

THE REMAINS OF THE EUROPEAN SABRE-TOOTHED CAT (*HOMOTHERIUM LATIDENS*) FOUND IN THE SPEAR HORIZON AT SCHÖNINGEN (GERMANY)

In the last 25 years, over 20 000 fossil animal remains were recovered at the Palaeolithic sites of Schöningen (Lkr. Helmstedt/D) and analysed by various researchers (van Asperen 2004; Voormolen 2008; van Kolfschoten 2014; van Kolfschoten/Buhrs/Verheijen 2015; van Kolfschoten et al. 2015; Starkovich/Conard 2015). The mammalian faunal assemblages include not only species that are common during the late Middle Pleistocene, but also species that are rare, for example the giant beaver (*Trogotherium cuvieri*) (Heinrich/van Kolfschoten 2007) and the water buffalo (*Bubalus murrensis*) (Serangeli et al. 2015a). Here we report the remains of another rare species, the European sabre-toothed cat, *Homotherium latidens* (Owen, 1846), found at the Schö 13II site (figs 1-2). In the preliminary description (Serangeli et al. 2015b), two individuals of *Homotherium* were described from the Spear Horizon site (layer Schö 13II-4a-4b/c) in Schöningen. A third individual, represented by eleven cranial fragments, was recently discovered in layer Schö 13II-4e, stratigraphically situated over 1 m below the level of the other *Homotherium* finds.

With an approximate age of 300 000-320 000, the three individuals from Schöningen are among the youngest remains of *Homotherium latidens* with clear stratigraphic provenance and in an archaeological context. The context, together with hominin modifications present on one of the humeri, confirms that Middle Pleistocene hominins shared their environment with the sabre-toothed cat. The presence of sabre-toothed cats certainly had an impact on Lower Palaeolithic hominin daily subsistence and behaviour.

HOMOTHERIUM LATIDENS

Homotherium was a wide-spread member of the Pliocene-Early Pleistocene carnivore guild of Africa, Eurasia and the Americas; the genus was only absent in Australia/Oceania and on the Antarctic continent (Rincón/Prevosti/Parra 2011). Its wide distribution indicates adaptation to various climatic zones and environments. However, several authors consider open landscapes as the typical habitat of members of the genus *Homotherium* (Antón 2013; Naples/Martin/Bibiarz 2011).

Some authors (e.g. Ficarelli 1979; Turner/Antón 1997; Sotnikova/Titov 2009) distinguish two chronospecies from the Eurasian fossil record: *Homotherium crenatidens*, with a Villafranchian age (± 3.0 -1.0 Ma), and *Homotherium latidens* with a post-Villafranchian age (< 1.0 Ma). The differences between these species are, however, so minimal that Antón et al. (2014) assume that all Pleistocene *Homotherium* remains from Europe should be referred to as one species, *Homotherium latidens*. The *Homotherium* assemblage from Incarcal (prov. Girona/E; Galobart et al. 2003) supports this assertion. The observed, large intraspecific variation in size and mandibular morphology is interpreted as sexual dimorphism.

