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MAMMUTHUS-COELODONTA FAUNAL COMPLEX FROM SIEGSDORF (CHIEMGAU, GERMANY) – OVERVIEW AND NEW ANALYSES

Abstract

Remains of Pleistocene large mammals were discovered near the village of Siegsdorf, south-eastern Bavaria, in 1975 and 1985. New radiocarbon dates of some of these finds show that the Siegsdorf fauna can be assigned to two phases of the Würm Glacial. Among the Siegsdorf bones were those of a cave lion with cut-marks. According to radiometric dating, these marks must have been made by Neanderthals. The traces represent the first evidence of the presence of Neanderthals in the SE of the German Pre-Alps. Due to the rapid embedding in the clayey-silty sediments of a former waterhole, the bone finds are exceptionally well preserved. For this reason, bone samples from the mammoth and cave lion from Siegsdorf are also included in various important palaeogenetic analyzes.

Keywords

Mammoth, cave lion, cut-marks, radiometric dating, palaeogenetics

INTRODUCTION – HISTORY AND FINDS

The village of Siegsdorf is situated between Rosenheim and Salzburg in the local government of Traunstein, ca. 10 km from Lake Chiemsee (**Fig. 1**). The site itself is located in the Gerhartsreiter Graben, 1.5 km from the village centre (**Fig. 2**). Here, in the summer of 1975, two schoolboys found bones of a woolly mammoth (*Mammuthus primigenius*) in the clay beds of a creek.

Approximately half of the mammoth skeleton was unearthed after several weeks of amateur excavations. It was supposed that the missing half would be found beneath the gravel deposits of a steep slope, however, it was not possible to remove the sediment without special equipment. Accordingly, excavations in this area halted, and then later continued in 1985. The village of Siegsdorf took over the costs, while the scientific responsibility lay at the Institute of Palaeontology and Historical Geology at the Ludwig Maximilian University of Munich and the Bavarian State Collections of Palaeontology and Historical Geology. Besides the second half of the skeleton and three tusks, as well as the remains of other woolly mammoths, the site yielded a well-preserved, partial skeleton of a cave lion (*Panthera spelaea*), a right and left mandible from a wolf (*Canis lupus*), mandibles, skull fragments and postcranial bones from three woolly rhinoceroses (*Coelodonta antiquitatis*), a right scapula from an Irish elk (*Megaloceros giganteus*), and a right juvenile tibia fragment and a right radius fragment from a steppe bison (*Bison priscus*). Moreover, the presence of cave hyenas (*Crocuta crocuta spelaea*) is indirectly confirmed by coprolites (**Fig. 3**) and numerous gnawing marks on the bones of the mammoth and woolly rhinoceros.

The well-preserved partial skeletons of the *Mammuthus primigenius* and *Panthera spelaea* represent significant findings. A comparative osteological analysis of these findings was conducted by Ziegler (1994) and Gross (1992), respectively.

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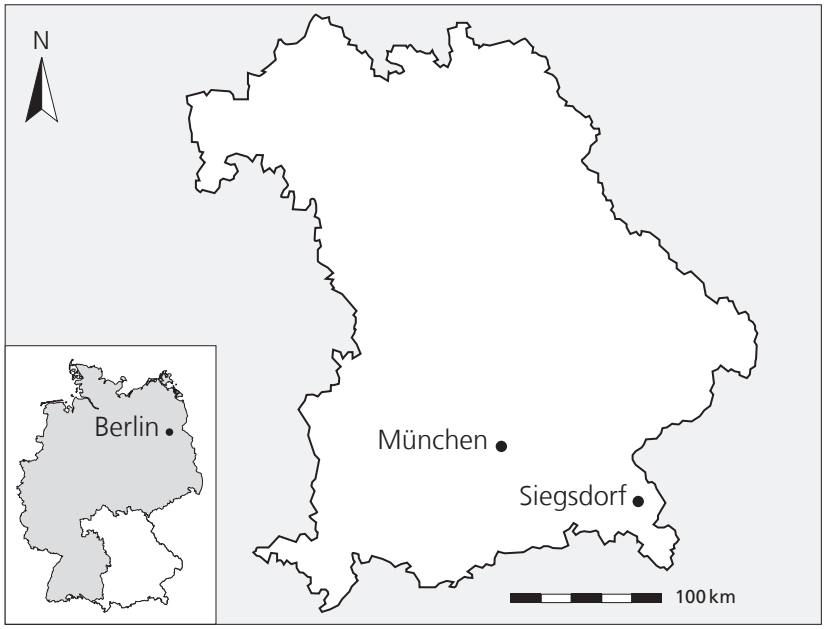


Fig. 1 Geographic location of Siegsdorf. – (Sketch: W. Rosendahl, *Reiss-Engelhorn-Museen* Mannheim).

