frontlets) found at Bedburg, lay adjacently some 10 metres from dry land and in this case must certainly have been carried together, perhaps tied or bound in a bundle, before their accidental loss or intentional discard. Similar associations of organic artefacts are known from other Holocene waterlogged contexts but by what mechanism or with what intention the Bedburg specimens were deposited remains unknown.

A quasi articulated radius and ulna of white stork probably represent an entire bird wing and their presence among human butchery waste may be the result of human discard or loss, although neither bone shows any modification. Other unmodified remains of small water birds (some in articulation) and fish probably reflect the natural background.

At the west of the excavated area an elongated area measuring some 3 metres in length from North to South contains a large amount of small-sized faunal material and an unusually high number of lithic artefacts. Material of equivalent small size is otherwise uncommon at the site, although wet-screening showed that smaller bone fragments are more numerous to the north of the site close to the water's edge. The heterogeneous lithic material includes both, well-made large blades and smaller lamellar forms, among them microlithic elements. The area yielded bone and tooth remains of the medium-sized mammal species beaver, badger and roe deer, among the latter a number of fragments of intentionally fractured roe deer limb bones. A scapula and femur of horse are among the few larger bones found close to this unusually dense scatter of bone at the west of the site. A complete articulated series of aurochs left carpal bones suggests that material was buried quite rapidly and demonstrates the lack of post-depositional disturbance in this part of the excavation.

The amount and range of material identified as roe deer in an area of less than 1 m² might also suggest remains of only one butchered individual and also underlines the rapid burial of material at this location. The sediment here was quite sandy, unlike the normally very fine gyttja matrix, and some of the fragmented long bones of roe deer are abraded. This and the linear distribution of the material suggest that the material was probably scoured from the bank and brought into the deposit as the filling of a small channel. Probably a small rivulet or stream flowed into the meander from the bank at this place and transported sediment and a selection of finds of smaller dimensions than those intentionally discarded into the water by humans. Possibly the valley extending into the meander from higher land to the north-west (**fig. 3**) drained water (perhaps seasonally) into the Erft valley at around the time the site was occupied. A source of fresh water may have played a major role in the choice of site location, while since occupation at Bedburg seems to have been in spring or summer, subsequent winter flooding of terrestrial areas and displacement of material is a probable scenario.

The heterogeneous "random sample" gives some idea of the range of material originally present in the terrestrial area of the site but lost due to recent destruction or perhaps much earlier due to weathering and other processes of site degradation. Furthermore, the close association of roe deer, badger and beaver with horse confirms the unity of the assemblage and demonstrates the contemporary ecological variation from woodland to more open grassland available to early Mesolithic hunters.

It is possible to identify a number of originally articulated associations of bone elements which have been moved apart underwater to a greater or lesser extent. The overall loss of material due to this process is impossible to quantify. The lack of strong currents indicated by the nature of the enclosing gyttja deposit might suggest that only small pieces are likely to have been seriously affected by winnowing. However, the recognition that material was probably discarded into the water at a time when infilling of the meander was not so far advanced leaves a period of unknown duration when scouring may have played a greater role.

Three carpal bones and a distal radius of *Bos primigenius* distributed over three neighbouring m² units show the movement of this articular unit subsequent to its removal from human influence.

Three semi-articulated cervical vertebrae of horse were found relatively deep in the gyttja horizon to the east of the site. A series of six red deer phalanges was found scattered over the same approximate area. It is unclear whether these finds might indicate the presence of another rapidly filled underwater channel and no anomalies such as different sediment matrix were noticed during excavation.

Site function and overview

The highly favourable nature of open swampland as feeding grounds for large ungulates has long been suggested as a major factor in the hunting strategies of early humans (e. g. Bay Petersen 1978). In the case of the aurochs, the largest terrestrial mammal prey species available to humans in the early Holocene, the etymology of the name (in German "flood plain" or "river meadow" ox) for this now extinct ancestor of domestic cattle would itself appear to betray the animal's ecological preferences. Moreover, various reconstructions of the ecology of the animal support this interpretation (e. g. Hall 2008; Van Vuure 2002).

Aurochs were certainly encountered, probably on a regular basis, by human hunters in the more open, flatland environments of river valleys. This is documented by a number of their skeletons recovered in various stages of completeness with clear evidence relating to human predation. Not

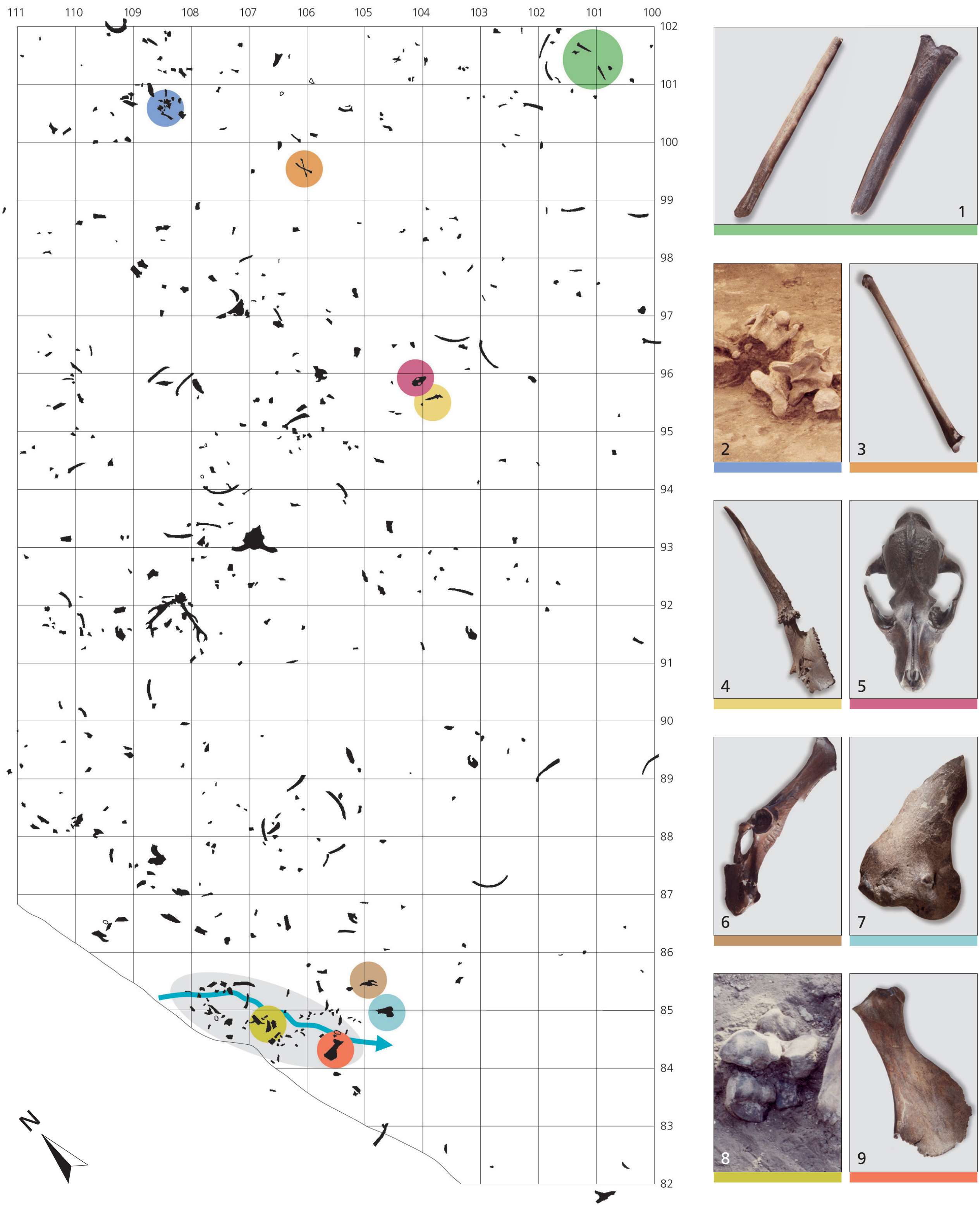

Fig. 9 Bedburg-Königshoven: Bone distribution patterns. Faunal remains in close spatial proximity represent primary anatomical associations or may in some cases reflect human activity or intention. Broken bone point and burnisher of red deer bone (1). Three articulated cervical vertebrae of horse (2) located close to six phalanges of a red deer foot probably disarticulated by water movement. The radius and ulna (3) of a white stork may represent human discard of an articulated wing. Close association of humanly modified skull bones of roe deer (4) and domestic dog (5) suggests they were discarded together. Other close spatial associations of material are probably due to rapid deposition, possibly caused by water run-off (blue arrow) from the bank (at left in plan). A small area of the excavation (grey shading) produced a collection of heterogeneous material including teeth and bones of roe deer (6), beaver and badger, articulated left carpal bones of aurochs (8), and a horse femur (7) and scapula (9).

all of these recorded episodes document successful hunts. Indeed, specific finds of entire aurochs skeletons associated with microlithic arrow points in early postglacial marshland deposits clearly represent wounded animals which evaded their hunters and died without being recovered. This is the case at the Danish sites of Vig (Hartz/Winge 1906; Noe-Nygaard 1973) and Prjelerup (Aaris-Sørensen 1984; Aaris-Sørensen/Brinch Petersen 1986). A complete aurochs skeleton reported from Holocene peat deposits in the Erft valley near Grevenbroich in 1912 (Krause 1912) might conceivably represent a similar episode located very close to the Bedburg Mesolithic camp.

The site of a successful early postglacial aurochs hunting episode was excavated at Schlaatz near Potsdam, where what remained of a butchered aurochs was found associated with a small number of flint blades (Benecke/Gramsch/Weisse 2002; Gramsch 1987; Gustavs 1987; Teichert 1987). The skull and axial skeleton of the massive bull were found in anatomical association and had undergone at most slight redeposition. All the limb bones and much of the rib cage were missing, and Schlaatz clearly represents the actual place of death ("kill-site"), from which the desired parts of the carcass have been removed.

The Bedburg faunal assemblage represents the next stage in carcass butchery (Street 1990), during which elements removed from the kill-site were further processed and the bones subsequently discarded as waste (Street 1989b). That so many elements of aurochs carcasses were transported to the Bedburg site indeed suggests that the animals were hunted and killed in the immediate vicinity at sites equivalent to Schlaatz, perhaps only some few hundred metres further out into the valley bottom marshland. Dismemberment of the prey and discard of elements too heavy to be transported took place before moving the required parts of the carcasses to the nearest dry land for further processing. This includes slabs of ribs fractured off the spinal column, whereby the proximal ends of ribs and vertebrae which are underrepresented at Bedburg correspond exactly to those elements found at Schlaatz.

There is some overlap of the elements found at the two sites, particularly the several aurochs skulls/mandibles at Bedburg. Their presence suggests that animals were killed close enough to the site to make transport of the detached heads profitable, since the brain, meat, tongue, marrow and horns were all desirable products. Nevertheless the skulls are only of much smaller cows and young animals and not of bulls equivalent to that at Schlaatz. This might suggest there was an upper weight limit for the readiness to transport elements, possibly also relative to the distance to the kill-site. Alternatively, the dominance of female and young animals might reflect the composition of targeted aurochs herds or higher potential risk in hunting larger males. Against these considerations would speak the clear presence of male elements among the postcranial material at Bedburg.

A number of further occurrences of early Holocene aurochs skeletons in varying stages of completeness are reported from equivalent river valley bottom contexts in the Rhineland and neighbouring regions (Auler 1999; Bos/Urz 2003; Lanser 1990; Prummel/Niekus 2011; Prummel et al. 2002; Richter et al. 2015; Urz 2000). It is probable that many of them are located along the spectrum extending from escaped prey of Mesolithic hunters to waste material discarded following their butchery of successfully hunted animals either at the kill-site or at a site occupied subsequently, perhaps for a number of other purposes.

The most plausible interpretation for the excavated part of the Bedburg-Königshoven site is as a waterside disposal area for butchering waste from a central residential camp occupied in spring/summer. The quantity of meat provided by the butchered mammals (at least 11 aurochs in addition to other species) would suggest a potential stay of at least two to three months over the summer by a group of e. g. eight adults and twelve children. This is implied by the heterogeneous character of the hunted faunal assemblage, the evidence for many episodes of lithic tool production, and the presence of a range of other items such as bone tools, tooth pendants and two antler frontlets. Indeed, the presence of the latter artefacts might suggest that the Bedburg site took on a role extending beyond the strictly economical into the social and/or spiritual and occupied a central position in the life of these early Mesolithic people, as has been argued for the early Mesolithic site Star Carr (Conneller 2004; Conneller et al. 2012).

Since the terrestrial land surfaces upon which prehistoric activities were primarily carried out will generally preserve faunal material poorly or not at all, it is self-evident that discard of organic waste into adjacent bodies of water will provide otherwise unavailable insights into butchery operations in the form of cut and impact marks which can show in detail how an animal carcass was processed. Material found in terrestrial contexts has by contrast a far greater potential for revealing the spatial dimension of the dynamics of human actions and activities.

The analysis of the early Mesolithic faunal assemblage at Bedburg-Königshoven, a site where no terrestrial deposits had survived, showed that an additional level of interpretation for butchering processes may in some cases be provided by meaningful spatial patterning even when the only surviving elements of the carcass are those that have been discarded into a sub-aquatic environment.

Clearly, in an ideal world we would hope to recover both the terrestrial and sub-aquatic parts of a lakeshore site and be able to examine their interaction in detail. When this is not the case, it appears that even the waste material discarded under water has its own tale to tell.

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LIFE AT THE PALAEOPOND: A DIACHRONIC RECONSTRUCTION OF THE LOWER PALAEOLITHIC INTERGLACIAL SITE OF MIESENHEIM I (CENTRAL RHINELAND, GERMANY)

Abstract

The Lower Palaeolithic site of Miesenheim I, located at the edge of the Neuwied Basin in the Central Rhineland of Germany, was investigated in a series of campaigns at the end of the 1980s and beginning of the 1990s. The site produced an interglacial fauna in association with an assemblage of lithic artefacts. Several lines of evidence suggest find-deposition took place in the backwaters of a former Rhine Valley, close to a floodplain pond. In this paper, data are drawn together to reconstruct the diachronic development of the site during an interglacial around 500,000 years ago and how hominins reacted to changing local biotopes and exploited these situations. In total, the finds and other evidence hint at a transient use of the site by hominins. This is in strong contrast to the evidence from interglacial sites such as Schöningen and Neumark-Nord, where hominins left behind abundant traces of their presence. Despite this, sites such as Miesenheim I are important, since they provide not only information on hominin movement and land-use, but also present another, ephemeral, facet of human behavioural adaptations in interglacials.

Keywords

Lower Palaeolithic, diachronic reconstruction, interglacial, transient occupation, biotopes, hominins

Introduction

The Lower Palaeolithic locality of Miesenheim I was discovered in 1982 by Karl-Heinz Urmersbach, after extensive commercial quarrying of pumice had truncated parts of the site on a stretch of land above the village of Miesenheim. Test-trenches put down between 1982 and 1984 brought to light animal bones from a series of layers sealed by volcanic ashes (Boscheinen et al. 1984). Extensive excavations carried out in the second half of the 1980s and beginning of the 1990s revealed abundant and extremely well-preserved faunal remains in association with lithic artefacts. Several lines of evidence suggest the finds had been deposited close to an open body of water, possibly a flood-plain pond. Just over 1100 faunal remains could be identified, comprising several species of small and large mammals, birds, amphibians and fish. A rich molluscan fauna was also recovered. The faunal assemblages include species typical of warm phases, and as a whole is representative of the type of community which would have been living in and around the Rhine Valley during an interglacial phase, some 500,000 years ago. Al-

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though lithic artefacts were recovered and refitting showed that lithic production had taken place at the site, the assemblage is relatively small (n = 114). Strong evidence of human interaction with the faunal remains is lacking. A conchoidal flake scar, similar to notches produced by humans when opening bone shafts to obtain marrow was observed on a fragment of a long bone of horse or a large bovine. Fine, linear incisions on three bones, superficially resembling cut marks, are probably of natural origin. Linear incisions on a fourth bone, a fragment from a mandible of red deer, may derive from cutting by a stone tool.

In an article published in 1999 and a monograph which appeared in 2000, I attempted to define the locality in terms of type of site (Turner 1999; 2000). My efforts to fit the evidence from Miesenheim I into categories formerly applied to Lower Palaeolithic localities, such as home base or central foraging site or short stay site, were inconclusive. I willingly attributed this result to what I claimed was a fundamental problem at the site, namely superimposed sequences of deposition and faunal remains subjected to varying degrees of modification by different agents, of which hominins were only one. Finally, I concluded that the low number of artefacts, lack of structures, absence of hearths and a paucity of human modification on the bones was more characteristic of a site visited only briefly by hominins.