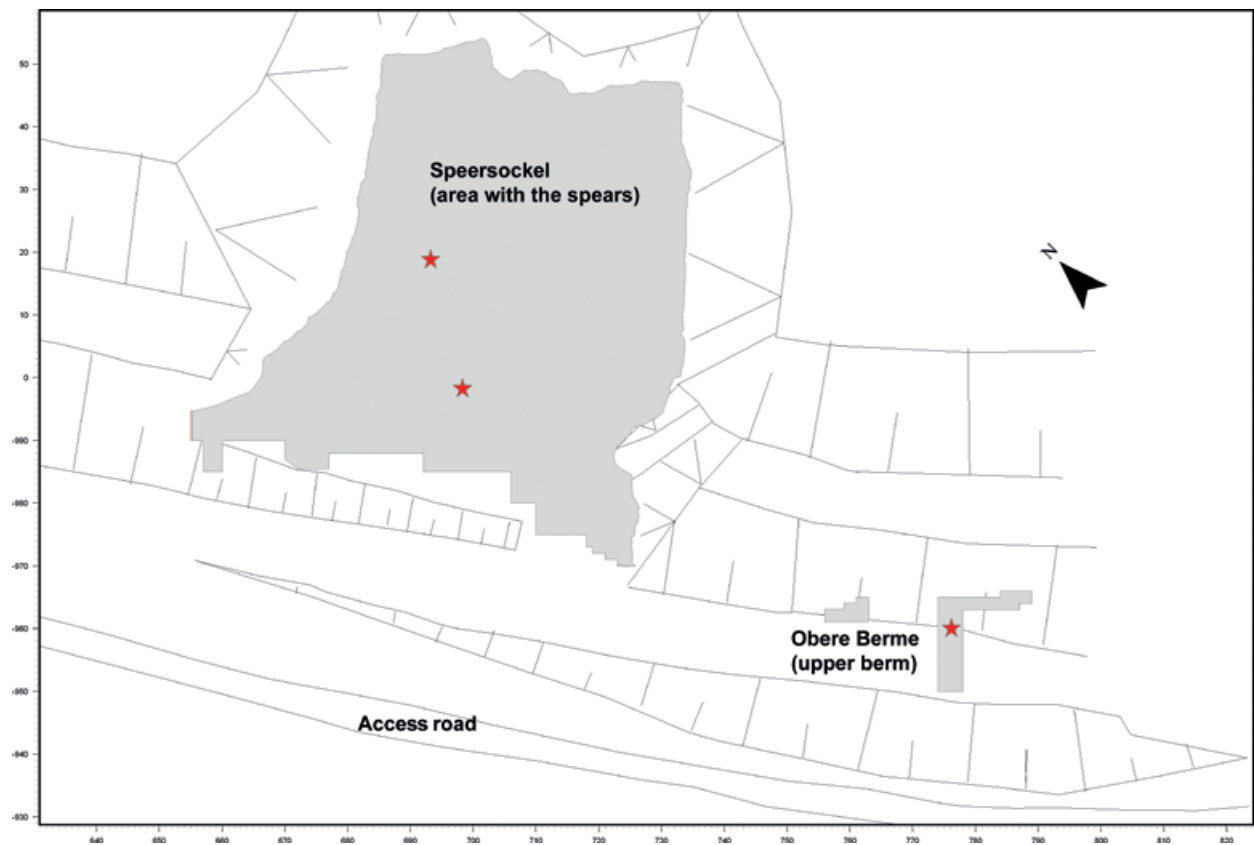
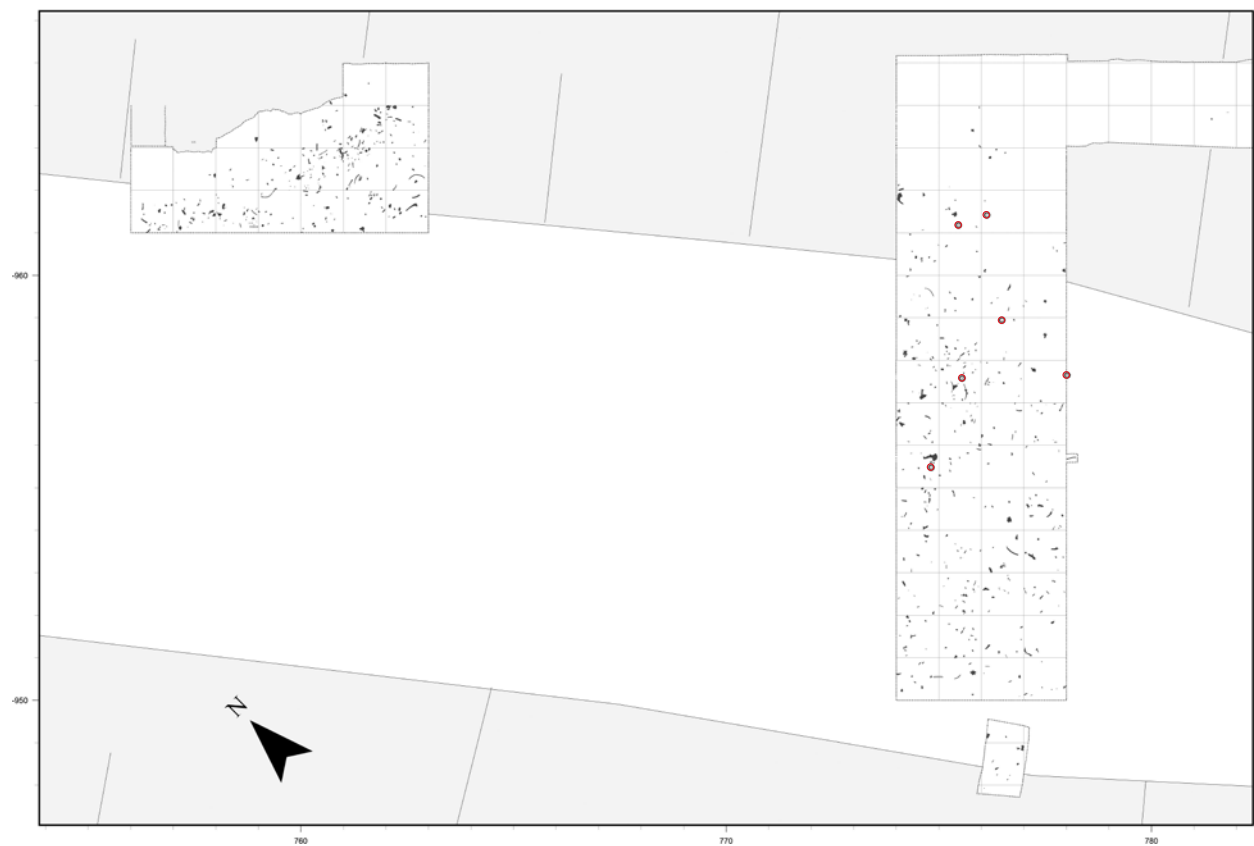


Fig. 1 Schöningen (Lkr. Helmstedt/D): Map of the excavated areas in the Spear Horizon, the »Speersockel« (the area with the spears; excavated from 1994 until 2012), and the new area »Obere Berme« (upper berm; excavated since 2011 until today). The stars indicate the position of the remains from the three *Homo*therium. – (Illustration J. Lehmann).



	description	individual	refit
ID 26509	I1 sup. sin.	1	
ID 26392	canine sup. medial fragment	1	ID 27746 ID 27872
ID 27872	canine sup. fragment of posterior cutting edge	1	ID 26392 ID 27746
ID 27746	canine sup. fragment of the posterior cutting edge	1	ID 27872 ID 26392
ID 27876	canine sup. (?) enamel fragment of the medial/lateral side	1	
ID 26238	P4 sup. (posterior half)	1	ID 26470
ID 26470	P4 sup. (anterior half)	1	ID 26238
ID 26367	M1 sup. sin./dex.	1	
ID 26229	i3 inf. dex.	1	
ID 27749	p3 inf. sin.	1	
ID 26549	m1 inf. dex.	1	
ID 26221	costa dex.	1	
ID 26207	scapula dex.	1	
ID 26234	humerus dex.	1	
ID 25885	humerus dex.	2	
ID 27378	right temporal/parietal	3	ID 27379, ID 27380, ID 27381, ID 27382, ID 27384
ID 27379	basioccipital and fragment of the ventral bulla tympanica	3	ID 27378, ID 27380, ID 27381, ID 27382, ID 27384
ID 27380	left frontal	3	ID 27378, ID 27379, ID 27381, ID 27382, ID 27384
ID 27381	occipital, fragment of the left mastoid and three fragments of the left glenoid fossa	3	ID 27378, ID 27379, ID 27380, ID 27382, ID 27384
ID 27382	medial part of the right and left parietal, three fragments of the right frontal bone	3	ID 27378, ID 27379, ID 27380, ID 27381, ID 27384
ID 27384	left temporal/parietal	3	ID 27378, ID 27379, ID 27380, ID 27381, ID 27382

Tab. 1 Overview of *Homotherium* finds from Schöningen, organized per individual. Anatomical refits are indicated in the last column.

Homotherium was, on average, about the size of a modern lion or tiger, with a withers-height of 0.9-1.1 m, a total length of 1.5-2 m and a weight of up to 200 kg (Turner/Antón 1997; Hemmer 2001; Antón/Galobart/Turner 2005; Antón 2013). Its long, powerful neck, long front legs and relatively short hind legs resulted in a stance that differs from other big cats and is more similar to that of a hyena or a bear (Hemmer 2001). The long sabre-like canines, together with the serrated incisors, canines and carnassials are the most distinctive characteristics of *Homotherium*. It is much more difficult to define specific features on postcranial elements to differentiate *Homotherium* from other large felids. This aspect, together with the fact that teeth are generally more resistant to natural weathering compared to bones, might explain why a disproportionate number of remains attributed to *Homotherium* are teeth.