In 2012, additional bones at the excavation area of the Siegsdorf mammoth were found. All belong to a horse and have the same color as the mammoth bones. Radiocarbon dating yielded an age of about 400 years for the horse remains (Darga, 2016).

The mammoth (**Fig. 4**) is identified as a bull, measuring 3.60 m at shoulder height. It represents one of the largest woolly mammoths known in Europe. The condition of its teeth indicates that it died at the age of around 50. Both last molars of the mandible were completely developed. The skeleton displayed only a few indications of arthritis, and no further signs of disease. The mammoth bones bear no traces of human impact as a result of either hunting or butchering. It is possible that the Siegsdorf mammoth simply became stuck in the clayey mire of the riverbed, and died there. Hyenas gnawed at significant portions of its cadaver, as evidenced by the gnawing marks on large bones such as pelvis, humerus and femur (**Fig. 4**). A probable explanation for the lack of cranial and facial bones of the mammoth could be the expansive force of grow-

Fig. 2 Aerial view of the site at which the Siegsdorf mammoth was found (top arrow), facing south toward the Alps. The road at the bottom left of the image is the Munich-Salzburg motorway. The Siegsdorf finds are displayed in the Southeast Bavarian Natural History and Mammoth Museum Siegsdorf (bottom arrow). – (Photo: Natural History and Mammoth Museum Siegsdorf).

Fig. 3 Hyena coprolites (maximum 3.5 cm in diameter). – (Photo: Natural History and Mammoth Museum Siegsdorf).

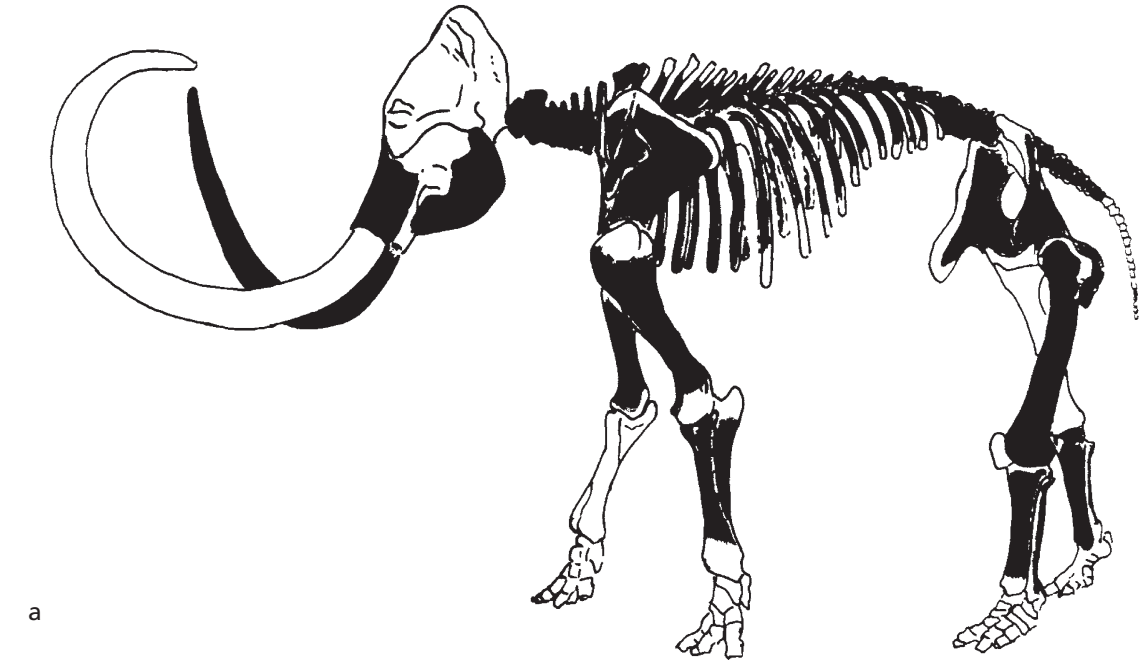
ing ice, which would have fragmented the perforated, spongy osseous mass of the skull into tiny pieces. The missing left tusk, like the tusk of another mammoth individual, probably decomposed in the weathering zone and was washed away down the creek.