With hindsight, the "short visit" tag seemed to be an almost apologetic response to a need to write something explicit about the site. In effect, this term was perceived as a best fit solution and overshadowed the fact that the rather fragmentary evidence from Miesenheim I was in itself potentially important information on facets of human behaviour in interglacials. In earlier analyses, a diachronic development of the site was discussed mainly in terms of stratigraphy and sedimentology, based on geological investigations undertaken during excavation. Applying a holistic approach, this paper focuses once again on a diachronic reconstruction of the site, but integrates aspects of find-deposition more securely into this framework. Only by placing the development of the site into the foreground, can a picture emerge of how hominins reacted to changing local interglacial biotopes and exploited these situations, or were affected by these conditions.

The context of the Miesenheim I site

Location, discovery and excavation

Miesenheim I is located on the south-western edge of the Neuwied Basin, a major geomorphological feature of the Central Rhineland of Germany. Today, the site lies on the slopes of the valley of the Nette River, at about 120-130 m above sea level, some 3 km from the Rhine River and approximately 1.5 km from the village of Miesenheim (**fig. 1**). However, several lines of evidence suggest that find deposition took place close to an open body of water – a lake or floodplain pond – in a former valley of the Rhine that extended far into the area occupied nowadays by the lower reaches of the Nette.

In 1982, commercial extraction of pumice near Miesenheim cut into underlying deposits, bringing well-preserved faunal remains to the surface where they were discovered by a local hobby archaeologist and collector, Karl-Heinz Urmersbach (Boscheinen et al. 1984). After reporting the discovery to the Monrepos Archaeological Research Centre and Museum for Human Behavioural Evolution, RGZM, in Neuwied (formerly Forschungsbereich Altsteinzeit, University of Cologne), a series of test-pits were opened at the site on behalf of the Landesarchäologie / Außenstelle Koblenz (formerly Denkmalpflege Rheinland-Pfalz), revealing remains of several large mammals associated with pieces of chipped stone, interpreted as debitage from the production of stone tools. A first publication appeared in 1984, describing the preliminary results (Boscheinen et al. 1984). Larger areas were investigated in 1984-1986 (Turner 1985) and in 1990-1991. By the end of the final season, five non-contiguous areas of varying size and depth, totalling 436 m^2, had been investigated (**fig. 1c**) (Turner 1999; 2000).

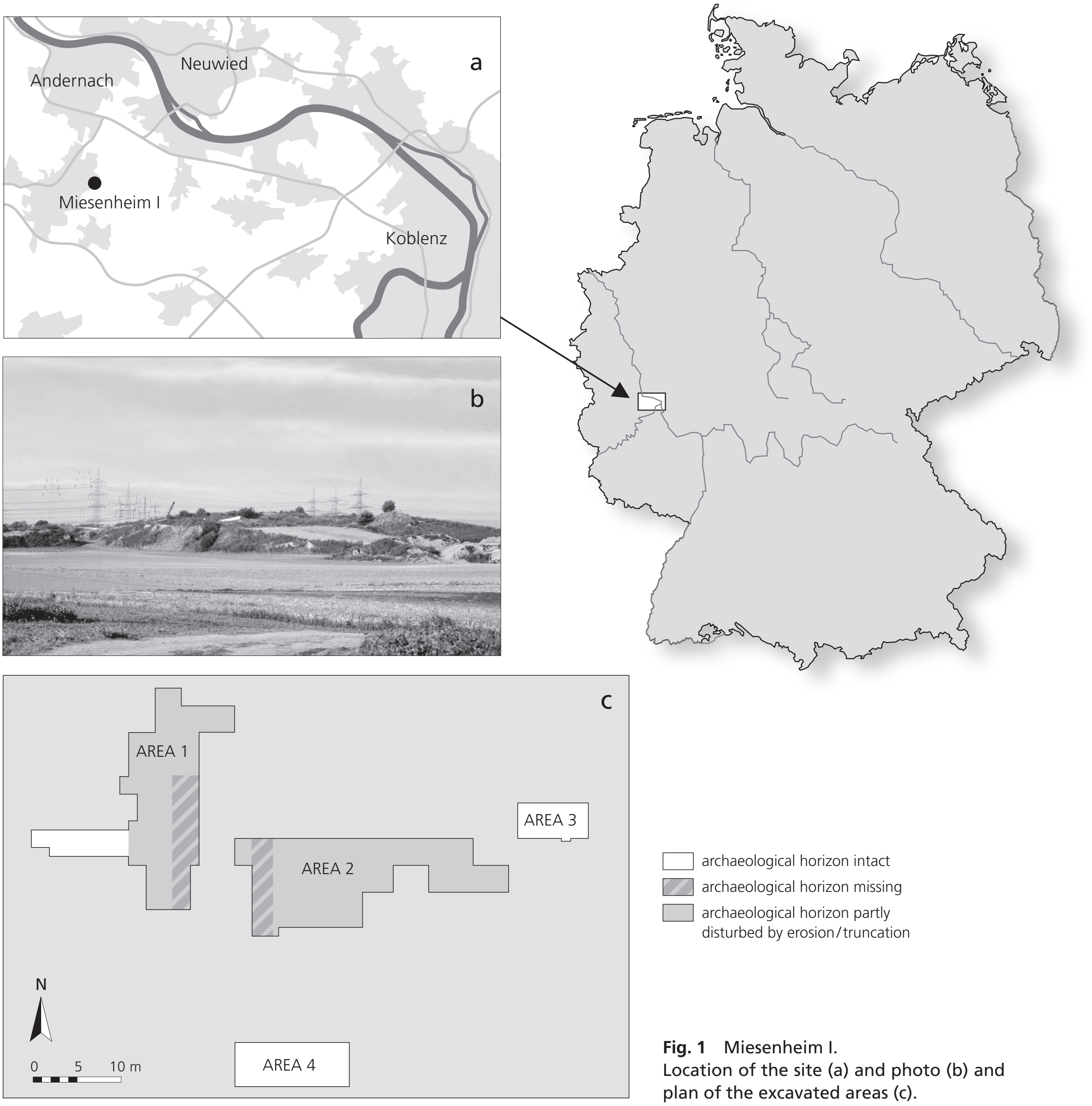

Fig. 1 Miesenheim I.
Location of the site (a) and photo (b) and plan of the excavated areas (c).

Stratigraphy, age and interpretation

During excavations at Miesenheim I, geological (Boscheinen et al. 1984; Hoselmann/Willems 1991; Müller 2000) and micromorphological (Boenigk/Frechen/Schweitzer 2000) analyses were undertaken. Since the results of these investigations have been published in detail elsewhere (Boscheinen et al. 1984; Hoselmann/Willems 1991; Turner 2000), only major phases relevant to the reconstruction of the biotope of the site during the period prior to and after find deposition are presented here, based mainly on Müller's (Müller 2000) analyses and descriptions.

Figure 2 depicts the section exposed in the western wall of area 3, where a more or less intact sequence of deposits was preserved. The oldest geological unit comprises up to 10 m of homog-

UNIT	LAYER	DATING	GEOLOGY	ENVIRONMENT	CLIMATE
10			REDEPOSITED SOIL, PUMICE AND ASH		
9		464 ± 4Ka	PUMICE AND ASH		
			EROSION		
8			CV HORIZON		INTERGLACIAL
			LOESS		GLACIAL MAXIMUM
7	**C**		SOLIFLUCTED DEPOSITS	VEGETATION-RICH OPEN WATER	EARLY GLACIAL
6			REDEPOSITED SILTS		
5	**F**		ANMOORGLEY	SILTING UP WATERLOGGED OPEN, RICHLY VEGETATED WATER FLUCTUATING WATER LEVELS	INTERGLACIAL
3-4	**G**		REDEPOSITED SILTS	OPEN GRASSLANDS SOME WOODLAND FENLAND OPEN WATER	INTERGLACIAL
			EROSION		
2	**H**	≈ 600 Ka	BROWN EARTH	TERRESTRIAL	
			MIESENHEIM SANDS	FLUVIATILE	

Fig. 2 Section through the deposits at Miesenheim I showing sequence of layers, dating, geology, environment and climate. Unit descriptions for the various layers given by Müller (Müller 2000); layer definitions were given on site during excavation.

enous fine to medium grained sands, representing a phase of strong fluviatile activity at Miesenheim I. Only the top of this deposit is exposed in the section in **figure 2**. Named the "Miesenheim sands" by Hoselmann and Willems (1991), the sands have been correlated by Boenigk and others (2000) to the Main Terrace Complex of the Rhine. Dating to between approximately 1 Ma ago and 600 thousand years before present (Ka B.P.), this complex consists mainly of braided river sediments deposited by repeated fluvial phases in a former Rhine valley, which was up to 8 km wide in places (Litt et al. 2008).

The brunification of the top of the sands represents the commencement of pedogenic processes (**fig. 2**, unit 2, layer H) and a transition to terrestrial conditions at the site. However, the development of the soil forming on the sands ("Braunerde") was interrupted by erosion and the onset of waterlogging, as revealed by the accumulation of redeposited silts, which already show the effects of gleying (**fig. 2**, units 3-4, layer G). On top of the silts, alternating autochthonous organic and clayey and silty allochthonous sediments (**fig. 2**, unit 5, layer F) were deposited by near-shore sedimentation or transportation during periods of higher water. At the height of waterlogging, an open body of calm, or sluggishly-moving water, was present at the site and mud, made up of organic materials and mineral particles, accumulated in the shallows. Waterlogging at the site led to further gleying of the underlying sediments (**fig. 2**, unit 3, layer G). Afterwards, the lake began to silt up and during processes of gleying, the mud deposits turned into an Anmoorgley or hydromorphic soil (**fig. 2**, unit 5, layer F). Wet conditions still prevailed at the site, as can be seen in unit 6 (**fig. 2**, unit 6, layer C), whose olive-green colouration was generated under reducing conditions.

A marked change in sedimentation was recorded in the upper part of the section where soliflucted deposits (**fig. 2**, unit 7, layer C) indicative of early glacial conditions were laid down. Loess accumulated during the following glacial maximum. A "Parabraunerde" formed on the loess (**fig. 2**, unit 8, layer C). The eroded Cv horizon is the only part of this soil visible in the section. Calcium-carbonate concretions in primary position in the uppermost part of the Cv horizon indicate that the pedogenic processes had taken place under interglacial conditions. There is a further break in the deposits at this point and small fluviatile channels filled with a sequence of *in situ* and redeposited pumices and ashes (**fig. 2**, unit 9) are visible. The eruption that produced these materials probably took place at the end of an interglacial and was followed, more or less immediately, by a further phase of erosion and redeposition of both soil and tephra (**fig. 2**, unit 10).

Another feature of the deposits at Miesenheim I is the many faults which have displaced the deposits from a few centimetres to several metres in height. It is not clear whether faulting was caused by true tectonics or tectonics associated with volcanic eruptions (Müller 2000). In places, the sedimentary sequence was also severely affected by erosion and, in addition, truncated during commercial exploitation of the younger tephra at the site, the Laacher pumice, dating to 12,960 cal BP (Baales et al. 2002).

Sanidines recovered from samples taken from the tephra deposits in the section described above (**fig. 2**, unit 9) were dated using the single crystal ^{40}AR/^{39}AR method to 464 ± 4 Ka (pers. comm. Paul v. d. Bogaard in: Turner 2000). The youngest relative date for the Miesenheim sands and the absolute date from the tephra bracket units 2-9 to between approximately 600-460 Ka B.P.

The palaeoenvironmental evidence from the faunal remains

The geological and sedimentological interpretation of the site reconstruction is supported by the results of analyses undertaken on the molluscan and vertebrate faunas. Analyses of bulk samples taken from layers G-C, undertaken by G. Roth (summarised in Turner 2000) produced 73 molluscan taxa. Isolated interglacial taxa are present in unit 2 (layer H) and, in particular, in units 3-4, including the type-fossil *Cepea nemoralis*.

The samples from units 3-4 (layer G) are dominated by land snails, indicating a more or less open environment. Freshwater species and those inhabiting the banks of open waters are also present, along with species typical of fenlands and damp woodlands. Molluscs inhabiting drier, wooded areas were recovered, indicating stands of trees close by.

Freshwater molluscs (81.5 %) dominate in unit 5 (layer F), and damp woodland species predominate among the land snails from this deposit. Dry woodland species and those inhabiting open land are conspicuously absent. Towards the top of layer F, the proportion of molluscs inhabiting vegetation-rich waters decreases and counts of fenland species and species inhabiting the edges of water increase. The molluscan fauna in the upper part of layer F also indicates deteriorating climatic conditions, so the accumulation of the underlying units 3-4 (layer G) can probably be placed in the second half of a warm phase.

Freshwater molluscs also dominate in units 6-8 (layer C) and throughout this layer the number of species inhabiting richly-vegetated, standing water increases once again. Pioneer species and species indicative of unstable biotopes, such as *Gyraulus laevis* and *Radix peregra*, appear, along with many species of the genus *Pisidium*, which all prefer cold conditions. The co-occurrence of *P. lilljeborgii, P. obtusale lapponicum* and *P. stewarti* is typically found in the early or late phases of a glaciation.

The remains of 43 small and large mammals, 8 species of bird, a small assemblage of amphibian remains and a single vertebra of a fish were recovered in units 3-4 and 5 (layers G and F) and identified by E. Turner and T. van Kolfschoten (in: Turner 2000). The fauna is diverse and representative of the type of vertebrate community living in a mosaic of biotopes in and around an extensive floodplain of the Rhine. Beavers, water shrews and water voles would have inhabited the immediate vicinity of the site. The dam-building activities of the beavers may even have contributed to the formation and conservation of the lake. Other species, such as roe deer, squirrels, wood mice and dormice, would have primarily inhabited woodland. Horse and large bovines, along with microtids and hamsters indicate the presence of open conditions along the edges of the floodplain. Wild boar and dormice are indicative of interglacial conditions.

Bird remains were found in units 3-4 and 5 (layers G and F) and although definition to species was difficult due to the fragmentary nature of the material, the avifauna appears to be dominated by several species of waterfowl, notably mallards, teals, tufted duck and coot.

Sampling for pollen was undertaken on two occasions by Urban (in: Boscheinen et al. 1984) and by Bittmann (2000). Urban interpreted her results as representing an end of interglacial situation, with dominant *Pinus* and *Betula.* Based on his analyses, Bittmann came to the conclusion that pollen at Miesenheim I had been strongly degraded, leading to a biased dominance of conifers. He concluded that the botanical remains, including fragmentary charcoal pieces, offered no information on either the stratigraphical position of the deposits or a reconstruction of the environment. Only the abundant algae in Unit 5 (layer F) indicated the presence of open water surrounded by lush vegetation

Summary

The environment and climate during the development of the site can be reconstructed by combining the results of the analyses (**fig. 2**). Three main phases can be recognised:

Phase 1 – strong fluviatile activity and the accumulation of thick sand deposits at the site, followed by terrestrial conditions. Interglacial. Miesenheim sands and unit 2, layer H.

Phase 2 – the terrestrial conditions prevailing towards the end of phase 1 continue into the following phase. The local biotope is characterised mainly by open grasslands dotted with bushes and some wooded areas. An open body of water, surrounded by fenlands and damp woodlands is present. Interglacial. Units 3-4, layer G.