Fig. 2 Schöningen (Lkr. Helmstedt/D): Map of the until July 2014 excavated Spear Horizon »Obere Berme«. The red circles indicate the position of the teeth. From top to bottom: ID 26470, ID 26238, ID 26229, ID 26549, ID 29392 and ID 26509. – (Illustration J. Lehmann).

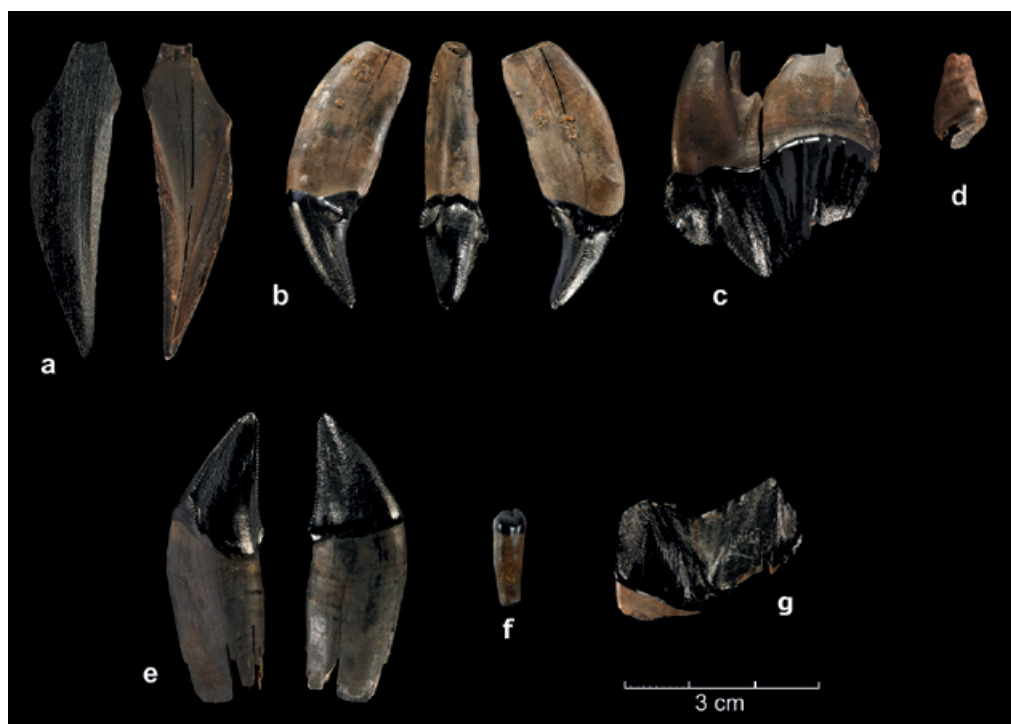


Fig. 3 Schöningen (Lkr. Helmstedt/D): *Homotherium latidens*, dentition: **a** fragment of an upper canine lateral and medial view (ID 26392). – **b** upper I1 sin. (ID 26509), posterior view and side views. – **c** upper P4 sin. (ID 26470, ID 26238), labial view. – **d** upper M1 (ID 26367), posterior view. – **e** lower i3 dex. (ID 26229), side views. – **f** lower p3 sin. (ID 27749), lingual view. – **g** lower m1 dex. (ID 26549), lingual view. – (Photos V. Minkus / I. Verheijen).

DESCRIPTION OF THE SCHÖNINGEN *HOMOTHERIUM* REMAINS

Here we present the remains of three different sabre-toothed cat individuals (**tabs 1-2**). The three individuals have a nickname to honor the person who discovered and excavated the remains.

Individual 1 (Martin, after Martin Kursch)

The seven teeth from the »Obere Berme« (a continuation of the Spear Horizon located to the south of the main concentration; **fig. 3**) are from a subadult *Homotherium* individual, a conclusion that is based on the extremely well-preserved serration of the teeth, with only minor signs of wear, and the open root of the incisors.

The partial denture, discovered in the »Obere Berme« area, is comprised of: 1) a fragmented upper canine, consisting of a medial part (ID 26392) and two small fragments of the posterior edge (ID 27746, ID 27872); 2) a left first upper incisor (ID 26509) with an open root; 3) a fragmented left fourth upper premolar (ID 26470, ID 26238); 4) an upper first molar (ID 26367); 5) a right third lower incisor (ID 26229); 6) a complete left lower p3 (ID 27749); 7) a partly preserved, fragmented first right lower molar (ID 26549). The teeth display a black, shiny patina, consistent with other finds from this horizon. The enamel is crenulated, with a smooth cingulum at the base. Most dental elements (with the exception of the upper M1 and the lower p3) have serration on the crown, with a frequency of 21 serrations per centimeter, observed on the first upper incisor. Several postcranial elements were found in association with the teeth. Their morphology is indicative



Fig. 4 Schöningen (Lkr. Helmstedt/D): *Homotherium latidens*, distal part of a right humerus: **a** medial view. – **b** posterior view. – **c** lateral view. – **d** anterior view (ID 25885). – (Photo V. Minkus).

of a felid and their bone quality corresponds well with that of a young individual. Due to their fragmentary nature, it is not possible to assign these to a specific species.

Several morphological features of the teeth, such as the basal tubercles on the incisors (Sotnikova/Tivov 2009), and in particular the presence of the serrations, led to the identification of these teeth as belonging to *Homotherium latidens*. In addition, the anterior edge of the parastyle of the upper fourth premolar displays the presence of a preparastyle. This characteristic was formerly associated with *Homotherium moravicum* (Sardella/Iurino 2012), which is now considered to be synonymous with *H. latidens* (Sotnikova/Tivov 2009).