The skeleton of the cave lion (**Fig. 5**) belongs to a senile individual, as evidenced by heavily worn teeth and the closed tooth sockets in the mandible, where teeth had already fallen out. It also appears that the Siegsdorf cave lion suffered from several or recurrent infections. This, at least, would explain the coarsely porous bone material found in a number of skull sections (Schouwenburg et al., 2009). It is fair to conclude that the animal may not have been particularly agile due to its age and infections, and its condition may even have rendered its continued survival impossible. It is a reasonable assumption that it did not seek an abode close to the waterhole or shallows in order to hunt, but instead, to feed on carrion.

ECOLOGY, CLIMATE AND CHRONOLOGY

The Siegsdorf fauna reveals a more temperate period within the Glacial, based on the ecological and climatic needs of the identified species. The presence of Irish elk *Megaloceros giganteus,* and the discovery of a snail belonging to the genus *Arianta arbustorum* (identified by R. Dehm in: Heissig and Bredow, 1987) contradict a high glacial climate. There are no traces of mixed fauna, e. g., due to redistribution processes, and the Siegsdorf fauna therefore can hence be considered homogeneous. Based on the size of the mammoth skeleton Ziegler (1994) ascribed the find into the Riss glaciation.

To clarify the chronostratigraphical position of the Siegsdorf Fauna an initial phase in reassessing the finds was started in 2001. Two bone samples, one from the mammoth and one from the cave lion, were dated by use of the radiocarbon method at the Leibniz Laboratory for AMS-^{14}C dating in Kiel (Germany). The cave lion sample (KIA 14406) revealed a radiocarbon age of 47,180 +1190 / -1040 ^{14}C BP and the mammoth sample (KIA 14407) an age of 45,180 +1130 / -990 ^{14}C BP. The age difference between these two samples is statistically insignificant. Most likely, both samples belong to the same period (**Tab. 1**).



a

b

Fig. 4 The Siegsdorf mammoth: **a** sketch of a mammoth skeleton (according to Abel, 1929) with the skeletal remains of the Siegsdorf mammoth highlighted in black. The bones in white are missing. The edges of the pelvis and many ends of joints and ribs were gnawed off by hyenas, as bite marks clearly show. – **b** cast of the skeleton of the Siegsdorf mammoth in the Natural History and Mammoth Museum Siegsdorf. – (a from Ziegler, 1994; b photo: Natural History and Mammoth Museum Siegsdorf).

