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Neanderthals in changing environments from MIS 5 to early MIS 4 in northern Central Europe – Integrating archaeological, (chrono)stratigraphic and paleoenvironmental evidence at the site of Lichtenberg

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Abstract

The resilience of Neanderthals towards changing climatic and environmental conditions, and especially towards severely cold climates in northern regions of central Europe, is still under debate. One way to address this is to investigate multi-layered occupation in different climatic intervals, using independently-compiled paleoenvironmental and chronological data. Unfortunately, most open-air sites on the northern European Plain lack a robust chronostratigraphy beyond the radiocarbon dating range, thereby often hampering direct

links between human occupation and climate. Here we present the results of integrative research at the Middle Paleolithic open-air site of Lichtenberg, Northern Germany, comprising archaeology, luminescence dating, sedimentology, micromorphology, as well as pollen and phytolith analyses. Our findings clearly show Neanderthal presence in temperate, forested environments during the Mid-Eemian Interglacial, MIS 5e and the latest Brörup Interstadial, MIS 5c/GI 22 (Lichtenberg II). For the previously known occupation Lichtenberg I, we revise the chronology from the former early MIS 3 (57 ± 6 ka) to early MIS 4/GS 19 (71.3 ± 7.3 ka), with dominant cold steppe/tundra vegetation. The early MIS 4 occupation suggests that Neanderthals could adjust well to severely cold environments and implies recurring population in the region between MIS 5 and MIS 3. The artefact assemblages differ between the temperate and cold environment occupations regarding size, blank production, typology and tool use. We argue that this distinctness can partially be explained by different site functions and occupation duration, as well as the availability of large and high-quality flint raw material. Raw material availability is in turn governed by changing vegetation cover that hindered or fostered sediment redeposition as a provider of flint from the primary source of the glacial sediments nearby.

1. Introduction

The "stereotype" Neanderthal is mostly perceived as a human species that lived in the cold and harsh climatic environments of the past glacial periods in Eurasia. But were Neanderthals indeed adapted to cold environments? This question has been a matter of debate in prehistory, biology and physical anthropology for a long time (e.g., Aiello and Wheeler, 2003; Churchill, 2008; Rae et al., 2011; Skrzypek et al., 2011; White and Pettitt, 2011). One way of addressing this open question is to analyze Neanderthal occupation at the northern extreme of their habitat, more precisely the northern part of Central Europe.

Currently, numerous sites suggest that Neanderthals settled in northern Central Europe during the Eemian Interglacial and during the first half of the last glacial cycle (Gaudzinski-Windheuser and Roebroeks, 2014; Hein et al., 2020; Litt and Weber, 1988; Nielsen et al., 2017; Richter, 2016; Thieme and Veil, 1985; Toepfer, 1958; Weber, 1990). However, the chronology of most late Middle Paleolithic sites is either poor and/or controversial (Jöris, 2004; Mania, 2002; Pastoors, 2009, 2001; Veil et al., 1994), and many of them are not dated at all. The majority of those sites are classified as late Middle Paleolithic by typological means only

(Kegler and Fries, 2018; Richter, 2016). Due to this lack of precise site chronologies, even though we know that Neanderthals occupied the northern regions, we lack evidence of whether they stayed there only during warmer periods of the last interglacial - glacial cycle or if they also persisted through cold stadial conditions. So far, the only indication for the latter is the site of Salzgitter-Lebenstedt, Lower Saxony/ Germany (Tode, 1982). At this site, the finds originate from layers containing cold climatic vegetation remains (Pastoors, 2001; Pfaffenberg, 1991; Selle, 1991), and are associated with glacial fauna. The presence of cranial and post-cranial Neanderthal remains (Hublin, 1984), clearly link Neanderthals to the accumulation of archaeological and faunal remains at the site. They hunted reindeer and manufactured bone tools from mammoth ribs (Gaudzinski, 1999, 1998). However, the dating of the site still lacks resolution. Uncertain ages at the upper limit of the ^{14}C time scale, together with contrasting stratigraphic interpretation, place the site either in the Marine Isotope Stage (MIS) 5a/4 (Jöris, 2004) or MIS 4/3 transition (Pastoors, 2009, 2001). Furthermore, the integrity of the lithic assemblage is unclear, as the artefacts were found in several geological layers (Pastoors, 2001). Evidence for occupation during warmer early last glacial interstadials only comes from two sites of the northern Central European Plain so far. The first site is Neumark-Nord 2/0 (Laurat and Brühl, 2006), Saxony-Anhalt/ Germany dating to either MIS 5c or 5a (Richter and Krbetschek, 2014; Strahl et al., 2010). The second site is Königsaue (Mania and Toepfer, 1973), Saxony-Anhalt/ Germany. Neanderthal occupation is here associated with peat layers at a paleo-lakeshore, dating most probably to MIS 5a (Jöris, 2004; Mania, 2002; Mania and Toepfer, 1973; but see Hedges et al., 1998 for a potential MIS 3 age of the site). However, with the scarce evidence outlined above, it is currently not possible to reconstruct the timing of human presence in northern Central Europe, as well as behavioral response to short-term climatic shifts.

To address these issues, we need to contextualize the northern Neanderthal occupations using detailed paleoenvironmental reconstructions, derived from the same chronostratigraphic frameworks as the archaeological material, preferably with a temporal resolution on the millennial scale of Greenland Interstadials (Rasmussen et al., 2014). Since the Middle Paleolithic period is mostly outside the radiocarbon range, this kind of precision is usually reserved for loess regions, where highly-resolved sediment-paleosol sequences occur (Locht et al., 2016). Beyond the loess belt, at the northern margin of the Neanderthal habitat and the European Plain, occupation is conceived to have been most particularly affected by climatic fluctuations (Depaepe et al., 2015; Hublin and Roebroeks, 2009; Roebroeks et al., 2011). Across these landscapes, however, shallow sediment deposits in unison with frequent cryoturbation features often hamper the establishment of such a precise chronostratigraphic framework (Hein et al., 2020; Wiśniewski et al., 2019). Instead, the dating resolution commonly does not exceed the much coarser scale of Marine Isotope Stages (Lisiecki and Raymo, 2005a).

Here we present new results of our recent research at the late Middle Paleolithic open-air site complex of Lichtenberg, Lower Saxony/Germany (Veil et al., 1994), which was initially discovered in 1987 and excavated until 1993 by the Niedersächsisches Landesmuseum, Hannover, Germany. Lichtenberg represents a Neanderthal site at the potential northern limit of their geographic range (Nielsen et al., 2017). The site yielded one of the most prominent late Middle Paleolithic assemblages of the northern Central European Plain, as well as a sediment sequence encompassing deposits from MIS 5e through MIS 3 (Veil et al., 1994). Neanderthal occupations at Lichtenberg were associated with a paleo-lakeshore (Hein et al., 2021). Therefore, the long-lasting highly resolved sediment sequence composed of intercalated organic and clastic sediments is an ideal location to study climatic and environmental shifts, and to investigate the Neanderthal population dynamics at the northern limit of their habitat.

Our multidisciplinary investigations combine archaeological investigations with detailed sedimentological, chronological and paleoenvironmental studies of the find-bearing and associated non-find bearing layers of the sequence. Our research focusses on the following aims: (1) Can we connect Neanderthal occupations of northern Central Europe to a chronological resolution of Greenland Interstadial-Stadial level and thus to changing climatic conditions? (2) Did Neanderthals inhabit specific environments only, or did they adapt to different environmental conditions? (3) To which extent do archaeological assemblages vary in different environments and climates? And, most importantly, (4) did Neanderthals live in northern Central Europe only during warmer, forested phases of the last glacial, or could they also cope with cold climatic conditions and open landscapes in the stadials of the Early Weichselian and the Pleniglacial?

2. Materials

2.1 Study area

Based on archaeological evidence and (paleo-)geographical considerations, the study region, here referred to as “northern Central Europe” or “northern Central European Plain”, consists mainly of the Northern German Lowlands above approximately 51° N, as well as the northern Netherlands. Today, the latter is part of the rather maritime North-Western Europe, but due to the lower sea level during the last glacial cycle, the northern Netherlands were part of a more extensive northern Central European Plain, and thus incorporated into the study region. Northern Poland is not included here, as we currently lack Middle Paleolithic archaeological sites from the area covered by the ice shield of the last Glaciation (see e.g., Wiśniewski et al., 2013).

2.2 Geological setting

The study site is located at latitude 52°55’ N in Northern Germany, eastern Lower Saxony (Fig. 1a). Throughout the Pleistocene, Scandinavian glaciers covered the region twice during the Elsterian (MIS 12) and three times during the Saalian (MIS 6) glaciation, and deposited >40 m of glacial tills and glaciofluvial sands (Ehlers et al., 2011; Lang et al., 2018). The ice-marginal valley of the River Elbe, as the major drainage channel of the region, assumed its course close to the study area, already during the late Saalian Warthe Stadial (Fig. 1) (Ehlers, 1990; Meyer, 1983). In contrast, Weichselian glaciers during MIS 4 and MIS 2 did not cross the Elbe lineament, with the margin of the furthest advance situated ca. 50 km to the NE (Duphorn et al., 1973; Ehlers, 2020) of the study area. The archaeological site is located at the southern declivity of the Öring, a confined Saalian plateau, which passes over into a major sediment basin that repeatedly hosted a lakescape since at least the Saalian-Eemian transition (Hein et al., 2021). Therefore, in the course of the Weichselian, the depositional regime was mainly characterized by slopewash and periglacial processes (Veil et al., 1994), which were presumably interrupted by episodic lake transgressions (Hein et al., 2021).

Neanderthal occupation took place on a small alluvial fan, which likely formed between the late Eemian Interstadial and early Weichselian Pleniglacial and provided a higher and hence drier ground, in comparison to the surrounding wetlands (ibid., Fig. 1b, Supplementary Figure S49b).

2.3 Previous Investigations

Archaeological Horizon Lichtenberg I

The site Lichtenberg with its archaeological horizon Lichtenberg I (hereafter: Li-I) was discovered in 1987 by one of us (K.B.) and was subsequently excavated from 1987 to 1993 (Veil, 1995; Veil et al., 1994). The assemblage consists of about 2500 artefacts, among them 405 artefacts with recorded provenience, including 76 retouched tools (Veil et al., 1994). All artefacts are made of Baltic Flint. Most of the bifacial tools were manufactured on natural blanks, such as frost shards transported from the Saalian glacial deposits upslope and potentially directly available on the land surface (Veil et al., 1994). Cores are entirely missing in the assemblage, but facetted flake platforms may hint at the existence of Levallois blank production (Veil et al., 1994). However, faceting may rather be the result of bifacial tool production (Veil et al., 1994; Wiśniewski et al., 2020) in this assemblage. Among the 76 tools are 19 bifacial backed knives or Keilmesser, 5 handaxes, as well as other types of bifacial tools. Keilmesser are asymmetric, mostly bifacial cutting tools with a natural and/or worked back opposite a working edge (Bosinski, 1967; Jöris, 2012, 2006; Veil et al., 1994). All of the tools have been interpreted as functionally slightly different cutting tools (Veil et al., 1994; Weiss, 2020). With a median dimension (largest width or length) of 86 mm (Supplementary Table S7) for 19 bifacial and 3 unifacial Keilmesser and one handaxe (Weiss, 2020), the tools are quite large. The assemblage is attributed to the late Middle Paleolithic Keilmessergruppen of central and eastern central Europe (Jöris, 2012, 2006; Mania, 1990; Veil et al., 1994). This represents a late Neanderthal archaeostratigraphic unit that ranges from MIS 5a to early MIS 3 (Hein et al., 2020; Jöris, 2006, 2004), and which is defined by the presence of Keilmesser. Furthermore, these assemblages are characterized by handaxes and other bifacial tools (Bosinski, 1967; Veil et al., 1994), as well as by varying blank production methods, including Levallois (Jöris, 2004; Richter, 1997). Most of the Keilmesser found in Lichtenberg I are still suitable for cutting with angles below 60° (Gladilin, 1976; Weiss, 2020), and several refits (Veil et al., 1994) evidence the production and use of the tools on the spot. This, as well as the functional uniformity point to a specialized assemblage that was produced during a short-term event, and potentially related to butchering activities, as indicated by use-wear analyses (Veil et al., 1994). The formerly-obtained thermoluminescence ages for the sediments containing the artefacts range from 66±14.6 ka to 52±6.8ka (Veil et al., 1994), displaying a rather high dating uncertainty most likely resulting from the cryoturbated context in which they were found.

Evidence for Eemian occupation

During our coring campaign, recently published in Hein et al. (Hein et al., 2021), we recovered a longitudinal broken flint flake (LIA-86, Supplementary Figure S13), another flint flake (LIA-187, Supplementary Figure S13), as well as a number of undetermined small chips and fragments from sandy Eemian half bog deposits of core PD.030 (6 m depth) (Fig.1c). Some of the flint fragments are highly weathered due to the acidic, humic sedimentary environment. The two artefacts are referred to as Lichtenberg Eemian and can be attributed to Eemian pollen zone E IVb/V (Hein et al., 2021). These finds make this the northernmost Eemian site besides Lehringen, Lower Saxony/ Germany (Hein et al., 2021; Nielsen et al., 2017; Thieme and Veil, 1985).

3. Methods

3.1 Fieldwork

In 2017, we localized the exact position of the 1987-1993 excavation and conducted a first attempt to locate non-cryoturbated sediments below the former trench. Then in 2019, we established geoarchaeological survey Trench 1 with a size of ca. 3 by 20 m and a depth of 2.20 m (Fig. 1c, Fig. 2a; Supplementary Figures S2 – S3). In order to better understand the stratigraphical situation of Li-I, we deliberately established Trench 1 at the southern edge of the former excavation area. Here, increasing accommodation space towards the adjacent sedimentary basin suggested less cryoturbational disturbance of the deposits. From there on, Trench 1 was extended 7 m to the south, and then, to gain a W-E profile, 7.50 m to the east and another 6 m to the south. The trench was excavated by a mechanical digger and every digger bucket was carefully searched for artefacts. If artefacts were found, the respective square meter was excavated following current standards of paleolithic excavation. We excavated the sediment by hand according to individual layers, recorded all individual finds with a total station at a size cut-off of 1.5 cm and screened the excavated sediment with a 4 mm and a 2 mm mesh.

Furthermore, we established a north-south trending coring transect of 11 sediment cores with depths of up to 11 m. The transect started upslope, and passed through the excavation area towards the valley bottom (Hein et al., 2021). The aim was to obtain high-resolution sedimentological data about the paleolake infill. Approximately 25 m north of Trench 1, at a depth of ca. 2 m, we detected lakeshore sediments. Therefore, in this area, we established the second survey Trench 2 (Figs. 1c, 2b/c; Supplementary Figure S8), using the same geoarchaeological survey methods as described above. At the end of the field campaign 2019, we detected the Lichtenberg II (Li-II) find horizon in sandy and peaty lakeshore sediments and excavated one square meter before the season ended.

In March and June 2020, we continued fieldwork and excavated parts of the new find horizon, Li-II. The find horizon was located about 30 cm above the ground water table, necessitating the installment of a protection and water management system (Supplementary Figure S9).

All three stratigraphies presented here (Trenches 1 and 2, core PD.028, Figs. 1c, 2) were carefully described in the field, according to German soil mapping standards (AGBoden, 2005). Documented parameters included textural composition, structure, Munsell color, carbonate and gravel content, as well as hydromorphic properties. Moreover, we documented sediment structures such as bedding and cryogenic features. This allowed for the comparison and correlation of sediment units between the stratigraphies, and facilitated optimal sampling and interpretation of luminescence samples. Further stratigraphic and landscape context was provided by the remaining cores of the more extensive drilling campaign in the study area (Hein et al., 2021).

3D models and Augmented Reality 3D models of both trenches can be found under https://marcelweiss.github.io/Lichtenberg/.