Individual 2 (Wolfgang, after Wolfgang Berkemer)

The second individual is represented by a right humerus (ID 25885), excavated from the »Speersockel« (the area where the wooden spears were discovered; **fig. 4**), located at a distance of 100m from the aforementioned finds from the »Obere Berme«. The proximal half of the bone is missing, and the distal epiphysis shows some damage as well. Therefore, multiple characteristics that can be used for a species identification are missing. One characteristic that can be used to differentiate *Homotherium* from other large felids is the shape and position of the supracondyloid foramen (**fig. 4**). In *Homotherium*, this foramen has an oval

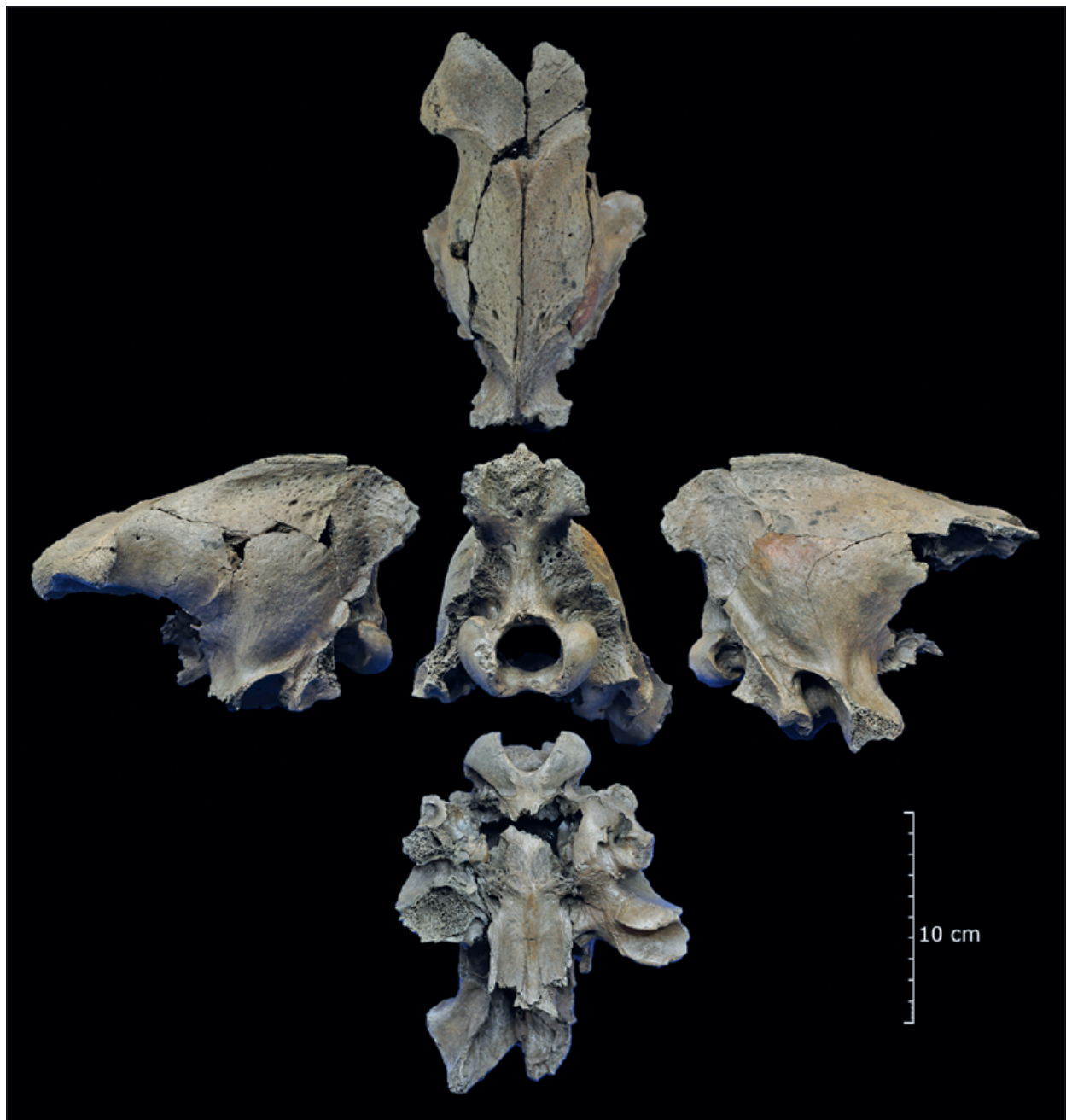


Fig. 5 Schöningen (Lkr. Helmstedt/D): Neurocranium of *Homotherium* individual 3 (Jörg) from layer Schö 13II-4e, after refitting. From top to bottom, left to right: dorsal view, lateral view (left side), posterior view, lateral view (right side) and ventral view. – (Photos I. Verheijen).

shape, whereas in lions it is more rounded. Besides that, in lions it is positioned less medially and higher above the condyloid. Finally, the foramen is not oriented horizontally in anterior-posterior direction, as in the European jaguar, *Panthera gombaszoegensis* (Hemmer 2001), but turns vertically, with a higher opening at the posterior end. The olecranon fossa has an irregular shape and forms a deep cavity in the posterior face. The crista epiconyle lateralis is reminiscent of a lion and a cave lion (van Logchem/Mol 2008), as it is more pronounced in comparison to other *Homotherium* specimens. This feature is interpreted as an indicator for strong muscle attachments, consistent with a large male individual, and not as a defying taxonomic charac-

teristic. Near the proximal edge of the fragment, the onset of the deltaloid ridge is present. The epicondyle and the proximal half of the bone are missing due to damage.

Individual 3 (Jörg, after Jörg Neumann Giesen)

The *Homotherium* neurocranium (fig. 5) from layer Schö 13II-4e was found in six larger and several smaller fragments, which were later refitted and fixed. Before restoration, all skull fragments were 3D scanned at Leiden University (the Netherlands), to enable the study of both the external and internal features. The bone preservation is excellent, allowing detailed study of specific features. The endocranial cavity reflects the external shape of the brain, which is of taxonomic and potentially of functional relevance. The third *Homotherium* from Schöningen will therefore potentially contribute to the understanding of the European sabre-toothed cat as a species. At the moment, the research on this specimen is at a preliminary stage; hence, only a short description is presented in this paper.