Later, the site is waterlogged. Damp woodlands and fenlands are still present. A lake with lush vegetation and fluctuating levels of water forms at the

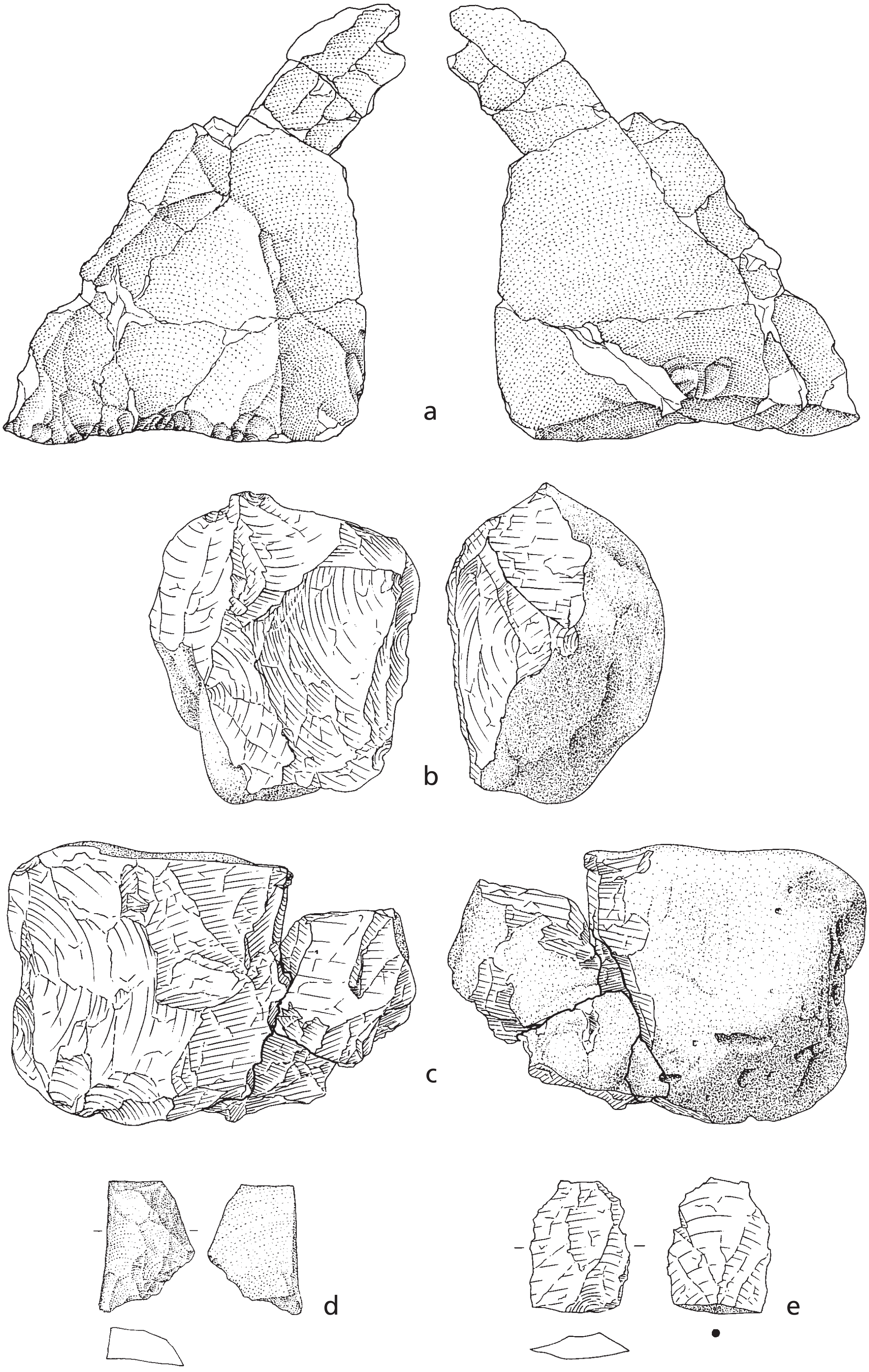

Fig. 3 Lithic artefacts from Miesenheim I. Fine-grained quartzite flake with retouch along the base (a); quartz core (b); quartz core with refitting angular debris (c); quartzite Burin de Siret (d); quartz flake (e).

Tab. 1 Counts and percentages of artefacts and raw materials at Miesenheim I.

material	core	flake	flakelet	angular debris	hammer-stone	burin	total	% total
KSC	–	1	1	–	–	–	2	1.8
QZ	4	13	21	64	–	–	103	94.5
QZT	–	1	–	1	1	1	3	2.8
RF	–	–	1	–	–	–	1	0.9
total	4	15	23	65	1	1	109	100.0
% total	3.7	13.7	21.2	59.6	0.9	0.9	100.0	

KSC = siliceous slate, QZ = quartz, QZT = quartzite, RF = river flint

Tab. 2 Counts of artefacts and raw materials in units 3-4, layer G and unit 5, layer F at Miesenheim I.

unit	material	core	flake	flakelet	angular debris	hammer-stone	burin	total
5 (layer F)	KSC	–	–	1	–	–	–	1
	QZ	–	6	6	23	1	–	36
	QZT	–	1	–	1	–	1	3
	RF	–	–	1	–	–	–	1
sub-total								41
3-4 (layer G)	KSC	–	1	–	–	–	–	1
	QZ	4	7	15	41	–	–	67
sub-total								68
totals		4	15	23	65	1	1	109

KSC = siliceous slate; QZ = quartz; QZT = quartzite; RF = river flint

site, but gradually silts up. Second half of an interglacial. Unit 5, layer F.

Phase 3 – open water with lush vegetation present again at the site. Early glacial conditions, followed by Glacial Maximum and the following warm phase. Units 6-8, layer C.

Find distribution

The lithic artefacts and faunal remains form a single horizon of finds stratified in the interglacial deposits of units 3-4 and 5 (layers G and F). In the few parts of the site where the stratigraphic sequence was intact, finds were distributed vertically up to 50-70 cms in depth. Close clusters of anatomically connected bone elements as well as short refits between bone fragments and between lithic artefacts indicates that the finds were recovered more or less *in situ*. However, the vertical distribution of the finds, evidence of deposition of some faunal remains during different seasons of the year (see below 4) and superimposed incidences of deposition suggest we are dealing here with an attritional assemblage.

Post-depositional factors, in particular phases of erosion and removal of tectonically-displaced portions of the site during the quarrying of pumice had resulted in a differential representation of finds over the site areas. Intact sediments containing finds were present in area 3 and the western part of area 1, but here find density was often less than 10 finds per square metre. In contrast, area 2 produced the densest concentration of finds even though the sedimentological sequence at this part of the site had been partially eroded (**fig. 1c**).

Lithics and larger vertebrates

The lithic assemblage

The presence of hominids at Miesenheim I is testified by an assemblage of 114 lithic artefacts (Turner 2000); and see Vollbrecht (1997). A total of 109 artefacts was recovered during excavation and 5 additional pieces were collected when the site was discovered. The excavated assemblage comprises artefacts of quartz, quartzite, siliceous slate and relict river flint, raw materials locally obtainable from the gravels of the Rhine River and its tributaries. Despite its relatively poor cleaving properties, quartz was the preferred raw material and 94.5 % of the lithic finds are made of quartz (**tab. 1**). The lithic artefacts are distributed vertically through units 3-4 (layer G) and 5 (layer F), but the majority of the finds are located in the gleyed silts of units 3-4 (*n* = 68) with less quantities in unit 5 (*n* = 41) (**tab. 2**).

The quartz artefacts comprise flakes, angular debris and several core-like pieces (**fig. 3**). An elongated quartz pebble shows damage at one end, consistent with its use as a hammerstone. Only two finds are retouched, a fine-grained quartzite flake (**fig. 3a**) and a flake of quartz. The absence of other retouched artefacts and the fairly large amount of debris, including some flakes produced during retouching (Vollbrecht 1997) suggests, on the whole, that finished artefacts were removed from the site.

An interesting accumulation of stones was revealed in area 2. Stratified at the base of units 3-4 (layer G), this feature comprised a single layer of mainly quartzite and some quartz pebbles, spread diagonally across the trench in the eastern part of area 2 (**fig. 7**).

The larger vertebrates

Out of a total of 1699 recorded faunal remains, 1146 bone, teeth and antler, representing 15 mammals, could be identified (**tab. 3**). These remains are excellently preserved, but highly fragmented due to pressure from overlying sediment after burial. Since the number of identifiable specimens (NISP) for many of the animals was not particularly high, more detailed assessments of minimum numbers of individuals (MNI) could be attempted by taking into account body-side, counting juvenile and adult bones separately, recording differently-sized bones of adult animals and defining eruption and wear stages and different patterns of morphology on teeth. The pattern that emerged after analysis was one of low numbers of identifiable fragments combined with high numbers of individuals for most animals. The discrepancy between NISP and MNI gives an impression of how much material from the individual animals either did not reach the site or, more likely, was removed after deposition. The activities of hominins, carnivores, phases of erosion and even the removal of parts of the site during the commercial extraction of pumice are all factors which contributed to the representation of bones at Miesenheim I. Finally, only four species – horse, a large bovine, red deer and roe deer – produced enough material for an in-depth analysis.

Strong visual evidence of human modification of the bones is lacking. Fine, linear incisions on three bones, superficially resembling cut marks and submitted for SEM analysis, are probably of natural origin, whereas linear incisions on a fourth bone, a fragment from a mandible of red deer, may derive from cutting by a stone tool (pers. comm. Jill Cook) (**fig. 4**). A conchoidal flake scar, similar to notches produced by humans when opening bone shafts to obtain marrow, was observed on a fragment of a long bone (humerus) of horse or large bovine (**fig. 8**).

The putative cut mark on the mandible and the impact notch on the long bone suggest hominins may have procured only red deer and horse/large bovine. In order to test this hypothesis, the skeletal part representations of these animals were compared to that of roe deer, which appears to bear no evidence of hominin modifications. Due to the relatively low counts of elements for all of these vertebrates, counts of minimum numbers of elements (MNE) were split into four carcass units (head, axial, limbs and feet) and expressed as percentages of the total number of elements (**fig. 5**). The skeletal representation of red deer is very similar to that of roe

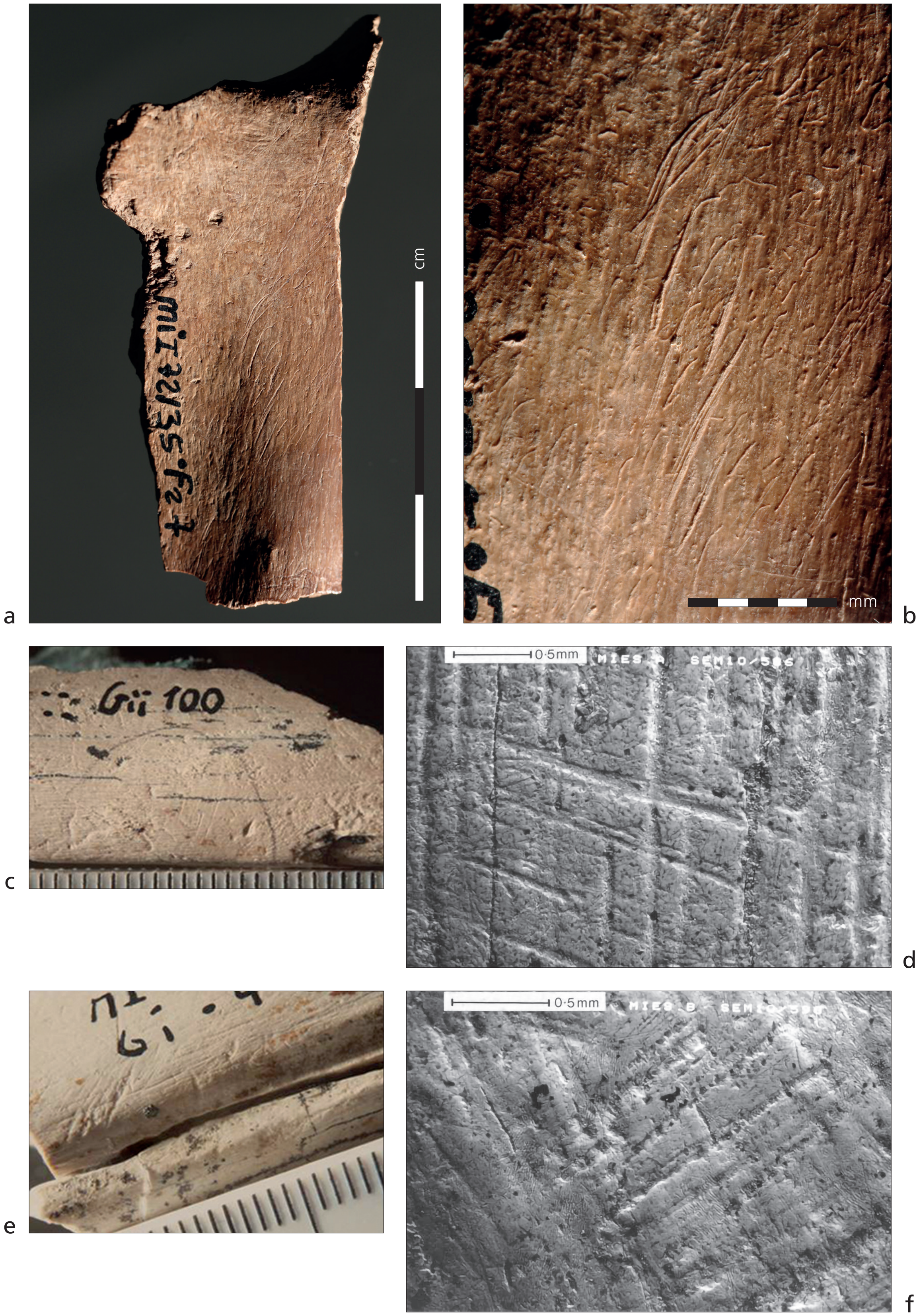

Fig. 4 Surface modifications on faunal remains from Miesenheim I. Putative cut marks on a mandible of red deer (*Cervus elaphus*) from Unit 5, layer F (a-b). (Photo Wolfgang Heuschen, RGZM). Surface scrapes on bone fragments from unit 3-4, layer G (c and e) (Photo Elaine Turner, RGZM) and details of marks taken by Scanning Electron Microscope (e and f). (Scans Jill Cook, British Museum).

deer. Horse has a more foot-dominated skeletal profile than the other animals, and the remains of the large bovine are characterised by larger quantities of axial elements than in the other species. With the exception of the large bovine (see below for description of bovine remains), there were no significant differences in the patterns of skeletal representation of horse, red deer or roe deer indicative of a specific targeting of a certain species by hominins.

Traces of carnivore gnawing were also observed on the bones, including those of the carnivores and 20.9 % of the total minimum number of elements of horse, large bovine, red and roe deer showed traces of carnivore gnawing.

Seasonality and behaviour of the animals

Cervid antlers are useful seasonal indicators due to their annual cycle of regeneration. The base of an unshed antler of red deer was recovered from unit 3-4 (layer G). The pedicle is slender, more typical of a young male. Red deer stags carry their antler from September through to spring (mid-February to March), when they are shed (Schmid 1972). Young males may carry them longer, shedding in April or even May, so the individual from Miesenheim may have died any time between September and May. Tooth eruption and wear patterns observed on a mandible of a juvenile red deer from Miesenheim were compared with those established by Legge and Rowley-Conwy (1988) for a sample of modern deer and indicate death of the individual from Miesenheim I during its second winter, thus providing supportive evidence for the presence of red deer at the site during the colder months of the year (**fig. 6**).

Roe deer undergo a different cycle of antler regeneration than red deer, carrying their antler from April and shedding in October/November. Shed antler of 14 individual roe deer were recovered at Miesenheim I. Based on the development of the antler, four of these animals were yearlings and the remaining ten animals were adults over two years of age. Time of death could also be established for three of the juvenile roe deer using comparative data from tooth eruption and wear patterns of teeth of a modern sample (Legge/Rowley-Conwy 1988). The three juvenile individuals from Miesenheim died between summer and winter.

Tab. 3 Numbers of identifiable specimens (NISP) and minimum numbers of individuals (MNI) of vertebrates present at Miesenheim I.

Common Name	Latin Name	NISP	MNI
Western polecat	*Mustela* (*P*) *putorius*	1	1
Steppe polecat	*Mustela cf. eversmanni*	1	1
Wild cat	*Felis sylvestris*	1	1
Elk	*Alces* sp.	2	1
Elephant	Elephantidae gen. et sp. indet.	2	2
Wild boar	*Sus scrofa*	4	1
Badger	*Meles* sp.	8	1
Mosbach wolf	*Canis lupus mosbachensis*	11	2
Deningers bear	*Ursus cf. deningeri*	12	2
Rhinoceros	*Stephanorhinus* sp.	33	3
Stehlins bear	*Ursus* (*Plionarctos*) *stehlini*	34	2
Horse	*Equus* sp.	110	4
Large bovine	*Bos*/*Bison* sp.	304	3
Roe deer	*Capreolus capreolus*	306	9-14
Red deer	*Cervus elaphus*	317	7
Sub-total		1146	
UL		396	
UM		110	
US		22	
Indet.		25	
Total		1699	

UL = Unidentified large vertebrates (cf. horse, large bovine); UM = unidentified medium vertebrates (cf. red deer, wild boar, bear) and US = unidentified small vertebrates (cf. roe deer, badger); Indet. = indeterminate fragments. MNI counts for roe deer based on teeth (MNI 9) and shed antler (MNI 14).