3.2 Luminescence dating

In total, 11 samples were taken for luminescence dating, utilizing stainless steel tubes. Sampling positions are indicated in Fig. 2a/b. The material was prepared under subdued light conditions with standard methods (Aitken, 1998). As the quartz grains showed signs of early saturation (occasionally at 80 to 100 Gy) and inconsistent dose recovery, all measurements were conducted on coarse grain K-feldspars (125-180 µm) using a Risø TL-DA-20 reader, equipped with IR light-emitting diodes, transmitting at 870 nm. The signal was filtered through a D-410 Chroma filter to allow detection in the blue-violet wavelength range. For sample irradiation, a calibrated $^{90}Sr/^{90}Y$ beta source was used with a dose rate of about 0.2 Gy/s. For each sample, we prepared 24 discs with very small aliquot sizes (0.5 mm) to perform multiple grain measurements applying the $pIRIR_{290}$ SAR protocol (Thiel et al., 2011) and using an a-value of 0.11 ± 0.02 (Kreutzer et al., 2014). Aliquots with a recycling ratio >10 % and a recuperation >5 % were excluded from age calculations. Dose rates were determined by high-resolution germanium gamma spectrometry in the VTKA laboratory Dresden (Supplementary Table S13). Further information on quality assessment and the results of dose rate determinations may be found in the Supplementary Section 6.

3.3 Palynological analysis

For biostratigraphic control and to obtain further paleoenvironmental information, we performed palynological analysis on 12 selected samples (see Fig. 2b/c, Tab. 1 and Supplementary Figure S59 for sampling positions and lithological descriptions). From Trench 2, a sequence of four samples from the peaty detrital mud (samples 4 to 7; layer 11b) and supplementing bulk samples (samples 1 to 3, 8) from layers 11 (a/b/b_2) and 10 were taken. Layers 9 and 7 in Trench 1 were also sampled, but contained no pollen. Additionally, four samples (9 to 12) were retrieved from organogenic segments of the adjacent sediment core PD.028 (Supplementary Figure S59). All samples were treated with standard methods (Faegri et al., 1989; Moore et al., 1991), after which, pollen and spores were identified using the atlases of Faegri et al. (1989), Moore et al. (1991) and Beug (2004). Micro-charcoal particles < 100 µm were counted in samples 1 to 8 and are presented alongside the pollen diagrams (Supplementary Figures. S 60 and 61). The pollen sum, on which percentages of all taxa are based, is solely composed of terrestrial taxa, excluding cryptogams, Ericaceae, Cyperaceae and aquatic plants. The curve “Ericaceae indeterminate” characterizes badly preserved and therefore indeterminable Ericaceae tetrades. The arboreal pollen (AP) sum includes trees and shrubs, whereas the non-arboreal pollen (NAP) sum covers Poaceae, *Cerealia*-type and the group of terrestrial herbs. Pollen percentages and concentrations were calculated and displayed with the software package TILIA (Grimm, 1990). For detailed results and interpretation, see section 4.3 and Supplementary Section 7.

3.4 Phytolith analysis

To complement the palynological findings, we vertically sampled sediment from Trench 1, layer 7 (one sample each from the eastern and southern profile: samples MH1 and MH3), layer 8 (MH4) and layer 9 (MH5), and also from layer 11a in Trench 2 (sample MH2)(Fig. 2, Supplementary Table S15). Phytoliths were extracted from the sediment using a version of the Rapid Phytolith Extraction method at the Max Planck Institute for Evolutionary Anthropology

(Katz et al., 2010). Phytoliths were counted on single and multi-cell counts using standard methods (Power et al., 2014). We aimed to count >200 phytoliths per sample but in some phytolith-poor samples, we could only reach 150-200. Phytolith concentrations based on the acid insoluble fraction (AIF) were also calculated to assess sediment diagenesis. Detailed sample preparation, results and interpretation can be found in Supplementary Section 8.

3.5 Micromorphology

We collected five oriented block samples for micromorphological analysis. Samples LIB 19 1 and LIB 19 2 were taken from Trench 1, samples LIB 19 3 to LIB 19 5 from Trench 2 (Fig. 2d, Supplementary Figure S50). Thin sections were prepared by G. MacLeod (University of Stirling, UK) and their analysis was performed on a petrographic microscope with a magnification of 20x to 200x using oblique incident (OIL), plane- (PPL) and cross-polarized light (XPL). Micromorphological descriptions follow established nomenclatures (Stoops, 2003; Stoops et al., 2010). Results and interpretation can be found in section 4.4 of the main text and in the Supplementary Section 5.3.

3.6 Grain size analysis

To support field descriptions and for the better assessment of sedimentary environments, we conducted grain size analysis on 28 bulk samples from most layers in both trenches (all except 1, 2, 8 and 11b) at the Leibnitz Institute for Applied Geophysics, Hannover/ Germany (see Tab. 1 for lab codes and positions). We utilized a Beckman-Coulter LS 13320 PIDS laser diffractometer, which detects a spectrum from 0.04 to 2000 µm. We mostly followed the measurement protocol described by Machalett et al. (2008). Deviating from this, for dispersion, we treated the samples with 1 % ammonium hydroxide solution (NH_4OH) and planted them in overhead rotators for > 12 hours. We refrained from removing organic matter and carbonates as pre-tests implied low contents, which were shown to be negligible for the grain size distribution (Beuselinck et al., 1998). All samples were subjected to a fivefold measurement and subsequently averaged, whereby sample clusters with a standard deviation >5 % were rejected.

3.7 Lithic analysis

The lithic artefacts were recorded using a detailed attribute recording system, published in detail recently (Weiss, 2019, 2015). For the aim of this study, mainly the following attributes were selected from the dataset (see Supplementary Sections 3.5 – 3.7): the raw material, the state of preservation, the blank type, maximum length, width, thickness, and weight. Here, the maximum dimensions were measured, whereby flake length was measured in flaking direction. The length of cores was measured in the direction of the last flake removal. The maximum length of flake tools was also measured in flaking direction, whereas the length of tools made from cores or natural blanks was measured along the technical axis (i.e., in direction of the longest working edge). Furthermore, for the flakes were recorded: the state of the platform, the exterior platform angle (EPA), the amount of worked surface on the dorsal face (i.e., flake scars), and the direction of the dorsal scars. For cores, the amount of worked (flaked) surface was recorded, as well as the number of flaking surfaces, the number of flake scars, the flaking (or striking) angle, the condition of the striking surface, and the flaking directions. Because the tools from Li-II are typologically diverse, and often combine several types on single tools together with recycling and reuse (see below), we could not always apply strict typological schemes. Where possible (e.g., notches, denticulates), types from the Bordian typology were adopted (Bordes, 1961; see also Pop, 2014 for the use of types in Eemian assemblages). Besides retouched flakes, flakes with possible macroscopic use-wear were also counted as flake tools.

The full attribute dataset is available as Supplementary Datafile (.csv).

3.8 Traceology

To provide additional data on the nature of the Neanderthal occupation at the Middle Paleolithic sites of Lichtenberg I and II, traceological analysis were conducted on a sample of 27 artefacts. Traceology (Semenov, 1964) aims to identify specific taphonomical, technological and functional traces or modifications, which allows us to reconstruct (i) specific technical behaviors, (ii) the post-depositional history of anthropic inclusions within sedimentary units, as well as (iii) how and for which purpose stone tools where made and used at a specific site. This is achieved by systematically scanning the edges and surfaces of stone tools under different magnifications ranging between 0.63x to 500x and plotting their location and distribution. The location and morphology of specific micro negatives, edge rounding, microscopic polish, micro scars and striations are compared to an experimental reference collection in order to establish the kinetics of stone tool use as well as the worked material (Chan et al., 2020; González-Urquijo and Ibañez-Estéves, 1994; Keeley, 1980; Vaughan, 1985). Here, we used a Carl Zeiss Stemi 508 stereo microscope and an Olympus BXFM reflected light microscope.

4. Results

4.1 Stratigraphy

General Stratigraphy

The sedimentary record within the Trenches 1 and 2 can be subdivided into 11 sediment layers (Fig. 2, Tab 1). The majority of these sediments are the product of the redeposition of Saalian glaciofluvial sands on the slope by different processes and over short distances (<100 m). These processes include solifluctive, niveofluvial, aeolian deposition. Furthermore, lacustrine deposits occur (see more detailed information in Supplementary Sections 5.1 and 5.2):

Solifluctive deposits (layers 2 and 3): Deposition and redeposition of solifluctive sediments happens in periglacial environments under the influence of seasonally thawing permafrost (French, 2008). This usually leads to unbedded sediments. However, as solifluction can alternate with slopewash or aeolian sedimentation, internal stratification of respective layers may occur, as is the case in layer 3.

Niveofluvial deposits (layers 4, 8 and 9): Niveofluvial deposition is a slopewash triggered by annual snowmelt in sparsely-vegetated environments together with possible involvement of aeolian input (Christiansen, 1998a; Menke, 1976; Zagwijn and Paepe, 1968). This results in the formation of thin wavy beds of fine and middle sands, and sometimes gravel.

Aeolian deposits (layer 5): Evidence for purely aeolian sedimentation of layer 5 is provided by its mean grain size (ca. 350 µm), good sorting and inclined bedding (ca. 15°), in combination with abundant surficial impact scars and a notably loose overall structure. There are indications that this aeolian material has been transported by saltation rather than in suspension (cf. Farrell et al., 2012; Schwan, 1988) (see Supplementary Sections 5.1 and 5.2).

Lacustrine deposits (layers 7, 10 and 11): In contrast to these slope and sensu stricto periglacial deposits from proximal sources, these layers are of lacustrine origin, i.e. their formation is connected to the presence of a paleolake (see directly below and Supplementary Sections 5.1 and 5.2).

Eight of the eleven layers were encountered in both trenches. Correlation was based on the agreement of macroscopic properties detected during field work, as well as micromorphological evidence and detailed evaluation of the grain size data (Figs 2 and 3, Supplementary Sections 5.2 and 5.3). The upper part of the sequence was subjected to likely multi-phased cryoturbation in the form of different involutions, both directed upwards and downwards (Fig. 2). With amplitudes of several decimeters to nearly one meter, these phenomena were likely produced by permafrost dynamics (cf. Vandenberghe, 2013). These features are frequent in layers 1 to 6, occasionally reaching down to layer 9, and result in a somewhat fragmentary appearance of archaeological find horizon Li-I (stratigraphic layers 7 and 8). Nevertheless, based on field observations, Li-I can predominantly be identified in an in-situ stratification. Find horizon Li-II in stratigraphic layer 11 remained entirely unaffected by those involutions.

Based on the lithological findings in Trenches 1 and 2, a schematic stratigraphy was established (see sections 5.2 and 5.3, Fig. 7), which in turn can be largely correlated with the sediment sequence of core PD.028, directly adjoining Trench 1 to the south (Figs. 1, 2; Supplementary Figure S59). The core penetrated most layers encountered in the excavations. In addition, it exposes three organogenic segments within and below niveofluvial sands, equivalent to layer 9: A peaty mud (230-250 cm coring depth) and a strongly humiferous sand (355-390 cm coring depth) surrounded by these niveofluvial sands, and a peaty layer (465-555 cm coring depth) directly at their base. These organic-rich deposits testify to the wetlands that surrounded the former occupation site on an alluvial fan (Fig. 1, Supplementary Figure S49b) (description of core PD.028 in Supplementary Table S11).

Stratigraphy of the find layers Li-II and Li-I

Because of their archaeological significance, the occupational layers deserve closer consideration. Layer 11, only present in Trench 2 is a two-part formation (11a and 11b), whose members interfinger with each other (Fig. 2c). Layer 11a (Li-II) is a slightly humic, unstratified silty fine sand, containing horizontally-oriented fragments of (charred) plant material and several thin humic drift lines, that are visible both macro- and microscopically (Supplementary Figures S52c, S59). We interpret this deposit as the beach facies of an adjoining water body (cf. Bridge and Demicco, 2008; Cohen, 2003), with the drift lines indicating fluctuations in the water-table. Layer 11b is a peaty and sandy, coarse-detrital mud with a thickness of ca. 10 cm. It grades into a humic silt (11b2) to the top and towards the intersection with layer 11a (Supplementary Figure S59). Layer 10 is a thin (<10 cm) veneer of laminated, fine-sandy, loamy silt, that covers layer 11a. It also contains a humic drift line, and it directly emerges from the peaty detrital mud (layer 11b) and wedges out on higher ground. This layer 10 is interpreted as a lacustrine muddy shore-face deposit, caused by a rising water table (see Supplementary Section 5.1). The artefacts are scattered between a total elevation of Z=18.84 m and Z=19.55 m [a.s.l.] within layer 11a. This scattering is mainly caused by the inclination of the find layer towards the shore. However, based on the distribution of screen finds < 1.5 cm within each quarter square, as well as the exact position of single finds > 1.49 cm, we could identify a main artefact scatter in the uppermost part of layer 11a, between Z = 19.10 m and Z = 19.21 m (Supplementary Section 2.2). This distribution pattern reduces the thickness of the main find horizon to 11 cm. In addition, some artefacts were obtained from the contact zone of the top part of layer 11a and the bottom part of layer 11b (as 11b interfingers with 11a).

Find horizon Li-I (primarily in Trench 1) is mainly contained within stratigraphic layer 7 but also includes the upper part of layer 8 (Fig. 2a). It is possible that we have evidence here for succeeding occupations, which needs to be clarified by future field work. Layer 8 is a massive to crudely-bedded, niveofluvial slopewash deposit, consisting of gravelly medium sands with gleyic properties. The layer is discordantly overlain by layer 7, a thin (<10 cm) whitish, very fine-sandy silt to silty very fine sand. Our layer 7 matches the sedimentological characteristics of the main Middle Paleolithic find horizon as described in Veil et al. (1994). In the thin sections, layer 7 stands out for its remarkably low porosity and fine horizontal layering. Because of these properties comparable with layer 10, we likewise interpret layer 7 as lacustrine shoreface deposit. In Trench 2, layer 7 intertongues with the underlying slope deposits of layer 9. The single tongues of interbedded lacustrine sediments from layer 7 unify on top of layer 9 towards higher ground (Fig 2c). This indicates alternating conditions of slope and lacustrine deposition, and testifies to their broad contemporaneity. Due to cryoturbation, layer 7 with the contained artefacts is occasionally deformed upwards in the form of diapirs or injections (then referred to as layer 7’). Based on the small number of artefacts recovered during our fieldwork (see below), we were not able to perform a statistical find distribution analysis for Li-I in our excavation. In this regard, the reader is referred to Veil et al. (Veil et al., 1994).

4.2 Luminescence Dating

Luminescence dating yielded ages between 53.5 ± 4.9 and 91.5 ± 9.1 ka (samples L-EVA 2010 and 2022) (Figs. 2 and 7, Tab. 2). The dated layers 6 to 11, including the archaeological find horizons are well aligned chronologically. For find horizon Li-I (stratigraphic layers 7 and top of layer 8), the three samples (L-EVA 2014, 2015 and 2017) range between 70.8 ± 8.0 and 71.6 ± 7.0 ka with a mean age of 71.3 ± 7.3 ka. Find horizon Li-II (stratigraphic layer 11) gave an age between 89.5 ± 8.2 and 91.5 ± 9.1 ka and a mean age of 90.5 ± 8.7 ka (samples L-EVA 2024 and 2022). Sample L-EVA 2010, taken in a position where find horizon Li-I was cryoturbated upwards, gave a cryoturbation age of 53.5 ± 4.9 ka. This is close to the previous TL-age of 57 ± 6 ka for this site (Veil et al., 1994). More details on data evaluation, equivalent dose (D_e) estimation and age calculation can be found in Supplementary Section 6.

4.3 Palynology

The pollen spectra and vegetation succession of sublayers 11a and 11b (incl. $11b_2$) from Trench 2 (Fig. 2b, c; Supplementary Figures. S60 and S61) are quite similar. They contain about 80 to 85% woody taxa (arboreal pollen, AP) consisting mainly of *Pinus* and *Betul*a and very few *Alnus, Larix, Myrica, Juniperus* and *Picea*, while the NAP (non-arboreal pollen) are represented by Poaceae, Cyperaceae and heliophile herbs, which is indicative of a densely wooded boreal conifer forest. Sparsely occuring pollen of aquatic and wetland taxa like *Sparganium spec.*, respectively *Montia* indicate open water and swampy environments. In layer 10, the strong increase of Poaceae (40%), different NAP, and the drop of *Pinus (*15%) associated with *Betula* amounts of about 30%, and occurrences of the cryptogams *Ophioglossum* and *Selaginella selaginoides* are interpreted as a strong opening of the landscape towards a tundra-like vegetation. This sequence (layers 11a, 11b, $11b_2$ and 10) is indicative of the late Brörup Interstadial, transitioning into the following Rederstall Stadial (Behre, 1989; Menke and Tynni, 1984; Veil et al., 1994; Supplementary Section 7).