The neurocranium is triangular in shape, both from a lateral and a posterior view, which is due to the high and pronounced sagittal crest. The occipital area has a rough texture and displays well-developed muscle attachments, related to the strong neck musculature. On the ventral surface, the muscle attachments of the longus capitus muscle are clearly visible in the basisphenoid-occipital suture area. This feature is also described for a *H. latidens* specimen from Incarcal (Antón/Galobart 1999, 777) and the *H. crenatidens* specimen from Senèze (départ. Haute-Loire/F; Ballesio 1963). The mastoid process is very large in comparison to that of modern felids and protrudes laterorostrally (Antón et al. 2004). The external auditory meatus is encapsulated by the frontal border of the mastoid process and the retroarticular process, resulting in a parallel sided slit with a dorsocaudal-ventro-rostral direction. The glenoid fossa is positioned ventrally, where in modern felids it is directed ventro-rostrally, which is related to the extended gape in sabre-toothed cats. All characteristics described above support the identification of the neurocranium as *Homotherium*.

element	feature	measurements in mm
I1 sin. (ID 26509)	height including root	40.4
	height crown (buccal)	19.6
	maximal width crown	11.3
	length crown (lingual-buccal)	12.3
P4 sin. (ID 26470, ID 26238)	height parastyle	12.2
	anterioposterior length parastyle	8.3
	width parastyle	8.4
	height paracone	19.6
	width paracone	11.5
i3 dex. (ID 26229)	height crown (buccal)	21.8
	maximal width crown	13.6
	length crown (lingual-buccal)	13.8
m1 dex. (ID 26549)	anterioposterior length paraconid	11.5
	height paraconid	14.7
humerus dex. (ID 25885)	smallest breadth diaphyse (SD)	34
	maximal width fossa epicondylar	9
	maximal length fossa epicondylar	27
	minimal thickness epicondylar bridge	5

Tab. 2 Measurements of all *Homotherium* skeletal elements from the site Schö 13II-4, taken with a digital caliper and were rounded to a tenth of a millimeter. Measurements were only performed on the non-frag-mentary parts of the skeletal elements.



Fig. 6 Schöningen (Lkr. Helmstedt/D): *Homotherium latidens*: medial view of the distal part of a right humerus showing carnivore gnawing marks (ID 25885). – (Photo V. Minkus).

Stratigraphic origin, spatial distribution and taphonomic aspects of the finds

The spatial distribution of the *Homotherium* dental elements from the »Obere Berme« is limited, though slightly dispersed (fig. 2), as two refitting parts of the upper P4 were found 70cm apart. Post-depositional processes, either alluvial or trampling, probably caused the distribution of the skeletal and dental elements.

The black, shiny patination of the tooth enamel is similar to other faunal remains at the site, and results from the preservation in humic, organic sediment. The enamel and the roots show hardly any signs of post-mortem weathering; only the root of the upper incisor shows some shallow surface scratches and iron oxide staining. Nonetheless, some of the teeth have been fragmented before final deposition.

Individual 2 (Wolfgang), represented by a distal humerus section, was recovered from the »Speersockel« as an isolated find. It originated from layer Schö 13II-4c, located about 30cm deeper than the base of the main concentration of remains from the Spear Horizon. In this area, a large fissure has been documented throughout the profiles starting at level 13II-4b and continuing to layer Schö 13II-4c. It has repeatedly been

documented that due to secondary post-depositional processes, intrusive remains originating from the layer Schö 13II-4b are located in the underlying layer Schö 13II-4c. Hence, we assume that the humerus, too, is intrusive in layer Schö 13II-4c and originates from the overlying archaeological layer. The humerus shows gnawing damage on the distal epiphysis (fig. 6) as well as polishing on the proximal edge of the broken diaphysis, probably caused by carnivore licking (fig. 7, 5) (Serangeli et al. 2015b). These taphonomic features correspond well with a medium to large-sized carnivore (e. g. wolf or large felid) and indicate the bone still contained nutrients within.

The cranial fragments, belonging to a third individual of *Homotherium*, originated from layer Schö 13II-4e, situated approximately 1 m below the Spear Horizon. The distribution of the cranial fragments is displayed in figure 8. The overall bone surface preservation of the skull fragments is good, with microstructures on the muscle attachment areas still present in great detail, indicating minimal weathering. Some fragments, such as the right parietal, show differential preservation with signs of iron oxidation, resulting in a rusty colour. This discoloration could be associated with post-depositional processes within the sediments, resulting in iron oxidation. No obvious taphonomic marks, such as cut marks or gnawing marks have been encountered on the skull fragments, though small unidentifiable scratches are present. Fragmentation appears to have occurred naturally; there is breakage along the thinner parts of the neurocranium, such as the mid regions of the parietal bones, and at the (former) sutures of the basioccipital region. Three specimens show additional cracks that have not resulted in more fragmentation: the left frontal, right parietal and basioccipital. The incomplete cracks and the fragmentation within the small cluster are most probably related to sedimentary pressure. Similar fractures are seen in the complete horse crania from the Spear Horizon site (Schö 13II-4a-4b/c) at Schöningen. The dispersal and earlier separation of the three segments that are not within the cluster must have occurred before deposition. The unweathered bone surface