Additional seasonal evidence was gleaned from the avian fauna. The crake, corncrake and song thrush are summer visitors to this region today. If their seasonal migration patterns were the same

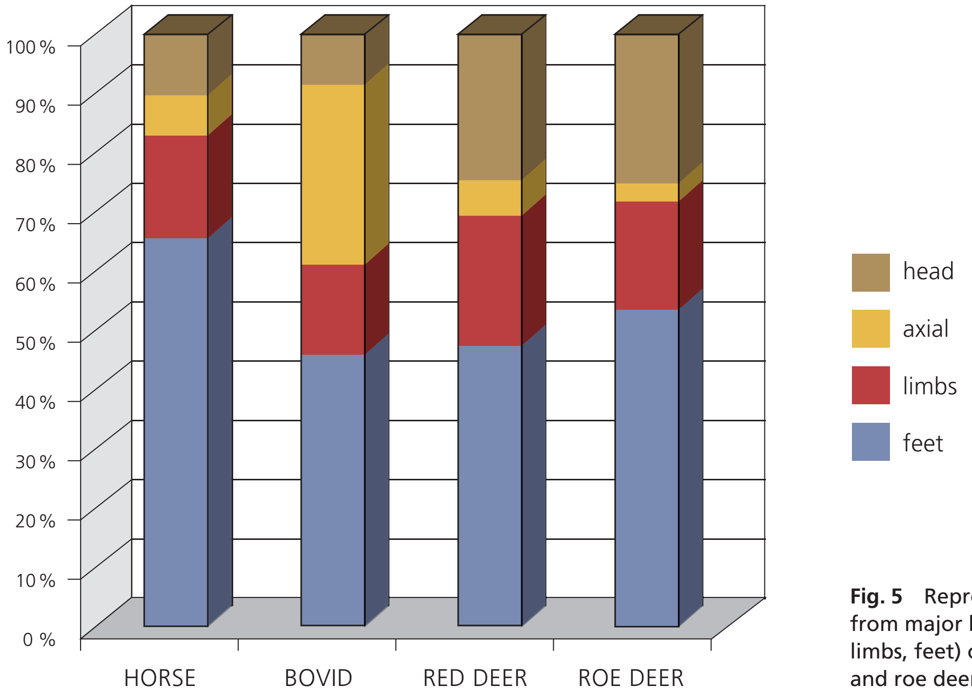

Fig. 5 Representation of elements from major body units (head, axial, limbs, feet) of horse, bovid, red deer and roe deer from Miesenheim I.

during the Pleistocene, this could be evidence for the deposition of some bird remains during the summer months. In summary, there seems to be evidence at Miesenheim I of the remains of animals and birds being deposited at the site practically all year round. This scenario gives additional support to the attritional character of the assemblage.

Roe deer are often recorded in marshy areas where they feed avidly on sedge-clover and seek refuge in thickets along riverbanks (Görner/Hackenthal 1988). Red deer are frequently found in floodplains. They seek out ponds and lakes as watering places; mud baths play an important role in their grooming. Thus, ideal conditions for both roe and red deer would have existed at Miesenheim I practically all the year round. However, there is evidence (cervid antler regeneration and cervid tooth eruption and wear) that deer were present at Miesenheim particularly during the cooler parts of the year, from autumn through winter (**fig. 6**).

The core unit of modern red deer comprises a hind and her young (calf and yearlings) (Ahlen 1965); stags form separate, temporary "bachelor" groups of varying sizes (Legge/Rowley-Conwy 1988). During the rut in September and October, red deer behaviour changes drastically as dominant males emerge from the bachelor groups and become territorial. Core unit size is temporarily increased as stags attempt to maintain a harem of females. After the rut, the larger groups disband and the smaller, sexually segregated, social groups re-form. In contrast, roe deer lead more solitary lives. They are usually encountered in small family groups, comprising a doe and her young, or as single animals (Strandgaard 1972). The bucks are usually solitary. Larger bands can form over winter (Prior 1968), when groups of mixed sexes congregate.

Both horse and large bovines would have used the floodplain to access water for drinking. Horses in particular are water-dependent and close proximity to watering places is an important requisite in their ranges. The main river courses of the Rhine would have been an optimal place for herds of both animals to access water on a regular basis throughout the year, especially in winter when other watering places may have been frozen over.

Thus, with herds of horses and large bovines and groups of cervids visiting the floodplain regularly as part of their natural ranges, Miesenheim I was an attractive place for foraging hominins. This situation

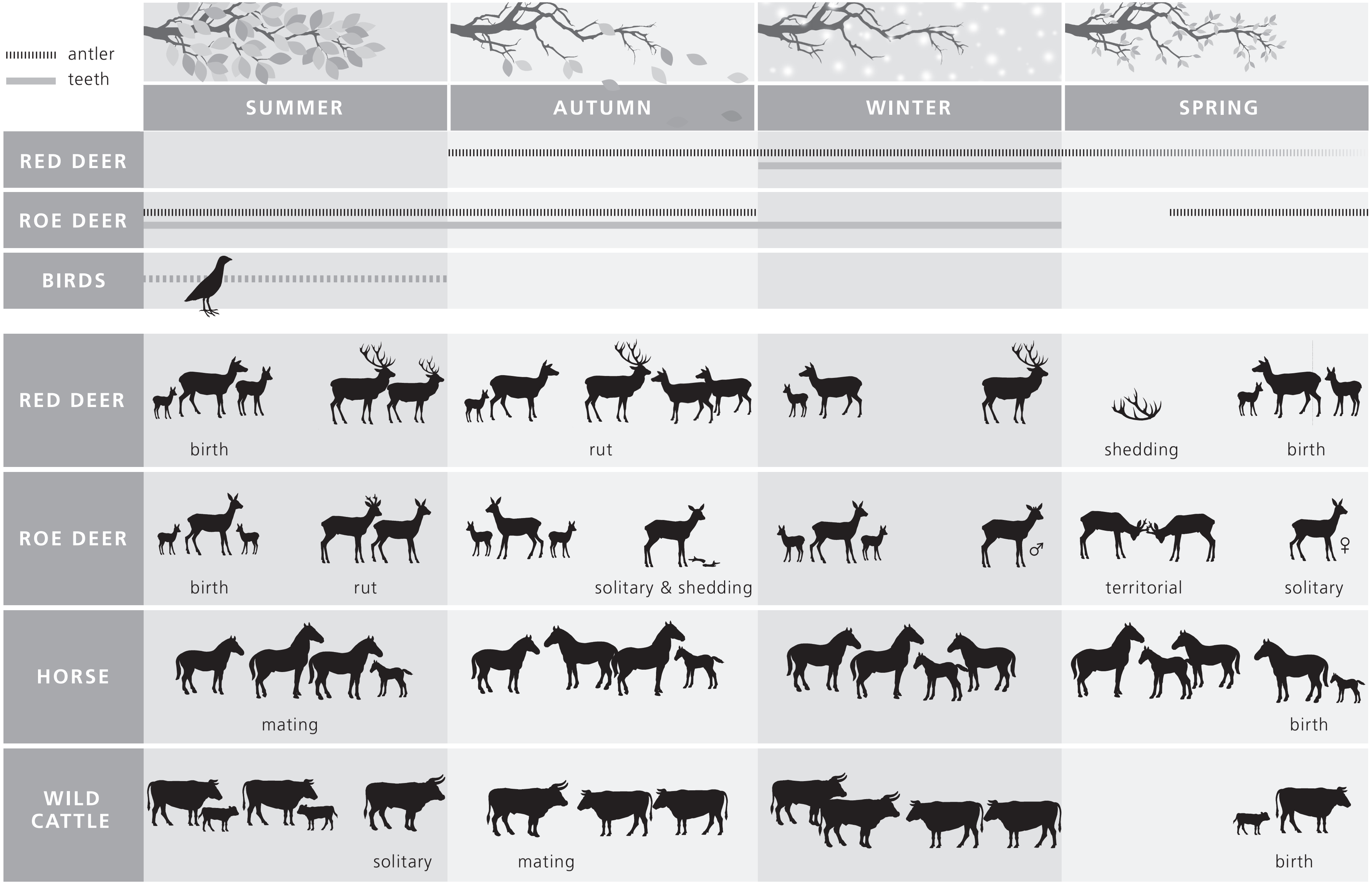

Fig. 6 Evidence of seasonality from Miesenheim I based on antler regeneration and age at death of red deer and roe deer and migration patterns of birds at the site (above), and comparative seasonal cycles of modern red deer, roe deer, horse and large bovine (below). Seasons given following the northern meteorological seasons. Spring = March – May; Summer = June – August; Autumn = September – November; Winter = December – February.

was probably optimised during the cooler months of the year, when increased numbers of cervids were present and horses and large bovines may have been using the site as a winter watering hole on a regular basis (**fig. 6**).

The diachronic development of the site of Miesenheim I and hominin activities

Phase 1

It is not surprising that there is no evidence of the presence of hominins at the site during this period of strong fluviatile activity. The locality itself and most parts of the surrounding landscape formed part of an extensive Middle Pleistocene Rhine Valley and were probably under water for an unknown period of time, but long enough to deposit several metres of sand. The transition to more terrestrial conditions, observable at the top of the sands, probably occurred as a result of downcutting of the main channel(s) of the river. As the river receded, the site and the immediate vicinity of the site became drier.

Phase 2

Erosion, redeposition of sediments, waterlogging, occasional higher water activity and the formation of an open body of sluggish water, which later silted up, all suggest a period of strongly fluctuating conditions at the site, corresponding to the location of Miesenheim I in the floodplain of the river during phase 2. Despite these, to my way of thinking, unstable conditions, hominins appear to have discovered and utilised the site only during this phase.

The oldest "feature" at Miesenheim I is the layer of pebbles discovered at the base of units 3-4, layer G (**fig. 2**). Located at the eastern end of area 2, this accumulation of stones was approximately 5 m long and distributed diagonally through the trench (**fig. 7**). Some isolated pebbles were recovered above this layer and probably represent stones derived from the feature. The pebble layer had been disturbed by a fissure-like fault running through the centre and truncated by a second, deeper fault at its eastern end. The two halves of the pebble layer had moved apart by between 10 and 40 cms and were displaced to approximately 15 cm in depth. The feature comprised pebbles of quartzite and quartz, typical raw materials of the region. There were no indisputable signs of a particular orientation of the stones, as would be expected, for example, in the natural bed of a stream. However, the movement and re-deposition of sediments in units 3-4 (layer G) may have led to a post-depositional re-alignment of water-borne stones. Significantly, none of the pebbles showed evidence of utilisation by hominins, indicating a non-anthropic accumulation of these finds. Thus, the preservation of the pebble layer as

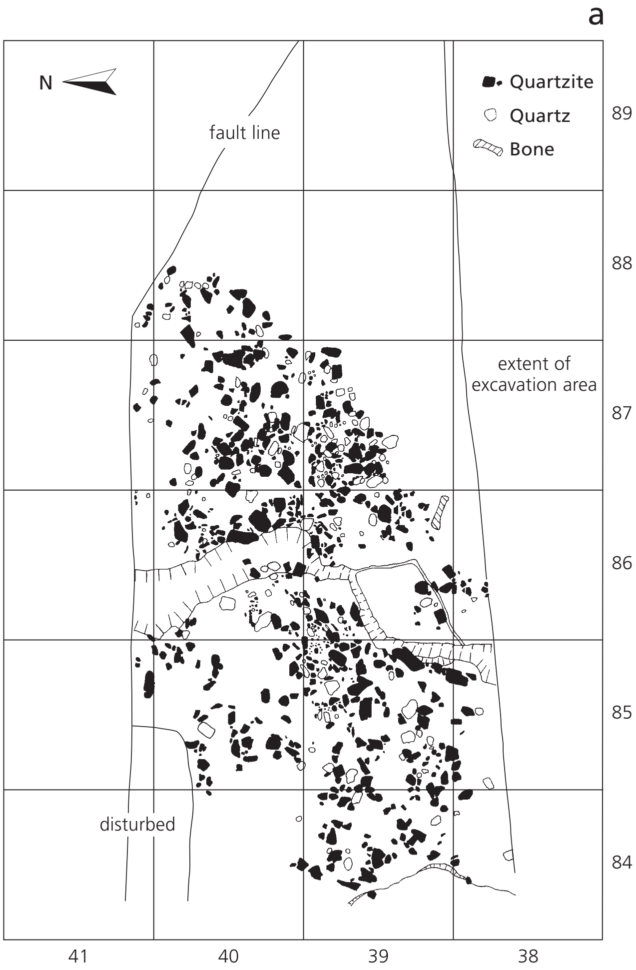

Fig. 7 The pebble layer in area 2 at Miesenheim I. Plan of the pebbles as revealed during excavation (a), plan of isolated pebbles removed prior to discovery of the layer = shaded area (b) and photo of the pebble layer (c).

revealed during excavation, gives few clues as to its genesis. Only two finds, a poorly preserved shaft of a radius of a juvenile horse and a small fragment of bone were laid close to, and almost on top of, this feature. They represent the oldest faunal remains from unit 3-4 (layer G); the rest of the animal bones and lithic artefacts were stratified above the pebble layer.

Important, however, is that the distribution of lithic artefacts at Miesenheim I show a very close spatial association with this feature. Lithic artefacts and lithic debris from units 3-4 and 5 (layers G and F) were recovered overlying the pebble layer, and spreading to the west (area 2) and east (area 3) of this feature (**fig. 8**). It is possible that the pebble layer was still visible or partly visible when hominins first visited the site. This feature may have provided them with an attractive, on-site, source of raw materials for their stone artefacts, or provided a more stable, drier surface, amidst waterlogged deposits, on which hominins could stay, or both. In the western part of area 1, areas 3 and 4, the number of artefacts is low (particularly in area 4). These areas are interpreted as peripheral to the main distribution of artefacts in area 2. Several refits between quartz core-like pieces, quartz flakes and angular debris are a major feature of lithic distribution in units 3-4 (layer G) in area 2 and clearly indicate that this raw material was worked here. In addition, a quartz hammerstone was recovered in area 2 and

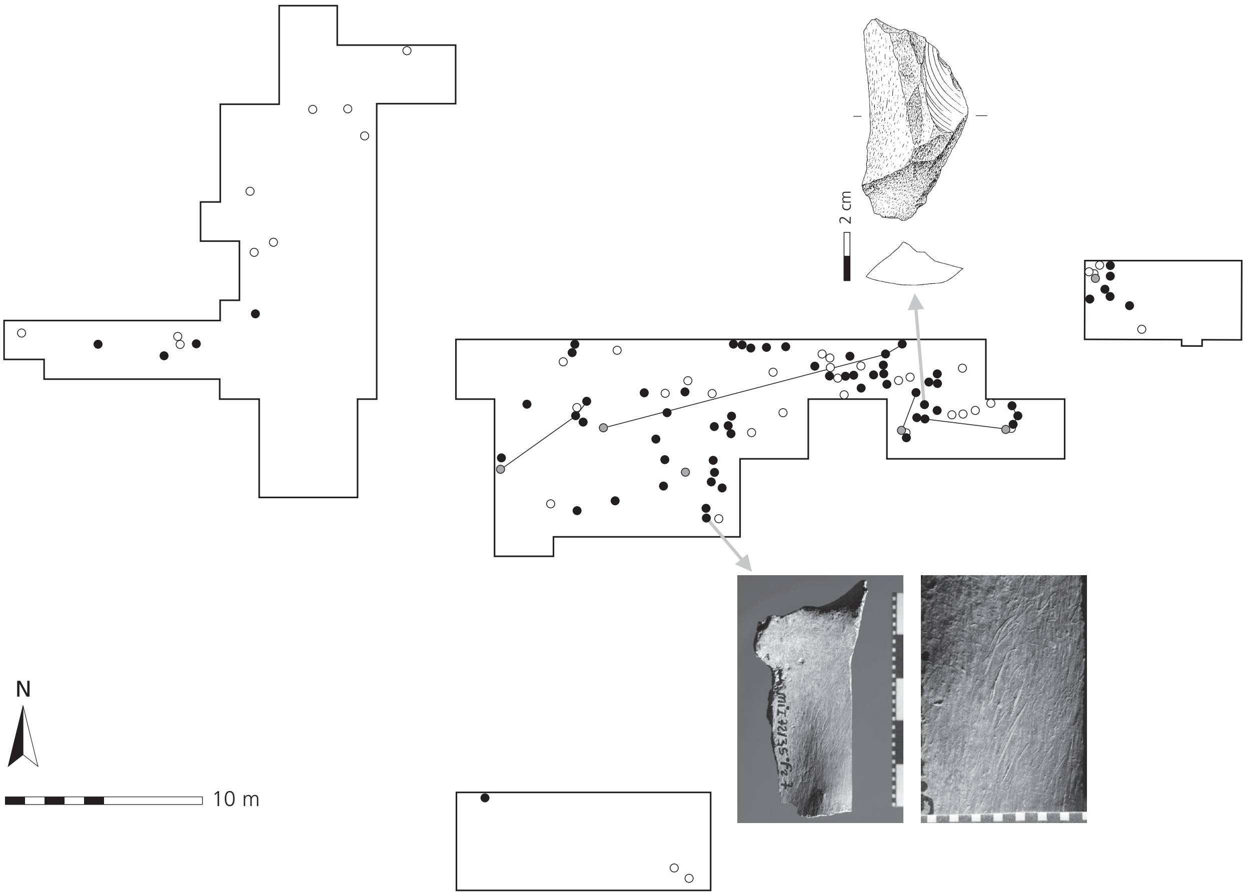

Fig. 8 Distribution of lithic artefacts in areas 1, 2, 3, and 4 and the positions of the bone with an impact notch (above) and the potentially cut-marked red deer mandible (below). Closed symbols – artefacts in units 3-4, layer G; open symbols – artefacts in unit 5, layer F. Shaded symbols – cores. Lines indicate refits between artefacts.

the fragment of a shaft of a humerus of horse/large bovine bearing the remains of a conchoidal, flake scar. A red deer antler frontlet from a young male, deposited sometime between September and April or May, was also found in this unit.