In core PD.028, the lower peat at 465-555 cm shows distinct interstadial conditions with AP spectra characterized by *Pinus, Betula, Picea* and *Larix*, which amount to 80-90% (Supplementary Fig. S62). A diverse heliophile pollen flora consisting of *Valeriana vulgaris*-type, *Matricaria*-type and *Artemisia* furthermore characterizes dry boreal forest habitats.

Both the sandy humiferous layer (355-390 cm) and the coarse detrital, peaty mud (230-250 cm) in superposition reveal pollen spectra dominated by NAP (up to 60%) with high amounts of Poaceae. The rich heliophile flora includes among others *Artemisia, Valeriana montana*-type*, Matricaria*-type, *Polygonum bistorta*-type*, Helianthemum oelandicum*-type*, Epilobium* and Chenopodiaceae. Among the wooden taxa, *Betula* reaches about 30%, whereas *Pinus* values have dropped down to <15%. The spectra therefore clearly reflect a phase of rather open landscape and dry and cold conditions, also indicated by the massive occurrence of colonies of the cold-tolerant green alga *Pediastrum kawraiskyi*.
The lowermost two bulk samples are correlated with the Odderade Interstadial, WF IVb (Behre, 1989; Menke and Tynni, 1984; Veil et al., 1994; Supplementary Figure S62), whereas the uppermost samples most probably represent early phases of the Schalkholz, WP I Stadial. Pollen diagrams and detailed interpretation are presented in Supplementary Section 7 and the main palaoenvironmental results and biostratigraphical subdivision can be found in Tab. 3 and Supplementary Tab. S14.

4.4 Micromorphology

The analyzed sequence is dominated by quartz sand, common clay and rare inclusions of organic material and mica. Anthropogenic remains, flint and charcoal are rare and only occur in the lithofacies associated with the archaeological layers. The microstructure and fabric, i.e., horizontal orientation of plant residues, channels filled with clay, and the good preservation of organic material indicate waterlain, potentially lacustrine environments with incipient soil formation (Bouma et al., 1990; Cohen, 2003; Taylor et al., 1998) for the lower part (layer 11a/b, 10). In contrast, for the upper part (layers 9 to 5) of the sequence the micromorphological analysis does not allow a differentiation between waterlain and aeolian deposition. Turbation features are overall rare and limited to individual layers, indicating good integrity of the archaeological assemblage. We did not, however, sample and analyze the cryoturbated parts of the sequence. The upper find horizon, Li-I, is associated with a fine and compact lithofacies (layer 7), however, the origin of this compaction was not apparent in thin section. No cementation features were observed at this scale of observations, instead the grains appear as very densely packed with very limited void space. The overlying coarse-grained layer 6 shows intense clay illuviation with the compacted, fine grained layer 7 presenting a barrier to the downward transportation of clay. This clay illuviation is not associated with further soil formation features, and it is therefore unclear whether this clay illuviation represents a soil formation process and to what former surface this process may be connected. For more details, see Figures S 50 to S 55 and Supplementary Section 5.3.

4.5 Phytolith Analysis

The ratio of grass short- to long-cells was measured to ascertain phytolith preservation, given that short-cells are more likely to preserve than long-cells due to their shape and higher silicification (Supplementary Table S16). Of the five analysed samples, MH3 and MH5 (layers 7 and 9) showed lower ratios, which is suggestive of poorer preservation (Madella and Lancelotti, 2012). However, the rarity and widespread absence of dendritic long-cells indicate some taphonomic alteration in all samples. The ratio and the presence of dendritic long-cells in MH2 (layer 11a) indicates that this sample has the least taphonomic alternation. Long-cells, such as psilate and sinuate types, dominate all the assemblages, and are typical of monocot plants, particularly Poaceae. We also found many short-cells and some bulliforms, which again shows the presence of grasses as a vegetation component. Less important were phytoliths produced by eudicot shrubs and trees. These include the two main categories; wood/bark and leaves. Eudicot leaf types were found in MH4 (layer 8). Wood/bark types occur in MH2 (layer 11a) and MH3 (layer 7). In addition, sclereids deriving from sclerenchyma were found in MH3 (layer 7). Unspecific eudicot types were found in all samples, except MH5 (layer 9). This indicates the presence of a shrubby vegetation component. The relatively low total numbers in most of the samples imply a low bioproductivity with constrained growing conditions that deposited only few phytoliths. In that way, samples MH1 and MH3 to MH5 (layers 7 to 9) are very similar. In contrast, the far richer assemblage in MH2 (layer 11a) indicates warmer and wetter conditions that fostered a plant-rich environment, including grasses and woody plants (see Supplementary Tables S16, S17; Supplementary Section 8).

4.6 Grain size Analysis

The 116 grain size fractions (0.04 - 2000 µm) for each sample were subjected to uni- and multivariate statistical analysis. Firstly, we calculated the sorting and the mean grain sizes (Blott and Pye, 2001; Folk and Ward, 1957) and displayed them as a scatter plot (Fig. 3a). Secondly, a principal component analysis (PCA) was conducted and the most significant principal components PC1 and PC2 were displayed, together accounting for 95.8% of the total data variance (Fig. 3b). In both graphs, we assigned each sample to the sedimentological process identified during field descriptions (and micromorphological analysis, if applicable) and constructed convex hulls around all processual clusters. Both graphs differentiate well between the different classes formed during fieldwork, encompassing aeolian, niveofluvial/niveoaeolian, solifluctive and lacustrine processes. This satisfactory discrimination was unexpected, seeing that the Saalian glaciofluvial sediments as main source material for the analyzed slope deposits crop out <100 m upslope, and grain size sorting is i.a. a function of transport distance. Moreover, all classes in the graphs contain samples from Trench 1 (dots) and Trench 2 (triangles), providing further evidence that layers 3, 4 , 5, 7 and 9 can be directly correlated in both trenches (Figs. 2 and 3, compare Tab. 1). A more detailed evaluation and interpretation of the grain size data is provided in Supplementary Section 5.2.

4.7 Archaeology

Lichtenberg I

During our initial survey in 2017, we found one Keilmesser (Fig. 4: 1) and one fragment of a bifacial tool (Supplementary Figure S1) in the cryoturbated layer 7' below the 1987-1993 excavation trench. In the course of our fieldwork in 2019, we excavated 17 flakes (Fig. 4: 2-7) and three cores from Trench 1. One flake was found in the cryoturbated layer 7' (Fig. 2a), 12 artefacts in layer 7 and seven artefacts in layer 8. All artefacts are made of Baltic Flint. Although being low in number and mostly typologically rather undiagnostic, finds like the Keilmesser from layer 7' as well as a relatively large flake that is potentially a product of bifacial reduction (Fig. 4: 6) helped, in addition to the sedimentological characteristics of the deposit (see section 4.1 above), to identify layer 7 as equivalent to the main find horizon of the 1987-1993 Keilmessergruppen assemblage (see Veil et al., 1994). One additional flake (Fig. 4: 8) was recovered from Layer 7 in Trench 2. This also supports an archaeological connection of the stratigraphies in Trench 1 and Trench 2.

Lichtenberg I - Traceology. Our preliminary traceological analysis (Supplementary Section 4, Supplementary Table S10) revealed neither use-wear traces on the two flakes analyzed, LIA-36 and LIA-50 (Fig. 4: 6, 7), nor on the bifacial tool fragment Li-6. For the analyzed Keilmesser Li-7 (Fig. 4: 1; Fig. 5), however, the wear traces suggest its use as a hafted butchering knife. The tool is made of dark Baltic Flint, and shows little signs of severe post-depositional mechanical damage or chemical weathering that could have hindered the preservation of wear traces. Traces indicating the natures of the transformed material, however, are subtle and constricted to lightly developed micro polishes zones located on the distal portion of the working edge (Fig. 5a: F1). Negative edge rounding and additional polished surfaces are found further inwards on the dorsal side of the working edge (Fig. 5a: F2). Directional markers, including striations running parallel to the working edge of the tool and generally associated with lightly developed polished spots are also located on the dorsal surfaces of the working edge (Fig. 5a: F3 and F4). In combination with the micro negatives located on the ventral side of the tool (Fig. 5a: F5 and F6), a longitudinal cutting motion under the excretion of pressure is suggested, what is comparable with the interpretation of previous traceological analyses from Lichtenberg (Veil et al., 1994). The lightly-developed polish and the presence of striations on the analyzed specimen indicates the processing of a soft organic material and occasional contact with harder organic substance. Therefore, we suggest the use as butchering knife.

The back of Keilmesser Li-7 shows a series of marked modifications and traces that are associated with intense mechanical stress (Fig. 5b). The distal portion of the back shows marked rounding and crouching that are evident by short continuous micro-negatives with step and hinge terminations (Fig. 5b: F1 and F2). Bright and semi-undulating cohesive polished areas were identified on the edges of the negatives located on the medial portion of the back, indicating the repeated contact with a hard organic substance (Fig. 5b: F3). Together, these signs may indicate the continued mechanical friction of the tool with a hard organic haft, thus possibly indicating the use of composite tools by Neanderthals at Lichtenberg. Regarding the common interpretation that Keilmesser were handheld tools (e.g., Jöris, 2006), we do not suggest that Keilmesser tools were generally hafted. However, our results make it paramount to conduct further investigations into the subject.

Lichtenberg II

We discovered 192 artefacts (Supplementary Table S3; Supplementary Table S9; Supplementary Datafile) in find horizon 11a (Fig.7). 173 artefacts are preserved in a fresh condition, 7 are rolled and 12 show light edge damage (see Supplementary Datafile). The assemblage is dominated by flakes, followed by cores and flake tools. The assemblage further includes shattered pieces and core tools. We also found three manuports and one piece that was typed as 'other' which are most likely raw material imports and/or hammerstones. If we exclude manuports (n = 3), other (n = 1) and shatter (n = 25), the remaining assemblage of 163 artefacts consists of 51.5% flakes (n = 84), 30.1% tools (n= 49) and 18.4% cores (n= 30). However, the category of tools also includes cores that were later transformed into tools, so that the original share of cores was higher (n = 42, see Supplementary Section 3.5, 3.7). Nevertheless, the share of tools is relatively high compared to Lichtenberg I (18.8% (Veil et al., 1994)).

Lichtenberg II - Raw material. The artefacts are made predominantly of Baltic Flint (n = 184; Supplementary Table S1). The raw material was of exceptionally small size, as is demonstrated by a controlled raw material sample from layer 11a that gave a median weight of 5.3 g (Supplementary Figure S33). Despite its small size, the flint was of rather good quality (Supplementary Table S2). Only one large core (Fig. 4: 20) shows internal cracks and flaws that hampered the core reduction and led to unexpected breaks of the resulting flakes. 14 (7.3%) artefacts show thermal alterations (Fig. 4: 10, 16; Supplementary Table S2), indicating the presence of artificial or natural fires at the site. Additionally to flint, six artefacts where made of quartzite (Fig. 4: 21).

Lichtenberg II - Size. The artefacts from Li-II are relatively small. Their median dimensions (either longest width or length) range between 19.48 mm for the flakes and 27.54 mm for the cores (Supplementary Table S5). Comparing the flakes from this site to 14 Central European assemblages ranging from the Eemian interglacial to early MIS 3, Li-II has the smallest artefacts (Supplementary Figure S36). Exceptional are the core LIA-335 (Fig. 4: 20), the quartzite flake LIA-513 (Supplementary Figure S41), and the quartzite flake tool LIA-504 (Fig. 4: 21). With their maximum dimensions of 114.7 mm, 106.3 mm, and 75 mm respectively, these by far exceed the median dimensions of the assemblage.

Lichtenberg II - Cores Fig. 4: 19,20; Supplementary Section 3.5). In the following analysis, we additionally included those cores that where later transformed into tools (see below). Most of the cores were only knapped up to half of their surface (72.5%, n = 29). Predominantly, the cores were exploited on a single (47.5%, n = 19) or two flaking surfaces (32.5%, n = 13). The angles between the striking platform and the flaking surface have a median value of 88° (min

= 64°, max = 108°, sd = 8.75). 35% (n = 14) of the cores have only one single flake scar, but 3 - 5 flake scars are common as well (in total 52.5%, n = 21). At a significance level of p = 0.05, a linear model (Supplementary Figure S37) reveals a weak significant relationship between core lengths and the number of flake scars (Multiple R-squared: 0.12, Adjusted R^2: 0.099, F-statistic: 5.312 on 1 and 38 DF, p-value: 0.03). This implies that larger cores have tentatively more flake scars and were thus exploited more intensively. In turn, the small raw material size tentatively led to low exploitation values on the small cores. Taking all flaking surfaces together, most cores where knapped unidirectionally (80.6%, n = 54). Most striking platforms consist of a natural (51.3%, n = 20) or plain (43.6%, n = 17) surface, whereas fine preparation of striking platforms does not occur in the assemblage. In conclusion, simple flaking methods dominated the blank production in Lichtenberg II. Core preparation was not common, if not entirely missing. The simple cores, sometimes just flaked once, may also be due to the small raw material size, as some nodules make only one-time flaking possible.

Lichtenberg II - Flakes (Fig. 4: 15, 22; Supplementary Section 3.6). We included 55 complete flakes into the analysis, as not all variables are preserved on flake fragments. The platform attributes reinforce the observation made on the cores that striking platform preparation (i.e., Levallois *sensu largo*) was not common, as platforms with natural (21.8%, n = 12) and plain surfaces (50.9%, n = 28) dominate the flake assemblage. Platforms that crushed during knapping also have a relatively high share of 23.6% (n = 13). The EPA has a median value of 85° (min = 58°, max = 109°, sd = 10.85°), comparable to the flaking angles observed on the cores. Most of the flakes originate from an advanced state of core reduction, as the share of fully cortical flakes is low (15.1%, n = 8). This may be a reasonable number, as cores naturally produce a lower share of fully cortical flakes than flakes with no or only remnants of natural surfaces. However, if we sum up all the flakes with remnants of natural surfaces on their dorsal face, we end up with 62.2%. This is more than half of the flake population and may be caused by the small size of the raw material. The observed dorsal scar directions on the flakes show the tendency that the blank production in Li-II was dominated by unidirectional flaking (51.1%, n = 23). This confirms the similar observation made on the cores.

Lichtenberg II - Tools (Tab. 4, Fig. 4: 9-14, 16-18; Supplementary Section 3.7). The tools from Lichtenberg II show a high typological diversity. They are dominated by flakes that were potentially used (Fig. 4: 9,17), tools with partial or limited edge retouch (Supplementary Figure S39) and endscrapers (Fig. 4: 12,13). They were manufactured from a diversity of blanks, such as natural pieces, cores and flakes, and are dominated by the latter (62.5%, n = 30). Endscrapers and endscraper combination tools were manufactured from thick blanks (Fig. 4: 12, 13; Supplementary Table S8), indicating special functional requirements. In addition, a rather steep endscraper edge can only be produced on a relatively thick blank. The high share of cores (25%, n = 12), as well as two shattered pieces that also served as blanks for tools, indicate the high importance of recycling within the Li-II assemblage. For example, the artefact LIA-379 was initially a core and then transformed into a hammerstone (Supplementary Figure S38). The traceology (see below) indicates that tool functions go beyond the current typological classifications and descriptions.

Lichtenberg II - Traceology (Fig. 6). The preliminary traceological analysis (Supplementary Section 4, Supplementary Table S10) of lithic material from Li-II indicates a heterogeneous pattern of activities, including the processing of soft animal materials, soft and abrasive vegetable materials and hard vegetable materials (wood). Notable are the traces located on the ventral distal working edge of artefact LIA-550 (Fig. 4: 9; Fig. 6a). They show a well-developed bright undulating polish with a high incidence of directional markers, indicating a crossed transverse motion. This bright well-developed polish likely formed by the contact with a highly abrasive and soft vegetal material, while the striations may be related to the admixture of mineral particles, possibly sand or grit, during scraping activity. The resemblance to cereal polish is remarkable (Clemente and Gibaja, 1998), indicating the working of silicate-rich grasses or sedges. The combination of percussive and pressure force was also found on the Li-II artefacts as well as the possible use of hafting technology. The latter was observed on artefact LIA-307 (Fig. 4: 12; Fig. 6b) based on the presence of G type polish (Moss, 1987; Rots, 2010) and the scaring on the dorsal surface along the edges of the central negatives. The general small-artefact characteristics of the assemblage, together with the high incidence of crushing, coupled with the high amount of force used during the different productive activities undertaken at the site, may suggest that artefact LIA-307 was not the only hafted tool. The absence of further hafting wear, however, constrains the further exploration of this possibility.