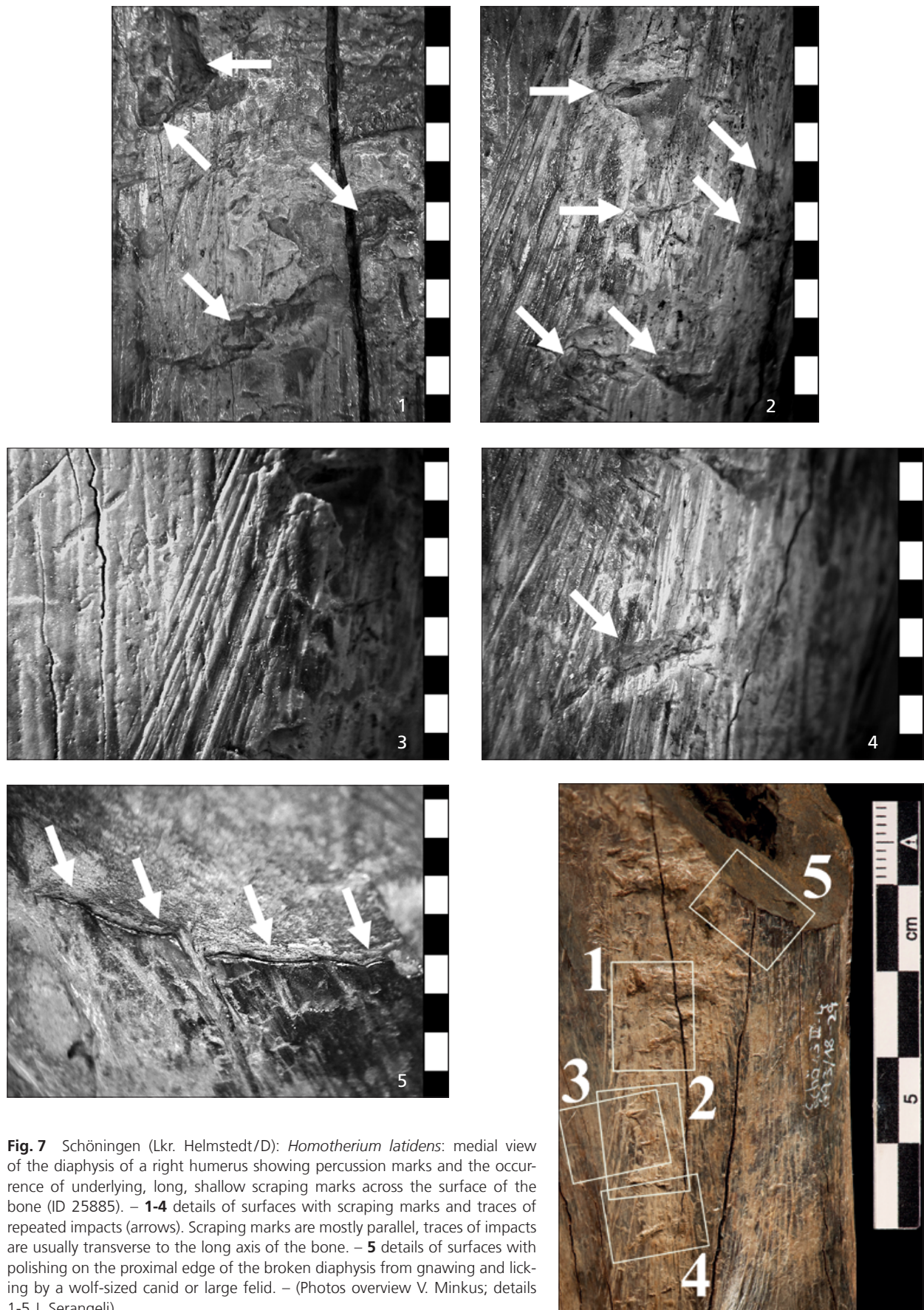


Fig. 7 Schöningen (Lkr. Helmstedt/D): *Homotherium latidens*: medial view of the diaphysis of a right humerus showing percussion marks and the occurrence of underlying, long, shallow scraping marks across the surface of the bone (ID 25885). – **1-4** details of surfaces with scraping marks and traces of repeated impacts (arrows). Scraping marks are mostly parallel, traces of impacts are usually transverse to the long axis of the bone. – **5** details of surfaces with polishing on the proximal edge of the broken diaphysis from gnawing and licking by a wolf-sized canid or large felid. – (Photos overview V. Minkus; details 1-5 J. Serangeli).

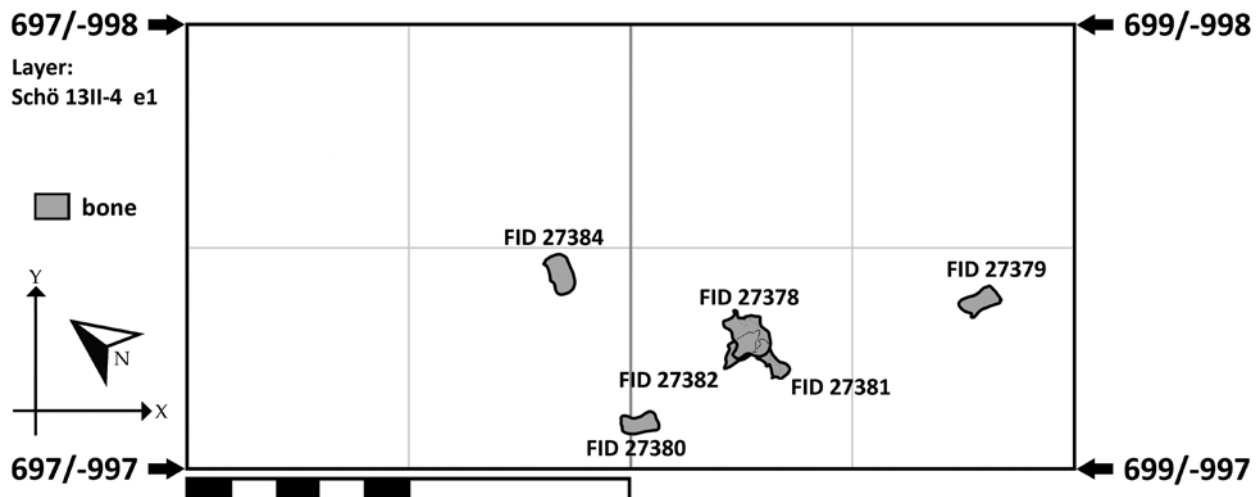


Fig. 8 Schöningen (Lkr. Helmstedt/D): GIS map of the six major fragments of the neurocranium of *Homotherium* (individual 3, Jörg) recovered in the square meters X 697 / Y -997 and X 698 / Y -997. It is important to underline here that the fragments lie in different heights with differences up to 22 cm (ID 27378 = right temporal/parietal bone, Z. 102,07 and ID 27382 = medial part of the right and left parietal and right frontal bone, Z. 101,85). – (Illustration D. Mennella).

preservation without root etching suggests that the cranium was not exposed to the elements over a long period. The distribution is therefore most probably related to trampling or movement within the body of water.