Of the four species of mammal that produced larger quantities of remains, only one, the horse, shows a clear association with units 3-4 (layer G), in which the bulk of the artefacts were also found. The open conditions in these units, indicated by the molluscan fauna, would have provided optimal habitat for the horse and may have led to the dominance of this species in layer G. Roughly 79 % of the remains of horse were recovered in this layer, in contrast to 19.2 % in the upper part of the deposits, in unit 5 (layer F). Fragmentary horse teeth and a few postcranial bones of this species are present in area 2, but on the whole, horse remains are peripheral to the main area of lithic distribution. One of the interesting aspects of the faunal assemblage from Miesenheim I is the presence of portions of animal carcasses preserved more or less in anatomical connection, and one of these examples – bones from the fore and rear legs of horse – was recovered in area 3 (**fig. 9**). This concentration of refitting fragments of bones and articulating elements is from an individual, juvenile, horse and comprises elements of the right and left fore and rear limbs and feet, a fragment of a rib and two lumbar vertebrae. These remains were spread over an area of some 16 m², with elements of the right side of the body located towards the south-east corner of area 3 and left elements more to the north-west. Several of the limb and foot bones showed traces of heavy gnawing by a carnivore and tooth scores on these elements were comparable in size to those

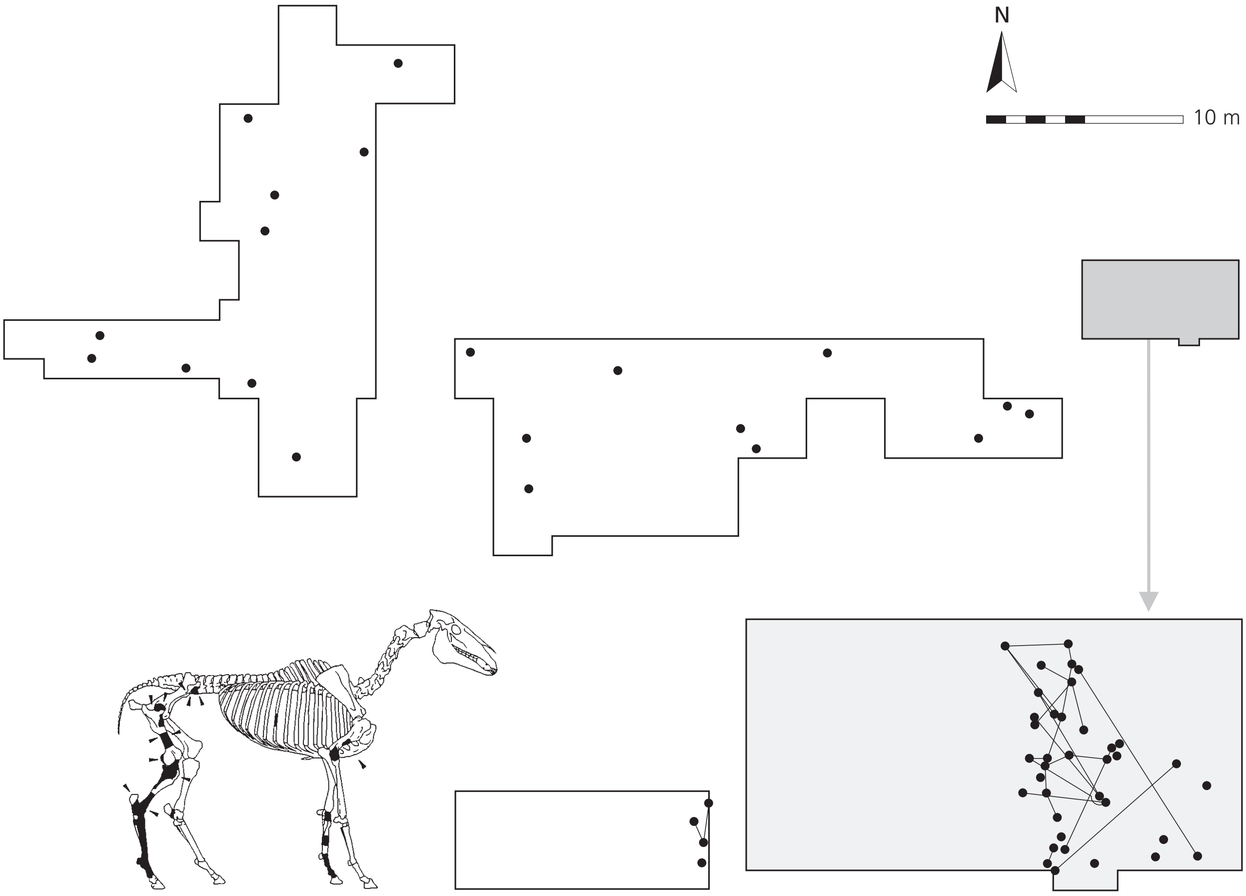

Fig. 9 Distribution of isolated horse remains in areas 1, 2, and 4 and the partial carcass of a horse in area 3. Lines indicate refits between bones.

produced by the wolf (Haynes 1983). The absence of any visible forms of hominin modification of the bones makes it difficult to interpret this assemblage of horse bones as a hominin kill which was later scavenged by carnivores, a carnivore kill which took place at the site when hominins were not present or a natural death of a young animal which was scavenged.

In contrast to horse, remains of red deer were vertically distributed more or less equally through units 3-4 and 5 (layers G and F) (52 % and 47.6 % respectively) and distributed throughout the site (**fig. 10**). Although fragments of red deer bones could be refitted, and elements re-articulated or attributed to an individual animal, articulating red deer carcasses comparable in preservation to that of horse in area 3 were not recovered. In fact, the red deer remains from Miesenheim I give the impression of a highly fragmented and widely scattered assemblage of bone. The mandible of red deer from unit 5 (layer F) with putative cut marks (**fig. 4**), was located in area 2, on the edge of the main area of lithic artefact distribution (**fig. 8**).

Teeth, fragmentary bones and antler of roe deer are widely scattered over the site, showing a state of preservation and distribution similar to that of red deer. Vertically, however, the remains of this cervid were associated with the upper part of the deposits, being predominantly found in unit 5 (layer F; 71.6 %), with fewer remains in units 3-4 (layer G; 28.4 %). A partially preserved carcass of an adult roe deer was recovered from the western edge of area 1 (**fig. 11**). This isolated assemblage of bones comprises elements from the left and right fore and rear legs of the animal, scattered over approximately ten m². Conjoins between the finds indicate displace-

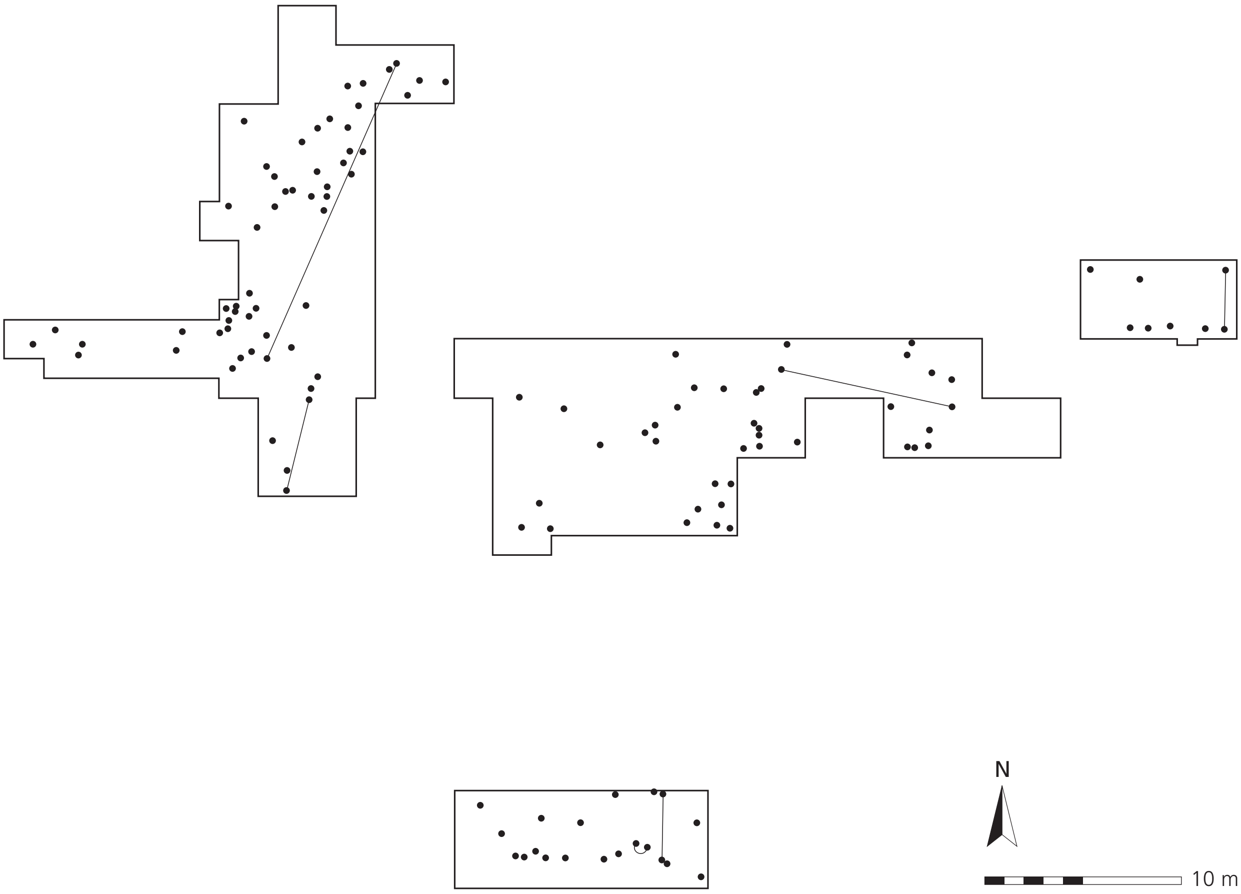

Fig. 10 Distribution of isolated red deer remains in areas 1, 2, 3 and 4. Lines indicate refits between bones.

ment of remains up to 4 m. Carnivore gnawing was observed on only one element from this assemblage and the horizontal and vertical distribution of the remains of this individual was more likely due to displacement due to faulting rather than other factors. Several closely-spaced fault lines transected the area in which the carcass had been embedded. Since this assemblage is located close to an area where pumice had been intensively worked, portions of this carcass may have been recently removed.

The remains of large bovines are almost exclusively associated with the upper part of the deposits and 96.1 % of the bones of these animals were stratified in unit 5 (layer F) and only 3.9 % in units 3-4 (layer G). In contrast to the distribution of both red deer and roe deer, remains of large bovines at Miesenheim I are concentrated in the eastern parts of areas 2 and 3, with only a few isolated finds in areas 1 and 4 (**fig. 12**). The partial carcass of one mature individual is very well-preserved in area 2 and comprised pieces of the cranium, vertebrae, ribs, limbs and feet of the animal. The scapulae, caudal vertebrae, right radiocubitus and pelvis, and the left humerus were not recovered, but these elements or fragments of them may be contained in deposits to the south-east, which have not been excavated. Typical for this assemblage are numerous, and occasionally long, conjoins in the horizontal plane between bone fragments which had fractured in a dry state, reflecting the strong post-depositional effects of, presumably, pressure of overlying sediment. The position of the elements from the different sides of the body suggests the carcass was laid on its right side with its fore quarters to the north-west, rear quarters to the south-east and the articulated spine in between. Since the carcass

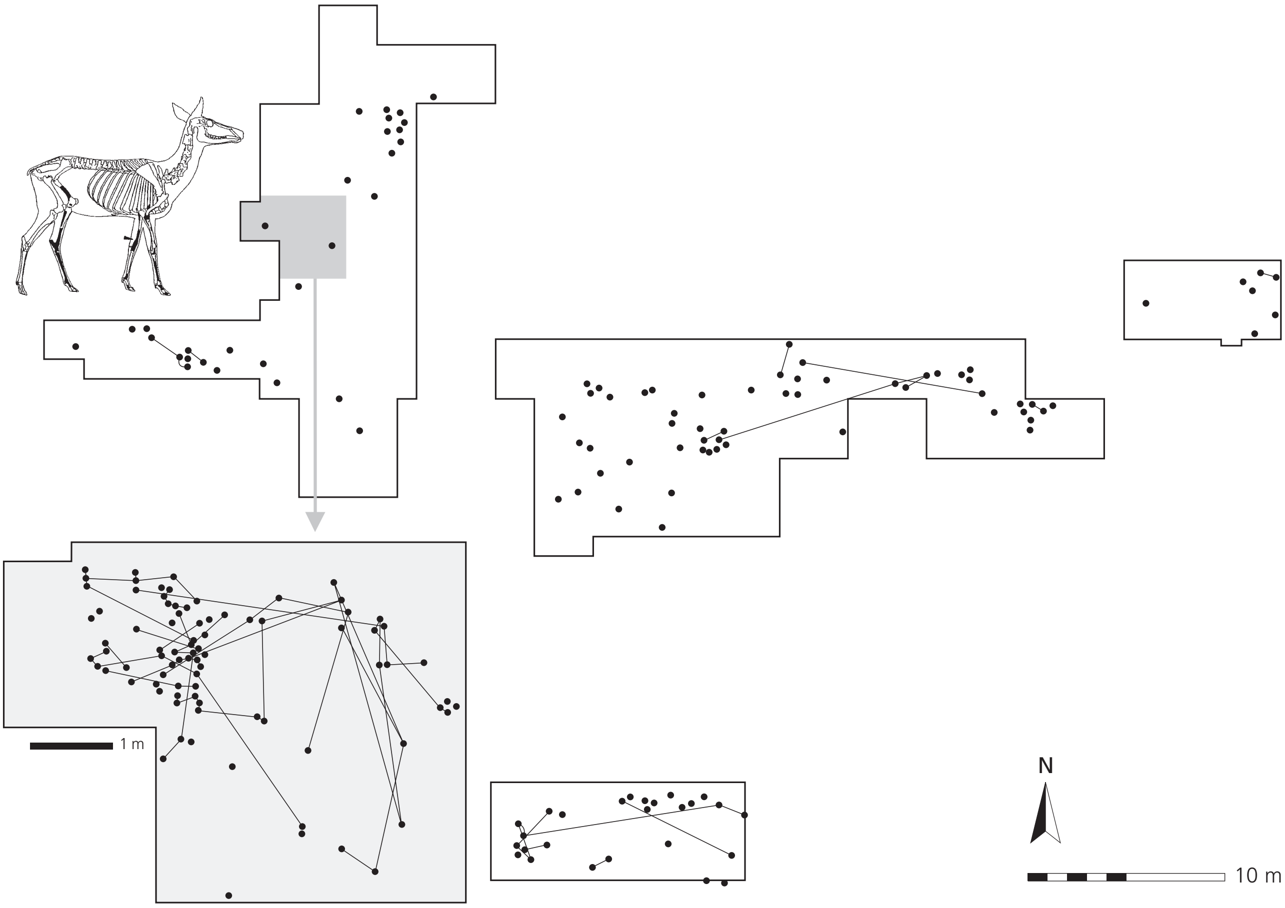

Fig. 11 Distribution of isolated roe deer remains in areas 1, 2, 3 and 4 and partial carcass of a roe deer in area 1. Lines indicate refits between bones.

of this individual was probably deposited at a time when very wet and muddy conditions prevailed at the site, the right side of the body may have sunk into the soft substrate. This would probably account for the fewer elements from the left side of the body being present, since these were more exposed to post-depositional factors, resulting in bone dispersal or destruction. Hominin modifications of the carcass were not observed and carnivore gnawing was found on only five bones.

Phase 3

As the interglacial ended and early glacial conditions took over, find deposition at Miesenheim I ceased and the site was abandoned. Even the reappearance of a body of water at Miesenheim I (**fig. 2**, unit 7, layer C) no longer seemed an attractive prospect under these colder conditions for a further occupation of the site by hominins.