5. Discussion

5.1 Comparison with previous geochronological data

Stratigraphic layer 7 (find horizon Li-I) is locally deformed upwards by cryoturbation, especially injection, but is still associated with lithic finds there (Fig. 2). To get an impression of the timing of deformation, we dated this cryoturbated sediment with luminescence and obtained an age of 53.5 ± 4.9 ka (L-EVA 2010, Fig. 7). This compares very well to the previous TL-age of 57 ± 6 ka for the find horizon Lichtenberg I (Veil et al., 1994). The origin of our sample from a cryoturbated context allows the following conclusions: (i) The previous age must likewise have been obtained from a cryoturbated deposit. This is supported by the fact that during the former excavation, a depth of ca. 1.2 m below surface was usually not exceeded. Our excavations revealed that in these higher stratigraphic positions only cryoturbated expressions of the find horizon occur (Fig. 2). (ii) In spite of considerable progress in luminescence dating during the last decades concerning measurement protocols and targeted signals (Buylaert et al., 2012; Murray and Wintle, 2003; Wintle and Adamiec, 2017), the similarity of the previous and newly-presented luminescence ages attest the remarkably high reliability of the former TL dates. Therefore, only lithostratigraphic challenges – i.e. the cryoturbations – apparently hindered a more accurate temporal estimation of the deposition and occupation at that time. (iii) The two dates imply a cryoturbation age that is time-equivalent to the early MIS 3. Even though permafrost – the probable driver for these deformations – was more widespread and effective in Central Europe during MIS 4 and MIS 2 (Bertran et al., 2014), it is known to have existed in MIS 3 as well (e.g. Van Huissteden et al., 2003; Van Meerbeeck et al., 2011). However, active permafrost is not a prerequisite for the partial deformation/injection of the find horizon Li-I. Instead, this can also be a function of loadcasting or cryogenic pressure during thaw degradation of the permafrost, which would be in agreement with the two independent ages suggesting a deformation during the more temperate early MIS 3 (French, 2008; Vandenberghe, 2013; Vandenberghe and Van den Broek, 1982). Nonetheless, according to our current state of knowledge, a cryoturbation age falling within the later MIS 3 or even MIS 2 cannot be completely ruled out. Therefore, a follow-up study will deal with the cryogenic capping sediments in Lichtenberg.

5.2 Comparison with global paleoclimate records

Find horizon Li-II

For layer Li-II, corresponding with stratigraphic layer 11a, two very similar luminescence ages from samples L-EVA 2022 and 2024 (91.5 ± 9.1 ka and 89.5 ± 8.2 ka) gave a mean age of 90.5 ± 8.7 ka. In the palynological data, we observe temperate, late interstadial conditions, characterized by an opening boreal pine-birch forest in layers 11a and the lower part of 11b, assigned to the Brörup Interstadial WE IIb (Tab. 3, Supplementary Section 7) (Behre et al., 2005; Behre and Lade, 1986; Menke and Tynni, 1984; Veil et al., 1994). The environment changed toward heliophyte and grass-rich, cold-stage tundra vegetation in the following Rederstall Stadial. In our sequence, this shift happens abruptly between layers 11a and 10, but gradually to the top of layer 11b. Therefore, the occupation of find horizon Li-II should have occurred during late phases of the Brörup Interstadial, whereby the obtained mean age of 90.5 ± 8.7 ka represents this terminal phase (Fig. 7). Compared with global paleoclimate records, this age for the end of Brörup Interstadial corroborates the correlation with the end of MIS 5c (peak at 96 ka in Lisiecki and Raymo (Lisiecki and Raymo, 2005b)) and with Greenland Interstadial (GI) 22 in the synchronized Greenland ice core records, dated to about 89 ka at its peak (Rasmussen et al., 2014). To our knowledge, for the Brörup Interstadial no direct numerical dates exist in its type region on the northern Central European Plain so far. Luminescence ages similar to ours for the end of equivalent interstadials have been obtained from loess records of Northern France at ca. 85 ka (Antoine et al., 2016) and Dolní Věstonice (CZ) at ca. 90 ka (Antoine et al., 2013; Fuchs et al., 2013). In the Alpine Foreland, the peak of the Brörup equivalent has been dated to around 96 ka (compiled by Preusser, 2004) and its end to ca. 89 ka in the highly-precise NALPS speleothem record (Boch et al., 2011). Altogether, these dates support our finding that the end of the Brörup Interstadial (mean age of 90.5 ± 8.7 ka in Lichtenberg) coincides with GI 22 and the termination of MIS 5c.

Find horizon Li-I

In find horizon Li-I (stratigraphic layers 7 and 8), three nearly identical luminescence ages for samples L-EVA 2014, 2015 and 2017 (71.6 ± 7.0 ka, 71.5 ± 7.0 ka and 70.8 ± 8.0 ka) gave a mean age of 71.3 ± 7.3 ka. Regarding lithostratigraphy, Li-I is under- and overlain by cold stage deposits (section 4.1, Supplementary Section 5.1), and the covering layers show clear permafrost features. This suggests a pre-pleniglacial age for Li-I (Jöris, 2004), because permafrost rarely occurred in Central Europe before MIS 4 (Bos et al., 2001; Vandenberghe and Pissart, 1993). Our chronostratigraphy implies that layer 9 (mean age of 72.5 ± 7.8 ka) is only slightly older than layers 7 and 8. Furthermore, as evidenced by the alternating deposition of layers 7 and 9 in the stratigraphy of Trench 2, these partially even occur contemporaneously (Fig. 2c). Accordingly, comparable cold-stage conditions for the formation of layers 7 to 9 are also suggested by similar phytolith results (section 4.5, Supplementary Section 8), which point to a grass-rich vegetation in these layers. However, layers 7 to 9 were pollen-sterile in the trenches, thus hindering their direct biostratigraphical assignment. In contrast, reliable information was obtained from core PD.028, directly south of Trench 1 (Figs. 1, 7): (i) A thick peat layer directly below the niveofluvial sands of layer 9 was characterized by dense *Pinus-Betula* forest, being characteristic for the Odderade Interstadial WE IVb (Tab. 3, Supplementary Section 7) (Behre et al., 2005; Behre and Lade, 1986; Menke and Tynni, 1984; Veil et al., 1994). Based on the bio-/lithostratigraphy and the luminescence ages for the overlying layers 8 and 9, we correlate the Odderade peat with GI 21 (Jöris, 2004; Stephan, 2014). (ii) Unlike in the trenches, the cold stage niveofluvial sands of layer 9 showed two interbedded organic-rich layers that were characterized by a grass- and heliophyte-rich open vegetation belonging to the early Schalkholz, WP I Stadial (Tab. 3, Supplementary Figure S62, Supplementary Tab. S14).

On the premise that these two organic-rich sediments represent low-magnitude climatic ameliorations (Hahne et al., 1994; Vandenberghe and van der Plicht, 2016), we cautiously regard them as minor interstadial oscillations seldomly described for Northern Germany (Supplementary Section 7). These minor oscillations following the Odderade, stratigraphically could be associated with GI 20 and 19 (Rasmussen et al., 2014), which would also agree with the mean luminescence age of layer 9 of 72.5 ± 7.8 ka (with a tendency to increase with depth, see Fig. 7). As for the find horizon Li-I, its mean luminescence age of 71.3 ± 7.3 ka and its superposition above the minor interstadial oscillations suggests correlation with Greenland *Stadial* (GS) 19 (Rasmussen et al., 2014).

Much like the Brörup, to our knowledge the Odderade Interstadial is mostly lacking an independent chronology in the type region of northern Central Europe, apart from previous dating attempts with ^{14}C (Behre and van der Plicht, 1992; Grootes, 1978) and unpublished luminescence ages, obtained by Thiel at the site of Osterbylund (Stephan et al., 2017). For Northern Germany, the Odderade was recently correlated with Greenland Interstadial (GI) 21

(Stephan, 2014). At a few sites (namely Keller, Schalkholz and Osterbylund), above the Odderade layer, but below the deposits of the first glacial maximum (~MIS 4), one or two weak Podzol paleosols exist, representing a slight climatic amelioration phase (Keller-Interstadial), ascribed to GI 20 and 19 (Menke, 1976; Stephan, 2014). Our chronological correlations compare very well with this northern German stratigraphy, but also with independently-dated loess and pollen/speleothem records in neighboring regions: Antoine et al. (2016) also correlated the Odderade/St. Germain II soils with GI 21 for the loess-paleosol-sequences in northern France and report this phase to end at ca. 80 ka. Above the Odderade/St. Germain II, there are two paleosols (Ognon I and II) relating to GI 20 and GI 19. The conclusion of this soil formation has been dated to ca. 71 ka (ibid.). Similarly, two paleosols in the loess-paleosol-sequence of Dolní Věstonice in the southeastern Czech Republic were dated to 73.1 ± 4.7 and 71.3 ± 4.9 ka, respectively, and were correlated with GI 20 and GI 19 (Antoine et al., 2013). Likewise, one or two minor interstadials in palynological records of South-Western Europe and southern Germany above the St. Germain II/Odderade Interstadial (e.g. Woillard, 1979) were ascribed to GI 20 and 19 (Ognon I/II and Dürnten), and the latter was dated to ca. 73 ka (Müller and Sánchez Goñi, 2007). Furthermore, in the NALPS speleothem record of the northern Alps, a minor interstadial related to GI 19 yielded an age of ca. 72 ka (Boch et al., 2011). Although for the Lichtenberg record, numerical dating of the Odderade peat and the overlying two minor interstadials cannot be presented yet, our chronological and biostratigraphic framework suggests their close coupling to the Greenland Interstadials GI 21 to 19. Consequently, the mean age (71.3 ± 7.3 ka) of the overlying find horizon Li-I (correlated with GS 19) represents a plausible age for the inception of the MIS 4 pleniglacial. Comparing our record with the marine chronology (Lisiecki and Raymo, 2005b), we regard the Odderade peat (GI 21) and the overlying two minor interstadials (GI 20 and 19) of core PD.028 to be part of MIS 5a, whereas stratigraphic layers 8 and 7 (find horizon Li-I, GS 19) are tentatively assigned to early MIS 4. This implies that the upper boundary of the Odderade Interstadial is not congruent with the end of MIS 5a, in this region (Behre, 1989a; Jöris, 2004; Stephan, 2014).

5.3 Site formation, paleoenvironment and humans

Neanderthals occupied the northern site of Lichtenberg during the Eemian (Hein et al., 2021), the following early Weichselian Brörup Interstadial (find horizon Lichtenberg II), through to the onset of the first Weichselian glacial maximum (find horizon Lichtenberg I). In the following, we will connect our sedimentological/paleoenvironmental and archaeological results to draw inferences about past human behavior in changing environments in Lichtenberg.

Lichtenberg occupation during the Mid-Eemian

Near the south-facing shore of a small lake, a half-bog formed just above the groundwater level during the mid-Eemian Interglacial (pollen zone E IVb/V). This was the time and position for Neanderthal occupation, as inferred from few artefact finds (2 flakes and a few small chips and fragments) within the core PD.030 (Hein et al., 2021). A densely-forested landscape was reconstructed for the area (>95% arboreal pollen), dominated by hazel (*Corylus*), alder (*Alnus*), lime (*Tilia*) and hornbeam (*Carpinus*), with the admixture of further thermophile taxa, such as elm (*Ulmus*), oak (*Quercus*) and yew (*Taxus*). Among the indicators for local swampy conditions are palynomorphs of ferns (*Polypodiaceae*), cattail (*Typha*) and bur-reed (*Sparganium*) (Behre, 1989; Menke and Tynni, 1984).
This fully-forested landscape contrasts with other contemporaneous Eemian sites from drier regions of central Germany (Gaudzinski-Windheuser and Roebroeks, 2014; Litt and Weber, 1988; Toepfer, 1958; Weber, 1990), where last interglacial Neanderthals are assumed to have lived in semi-open landscapes (Pop and Bakels, 2015). Thus, contrary to earlier hypotheses (Pop and Bakels, 2015), we suggest that the Lichtenberg-Eemian Neanderthals adapted well to wooded paleoenvironments. However, so far we have too few artefacts to draw inferences about Neanderthal behavior in Lichtenberg during the last interglacial. Therefore, future excavations are planned to reveal more about the structure and spatial pattern of the Eemian settlement at the Lichtenberg lakeshore.

Li-II: Late Brörup Interstadial to Rederstall Stadial

During the Brörup Interstadial a beach sediment (layer 11a) was deposited at the shoreline of a small lake (ca. 1.5 km^2, cf. Hein et al., 2021) with fluctuating water tables. In the late interstadial the water table was rising, as evidenced by the formation of a peaty deposit (layer 11b) partially covering the beach, but also interfingering with its deposits. Such a hydrological shift is typical for transitional phases between forested and unforested periods due to the loss of woodland and associated decreasing evapotranspiration values (Behre et al., 2005; Tucci et al., 2021). Vegetation was characterized by boreal forests, with pine (*Pinus*) and birch (*Betula*) being the main tree species (Caspers and Freund, 2001). Likewise, phytolith analysis indicates a relatively high bioproductivity (section 4.5). On the beach, local sandy to humic open stands were dominated by wet meadows, fern and heathland, and a diverse heliophytic flora. For the peaty deposit, we conclude there was a shallow water body with swampy conditions that featured rich stands of cattail (*Typha latifolia* type), reed and sedges. In this environment, the occupation of Li-II took place directly by the shoreline. Regular occurrence of macroscopic and microscopic charcoal fragments (Supplementary Sections 5.3 and 7.2) document episodic burning events, either in connection with natural wildfires or Neanderthal fire use (Dibble et al., 2018; Glückler et al., 2021; Roebroeks et al., 2015). For the site of Gröbern (Central Germany), reconstructed summer temperatures of ca. 16°C and winter temperatures of ca. -15°C in the late Brörup (Kühl et al., 2007) demonstrate a highly continental climate that was caused by a lower sea level at that time (Lambeck, 2004). During the late Brörup stage WE IIb transitioning into WE III, the local water table in Lichtenberg kept rising as the woodlands gradually opened up and gave way to more heliophilous plants. Wave activity on the beach reworked plant material, charcoal and also small lithic fragments, thereby creating distinct driftlines. Eventually, during Rederstall Stadial, vegetation had changed into a grass- and heliophyte-rich tundra. The former beach was largely inundated by the rising lake level due to starkly decreased evaporation values in this non-forested environment (Behre et al., 2005). Subsequently, stadial conditions are recognized in the muddy shoreface deposit of layer 10 and the uppermost part of layer 11b. Layer 10 emerges from layer 11b, that unconformably overlies layer 11a, and wedges out toward higher ground. This suggests that the top of layer 11a might have been eroded prior to being covered.