HOMININ MODIFICATION

The humerus shows various taphonomic markers inflicted by both hominin, carnivore and natural actors (fig. 7; Serangeli et al. 2015b; van Kolfschoten et al. 2015). The exfoliated surface of some parts of the cortical bone is the result of weathering, prior to other taphonomic damage. On the medial and lateral side, hominin scraping marks and percussion marks from (re)sharpening flint tools are present, all related to its use as a percussor tool (van Kolfschoten et al. 2015; Serangeli et al. 2015b). The hominin scraping marks result from the removal of (remnants of) the periosteum to clean the bone surface, by scraping with the sharp edge of a flint tool in a slightly oblique position over the bone surface with a direction perpendicular to the long axis of the bone. The scraping marks continue straight until the edge of the proximal break of the diaphysis, suggesting this break occurred after the scraping marks were produced. After this cleaning process, the bone was used as a percussor, leaving pits that are fundamentally different from bite scars produced by other animals; the V-shaped section of the marks is indicative of its artificial origin and do not correspond with bite marks, which are usually more shallow and U-shaped. As a final stage of the taphonomic history, the proximal edge of the breakage was polished as a result of carnivores licking the bone. Carnivore gnawing marks are also present on the distal epiphysis, but it cannot be determined if these were inflicted prior to or after hominins utilized the specimen.

The use of bones as a percussor tool at the Schöningen sites is relatively common; van Kolfschoten et al. (2015) describe a multitude of these tools, made of bones from different taxa (e. g., horse, large bovids, red deer and giant deer). The use of (partially) weathered bones for this purpose is not unique, as indicated by a weathered bison radius (ID 7131) that was discovered c. 6 m from the *Homotherium* percussor.

THE YOUNGEST EVIDENCE OF *HOMOTHERIUM LATIDENS* IN EUROPE

The regional extinction of *Homotherium*, and especially the dating of its latest occurrences, is a matter of ongoing debate. Between 1 Ma and 500 000, *Homotherium* first disappeared from the African fossil record, and subsequently around 500 000 in southernmost Europe. Until the end of the 20th century, it was assumed that the presence of the genus *Homotherium* slowly declined in Eurasia until they disappeared around 300 000 years ago. In North America, the genus persisted until the Late Pleistocene, around 12 000 BP as *Homotherium serum* (Turner/Antón 1997; Antón 2013).

Multiple claims have been made for the Late Pleistocene survival of *Homotherium* in Europe. At Kents Cavern (Devon/GB), several dental remains were discovered in association with Upper Palaeolithic artefacts. The teeth were found to be intrusive to the cave sediments, given their dissimilar uranium and fluorine uptake in comparison to other faunal remains from the same location (McFarlane/Lundberg 2013). In 2003, a mandible was dredged from the bottom of the North Sea. It was dated to c. 28 000 BP using radiocarbon dating, and is the youngest dated find of *Homotherium* in Europe (Reumer et al. 2003; van Logchem/Mol 2008; Mol et al. 2008). The exact stratigraphic origin of the find is unknown, although the preservation and mineralisation correspond with other Late Pleistocene faunal remains from the area. It was originally ascribed to *Homotherium latidens*, other authors however highlight its similarities in morphology to the Late Pleistocene species *H. serum* (Antón et al. 2014).

Excavations in the municipality of Mealhada (distr. Aveiro/P) during the 19th century yielded an astragalus, ascribed to *Homotherium latidens* (Antunes 1986). The river terrace sediments where the faunal remains were recovered were initially correlated with the Riss-Würm (=Eemian, MIS 5e) interglacial (Antunes 1986), but these were later correlated to an interstadial of the Riss (=Saalian; Antunes/Cardoso/Faure 1988; Cunha-Ribeiro 1999). Dental remains discovered in layer Va of Artenac Cave (dép. Charente/F) consist of a canine, an upper P3 and P4. The chronological assignment of these finds is problematic, as only the adjacent layers have been dated using the uranium/thorium dating technique: the overlying stalagmite floor (PL V) is dated to c. 110 000/100 000 years ago, whereas the underlying layer (PL-IV) is 345 000/178 000 years old (Delanges et al. 1999). The associated faunal assemblage shows similarities with other fauna complexes attributed to the Mindel-Riss interglacial or the beginning of the Riss (Beden et al. 1984) and can therefore either be correlated with marine oxygen isotope stage (MIS) 7, MIS 9 or MIS 11.

At Steinheim an der Murr (Lkr. Ludwigsburg/D), a canine of *Homotherium* was found in a layer dated to the Holsteinian Interglacial or the beginning of the Saalien (Adam 1961). In the very same layer, the Steinheim skull, hominin cranial remains most likely belonging to *Homo heidelbergensis* were recovered, indicating the contemporaneity of both taxa.

The finds from Schöningen originate from a layer dated to MIS 9 (320 000-300 000 BP; Sierralta/Frechen/Urban 2012; Richter/Krbetscheck 2015). Their well-documented archaeological context adds to their scientific value, as one of the latest occurrences of *Homotherium* within Europe.

DISCUSSION AND CONSEQUENCES FOR HUMAN EVOLUTION

Apart from Schöningen, there are other archaeological sites in Europe where remains of sabre-toothed cats (*Homotherium* or *Megantereon*) were found: Czech Republic: Stránská Skála (okr. Brno-město/CZ), c. 780 000-400 000 (Sardella/Iurino 2012); Spain: la Trinchera Dolina de Atapuerca (prov. Burgos/E), layer TD5, 900 000-800 000 (García/Arsuaga 1999) and layer TD10, c. 400 000 (Antón/Galobart/Turner 2005);

Italy: Pirro Nord (prov. Foggia/I), 1 700 000-1 300 000 (Gliozzi et al. 1997; Arzarello et al. 2007) and Fontana Ranuccio (prov. Frosinone/I), c. 450 000 (Bittiddu et al. 1979; Gliozzi et al. 1997); Germany: Steinheim an der Murr, c. 400 000-300 000 (Adam 1961) and Mauer bei Heidelberg, 600 000-500 000 (Freudentberg 1929); Hungary: Vértesszőlős (Kom. Komárom-Esztergom/H), c. 600 000-300 000 (Sardella/Iurino 2012); Greece: Petralona (Chalkidiki/GR), c. 600 000-400 000 (Kurtén/Poulanos 1980). Nonetheless, the co-occurrence of both hominin fossils or artefacts, and saber-toothed cat remains at a site, or even within the same archaeological horizon, does not necessarily prove the contemporaneity of the two taxa; at Kent's Cavern in England, the *Homotherium latidens* dental remains were found to be intrusive to the archaeological sediments, and are now interpreted as potential Upper Palaeolithic trade goods (McFarlane/Lundberg 2013).