Conclusion

Detailed analyses undertaken at Miesenheim I have revealed the genesis of a Lower Palaeolithic interglacial site from the time when the locality was part of the fluviatile system of the Middle Pleistocene Rhine River (Phase 1), its assimilation into the backwaters of the flood plain (Phase 2), burial below soliflucted deposits and loess during the oncoming glaciation (Phase 3), integration into the volcanic area of the East Eifel region and burial by younger cold stage sediments towards the end of the Glacial cycle.

In addition, the results of the geological, micromorphological and molluscan analyses of the find-

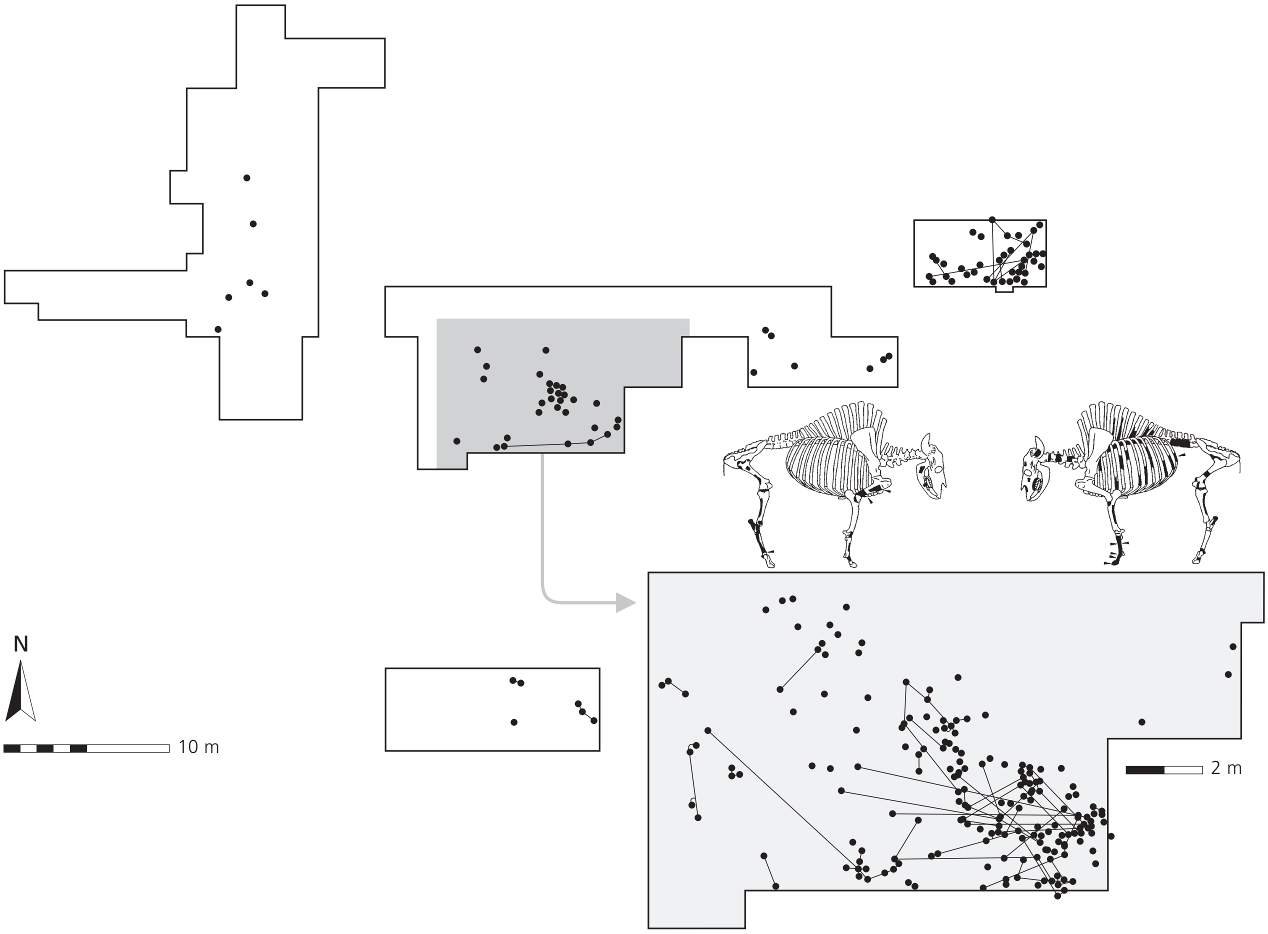

Fig. 12 Distribution of isolated bovid remains in areas 1, 2, 3 and 4 and carcass of a bovid in area 2. Lines indicate refits between bones.

bearing deposits provide the background to the hominin use of the site. During the second half of the interglacial phase, and at a time when the locality was situated in the floodplain of the Rhine, hominins utilised the site. During interglacials, valleys with wide floodplains probably teemed with wildlife, representing a high biomass with strong seasonal fluctuations. At Miesenheim I, the close proximity of an open body of water would have been an added attraction to hominins, not only as a source of water for themselves, but also as a watering hole for animals they regarded as prey.

What is lacking at Miesenheim is stronger evidence of hominin interaction with the faunal remains. The conchoidal flake scar on the long bone of horse or large bovine and the putative cut marks on the red deer mandible offer a tantalising indication of which animals hominins were interested in, but no more than that. In contrast, the lithic assemblage gives us some information about hominin activities here. Miesenheim I was a place where hominins produced stone tools made of local raw materials, which they may even have acquired at the site itself. The distribution of the debris they left behind indicates that at this time at least, areas 2 and 3 must have been relatively dry, representing a land surface which hominins could move over and where they could produce lithic tools.

Hominins were well aware of the potential of localities such as Miesenheim I, and this site may have been just one of a number of areas that were visited either once or even on a regular basis as part of hominin movement and land-use in this area of the Central Rhineland. The use of these sites may also have seasonally fluctuated. Although there is evidence at Miesenheim I for deposition of faunal remains throughout the year, seasonal indicators suggest deposition of many remains during the colder periods of the year when numbers of some species increases, during the rut, for example. These situations could have been observed and specifically exploited by hominins. Recent analysis of tracks of *Homo erectus* footprints at Ileret in north-western Kenya indicates repeated use of lakeshore habitats by hominins (Roach et al. 2016). The orientation of the tracks suggests hominins generally moved along the lakeshore, following the land-water ecotone. This is not only an effective way of foraging for both plants and animals, but also mirrors patterns of land-use by modern-day carnivores, which follow fixed waterways where densities of prey are high and where washed ashore carcasses offer scavenging opportunities, a strategy that reduces both search and stalking efforts (Roach et al. ibidem). A similar scenario can be extrapolated to the Rhine Valley during a Middle Pleistocene interglacial. Here hominins would have moved over the landscape following the banks of a changing system of braided river channels, ox-bow lakes and flood-plain ponds, where they would have encountered high densities of prey and stranded carcasses of animals. Close to one of the ponds, hominins stayed on a relatively dry area of land and produced artefacts of quartz, quartzite, siliceous slate and river flint. They smashed open a long bone to procure marrow and may have disarticulated the carcass of a red deer, before moving on again. This ephemeral use of the site appears to have been limited to the interglacial phase; since the same pond or lake-side site was no longer attractive during the following glaciation.

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MARKUS WILD

“ANTLER HEADDRESSES” AND THE PREBOREAL SITE OF BEDBURG-KÖNIGSHOVEN: THE BEGINNING OF MESOLITHIC BEHAVIOUR IN THE NORTHERN EUROPEAN LOWLANDS

Abstract

Bedburg-Königshoven is the oldest Mesolithic site in the southernmost part of the Northern European Lowlands. Excavations at the site have exposed a rich spectrum of organic remains. The nature of the site as a secondary butchering camp with possible additional functions is well published, but evidence for other activities and site functions have been, thus far, in the shadow of the prominent find categories of faunal and lithic remains. Two perforated red deer (*Cervus elaphus*) crania with attached antler were recovered from this site and, due to a systematic review of the find category, are identified as so-called antler headdresses – an extremely rare type of object at Mesolithic sites. Presented in this paper is the detailed study of this find group that leads to the discussion of whether the adjacent dry-land area was the location of manufacture for at least two half-finished examples of these rare objects. The combination of this study with existing analysis of environmental and archaeological data reinforces the interpretation of Bedburg-Königshoven as a residential type site of the Early Mesolithic where a rapid adaptation to the changing environment of the Holocene is well documented.

Keywords

Antler frontlet, Antler headdress, Early Mesolithic, site function, adaptation

Introduction

The Early Mesolithic site of Bedburg-Königshoven (District Rhein-Erft-Kreis / D), was discovered in 1987 at the centre of the vast Garzweiler opencast lignite mine, and was excavated until 1988.

Artefacts were preserved in the calcareous sediments, but mining activities had already removed terrestrial sediments behind the excavated littoral zone where the centre of the settlement area had presumably been located (Street 1989a; 1991; 1993).

Data from palynological analysis (Behling 1988) and radiocarbon dates for the sediment layer containing archaeological material (KN-3999: 9780 ± 100 BP / 9176 ± 174 calBC[1]; KN-3998: 9600 ± 100 BP / 8998 ± 163 calBC[1]) suggest that the deposition of the Early Mesolithic finds had taken place during the middle Preboreal (Street / Baales / Weninger 1994).

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[1] Calibrated with CalPal Online using the CalPal_2007_HULU calibration curve.

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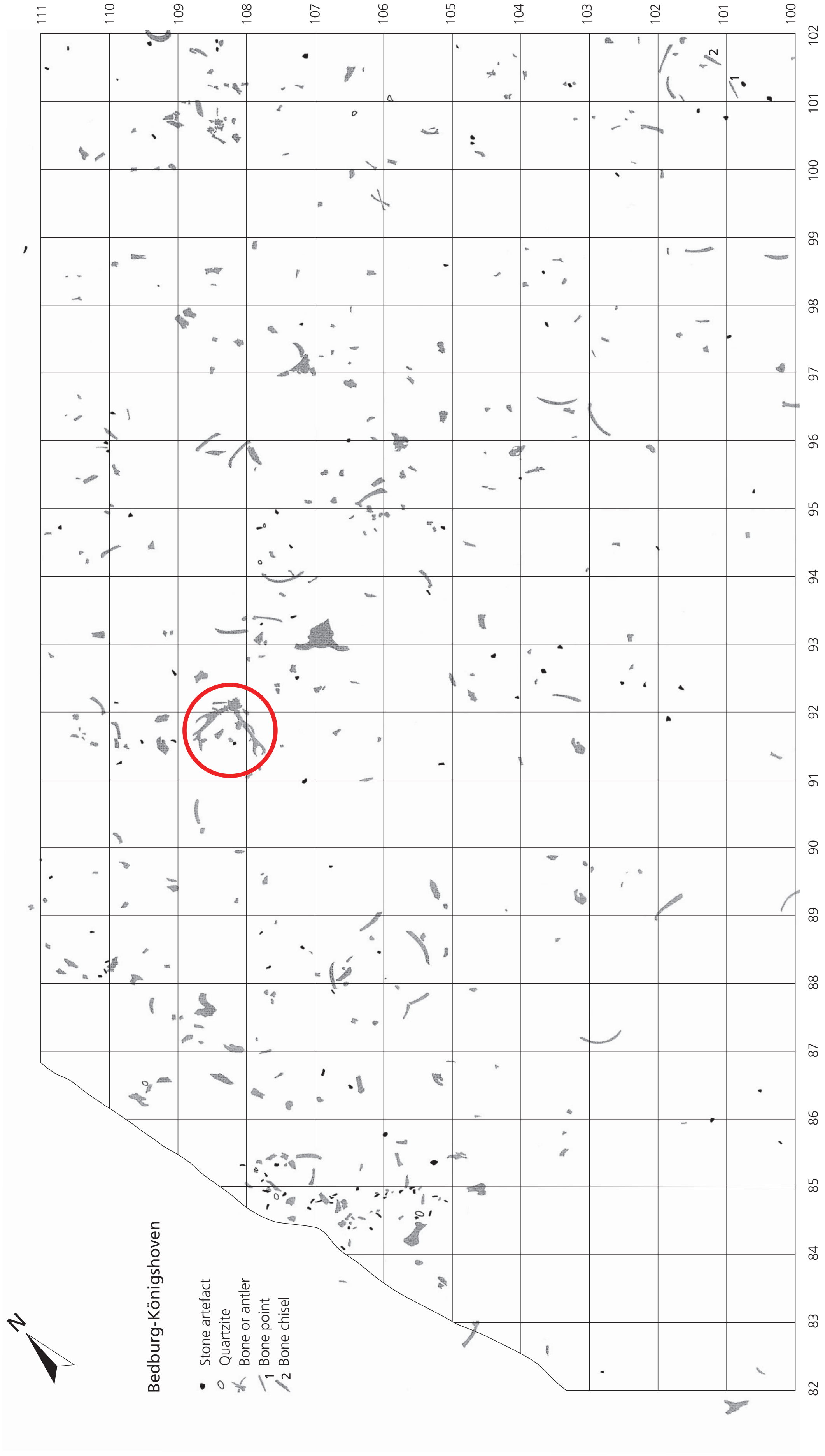

Fig. 1 Excavation plan of Bedburg-Königshoven. Frontlet 2 (E115/91-2) (circled) was found approximately 3-4 m away from the ancient shore in the North. – (Street/Wild 2015, 210 fig. 2).

The preserved part of the site (**fig. 1**) has been interpreted as an outcast zone, with the ancient shore line roughly parallel to the north-western edge of the excavation (Street 1989a). The faunal assemblage is dominated by discarded remains of large mammals. These show clear signs of anthropological modifications in the form of butchering marks (Street 1989a; 1990; 1993; 1999). It can be assumed that the animals had been hunted in the vicinity of the site (see Street 1989a, 41 ff. for further detail) with secondary butchering activities taking place at the transition area from dry land to open water at Bedburg-Königshoven. These activities resulted in waste material being disposed in an abandoned meander of the river Erft (Street 2020). The small lithic inventory – containing only 196 pieces of worked flint – supports this idea as it is composed of large lamellar lithic debitage and a few retouched artefacts possibly used for butchering. The assemblage is complemented by five blade and flake scrapers, three microliths and a heavy-duty pick (Street 1998) of 805 g. The tools indicate activities like hide working or the manufacturing of tools or the discard of parts of the lithic toolkit that were not used during the human occupation of the site. Although this interpretation is not definitive, other finds suggest that the bulk of the activities (e. g. re-tooling, tool production, hide working etc.) are those carried out at a base camp and hint at a more centralist character for Bedburg-Königshoven within the broader hunter-gatherers' settlement structure.

In the absence of any butchery marks on the fish and bird remains, it has been suggested that these species are a natural 'background' fauna (Krey 1990; Street 1989a; 1990). The only exception might be a stork (*Ciconia ciconia*) whose sole *in situ* excavated bones were an articulated right wing without anthropogenic modifications. Nevertheless, articulated stork wing bones are known from other Mesolithic contexts (Street / Peters 1991; Street 1993, 196). The presence of dogs (*Canis lupus familiaris*) is quite common on Early Mesolithic sites. Cut marks on the cranium of at least one of two dogs present at Bedburg-Königshoven indicate not only their use as a hunting aid, but as a source of ritual, food and / or raw materials (Street 1989b). An upper canine of red deer with a broken out perforation, a second upper canine and an incisor of red deer with a grooved cut across the tooth's axis as well as

Fig. 2 Bone point made of a long bone of an aurochs. – (J. Vogel / LVR LandesMuseum Bonn).

Fig. 3 Bone chisel made of the radius of a red deer. – (J. Vogel/LVR LandesMuseum Bonn).

a notched canine of a wild boar (*Sus scrofa*) were also found in the littoral zone (Street 1989a, 39 ff.). These remains can be interpreted as either discarded or lost. At the easternmost part of the excavation area, approximately 10 m away from the Mesolithic shore line, a pair of bone tools was found in close proximity which suggests a possible relationship. A bone point (**fig. 2**) made from a metapodial bone of an aurochs (*Bos primigenius*) is broken at its terminal end. A 223 mm long chisel (**fig. 3**) made of the radius of a subadult red deer shows use-traces at its working edge. While there seems to be no reason for the discard of these two artefacts, the great distance to the Mesolithic shore line as well as the small area in which they were found might indicate intentional deposition or accidental loss (Street 1989a, 38 f.), perhaps during swimming, wading or sitting in a dugout canoe.