Li-I: Odderade Interstadial to early Schalkholz Stadial

Within our record, the Odderade Interstadial is only detected in core PD.028 on account of higher accommodation space in the basin, south of the alluvial fan (Fig. 1, Supplementary Figure S49). However, the Odderade was also represented in the previously investigated core Veil 1, only about 10 m apart from core PD.028 (Veil et al., 1994). In both parallel cores, the Odderade peat occurs at the same depth, marking the ground water/lake level of that time. Vegetation was characterized by a dry boreal pine-birch forest with admixed spruce, juniper and larch. A rich but subordinate herbal flora indicates open stands nearby. Main peat formers were likely sedges and ferns. Following the Odderade, in the earliest Schalkholz Stadial, niveofluvial slope deposition started, triggered by annual snow melt in a sparsely vegetated landscape (Christiansen, 1998b, 1998a). The grain size data show a coarsening trend from fine-sandy, slightly silty and slightly humic deposits above the Odderade peat in core PD.028 to the fine/medium sandy sediments of layer 9 in both the core and the trenches, and finally to more gravelly layer 8. This coarsening possibly indicates a raise of base level caused by a rising lake level. In our trenches, these niveofluvial sediments (layers 9 and 8) form a relatively coherent unit, but in core PD.028 with larger accommodation space, they are interbedded with two organogenic and lacustrine deposits. These attest to a continuously rising water level, interrupted by longer spells of relative landscape stability that were induced by denser vegetation. Stability would have slowed down the lake level rise and niveofluvial slope wash alike, and allowed these lacustrine/organic-rich deposits to form. Therefore, we regard these to represent minor local interstadial oscillations (see section 5.2, Supplementary Section 7). The dominating vegetation type during both oscillations indicates an open, grass-rich habitat. Among the woody taxa, *Betula* (likely dwarf birch), juniper and heath species, such as *Calluna*, *Empetrum* and *Vaccinium* stand out. Because these minor interstadial oscillations have not yet been described for Northern Germany by palynological findings, no direct paleotemperature estimation exists. However, in the Alpine Foreland, based on a chironomid record at the site of Füramoos, summer temperatures between 9-11°C were reconstructed for the two-part Dürnten Interstadial, the latter correlated with GI 19 (Bolland et al., 2021). For Northern Germany, the pleniglacial Oerel Interstadial (WP II) shows a similar pollen spectrum to those oscillations in Lichtenberg, hence, the reconstructed mean summer and winter temperatures for Oerel (9°C and -17°C) might be a fair approximation (Walkling, 1997). In Lichtenberg, at the culmination of lake level rise after the Odderade, large parts of the study area were inundated and an organic-free, thin, muddy shoreface sediment was deposited (layer 7). This is only missing at the higher ground in the northern part of Trench 2, which was not flooded apparently. Direct pollen information is lacking in this lacustrine deposit, but the results of phytolith analysis provide evidence that the conditions of layer 7 resembled those of the cold-stage, sparsely-vegetated niveofluvial layers 8 and 9 (section 4.5, Supplementary Section 8). Neanderthal occupation of Li-I (layer 7 and top of layer 8) occurred after the upper minor interstadial oscillation in a severely cold environment, as is further proposed by the modelled annual mean temperature (Gamisch, 2019a, 2019b) displayed in Figure 8b. We suggest that the occupational surface was topmost layer 8 near the lake shoreline. The artefacts must have been smoothly embedded by the muddy shoreface sediments of layer 7 during lake level rise, leaving no distinct taphonomical marks on the lithic finds.

Comparing Li-II to Li-I: Human behavior in changing environments

The Lichtenberg find horizons represent two distinct site types, connected to different paleoenvironments and climatic conditions (Fig. 8b). Li-I and Li-II differ in raw material attributes and use, artefact size, as well as blank production, typology, and tool use.

Lichtenberg II has a high typological tool variability (Tab. 4, Fig. 4, Fig. 6). Edges with different functionalities on some artefacts (Supplementary Table S10) demonstrate that the tools often had several use-cycles. Further evidence for this recycling behavior comes from the cores and shattered pieces that were also recycled to tools. Traceology further suggests that the Li-II Neanderthals exploited the still richly-vegetated environment of late MIS 5c, and processed wood, plants, and other soft and hard organic material. All these assemblage characteristics indicate a longer and/ or repeated stay(s) at the lakeshore with a variety of domestic activities. Under these still temperate continental conditions at the lakeshore, we see the use of small and diverse raw material, what was possibly linked with the lack of accessible natural resources. We argue that relatively stable and densely vegetated landscape surfaces inhibited sediment erosion and favored weathering, and thus reduced the availability of fresh flint from the surrounding Saalian glacial deposits (Supplementary Section 3.4.4). Recycling and intensive tool use can also be related to this shortage of high-quality and large sized raw material. Faced with small and low-quality raw material in a forested landscape, Neanderthals at the site displayed an economic raw material management behavior. This may also explain the lack of more complex blank production techniques (e.g., Levallois, and/or discoidal methods), as the small-sized nodules in Li-II potentially did not allow for extensive core preparation (see for comparison Pop, 2014). Neanderthals mostly knapped small flint pieces a few times to obtain some larger flakes for further use, and/or to establish working edges on natural flint pieces. This behavior, as well as the small artefact size, the typological variety of tools and the recycling behavior are also known from the Eemian site of Neumark-Nord 2/2 (Pop, 2014), as well as from the subsequent MIS 5c or 5a (Richter and Krbetschek, 2014; Strahl et al., 2010) assemblage Neumark-Nord 2/0 (Laurat and Brühl, 2021, 2006). It seems that forested to semi-open landscapes (Pop and Bakels, 2015), temperate organic rich environments, as well as lakeshore areas with limited raw material availability, probably induced similar Neanderthal settlement behavior and resource management strategies on the northern European Plain between the Eemian and late MIS 5. However, besides paleoenvironmental triggers, we cannot rule out certain techno-cultural influences on the presence of typologically diverse small tool assemblages in Central Europe during the early last glacial, as these are also found in probably paleoenvironmentally slightly different, more southern regions of Central Europe. Examples are the lower layers of the Sesselfelsgrotte (Weißmüller, 1995), Bavaria/ Germany, and in layer 11 of the Kůlna Cave (Moncel and Neruda, 2000; Valoch, 1988), Czech Republic. Based on these typological similarities, Li-II fits well into early last-glacial technocomplexes of Central Europe.

In contrast to Li-II, the Li-I artefacts were exclusively manufactured on large, high quality flint pieces, such as frost shards that could be recovered in this area (Veil et al., 1994). This coincides with a sparsely-vegetated landscape, fostering sediment redeposition and providing freshly eroded flint from the Saalian glacial deposits (<100 m upslope). As suggested by former use-wear and techno-functional analyses (Veil et al., 1994; Weiss, 2020), the majority of Li-I tools served mainly for cutting soft tissue, potentially meat (Veil et al., 1994). This usage of Keilmesser as cutting tools confirmed by our traceological analyses of the Keilmesser Li-7 (Fig. 4: 1). Furthermore, we recently showed (Weiss, 2020) that the Li-I Keilmesser were mostly discarded shortly before the edge angle of the working edge exceeded 60° (Gladilin, 1976), in other words, when the Keilmesser subsequently lost their functionality as cutting tools. In general, the functional focus of the Li-I tools led to a relatively low typological diversity in the presence of scrapers, bifacial scrapers, handaxes and Keilmesser. Based on the lack of cores and primary blank production in the assemblage, artefact refits that evidence on-site tool production, and the use-wear traces related to butchering activities (Veil et al., 1994), we suggest a short-term occupation event at the lakeshore with a specialized objective, i.e., a hunting/ butchering stay.

Altogether, Li-I most probably represents a single, short-term event related to butchering activities in a harsh and cold environment. In contrast, Li-II is interpreted to result from repeated and probably longer stays at the lakeshore under still temperate continental climatic conditions, with a variety of activities that were carried out at this site.

5.4 Northern Neanderthals in the cold: occupations between MIS 5a and early MIS 3

From the last interglacial through to the end of MIS 5a/early MIS 4, the paleoenvironment of the European Plain gradually changed from temperate towards colder climatic conditions and open landscapes (Fig. 8b) (Caspers and Freund, 2001). The same trend is also documented in the sediment sequence of Lichtenberg (see above). Besides the subsequent replacement of the Eemian interglacial fauna by the mammoth fauna after the Eemian, we also expect to see a shift from a more local roaming behavior (Kindler et al., 2020) of the potential prey species to large herds with extended seasonal migration ranges. These changes and shifts in climate, paleoenvironment and the fauna coincided with a shift in the archaeological record of northern Central Europe. The early last-glacial small-tool assemblages such as those of Li-II gradually disappeared. On the other hand, we see that in the upper part of the lower layers in Sesselfelsgrotte or in Neumark-Nord 2/0 (Laurat and Brühl, 2021, 2006) bifacial tools, like Keilmesser start to appear in low frequencies. This transition ended during MIS 5a with the appearance of the late Middle Paleolithic Keilmessergruppen (Hein et al., 2020; Jöris, 2004; Mania, 1990) that persisted in northern and eastern Central Europe until the early MIS 3 (Fig. 8a) (Jöris, 2004; Richter, 2016; Weiss, 2015), and probably extended as far east as the Altai Mountains (Kolobova et al., 2020). Based on the short-term nature of their sites (Picin, 2016), land-use systems with scattered special task and ephemeral camps (Richter, 2016, 1997), as well as raw material transport over large distance in Central Europe (Féblot-Augustins, 1993), the Neanderthals of the Keilmessergruppen are interpreted as highly mobile groups. This is further expressed by the assumed mobile nature of the Keilmesser itself, enabling their long-term use and transport through special re-sharpening possibilities (Iovita, 2010; Jöris, 2012, 2004; Weiss, 2020). Our evidence for hafting the Li-I Keilmesser supports this interpretation of a tool concept with a long use-life.

As Keilmessergruppen Neanderthals of Li-I were present in the northern latitudes at the onset of the cold climatic MIS 4 (GS 19), we suggest that the increased residential and long-distance mobility inferred from the Keilmessergruppen assemblages is one aspect of Neanderthal behavioral adaptations to the cold climate and the related paleoenvironmental conditions. In contrast to this, although last interglacial Neanderthals are also interpreted as highly mobile, it was inferred from the archaeological and faunal assemblage of the Eemain site Neumark-

Nord 2/0 (Kindler et al., 2020) that their mobility must have been more local instead of travelling large distances.
As mentioned above, the site Salzgitter-Lebenstedt is another proof of Neanderthals living under cold climatic conditions, as the find layers contain remains of a cold climatic vegetation (Pastoors, 2001; Pfaffenberg, 1991; Selle, 1991). Furthermore, that sequence shows a succession from subarctic (find horizon) to arctic conditions (silts covering the find horizon) (Pfaffenberg, 1991; Selle, 1991), comparable to the sediment sequence of Li-I. Given our paleoenvironmental results and the age of Li-I, the formerly suggested MIS 5a/4 (Jöris, 2004) age for Salzgitter-Lebenstedt seems very plausible by analogy. This implies a repeated or continuous Keilmessergruppen Neanderthal occupation of cold climatic northern latitudes with specific adaptations to these environments, like e.g., seasonal hunting of migratory game herds, such as late summer/ early autumn reindeer hunting, as evidenced in Salzgitter-Lebenstedt (Gaudzinski, 1999, 1998). The latter suggests that late Neanderthals stayed at least until early autumn in northern regions of Central Europe. But even for that season, reconstructed summer temperatures of <9-11° C (Bolland et al., 2021; Walkling, 1997) for minor interstadial phases such as in Li-I or in Salzgitter-Lebenstedt (Pastoors, 2001) suggest cold summers in tundra-like landscapes, forming a challenging environment for Neanderthals. Further evidence of their successful adaptation to the cold climatic conditions of late MIS 5a, the onset of MIS 4, and early MIS 3 in northern Central Europe also comes from a large number of late Middle Paleolithic Keilmessergruppen sites and surface collections (Fig. 8a) that are aggregated along the river valleys and associated with sediments mainly dating to early MIS 3 (Mol, 1995; Weiss, 2015; Weiss et al., 2018; Winsemann et al., 2015). These assemblages, although only typologically attributed to the Keilmessergruppen, show that Lichtenberg is not the northernmost limit of the Neanderthal habitat (Nielsen et al., 2017), as late Middle Paleolithic sites, such as Ochtmissen (Thieme, 2003), Lower Saxony/ Germany and Drelsdorf (Hartz et al., 2012), Schleswig-Holstein/ Germany are located even further north (Fig. 8a).

Currently, we are missing direct evidence for Neanderthal occupations of northern Central Europe during the peak of MIS 4. Whereas some authors suggest that Neanderthals migrated south (Jöris, 2004) during that period, others even consider local extinctions of Neanderthal groups (Hublin and Roebroeks, 2009). However, the Keilmesser tools show technological continuity that connects MIS 5a with early MIS 3 assemblages (Fig. 8c). This is demonstrated in the assemblages of Königsaue A and C (MIS 5a (Jöris, 2004; Mania, 2002; Mania and Toepfer, 1973)), Salzgitter-Lebenstedt (MIS 5a/4 or MIS 4/3 (Jöris, 2004; Pastoors, 2009, 2001)), and Pouch, Saxony-Anhalt/ Germany (MIS 3 (Weiss, 2015; Weiss et al., 2018)), where the Keilmesser share the main technological and morphological features with those from Lichtenberg (Weiss, 2020) (Fig. 8c). Furthermore, some of the MIS 3 Keilmesser from the G-Complex of the Sesselfelsgrotte (Richter, 2002, 1997) also show morpho-technological similarities to those from Lichtenberg (Delpiano and Uthmeier, 2020), potentially indicating seasonal, migrations to southern regions of Central Europe during the late Middle Paleolithic. Altogether, the techno-typological continuity of late Neanderthal assemblages in northern Central Europe between MIS 5a and MIS 3, as well as the successful adaptation to cold environments, favor the hypothesis of seasonal migrations during cold periods instead of local extinctions.

In summary, Li-I proves the presence of Neanderthals in the north during cold, stadial climatic conditions. This assemblage represents a short-term butchering stay associated with the central and eastern European Keilmessergruppen. We suggest that Neanderthals populated the north intensively until early MIS 3, and adapted their life ways to the regional cold climatic conditions.

6. Conclusion

(1) In Lichtenberg, we have established a high-resolution chronological framework based on the luminescence dating results as well as sedimentological, paleoenvironmental, and archaeological analyses. This allowed us to connect the northern Neanderthal occupations to climatically different phases of the last interglacial-glacial cycle, with a chronological resolution close to the millennial scale of Greenland Interstadials/Stadials (section 5.2).

(2) The chronostratigraphic results led to a revision of the timing for the occupation Li-I in Lichtenberg. We obtained consistent ages for this find layer with a mean of 71.3 ± 7.3 ka replacing the former mean age of 57 ± 6 ka, which was likely rejuvenated by post-depositional cryoturbation. Our new age complies with the stratigraphic and paleoenvironmental findings and is therefore considered robust and reliable.

(3) By reporting the age for the occupation Li-II (mean of 90.5 ± 8.7 ka), we also present the first independent ages of the latest Brörup Interstadial WE IIb in its type region in northern Central Europe. The age suggests that the terminations of the continental Brörup and MIS 5c broadly coincide (section 5.1). This is valuable information for numerous paleoenvironmental and archaeological sites in the area, where the chronologies rely on biostratigraphical evidence alone.

(4) The high-resolution chronological framework enabled us to show that Neanderthals inhabited the northern regions of central Europe during the Eemian, the early last glacial interstadials, as well as during the onset of the first glacial maximum. We conclude, they lived in changing environments: a wooded landscape during the Eemian pollen zone E IVb/V, a boreal landscape opening up during late MIS 5c and a dry tundra-like environment during earliest MIS 4.

(5) The changing archaeological record tentatively implies resilient adaptations to changing environments. These are inferred from different raw material availabilities and resulting management strategies, as well as a high-typological tool diversity in Li-II versus specialized cutting tools and a potentially highly-mobile tool kit in Li-I. This is supported by the use-wear analysis that demonstrated a variety of tasks in Li-II in contrast to potentially specialized cutting tasks in Li-I only. Furthermore, raw material availability can also be explained by geomorphic factors. Sediment redeposition, which provided high-quality and large flint raw material from the primary source of the glacial sediments nearby was hindered in the forested intervals (Li-II and the Eemian occupation) and fostered in the much more sparsely-vegetated phases (Li-I). Future work is planned to evaluate our preliminary results.

(6) Most importantly, we could show that Neanderthals occupied the northern regions of central Europe also during the cold phases of the last Glacial (section 5.5). Similarities in the archaeological record, especially the technological similarities of Keilmesser manufacture (see above) between Li-I and the posterior early MIS 3 sites further suggest the potential recurrence of populations in the region. That Neanderthals successfully adapted to the harsh northern climatic conditions is corroborated by the fact that early MIS 3 sites are by far the most numerous Middle Paleolithic sites in the North.