By reconstructing the diet of extinct carnivore species with no modern analogue like *Homotherium*, we can hypothesize about the degree of overlap in prey-preference with hominins and the potential for competition over resources. The only direct evidence for the prey-preference of *Homotherium* originates from Friesenhahn Cave (Texas/USA). Here, an accumulation of young proboscidean remains with gnawing marks and the remains of several individuals of sabre-toothed cats with a wide age range were found (Marean/Ehrhardt 1995). If indeed *Homotherium* was actively hunting or scavenging from these large-sized prey animals, most of the large mammal taxa found in Schöningen would also fall into this range; giant deer, bovines, rhinos, large Pleistocene equids and proboscideans have all been discovered at Schöningen, and the majority of them contain hominin butchering marks as well. Therefore, the potential overlap in prey taxa between hominins and *Homotherium* should not be underestimated. In the past, hominins were mainly ascribed a passive role in this relationship, as practicing kleptoparasitism, eating the »leftovers« of *Homotherium* kills (Marean/Ehrhardt 1995; Antón/Galobart/Turner 2005; Antón 2013). The super-positioning of cutmarks and gnawing marks is used as an indicator of primary access to a carcass. In the case of Schöningen, the predominance of gnawing marks overlaying cut marks argues for primary access by hominins (Voormolen 2008; Starkovich/Conard 2015). This pattern is also described for other Lower Palaeolithic, such as Boxgrove in England (West Sussex/GB; Smith 2012; 2013).

The occurrence of *Homotherium* in the archaeological site Schö 13II-4 requires a re-interpretation of the wooden spears solely as hunting weapons; self-defence against large carnivores might have also played a role for carrying weapons while acquiring food through hunting or scavenging.

CONCLUSION

The Schöningen remains are the best-documented finds of *Homotherium* within an archaeological setting. They originate from deposits dated to MIS 9 and are therefore one of the youngest findings of the species *H. latidens* in Europe. Other finds of similar or assumed younger age often originate from poorly documented excavations (e.g. Adam 1961; Antunes 1986) or show more similarities with the American species *H. serum* (e.g. Reumer et al. 2003).

The *Homotherium* humerus with flint percussion marks indicates that the European saber-toothed cat and hominins shared the Middle Pleistocene landscape at around 300 000 years ago. It highlights the potential competition between the two species, as they probably hunted a similar suite of prey taxa. And it sheds new light on the technological adaptations (e.g. the Schöningen spears) hominins were using, not only as active weapons for hunting, but possibly also for self-defence.

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SUMMARY / ZUSAMMENFASSUNG

The Remains of the European Sabre-toothed Cat (*Homotherium latidens*) Found in the Spear Horizon at Schöningen (Germany)

The discovery of remains of a European sabre-toothed cat (*Homotherium latidens*) in the Spear Horizon is one of the most important discoveries of the last years at Schöningen (Lkr. Helmstedt/D). Here we present the remains of three individuals: (1) seven teeth and associated postcranial elements, (2) a distal humerus fragment and (3) a neurocranium. The remains of the first two individuals were found in the archaeological site Schöningen 13II-4, layers 4a-4bc, the so-called Spear Horizon, the approximately 300 000-320 000-year-old layers where the world's oldest preserved wooden spears were discovered. The teeth were found in close proximity to each other and all belong to a c. 2-3-year-old sub-adult individual. Conversely, the humerus is from a large and robust individual, probably a male. It displays evidence of hominin scrape and impact marks that indicate it was used as a percussor for working flint. To date, this is the only known bone of a *Homotherium* that has been modified and used by hominins. The cranial fragments of the third individual were excavated in 2015 from the Schöningen 13II-4, layer 4e, situated approximately 1 m below the other finds. Six larger fragments were 3D documented and refitted, and together they form the neurocranium of an adult specimen.

The *Homotherium* remains from Schöningen have an age of c. 300 000-320 000 years and are therefore amongst the youngest specimens of *Homotherium latidens* from Europe. The presence of this large carnivore competitor would certainly have had a major impact on the existence of late Middle Pleistocene hominins. From this perspective, one can hypothesize that the wooden spears were not only used for hunting large mammals, but probably also as a weapon for self-defence.

Die Überreste des Europäischen Säbelzähntigers (*Homotherium latidens*) im Speerhorizont bei Schöningen (Deutschland)

Der Fund von Überresten einer Europäischen Säbelzahnkatze (*Homotherium latidens*) im Speerhorizont ist eine der wichtigsten Entdeckungen der letzten Jahre bei Schöningen (Lkr. Helmstedt/D). Hier präsentieren wir die Überreste von drei Individuen: (1) sieben Zähne und zugehörige postcraniale Elemente, (2) ein distales Humerusfragment und (3) ein Neurocranium. Die Überreste der ersten beiden Individuen wurden in der archäologischen Stätte Schöningen 13II-4, Schichten 4a-4bc, dem sogenannten Speerhorizont, gefunden – den etwa 300 000-320 000 Jahre alten Schichten, in denen die ältesten erhaltenen Holzspeere der Welt entdeckt wurden. Die Zähne wurden in unmittelbarer Nähe zueinander gefunden und gehören alle zu einem ca. 2-3 Jahre alten subadulten Individuum. Der Oberarmknochen hingegen stammt von einem großen und kräftigen Individuum, wahrscheinlich einem männlichen Tier. Er weist Schürf- und Schlagspuren von Homininen auf, die darauf hindeuten, dass er als Schlaginstrument zur Bearbeitung von Feuerstein verwendet wurde. Bislang ist dies der einzige bekannte Knochen eines *Homotherium*, der von Homininen verändert und benutzt wurde. Die Schädelfragmente des dritten Individuums wurden 2015 in Schöningen 13II-4, Schicht 4e, etwa 1 m unter den anderen Funden ausgegraben. Sechs größere Fragmente wurden 3D-dokumentiert und nachbearbeitet und bilden zusammen das Neurocranium eines erwachsenen Exemplars.

Die *Homotherium*-Reste aus Schöningen haben ein Alter von ca. 300 000-320 000 Jahren und gehören damit zu den jüngsten Exemplaren von *Homotherium latidens* aus Europa. Die Anwesenheit dieses großen fleischfressenden Konkurrenten hätte sicherlich einen großen Einfluss auf die Existenz der spätmittelpleistozänen Homininen gehabt. Unter diesem Gesichtspunkt kann man annehmen, dass die Holzspeere nicht nur für die Jagd auf große Säugetiere, sondern wahrscheinlich auch als Waffe zur Selbstverteidigung verwendet wurden.