Going beyond the interpretations already mentioned, three microliths (found in squares 101/104, 84/105 and 95/106 see **fig. 1**) were distributed over a large distance within the excavation area. In a slightly younger context at Hohen Viecheln (Nordwestmecklenburg/D) at least four microliths were perceived as deriving from a single arrow (Schuldt 1961, 103) – a scenario that is not likely to have parallels in Bedburg-Königshoven (see also Street 1993, 157). Instead it has been suggested that the microliths in the off-bank discard zone at the palaeochannel of the river Erft were accidentally or intentionally discarded with the bones, cartilage or sinews into which they had been shot. For the Final Palaeolithic (Ahrensburgian) site of Stellmoor, reindeer (*Rangifer tarandus*) remains show at least 32 hunting lesions with embedded fragments of flint point (Bratlund 1991; 1996, 23). Thus, the projectiles would probably reflect the hunting event and not any activity that had taken place at the site of Bedburg-Königshoven itself.

Another group of artefacts has not yet been incorporated into an overall interpretation of the site: two perforated antler frontlets[2] (**fig. 4-7**) – one of them the initial find at Bedburg-Königshoven (**fig. 4-5**) – that have only been discussed, to date, in relation to comparable artefacts and their inter-

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[2] For these and all other objects in this paper mentioned by the authors refer to the first described 'antler frontlets' from Star Carr.

Fig. 4 Bedburg-Frontlet 1 (E115/91-1). – (J. Vogel / LVR LandesMuseum Bonn, modified by M. Wild).

Fig. 5 Bedburg-Frontlet 1 (E115/91-1): detail of the perforation on the right side. – (J. Vogel / LVR LandesMuseum Bonn, modified by M. Wild).

Fig. 7 Bedburg-Frontlet 2 (E115/91-2): detail of the perforation on the right side. – (J. Vogel / LVR Landes-Museum Bonn, modified by M. Wild).

Fig. 6 Bedburg-Frontlet 2 (E115/91-2). – (J. Vogel / LVR LandesMuseum Bonn, modified by M. Wild).

pretation as shamanistic garb or hunting aids (Street 1989a; 1993). These circumstances were crucial to a proposed revision of the group of so-called 'Mesolithic antler frontlets' (Street / Wild 2015) leading to the question why these artefacts were discarded at Bedburg-Königshoven alongside butchery waste. Moreover, the site's function as well as its role in the surrounding settlement structure will be discussed in the light of altered survival strategies and an emerging 'Mesolithic (behavioural) package' in the Northern European Lowlands at the beginning of the Holocene.

Mesolithic antler frontlets

Since their discovery, the Bedburg-Königshoven specimens have been interpreted as antler frontlets (Street 1989a; 1993; Street / Wild 2014) comparable to similar finds from Early Mesolithic Star Carr (Borough of Scarborough / GB) originally described by Clark (Clark 1949; 1950; 1954; Walker / Godwin 1954, 59 ff.). In addition to artefacts from these two sites, frontlets are mentioned from six other early Holocene contexts: Berlin-Biesdorf (State of Berlin / D) (Reinbacher 1956), Hohen Viecheln (Gehl 1961a; Schuldt 1955; 1961, 130 f.), Plau (Ludwigslust-Parchim / D) (Schoknecht 1961; Knape / Brande 2008, 106), Friesack 4 (Havelland / D) (Gramsch 1987; Pratsch 1994; 2006, 71), Bad Dürrenberg (Saalekreis / D) (Grünberg 2000, 204; 2004) and Thatcham II and V (District of West Berkshire / GB) (Overton 2014, 290 ff.). In addition to these nine sites, Rust (Rust 1958, 107 f.) published another skull of a reindeer with worked antler from the late Palaeolithic (Hamburgian) site of Poggenwisch (Kreis Stormarn / D). From these ten sites a total of 39 potential antler frontlets are reported, dominated by 21 from Star Carr (Clark 1954, 168 ff.). The site of Friesack 4 brought a total of three (Pratsch 2006, 71), four (Pratsch 1994, 53, 90 fig. 39) or probably six specimens (B. Gramsch, *pers. comm.*) to light. For Hohen Viecheln the authors refer to one (Schuldt 1956, 120), two (Schuldt 1955, 28; 1961, 130 f.) or four specimens (Pratsch 2006, 71). While Bedburg-Königshoven yielded two possible frontlets, the remaining sites produced evidence for a maximum of one antler frontlet (Reinbacher 1956; Rust 1958, 107 f.; Schoknecht 1961; Grünberg 2000, 204; Overton 2014, 290 f.).

Approaching antler frontlets

As these kind of artefacts have never been described, and to further understand the characteristics and features of the two modified red deer antler frontlets from the site of Bedburg-Könighoven, the entire category had to be reviewed and compared systematically. From the total of 40 specimens, 16 from eight sites (**tab. 1**) were available for a systematic review in an approach combining zooarchaeological, morphometrical and technological data. Parameters recorded included: species, minimum age measured on the development of antler (after Wagenknecht 2000, 139 f.), weight, existence of other bones as well as parts of cranium and antler, whether parts were fully or only partially preserved, intentional fractures, presence of surface modifications (cut marks) on the bones and antler, presence of anthropogenic surface modifications in general (notches, grooves, chopping marks etc.) anthropogenic perforations and their locations, and traces of different techniques used to perforate the bone. This information was supplemented by morphometrical data including the dimensions of the specimens in total length, width, and height as well as the length of beams and tines, and finally, length and width of the perforations. Three of the original specimens included in this review were not directly accessible. To gain as much data as possible all available information from casts, literature, detailed drawings and photographs were used instead (Wild 2014).

Defining and discussing antler frontlets

The results of the analyses of the recorded parameters show the antler frontlets can be divided into two major groups, antler headdresses (= Hirschgeweihkappen *sensu* Wild 2014) (**fig. 8-9**) and a group of

Tab. 1 Overview of available information about antler frontlets. Grey background: not included in the study but presented in Wild 2014. In brackets: Information available for some of the artefacts.

Site	Artefact/s	Reference	#	Artefacts	Cast	Litera-ture	Museum	Detail drawings
Bad Dürrenberg	Rehgehörn	Grünberg 2000	1	✓	–	✓	✓	–
Bedburg-Königshoven	E115/91-1; E115/91-2	Street 1989a	2	✓	✓	✓	✓	✓
Berlin-Biesdorf	I/82/26	Reinbacher 1956	1	✓	✓	✓	✓	–
Friesack 4	K127; K245; K280; K705	Pratsch 1994	4	✓	–	✓	–	–
Friesack 4	K356; K711	B. Gramsch, pers. comm.	2	✓	–	–	–	–
Hohen Viecheln	HV 5863	Schuldt 1956	1	✓	✓	✓	–	✓
Hohen Viecheln	HV 3412	Schuldt 1961	1	✓	✓	✓	–	–
Hohen Viecheln	HV 5774; HV 6162	Pratsch 2006	2	✓	–	✓	–	–
Plau	2178g	Schoknecht 1961	1	✓	–	✓	–	–
Poggenwisch	Tanzmaske	Rust 1958	1	✓	–	✓	–	–
Star Carr	AF2	Clark 1954	1	–	✓	✓	–	–
Star Carr	AF8	Clark 1954; Street/Wild 2015	1	–	–	✓	–	✓
Star Carr	AF1-21 (exc. AF2/AF8)	Clark 1954	19	–	–	(✓)	–	–
Thatcham II	upturned red deer antler	Overton 2014	1	–	–	✓	–	–
Thatcham V	right roe deer frontlet	Overton 2014	1	–	–	✓	–	–

Tab. 2 The revision of the antler frontlets resulted in the distinction of two major groups. The presented data manifests this division.

parameter	antler headdress	exploitation waste	BK: E115/91-1	BK: E115/91-2
age termination				
level of antler growth	4.67	2.13	7	6
minimum age of animal	3	2.38	3	3
weight				
in g	1137.5*	319.88	2800	2384
preservation				
os frontale	100 %	100 %	(✓)	(✓)
os parietale (sin.+dex.)	100 %	43.75 %	(✓)	(✓)
os temporale (sin.+dex.)	83.33 %	6.25 %	(✓)	(✓)
os interparietale	100 %	62.50 %	✓	(✓)
os sphenoidale	0 %	62.50 %	–	–
os temporale (sin.+dex.)	40 %	0 %	✓	✓
os interparietale	50 %	0 %	–	–
cut marks				
os nasale	50 %*	–		✓
os frontale	100 %	87.50 %	✓	✓
os parietale (sin.+dex.)	100 %	0 %	✓	✓
os temporale (sin.+dex.)	77.50 %	0 %*	✓	✓
os interparietale	66.67 %	0 %	–	✓
os supraoccipitale	33.33 %	0 %*		
os sphenoidale	–	0 %		
tabula interna	100 %	25 %	✓	✓
antler	100 %	66.67 %	–	
other modifications				
os nasale	0 %*	–		–
os frontale	50 %	25 %	–	–
os parietale (sin.+dex.)	66.67 %	0 %	✓	✓
os temporale (sin.+dex.)	45 %	0 %*	✓	✓
os interparietale	33.33 %	0 %	–	–
os supraoccipitale	0 %	0 %*		
os sphenoidale	–	0 %		
tabula interna	66.67 %	0 %	–	✓
antler**	100 %	25 %	–	–

(*≤ 2 specimens; **as the frontlets from Bedburg-Königshoven are supposed to be half finished products their antler has not been taken into account) objects that resemble simple butchering and raw material exploitation waste (**fig. 10**). While the former group shows clear signs of modifications which are the result of motivation, finds in the latter group displayed no unambiguous intention in their actual form. The category antler headdress encompasses one specimen from Hohen Viecheln (**fig. 8**) and the reviewed objects from Star Carr (AF2 & AF8 [**fig. 9**] [Clark 1954]), the single find from Berlin-Biesdorf as well as the two deer crania from Bedburg-Königshoven (**fig. 4-7**) discussed in this paper. The waste group contains the reviewed material from Friesack 4, a specimen from Hohen Viecheln (**fig. 10**) and the half reindeer cranium from Poggenwisch[3].

The entire group of analysed headdresses can be distinguished from the other frontlets by different parameters. Although the examined artefacts show a diverse range of species – elk (*Alces alces*), red deer, reindeer and roe deer (*Capreolus capreolus*) – only red deer was used for the manufacturing of antler headdresses so far. Thus, they should be called red deer antler headdresses without excluding the possibility of such an object being made of a cranium of another species. Importantly, red deer does not play a predominant role either as a food or a raw material source at each of the sites where these artefacts occur (**fig. 11**) (Gehl 1961b; Legge/Rowley-Conwy 1988; David 1999; Street 1999; Street/Wild 2015; Street 2020). Moreover, the Star Carr headdresses were associated with the production and hafting of antler points (Elliott/Milner 2010), while comparable bone points at Bedburg-Königshoven and Hohen Viecheln are produced from raw materials of other species (Schuldt 1956; David 1999). Apart from this, other parameters help to distinguish the different classes of object. In comparison with the antlers of the group of antler headdresses, antler growth as a means to determine age, is noticeably lower in the waste group. This, as well as the poorer preservation of crania and antlers results in lower morphometrical values among the waste group. But while the cranium of the waste material was worked down more intensively, abiotic modifications like cut or scraping marks and impact scars are less numerous than observed in the headdress group (**tab. 2**). This can possibly be explained by a long term usage of antler headdresses and therefore an increase of use traces, while prompt disposal of waste can be assumed when crania and antlers were exploited solely for raw materials, resulting in fewer modifications.

Hitherto, the first success of the review is apparent in a simple classification of antler frontlets. But a much more important result of the review is the recognition that several features on the different specimens are regularly observed and thus describe a definition of antler headdresses:

- frontal, parietal and interparietal bones are always present
- antlers, frontal and parietal bones are only partially preserved
- a minimum of 75 % of the present bones of the cranium (including the antlers and the *tabula interna*) show anthropogenic modifications
- temporal, parietal and interparietal bones show a minimum of two artificial perforations and a maximum of two complete perforations
- antler beams and tines are longitudinally split and often shortened.

At present, this interpretation is the best fit for these artefacts based on common features and morphology. Additionally, the nasal bone (*os nasale*) is absent in all cases but two; for the reviewed artefacts it seems it had not been removed intentionally. Only the second specimen from Bedburg-Königshoven includes a complete nasal bone. In comparison to the other sites, Bedburg-Königshoven was the only one carefully excavated layer by layer, thus, increasing the chance of finding complete artefacts *in situ*. Therefore, the frequent loss of the nasal bone may have resulted from taphonomic factors. One has to come to the conclusion of a probable

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[3] Not included in this first study of antler headdresses were a handful of finds. Two artefacts from Hohen Viecheln mentioned by Pratsch (Pratsch 2006, 71) but not available for studying before 2015, and two further objects from Thatcham, described as possible antler frontlets by Overton after the completion of the first study (Overton 2014, 190 ff.). All of these objects were tested on the definition of antler headdresses (see below). They fall entirely in the group of waste material.

Tab. 3 Overview of artefacts mentioned in the text tested on the definition of a headdress *s.s.* (*sensu stricto*). 1: Presence of *os frontale, os parietale* and *os interparietale*; 2: *os frontale, os parietale* and antler only partially present; 3: 75 % of the bones of the skull (including antler and *tabula interna*) are anthropogenically modified; 4: Perforations on the caudal part (*os temporale, os parietale, os interparietale*); 5: Antler is longitudinally split and sometimes shortened. Grey background: not possible to determine because of breakage.

feature/find	BD: Roe deer antler	BK: E115/91-1	BK: E115/91-2	BB: I/82/26	F4: K127	F4: K245	F4: K280	F4: K356	F4: K705	F4: K711	HV: H.V. 5863	HV: HV 3412	HV: HV 5774	HV: HV 6162	HV: HoVi 387	PL: 2178g	PO: Mask	SC: AF2	SC: AF8	TH II: -	TH V: -
1		✓	✓	✓	✓	✓	✓	✓			✓			✓				✓	✓		
2	✓	✓	✓	✓		✓	✓				✓		✓	✓	✓	✓		✓	✓	✓	✓
3		✓	✓	✓							✓		✓		✓	✓		✓	✓		
4		✓	✓								✓							✓	✓		
5				✓							✓				✓	✓	✓	✓	✓		

BD: Bad Dürrenberg; BK: Bedburg-Königshoven; F4: Friesack 4; HV: Hohen Viecheln; PL: Plau; PO: Poggenwisch; SC: Star Carr; TH II: Thatcham II; TH V: Thatcham V

link between the loss of the nasal bone and taphonomic factors. Anyway, due to several reasons (e. g. taphonomic factors, use, stage of manufacturing) not all the specimens reviewed fit the definition of antler headdresses in its entirety (**tab. 3**).

The specimen from Hohen Viecheln (**fig. 8**) and at least the two examined frontlets from Star Carr (**fig. 9**) can easily be called typical headdress, while the group belonging to artefacts from Plau, Berlin-Biesdorf and Bedburg-Königshoven must be discussed further.

The red deer cranium from Plau has its inner surface (*tabula interna*) worked down to a high degree. The frontal bone is the only bone preserved and is too small for recognition of further details. In addition, there was a fire in the building where the materials were curated, which destroyed the surface of the bone (Schoknecht 1961). This makes it almost impossible to recognise and distinguish modifications and determine its status as an antler headdress.

The inner surface of the Berlin-Biesdorf specimen is worked down and smoothed. Frontal, parietal and interparietal bones are present, frontal and parietal at least partially. Antlers and pedicles have been reduced by removing the anterior surface of beams and tines but still preserving the form of the antler in its frontal aspect. Although this frontlet lacks perforations, the unusual treatment of the beams and tines cannot be explained simply with the production of tools. The resemblance to thinned pedicles and brow tines of two reviewed antler frontlets (**fig. 8-9**) puts the Berlin-Biesdorf specimen into the category of antler headdresses.

Both red deer crania from Bedburg-Königshoven show minor modifications through isolated cut marks on their inner surface. Frontal, parietal and interparietal bones are present and frontal and parietal are partially preserved. On the parietal-temporal *suturae* of both specimens a perforation was notched into the bone, however, the antlers are almost complete and show no traces of intentional modification. As the affinities in the shape of the cranium and perforations to some Star Carr frontlets are unambiguous and other analogies are yet unknown, it should be assumed that both Bedburg-Königshoven specimens are antler headdresses, even if their antlers look atypical (**fig. 4, 6**).

Discussing the headdresses from Bedburg-Königshoven

Already mentioned was the fact that the definition can hardly be a final and inescapable measurement but the closest possible approximation of the antler headdress (*sensu stricto*)-character. Thus, some ex-

Fig. 8 "Antler headdress" H.V. 5863 from Hohen Viecheln. – (M. Wild/LaKD Mecklenburg-Vorpommern).