Figures

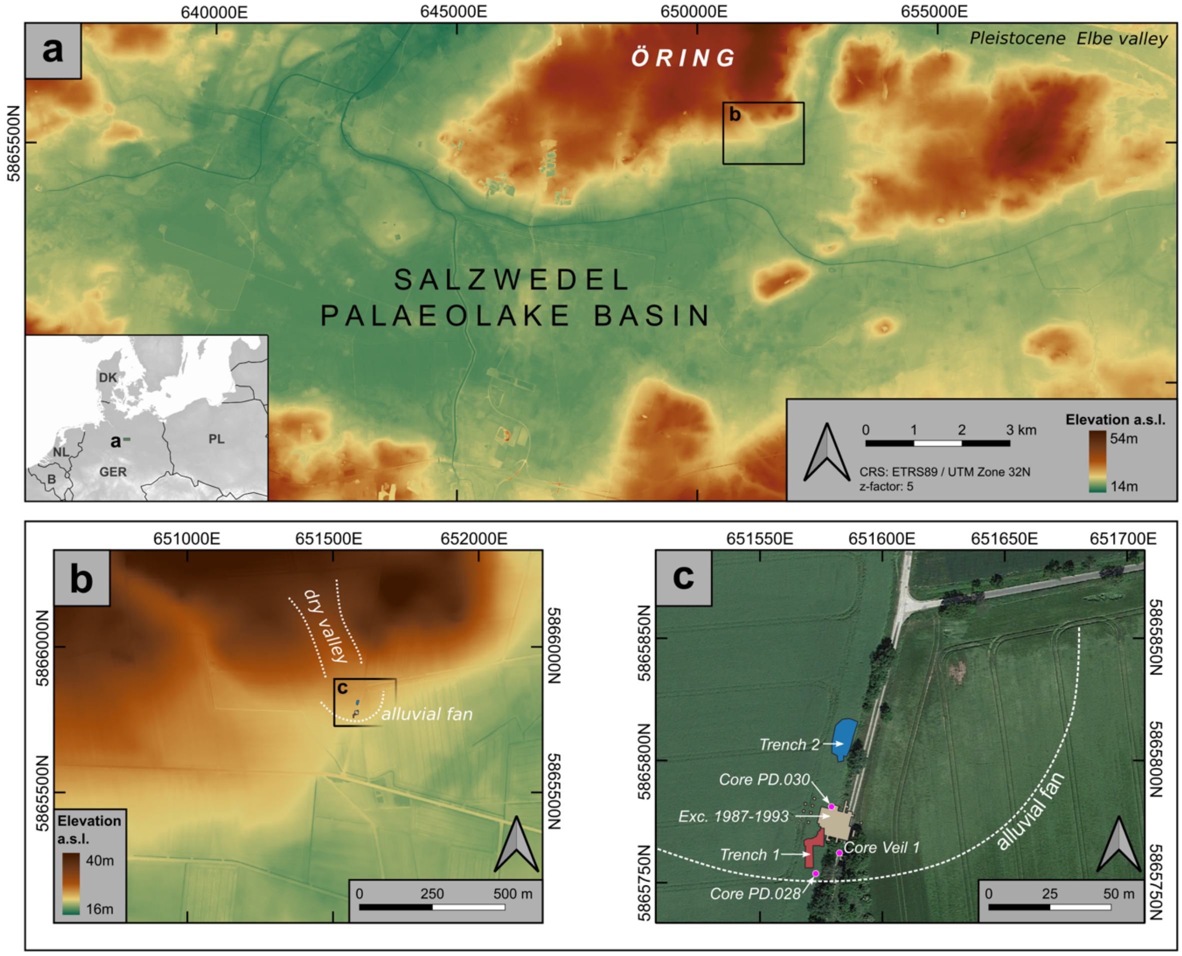


Figure 1: Location of the study area in Northern Germany (a). The sites are situated on a small alluvial fan surrounded by lowlands (b). Panel c indicates the position of the archaeological trenches 1 and 2, the previous excavation area (1987-1993) and three sediment cores mentioned in the text (PD.028, PD.030, Veil 1). Digital elevation model (DEM 1) provided by the State Offices for Geoinformation and Land Survey in Lower Saxony and Saxony-Anhalt.

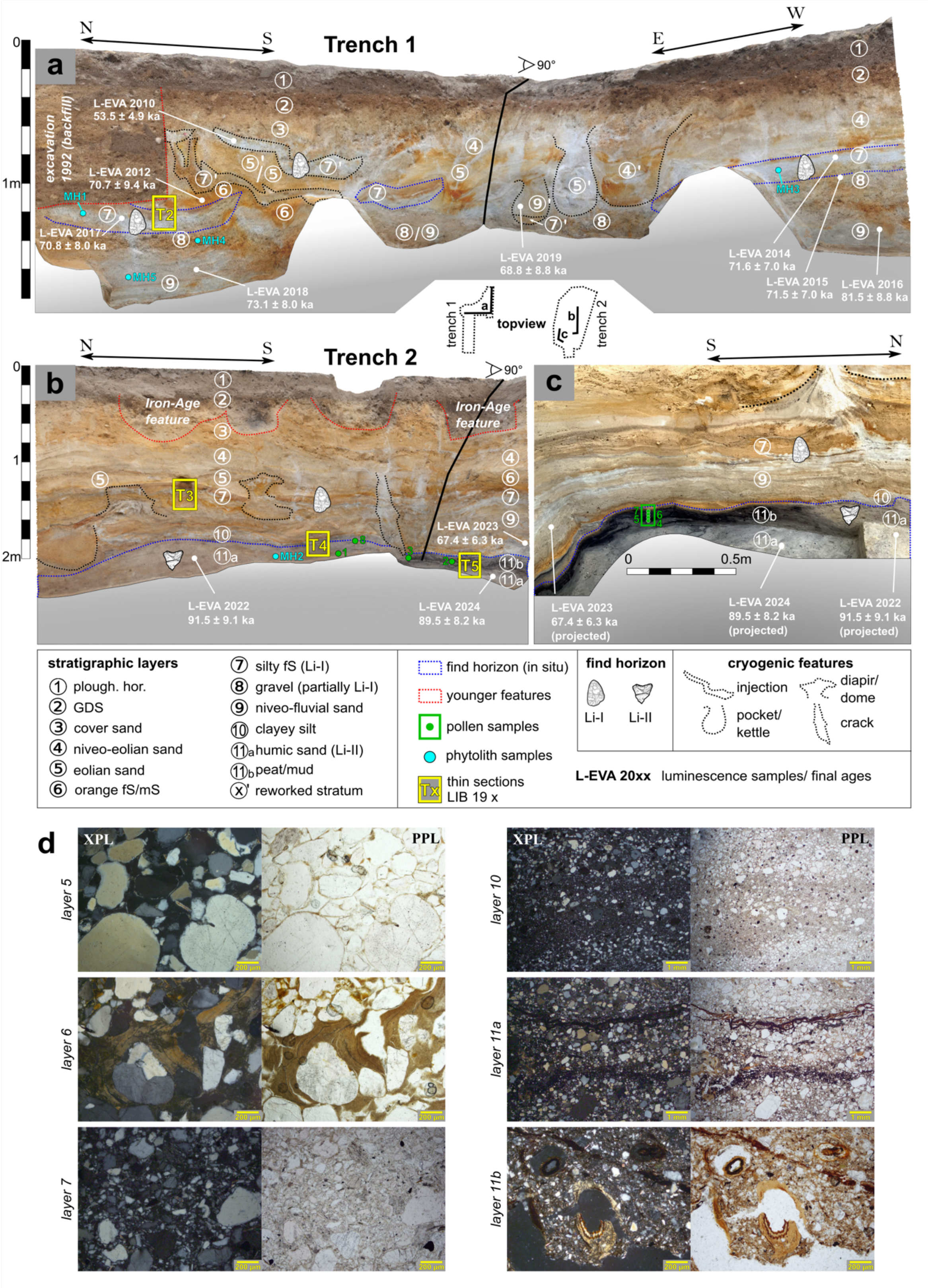


Figure 2: Stratigraphic features and archaeological horizons, along with sampling positions for luminescence dating, pollen analysis and micromorphology in Trench 1 (a) and Trench 2 (b and c). GDS refers to "Geschiebedecksand" a late Weichselian solifluction layer (Tab. 1, Supplementary Section 5.1). (d) Microphotographs of thin sections in cross-polarized (XPL) and plane-polarized (PPL) light. Photograph of layer 5 taken from sample T3, layer 6 from T1,

layer 7 from T2, layers 10 and 11a from T4 and layer 11b from T5. Layer 5 is dominantly composed of coarse sand to silty quartz grains in a massive microstructure; layer 5 shows the same composition as layer 6, but here void space is filled by clay illuviation; layer 7 shows a poor sorting for fine sand to silt sized quartz grains in a dense microstructure that presents a barrier for the clay moving down with pore water; layer 10 shows bedding of silty to coarse-sand sized quartz; layer 11a is characterized by organic-rich bands composed of amorphous staining, plant cells and tissues with rare bioturbation voids; in layer 11b organic residues increase in size as well as number and bioturbation voids are more ubiquitous.

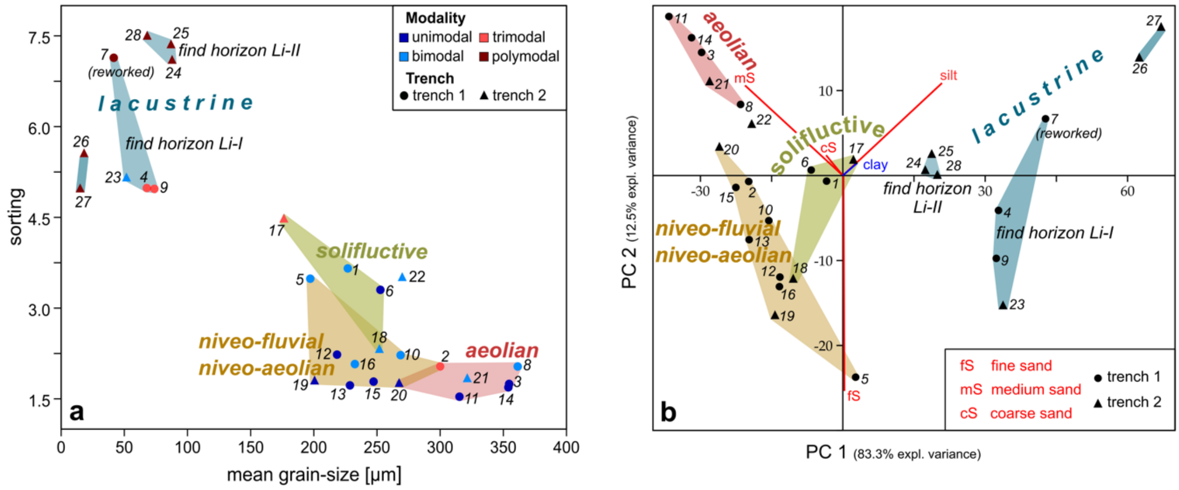


Figure 3: Statistical analyses of grain size results. (a) Scatter plot of sorting and mean grain size. (b) Principle component analysis (PCA) with the most significant principle components (PC1 and PC2) shown. Convex hulls of sedimentary processes according to classification during field description. Stratigraphic layers related to the sample codes indicated in Tab. 1.

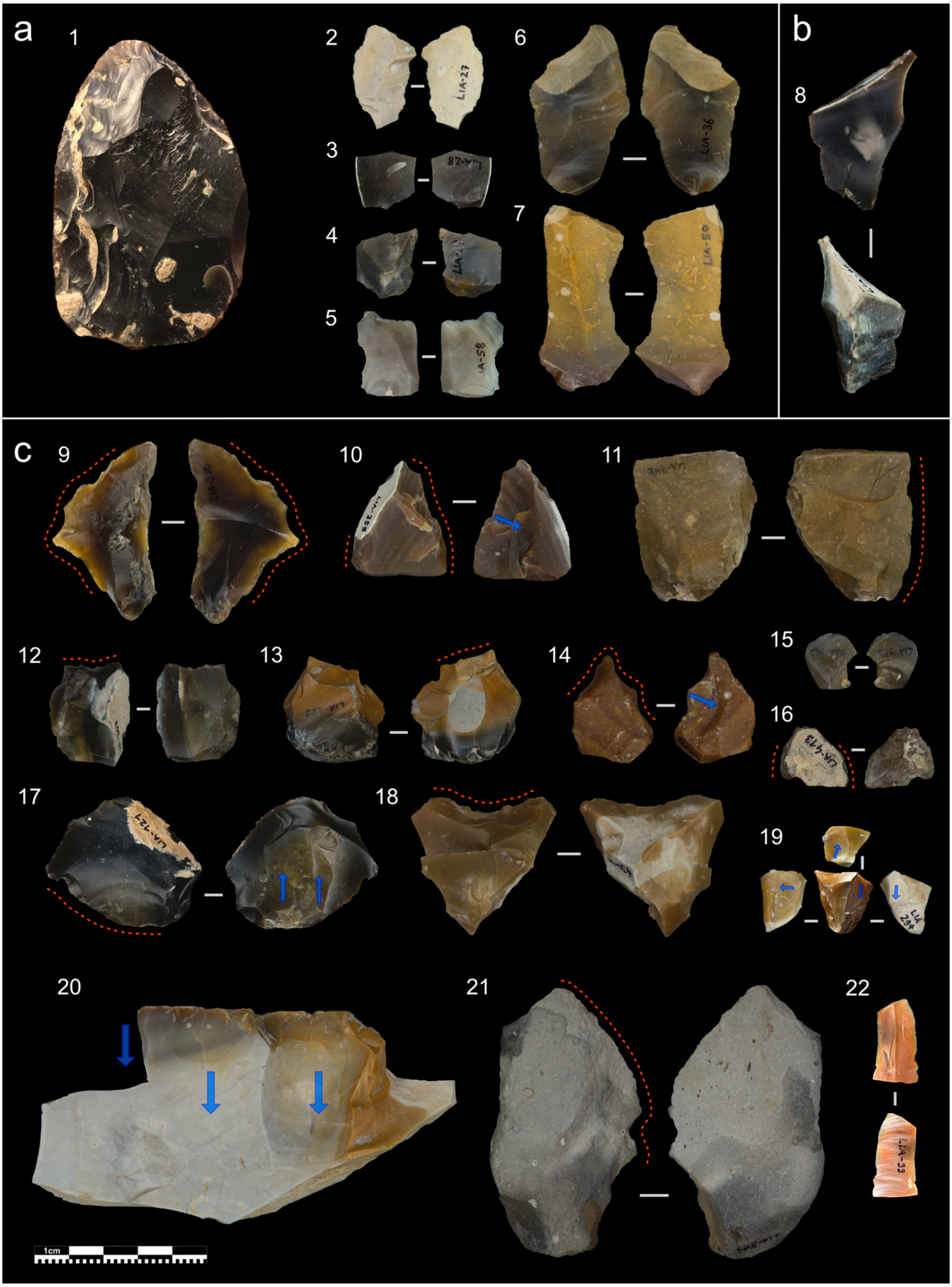


Figure 4: Artefacts from Lichtenberg I (a), (b) and II (c) discovered in Trench 1 (a) and Trench 2 (b), (c). (a) 1 – Keilmesser (Li-7; Layer 7'); 2 – flake (LIA-27; Layer 7); 3 – proximal flake (LIA-28; Layer 7); 4 – flake (LIA-29; Layer 7); 5 – flake (LIA-58; Layer 8); 6 – flake from bifacial tool production (LIA-36; Layer 7); 7 – flake (LIA-50; Layer 8); (b) 8 – flake (LIA-74; Layer 7); (c) (all Layer 11a): 9 – flake with heavy macroscopic use-wear (LIA-550); 10 – scraper with ventral surface removal and thermal alteration (LIA-359); 11 – backed knife with macroscopic use-

wear (LIA-342); 12 – endscraper on thick flake (LIA-307); 13 – endscraper on thick flake (LIA-285); 14 – denticulate on thick flake with dorsal surface removal (LIA-377); 15 – small flake with fresh, sharp edged preservation (LIA-330); 16 – distal scraper fragment with thermal alteration (LIA-413); 17 – flake with macroscopic use-wear and with ventral surface removals (LIA-121); 18 – complex notch on core (LIA-154); 19 – small irregular core (LIA-294); 20 – large core on low quality raw material with internal cracks (LIA-335); 21 – flake tool with notch and sharp edge on large quartzite flake (LIA-504); 22 – medial blade fragment (LIA-99). Red dotted lines mark macroscopic working edges, blue arrows mark larger surface removals and removals on cores. Photos: MPI EVA.

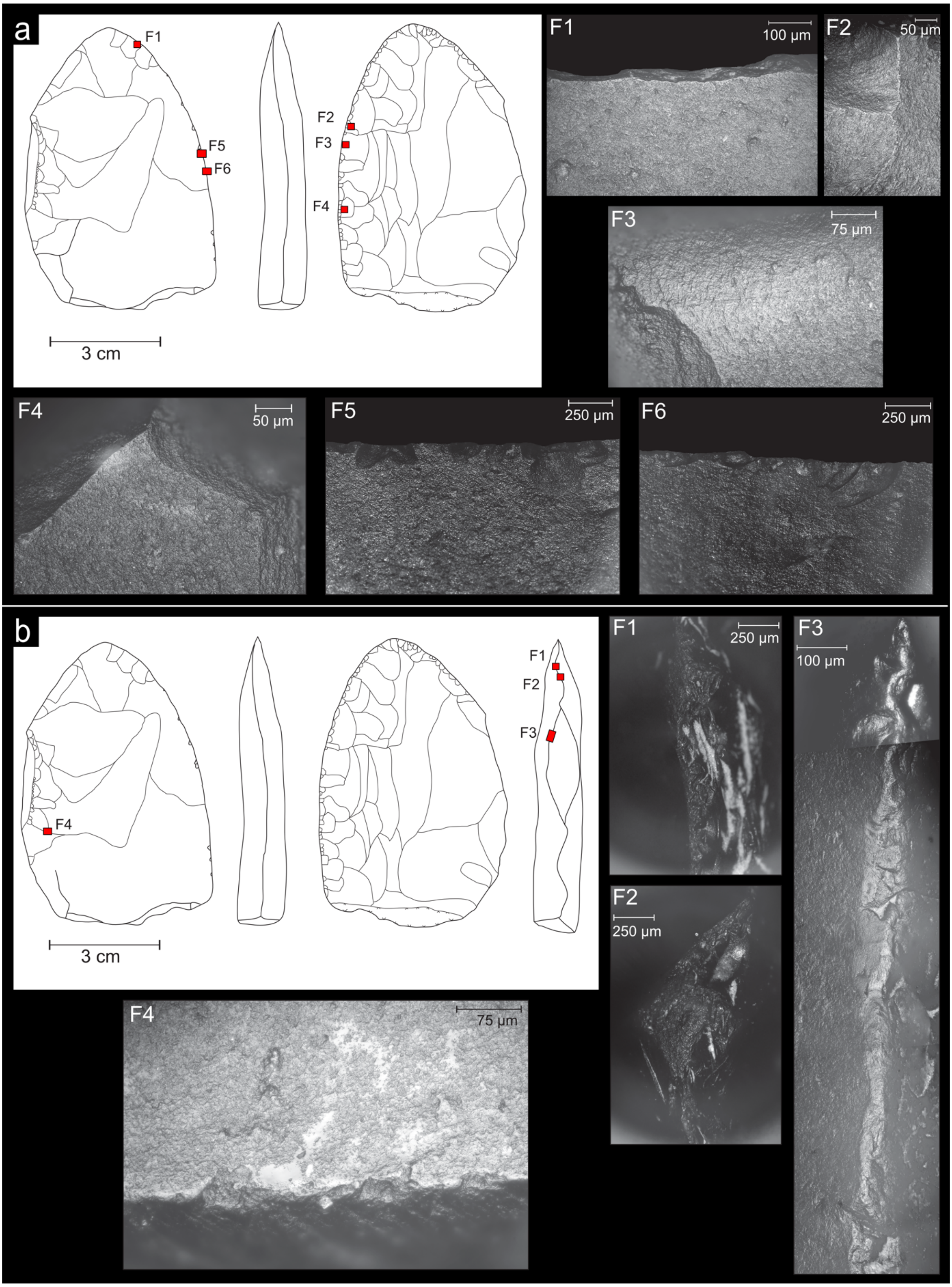
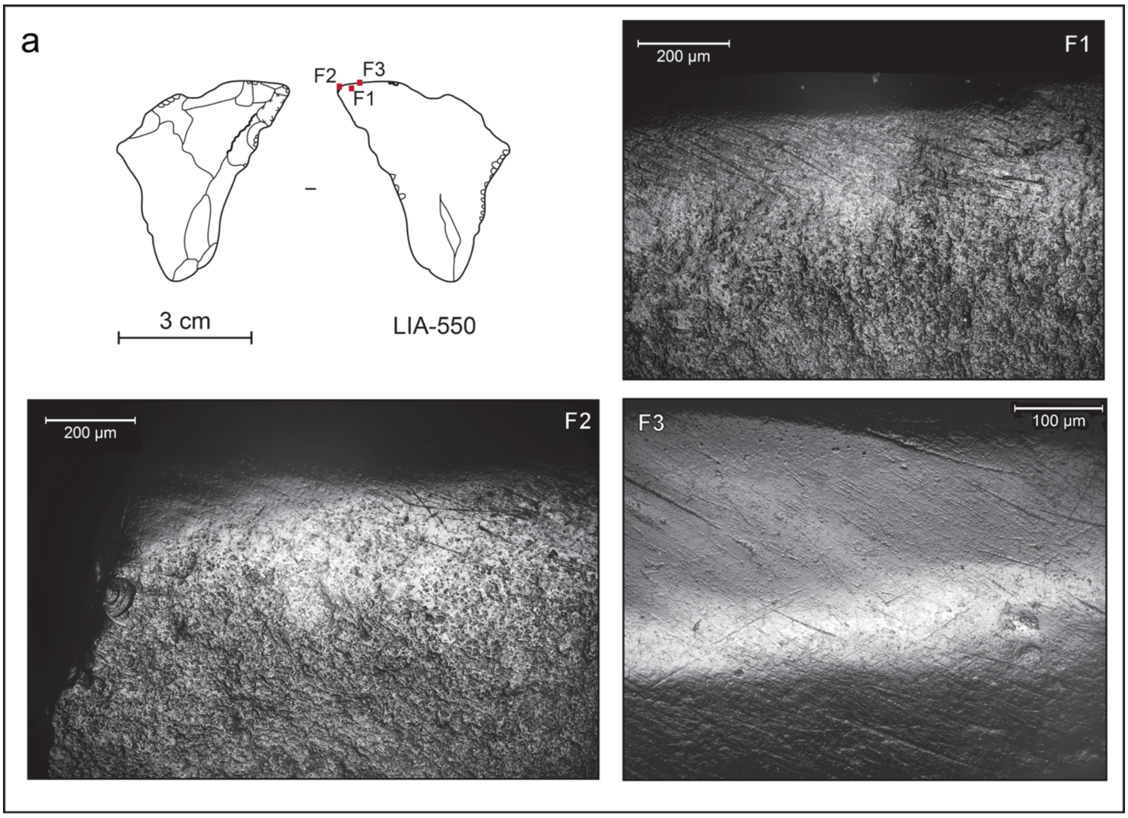


Figure 5: Results of the traceology for the Keilmesser Li-7. (a) Use-wear traces along the working edge. F1 - taken at magnification 200x, micrograph of the light developed bright polish on the edge of the active zone of the tool; F2 - taken at magnification 200x, micrograph showing the rounded and polished edges of the negatives on the dorsal surface of the working edge; F3 and F4 – both taken at magnification 200x, micrographs of the striations on the interior of the dorsal side of the tools' working edge; F5 and F6 – both taken at magnification

50x, micrographs of the micro-negatives on the ventral surface of the working edge. (b) Traces on the prehensile/hafting zone of the Keilmesser Li-7. F1 and F2 - both taken at magnification 50x, crushed and abraded edges on the back of the tool; F3 - taken at magnification 200x, composed micrograph images showing the undulating bright and well interconnected polish on the edge of the negative forming the back of the Keilmesser; F4 - taken at magnification 200x, bright undulating G type polish on the ventral surface of the tool. Drawings and photographs: Y. H. Hilbert.


a
F2
F3
F1
3 cm
LIA-550
200 µm
F1
200 µm
F2
F3
100 µm

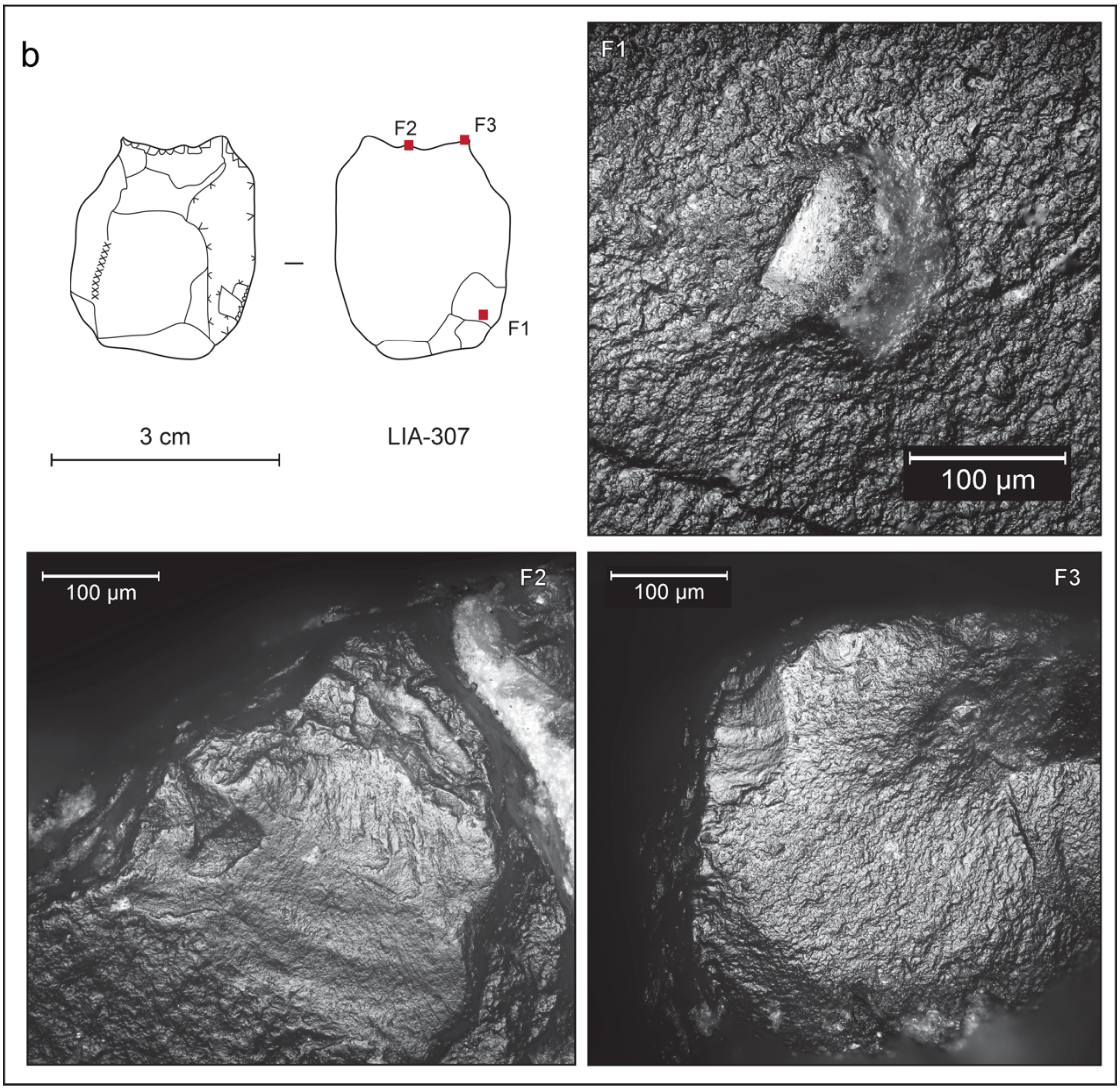

b
F2
F3
F1
3 cm
LIA-307
F1
100 µm
100 µm
F2
100 µm
F3

Figure 6: Results of the traceology for the Lichtenberg II assemblage. (a) Schema of artefact LIA-550 and the location of the micrographs showing the use related polish. F1 – taken at magnification 100x, bright undulating extensive polish located on the distal portion of the working edge; F2 – taken at magnification 100x on the edge of the working surface showing the spread of the bright undulating extensive polish, note the high incidence of striations and scratches; F3 – taken at magnification 200x at the center of the maximum extension of the micro polished surface on the working edge of the tool. The spread and connectedness of the polish is very high and the surface is extremely smoothened, again the criss-cross patterned motion of tool use is particularly evident by the striations and scratches. The resemblance to cereal polish is remarkable. Worked material: soft vegetal/ hard organic. (b) Schema of artefact LIA-307 and the location of the micrographs showing use and hafting related polish. F1 – flat bright polish located on the eminence of the micro topography on the ventral surface of the tool; F2 and F3 – negative edge rounding and bright undulating extensive polish on concave working surface. All micrographs taken at 200x. Worked material: hard organic/ wood. Drawings and photographs: Y. H. Hilbert.

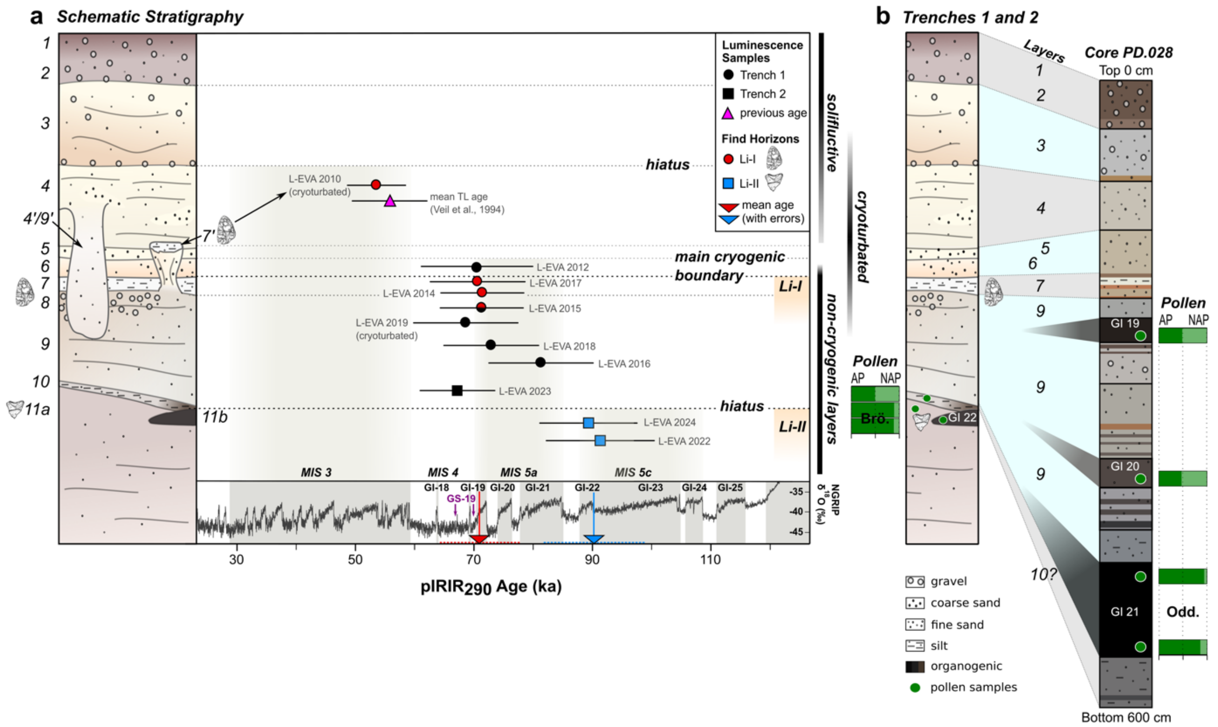


Figure 7: (a) Schematic stratigraphic column of Trenches 1 and 2 and luminescence dating results (1σ error); position of the find horizon is highlighted and indicated by a representative artefact symbol. On the x-axis, the time line and the NGRIP $\delta^{18}O$ Greenland temperature proxy is provided (NGRIP Members, 2004). (b) Correlation of the schematic stratigraphy of the trenches with sediment core PD.028 (location in Fig. 1) and simplified results of palynological analysis. AP = arboreal pollen, NAP = non-arboreal pollen.