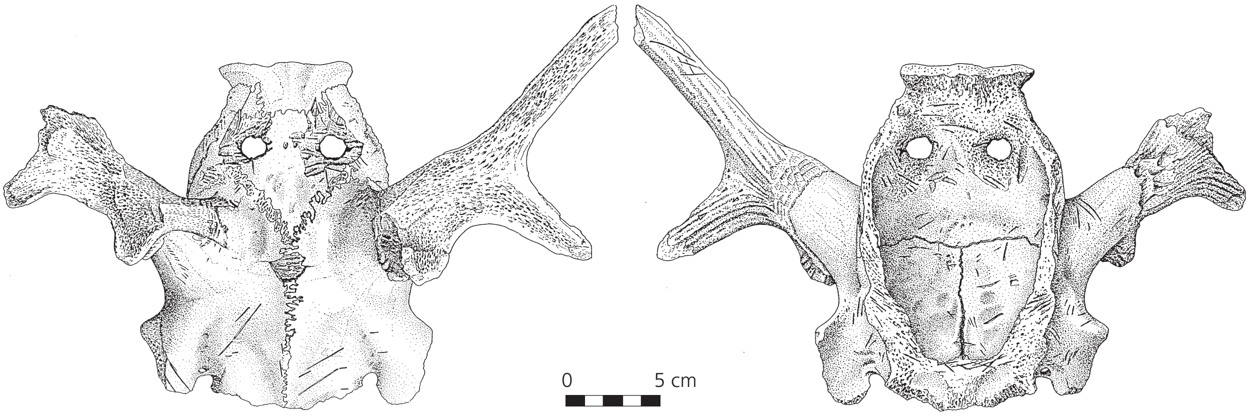

Fig. 9 "Antler headdress" AF2 Star Carr. – (Street/Wild 2015, 216 fig. 8B, 217 fig. 8E, modified by M. Wild).

Fig. 10 Possible butchering waste Hohen Viecheln: a) frontal perspective b) caudal perspective. – (M. Wild/LaKD Mecklenburg-Vorpommern).

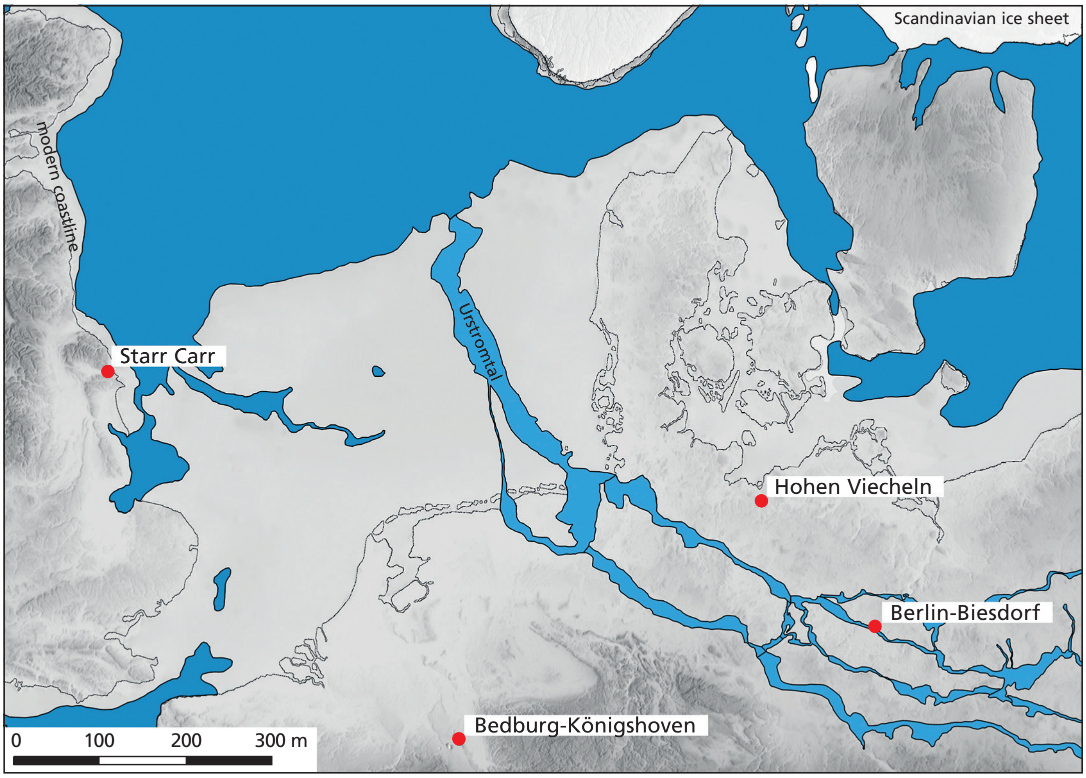

Fig. 11 Sites with headdresses. – (Background map based on Grimm 2009 [and supplemented by Groß 2014] after Björck 1995a; Björck 1995b, Björck 1996; Björck/Anonymous 1992; Boulton et al. 2001; Brooks 2006; Clarke et al. 2004; Coope et al. 1998; Ivy-Ochs et al. 2006; Lundqvist/Wohlfahrt 2001; Weaver et al. 2003, modified by M. Wild).

planations for the completeness of the antlers from Bedburg-Königshoven frontlets are conceivable:

1. Antler was not exploited as a source of raw material, and so reduction was not necessary. Indeed the small antler assemblage of Bedburg-Königshoven shows no signs of an intense exploitation for the manufacturing of points or axes as documented at other sites with antler headdresses (**fig. 12**) (David 1999). But the presence of four tines with clear signs of modifications and use traces (Street/Wild 2015, tab. 2) makes this hypothesis almost untenable.

2. The specimens are a subform of antler frontlets whose antlers vary from the others significantly. Although there is no argument against this explanation, Clark observed the gouging and hollowing of antlers at Star Carr (Clark 1954, 168). He saw this as a method of reducing the weight of the antlers while at the same time accentuating their shape (Clark 1954, 169). The same line of argument with a differing result can be assumed for the Berlin-Biesdorf specimen too.

3. The work on the red deer crania was not complete. Compared with the weight of the Berlin-Biesdorf specimen (1850 g) and the Hohen Viecheln frontlet (321 g), the objects from Bedburg-Königshoven are strikingly heavy (2800 g and 2384 g). Besides the exceptional weight, the location of the frontlets at a distance of roughly 5 m from the Early Mesolithic shore line (**fig. 1**) suggests disposal or possible storage for later use. As both the perforations of Frontlet 2 are broken, the reason for a possible disposal seems to be clear. But as Frontlet 1 has no traces of non-intentional ancient fractures, its disposal might be doubted. Storage of the objects under water would be beneficial from two perspectives: Mesolithic people could preserve the antler frontlets from gnawing by dogs and the antler would have been water-soaked. This pre-treatment softens antler and simplifies later processing

(MacGregor 1985, 27. 63-65). When compared with other antler headdresses the low amount of cut marks, notches and other anthropogenic modifications on the surface of the Bedburg-specimens is notable (**fig. 5, 7, 9**). As these traces do not follow a clear pattern that points to the manufacturing of the headdresses this indicates a shorter period of life of Frontlet 1 and 2 from Bedburg-Königshoven. Furthermore, in a recently conducted experiment (Wild 2014), the author was able to show the possibility of replicating antler headdresses comparable in form to those from Bedburg-Königshoven with tool types found at this site (Street 1989a; 1998). In combination, these arguments lead to the hypothesis that the dry land at the abandoned meander of the river Erft was the place of manufacture of the laterally perforated deer crania, and that these appear to represent half-finished antler headdresses.

There is, however, still an unsolved problem to this kind of explanation since the red deer crania were found in the outcast zone at Bedburg-Königshoven. As already mentioned, the first specimen seems to be complete, calling into question whether it was discarded. On the other hand, the second specimen was not complete and its perforations were broken. With the exception of the artefact from Berlin-Biesdorf, the review of antler headdresses speaks for the presence of two symmetrically located perforations, to which a third can be added if one of the perforations had been broken. This is why a third perforation always overrides the existing symmetry. If not already broken during the manufacturing process, a frontlet with a third perforation should have been in use for a longer period of time than a frontlet with only two. This contradicts the hypothesis of half-finished products since one of the frontlets had a 'longer' use of life. A possible explanation lies in the breakage patterns of Frontlet 2. The force, necessary to crack the bone at both sides, seems to have worked simultaneously off the bone and, in the same direction, away from the antler and the frontal cranium. If Mesolithic people strung the frontlets through the perforations prior to submergence and did not tie the cord around the antlers (which would seem to be the easiest solution), they could try to lift the object out of the water by pulling the string. If the frontlet had become deeply embedded within the fine, wet sediment, the perforations may have broken during attempts to retrieve the antler. Obviously, this explanation is hypothetical, but it would be even more hypothetical to assume that both perforations had broken simultaneously as the frontlet was worn. In this case it would be more likely that one perforation breaks, the frontlet loses its stability and falls off. Afterwards, a third perforation could be notched into the bone. This explanation still does not solve another problem. Why was Frontlet 1 left 'unbroken' in the shallow waters?

Another striking aspect is the estimated season of occupation at Bedburg-Königshoven. Street (1989a, 49) argues that unshed antlers are most common during winter, while most of the remains in Bedburg-Königshoven indicate an occupation in summer. In this case, the perforated artefacts could have been brought to the site from somewhere else instead of being produced there. A few seasonality indicators, young calves and two other individuals of aurochs as well as the cranium with attached antlers from roe deer and the remains of stork, point to the presence of Mesolithic people at the site between April and late summer (Street 1989a, 43). The yearly cycle of antler growth starts, by contrast, around April and is completed around June. Subsequently the deer starts to rub off the velvet of the antlers. Around March or April the yearly cycle ends with the casting of the antlers (Legge/Rowley-Conwy 1988, 5 fig. 2; Wagenknecht 2000, 127). Following this yearly cycle, all seasonal indicators mentioned earlier for the occupational period as well as the two unshed red deer antlers could overlap in springtime. This would push the potential starting point of Mesolithic visits at Bedburg-Königshoven to March or April with a possible continuation into the summer.

Possible functions of antler headdresses

The possible shift in the interpretation of the season of occupation of Bedburg-Königshoven does not argue against Street's interpretation of the headdresses as hunting aids, though ethnographic analogies illustrate that these artefact types are not as realistic as one might expect (e.g. Halls 1984), especially considering that the occupation of the site occurred when red deer do not possess fully grown antlers. Since a solely functional use of the deer skulls as secular tools does not seem to show up, it might be more likely to interpret the find category as the remains of an ancient custom. Clark (1954) favoured a shamanistic interpretation of the frontlets, but other hypotheses have been postulated and seem to be equally conceivable. Conneller (2004) puts forward the idea of a much more complex worldview for Mesolithic hunter-gatherers more than just a clear distinction between profane and ritual, and places the frontlets of Star Carr into a supernatural context at a special site. This interpretation and the role of ritual have been critically reviewed by Mellars (2009), who still interprets the distribution patterns of organic artefacts and the site's character in a more pragmatic way. However, despite the intensification of discussions about Mesolithic rituals it must be clearly stated that, to date, ritual or religious customs cannot be unambiguously verified and other interpretations have been discussed in the last 65 years.

For example Pratsch (2006) seized Clark's idea that red deer crania were used as a kind of (hunting) trophy (Clark 1954, 170) and assumed this again for the alleged antler frontlets from Friesack 4. Recently, Street and Wild (2014; 2015) introduced the interpretation of a reindeer crania from the Final Palaeolithic site of Stellmoor (Kr. Stormarn/D) fixed on a rod as a static element of a hunting drive system (Bokelmann 1991). Nevertheless, the intensive modifications of the frontlets seem to exceed what would be required to display red deer crania as a kind of trophy. As the discussed phenomenon only exists in a limited area during a short period at the beginning of the Holocene, other explanations could be possible as well. The frontlets might have been identity-establishing symbols of a group of people who wanted to show their basic convictions and displayed these either on their head, as a trophy, a decoration on top of their tent, etc. In the future more detailed use-wear investigations could illuminate the functional question of the artefact group and contribute to discussions about their exact use.

Bedburg-Königshoven: an Early Mesolithic type site?

Based on spatial analysis of faunal and lithic remains as well as archaeozoological and lithic technology studies, Bedburg-Königshoven was interpreted as a place where secondary butchering activities (Street 1989a; 1991; 1993; 2020; Street/Wild 2015), and other 'domestic' tasks had taken place (Street 1989a, 43). The site is situated at a particularly advantageous spot in the landscape. At the northernmost part of an abandoned meander, sheltered by hills in the North from the prevailing west wind, and connected with the surrounding marsh of the valley by a dry promontory (Behling 1988; Ikinger 1989), the place chosen by Mesolithic people offered many opportunities.

This setting with a mosaic of ecological niches supported an opportunistic style of hunting for different species inhabiting the Northern European Lowlands at the beginning of the Holocene. In one scenario, widely accepted for the Mesolithic site of Bedburg-Königshoven, a group of people used this privileged area as a central camp to which selected faunal elements of nearby hunted prey were brought (Street 1989a, 41 ff.). Re-fitting of bones over distances of more than 10 m (Street 2020) and a homogenous find layer also indicate a more ephemeral character of a short visit of people at the site. However, the assumption that the site is not the place of disposal but the area adjacent to the place of manufacture of two antler frontlets again suggests a longer stay or repeated visits over a short period as the working of the antler headdress probably begins with the end of the butchery process. Furthermore, this adds another possible activity to the already mentioned secondary butchering and further 'domestic' tasks. Therefore, antler headdress manufacture underlines the site's character as a place where different activities had been performed and it seems that the excavated outcast zone, with its bias towards butchering waste, just reflects a highly specialised part of a camp where certain activities took place. This is supported by the observation of other contexts where loci of secondary butchering are situated in close vicinity to central camps (Lyman 1992, 247 f.) where the final stages of processing (e. g. eating) takes place. Furthermore, use-wear analysis of discarded lithics from Bedburg-Königshoven would be useful as it could add more information about the activity spectrum, e. g. hide fleshing, thus possibly substantiating the claim.

Finally, extending beyond this small scale interpretation of Bedburg-Königshoven the present paper is part of the conference proceedings of the 2014 UISPP world congress session B30 'A diachronic perspective of human behavioural adaptations to interglacial lakeshore environments during the European Pleistocene to early Holocene'. Formulated in the introduction of the session the 'ultimate goal' will be to evaluate how survival strategies in similar environmental situations evolved throughout the course of our history (García-Moreno et al. 2014). As has been shown, Bedburg-Königshoven, as one of the earliest well-dated Mesolithic sites in the Northern European Lowlands, demonstrates a picture of survival strategies that are assumed to be typical for the Early Mesolithic in Northern Central Europe (Baales 1996, 338). This includes the use of dry areas in marshy environments for camps which were visited regularly over a long period (Groß 2015; 2020) as well as an opportunistic way of hunting. With this choice, Mesolithic strategies in the developing environment are different from earlier adaptations in comparable environments, for example in the Allerød: During this period, comparable camps are conglomerations of small specialised spots distributed over a larger area of sand ridges, e. g. Rekem (Prov. Limburg / B) (De Bie / Caspar 2000).

Therefore, it is striking that with the appearance of this 'Early Mesolithic behaviour' new items, like the antler frontlets, immediately appeared, completing this somehow new package of adaptation to a more humid and densely vegetated environment. As the oldest site showing this package, Bedburg-Königshoven seems to be a pioneer for a set of human behavioural traits that was typical to a certain degree throughout the Early Mesolithic in Central and Northern Europe.

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During the course of human evolution, we have successfully adapted to various climates and habitats.

Interglacial environments, in particular, offer an excellent opportunity to study these adaptations.

On the north European plain, interglacials often correlate with the flooding of basins, resulting in the appearance of lacustrine landscapes. These environments exhibit remarkable ecological diversity with highly concentrated and predictable resources. Numerous archaeological sites from the Palaeolithic to the Mesolithic are preserved in these lacustrine landscapes, providing rich sources of potential data.

Many of these archaeological sites are well-known as locations for the procurement and butchering of animals, lithic provisioning, gathering vegetal and aquatic resources by humans.

These sites are embedded in wetland deposits with favourable conditions for the preservation of organic and botanical remains and are thus exceptional archives for detailed analyses of human adaptations to changing, dynamic environments.

In a diachronous perspective from the Middle Pleistocene to the Holocene, the current anthology collates studies on differing aspects of interglacial archaeological lakeland sites, illustrating human survival strategies under similar environmental conditions through the ages.

This volume contributes to a core research theme "Human behavioural strategies in interglacial environments" of the MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution (RGZM) (Neuwied, Germany). The aim of the research is to undertake a holistic and diachronic analysis of survival strategies under similar environmental parameters, in order to document the evolution of hominin subsistence behaviour and to gauge whether certain subsistence adaptations arose in direct response to distinct environmental conditions.

Propylaeum