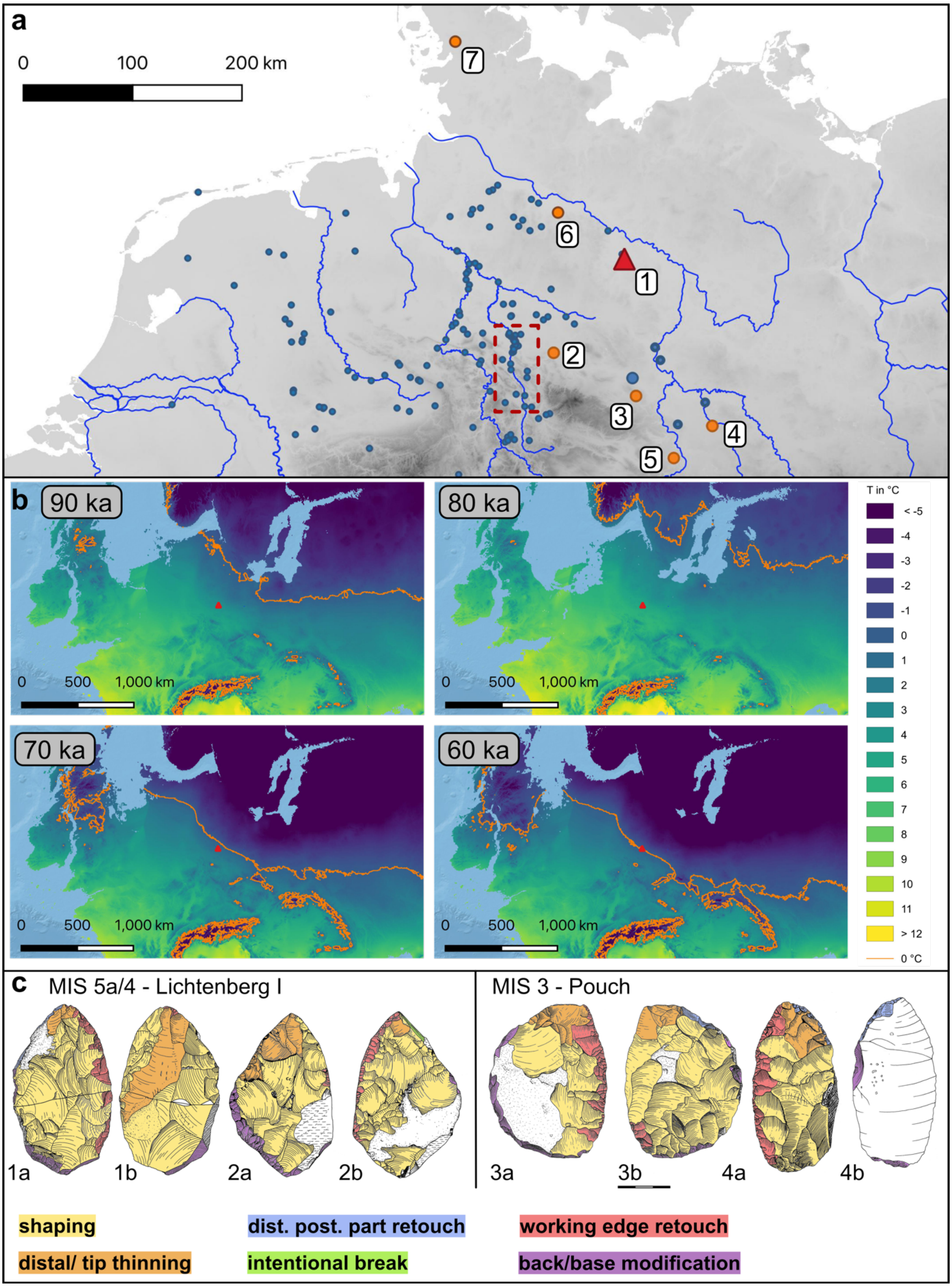


Figure 8: Distribution of late Middle Paleolithic sites in the study area (a), mean annual temperature change between 90 ka and 60 ka (b), and Keilmesser technology (c). (a) Displayed are the late Middle Paleolithic sites documented in the database of the State Service for Cultural Heritage Lower Saxony, Hannover, Germany. Most of them are surface collections. To make sure that they date between MIS 5a and MIS 3, only collections that include Keilmesser, Handaxes, and sometimes leafpoints as late Middle Paleolithic type

fossils were selected. Sites located in the rectangle were collected from a river terrace of the Leine Valley that was dated to early MIS 3 (Winsemann et al., 2015). 1 – 6 are sites mentioned in the text: 1 – Lichtenberg; 2 – Salzgitter-Lebenstedt; 3 – Königsaue; 4 – Pouch; 5 – Neumark-Nord; 6 – Ochtmissen; 7 – Drelsdorf. The map is based on SRTM data V4 (http://srtm.csi.cgiar.org) (Jarvis et al., 2008; Reuter et al., 2007) and was generated in QGIS v3.12. (b) Change of the mean annual temperature with focus on northern central Europe. Red triangle: Lichtenberg; orange line: 0 °C isotherm. The map was created with the oscillayers dataset (https://doi.org/10.5061/dryad.27f8s90) (Gamisch, 2019a, 2019b) and generated in QGIS v3.12. (c) Technological comparison of Keilmesser from the MIS 5a/4 transition (Lichtenberg) and early MIS 3 (Pouch). The Keilmesser from both sites can be classified as type Lichtenberg. They show the same shaping technology, and moreover the Keilmesser from both sites are highly comparable regarding overall morphology, working edge morphology and treatment, as well as edge angle configurations (Weiss, 2020).

Layer	Pre-sence	Thickn. (cm)	Sediment Description	Interpretation	Grain Size Sample
1	Tr1, Tr2	< 40	Gravelly, slightly silty sand; very poorly sorted; humic (ca. 2%), related to layer 2	**ploughing horizon** formed in layer 2	**–**
2	Tr1, Tr2	< 25	Gravelly, slightly silty sand; very poorly sorted; coincides with brunified horizon (Cambisol); unbedded; higher gravel content than in layer 3	periglacial cover bed, 'Geschiebedecksand' **(GDS)**	**1, 17**
3	Tr1, Tr2	50	Slightly gravelly and silty, poorly sorted, yellow medium sand; weakly-bedded; stoneline at its lower boundary	**cover sand**, solifluctive/colluvial facies	**6, 18**
4	Tr1, Tr2	50	Thin-bedded, wavy, moderately to poorly sorted, fine to medium sands; pale yellow; interbedded with thicker lenses of better sorted (aeolian) medium sands which are similar to layer 5	**niveofluvial** to **niveo-aeolian** facies, partially reworking layer 5 (?)	**2, 19, 20,**
4'	Tr1	pocket	Original structure of layer 4 recognisable, but deformed and slightly mixed within a pocket (ca. 50 cm deep); hydromorphic overprint	**cryoturbation pocket** affecting layer 4	**13, 15**
5	Tr1, Tr2	10/30	Very loose, yellow medium sand, better sorted than surrounding layers; inclined bedding to sheet-like (unbedded)	**aeolian sand** (saltation)	**3, 8, 11, 21**
5'	Tr1 (Tr2)	various	Similar characteristics as layer 5 but with cryogenic overprint (injections or pockets)	**cryoturbation** affecting layer 5	**14**
6	Tr1, Tr2	20	Poorly to moderately sorted, fine to medium sands, orange oxidation color; unbedded	no interpretation (may belong to adjacent layers)	**22**
7 Li-I	Tr1, Tr2	< 15	Fine sandy very coarse silt to silty very fine sands; whitish, brown-orange ferrugination on top with drop-shaped boundary on mm to cm-scale; very poorly sorted; contains **find horizon Li-I**	lacustrine **shoreline facies**	**4, 9, 23**
7' Li-I	Tr1 (Tr2)	10/20	Main characteristics similar to layer 7; distorted; mixing with medium sand; contains artefacts of **find horizon Li-I**	layer 7 injected upwards by **cryoturbation**	**7**
8	Tr1	20/40	Fine to medium gravelly, medium sands; poorly sorted; gleyic (greyish-light br.), crudely bedded, contains lithic artefacts in the upper 5 cm (lower part of **find horizon Li-I**)	higher-energy **niveofluvia**l **slopewash**	**–**
9	Tr1, Tr2	40/> 100	Thin-bedded, wavy, moderately to poorly sorted fine to medium sands; gleyic (greyish-light brown)	**niveofluvial slopewash**	**5, 10, 12**
9'	Tr1	pocket	Gleyic, poorly sorted fine sand, characteristics of layer 9 discernable, even weak wavy bedding	**cryoturbation pocket** affecting layer 9	**16**
10	Tr2	< 10	Gleyic, fine sandy to loamy silt; covers layer 11b as a thin veneer; contains very thin humic bed (drift line)	**lacustrine facies**, with contained **drift line**	**26, 27, (28)**
11a Li-II	Tr2	> 100	Very coarse-silty fine sand, slightly humic (<0.5%); very poorly sorted; unbedded; contains **find horizon Li-II** and abundant small pieces of charred organic matter (both esp. in the uppermost 11 cm)	**colluvial to lacustrine** shoreline/**beach** facies, contains drift lines	**24, 25, (28)**
11b (Li-II)	Tr2	< 20	Peaty organic mud, interfingering with layer 11a, contains some artefacts at the lower boundary (**find horizon Li-II**); in places overlain by thin (<1 cm) grey silt (part of layer 10?)	lake moor near the shoreline	**–**

Table 1: Sedimentary properties of the stratigraphic layers, including their interpretation (cf. Supplementary Section 5) and the sample codes for grain size analysis. Grain size samples taken layer-wise: samples 1-16 from Trench 1, samples 17 to 28 from Trench 2. The column "presence" indicates in which trench the respective layer occurs, Trench 1, Trench 2 or both (Tr1, Tr2).

Lab.-ID (L-EVA)	Layer	D_e (Gy), 1σ	DR_{total} (Gy/ka)	Age (ka), 1σ	OD (%)	No. al.	Dose Model[1]
2010	7'– **Li-I**	131.9 ± 4.3	2.46 ± 0.21	53.5 ± 4.9	14.7 ± 0.4	24	MAM
2012	6	110.7 ± 4.3	1.57 ± 0.20	70.7 ± 9.4	16.0 ± 0.5	24	MAM
2014	7 – **Li-I**	160.8 ± 3.8	2.25 ± 0.21	71.6 ± 7.0	11.3 ± 0.4	23	MAM
2015	8 – **Li-I**	174.8 ± 7.5	2.44 ± 0.21	71.5 ± 7.0	19.4 ± 0.6	24	CAM
2016	9	163.3 ± 5.0	2.00 ± 0.21	81.5 ± 8.8	11.8 ± 0.5	17	MAM
2017	7 – **Li-I**	143.9 ± 8.2	2.03 ± 0.20	70.8 ± 8.0	21.4 ± 0.6	24	MAM
2018	9	137.3 ± 3.4	1.88 ± 0.20	73.1 ± 8.0	11.7 ± 0.4	24	CAM
2019	9'	112.4 ± 3.4	1.63 ± 0.20	68.8 ± 8.8	13.9 ± 0.4	24	CAM
2022	11 – **Li-**	254.7 ± 16.7	2.78 ± 0.21	91.5 ± 9.1	29.4 ± 1.0	21	CAM
2023	9	155.0 ± 4.8	2.30 ± 0.20	67.4 ± 6.3	14.7 ± 0.5	24	CAM
2024	11 – **Li-**	241.1 ± 12.7	2.69 ± 0.20	89.5 ± 8.2	20.9 ± 0.7	22	WM

Table 2: Results of the De-measurements along with the final $pIRIR_{290}$ luminescence ages. OD = Overdispersion value. No.al = Number of aliquots included in the age calculations. CAM = Central Age Model, MAM = Minimum Age Model, WM = Weighted Mean. [1]σb value of 0.11 was used for MAM. The choice of age model is explained in Supplementary Section 6.3

Trench 2, excavation 2019		***Trench 2, excavation 2020***		***Core PD.028***			
Layer (Sample)	**Vegetation**	**Layer (Sample)**	**Vegetation**	**Layer (Sample)**	**Vegetation**	**Biostratigraphy**	**MIS**
n.r. n.r.	- -	n.r. n.r.	- -	peaty mud (12) hum. sand (11)	open landscape with dominant NAP (Poacea and heliophile herbs), *Pediastrum*	two minor interstadial oscillations in the **earliest Schalkholz (WP I)**	**4**
n.r.	-	n.r.	-	Peat (9, 10)	dense boreal forest with *Pinus*, *Betula*, *Juniperus* and *Larix*	**Late Odderade Interstadial WE IV b**	**5a**
10 (8)	*Betula*, very few *Pinus,* Poaceae, heliophyte-rich open vegetation, micro-charcoal peak	11b (7)	*Betula*, very few *Pinus,* Poaceae, heliophyte-rich (*Ophioglossum*) open vegetation, micro-charcoal peak	n.r.	-	**Early Rederstall Stadial WE III**	**5b**
n.r.	n.r.	11b (6) 11b (5)	Decrease of *Pinus*, increase of *Betula* and heliophytes	n.r.	-	Transition of **WE II b to WE III**	**5c/5b**
$11b_2$ (3) 11b (2) 11a (1)	Boreal forest opening up; *Pinus*, *Betula*, *Juniperus*, very few *Picea*, *Alnus* and *Larix*; Poaceae; *Selaginella selaginoides*, *Ophioglossum*, *Botrychium*	11b (4)	Boreal forest opening up; *Pinus*, *Betula*, *Juniperus*, very few *Picea*, *Alnus* and *Larix*; Poaceae; *Selaginella selaginoides*, *Ophioglossum*, *Botrychium*	n.r.	-	**Late Brörup Interstadial WE II b** **find horizon Li-II**	**MIS 5c**

Table 3: Comparison and correlation of pollen samples 1 to 8, taken from layer 11 and 10, trench 2 (2019 and 2020 excavations) and samples 9 to 12 (core PD.028). Biostratigraphic assignment follows Menke and Tynni (1984); Behre and Lade (1986). For sampling codes and positions, see Fig 2b/c, Supplementary Figure S59. n.r. = not resolved. Correlation with Marine Isotope Stages (MIS) follows Lisiecki and Raymo (2005) and the lithostratigraphic

lexicon LITHOLEX of the German Federal Institute for Geosciences and Natural Resources, BGR (https://litholex.bgr.de).

tool type	number	percent	example
backed knife	1	2%	Fig. 4: 11
denticulate	3	6.3%	Fig. 4: 14
(limited) edge retouch	8	16.7%	Supplementary Figure S39
endscraper	8	16.7%	Fig. 4: 12, 13
endscraper, reused as hammerstone	1	2%	-
endscraper-scraper	1	2%	-
hammerstone	3	6.3%	Supplementary Figure S38
naturally backed knife	1	2%	Supplementary Figure S40
notch	11	22.9%	Fig. 4: 18, 21
scraper	2	4.2%	Fig. 4: 10, 16
flakes with possible use-wear	9	18.8%	Fig. 4: 9, 17
not identifyable	1	-	-
total	**49**	**100%**	-

Table 4: Tool types Lichtenberg II.

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Author Contributions

All authors made substantial contributions to the study and approved the final manuscript. M.H. and M.W. equally contributed to the study with respect to research design, fieldwork, data analyses, interpretation of data and the writing of the manuscript. They actively took part in the different analyses listed below and amalgamated the various data. B.U. and M.T. conducted palynological analysis; M.C.S. and S.H. conducted micromorphological analysis; Y.H.H. performed traceology on the artefacts; R.C.P. did phytolith analysis; H. v.S. co-supervised M.H. s doctoral thesis and supported fieldwork; T.T., U.B., F.K. provided additional archaeological data of the region and supported fieldwork; S.V. and K.B. discovered and excavated the original site; J.S. supported grain size analysis; D.C. supported luminescence dating; D.C.T. and M.F. provided methodological and geological information; T.L. supervised M.H. s doctoral thesis, contributed to the research design and supported luminescence dating. All authors contributed to the preparation of the manuscript.