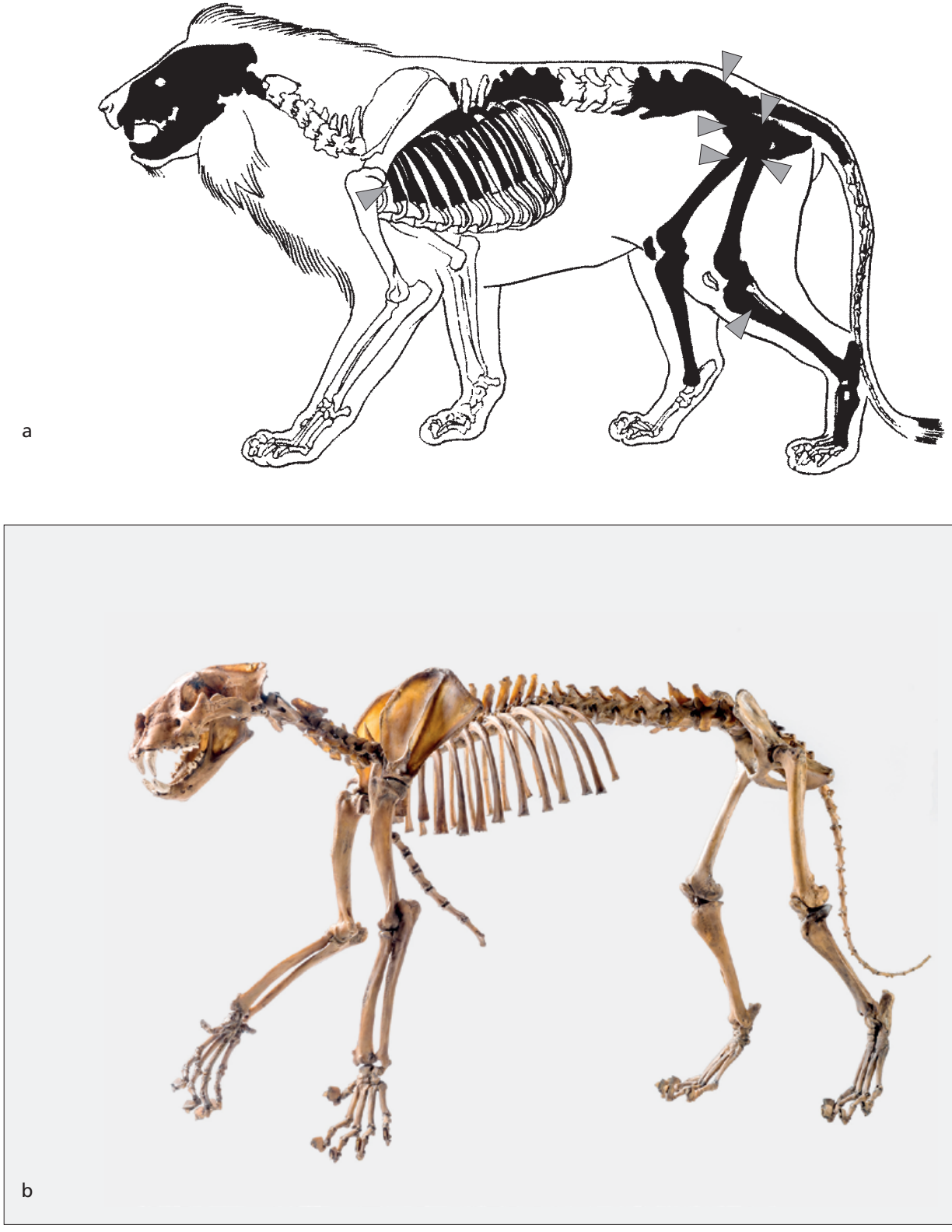


Fig. 5 The Siegsdorf cave lion: **a** sketch of a lion skeleton, with the skeletal remains of the Siegsdorf cave lion highlighted in black; arrows show the position of the cut-marks; **b** cast of the skeleton of the Siegsdorf cave lion. – (a sketch: W. Rosendahl, *Reiss-Engelhorn-Museen* Mannheim; b photo: T. Schwerdt, *Reiss-Engelhorn-Museen* Mannheim).

Fig. 6 Mandibles of two woolly rhinoceroses (to the left) and the mandible of a wolf (to the right). (Photo: Natural History and Mammoth Museum Siegsdorf).

In 2020 a second phase of reassesing faunal remains was started and bone samples from *Coelodonta antiquitatis, Megaloceros giganteus* und *Bison priscus* were dated with the radiocarbon method at the *Curt-Engelhorn-Zentrum für Archäometrie gGmbH* in the *Reiss-Engelhorn-Museen* in Mannheim. All dates obtained fall into Oxygen Isotope Stage (OIS) 3 and cluster between ~45,000 and ~50,000 cal BP; only the date obtained on the woolly rhinoceros (**Fig. 6**) turns out some 4,000-5,000 years younger than the majority of the Siegsdorf fauna (**Tab. 1**).

The recently produced AMS results confirm the dates obtained earlier from mammoth and cave lion. These results permit us to state that the majority of the mammal fauna from Siegsdorf is chronological homogenous and dates into a Middle Würmian period of OIS 3. In climatic-ecological terms, this period correlates with a more temperate climate in the middle part of the last Glacial. Vegetation in this period was typically characterized by open woodlands with pine trees (*Pinus*), spruce (*Picea*) and birch (*Betula*) (van Andel and Tzedakis, 1996). The annual average temperature was approximately 4 degrees Celsius below current levels (Guiot et al., 1989). The woolly rhinoceros, on the other hand, dates into a cooler period, close to the Heinrich 4 cold episode.

TAPHONOMY

The deposits in which the osseous remains were embedded consist of grey silt with a small proportion of clay, holding a few sharp pieces of carbonate stone and scree. The average granular diameter of the sediment is 0.020 mm (coarse mid-silt), and it is extremely well-sorted. The analyses were conducted on one kilogram of sediment taken from a reserve sample of material found at the site during the excavation in 1985.

The silt is a product of weathering in the Gerhartsreiter beds. These are clay-like, marly deposits from shallow waters belonging to the Helvetic Late Cretaceous period. These beds extend approximately 100 m southward around the Gerhartsreiter Graben, where they form the bedrock. A smaller expanse of stagnant water, fed by a minor tributary brook, emerged in the area of today's Gerhartsreiter Graben during the lifetime of the Siegsdorf fauna. Clay sludge from weathered Gerhartsreiter layers settled on its floor. Older, water-permeable quaternary sedimentation, for instance gompholite, formed the immediate vicinity around the pool. It is likely that the animals in the surrounding areas used the pool as a watering hole. It is possible that if one of these animals died and fell into the water or into the clay-like sludge, it would have become embedded in the material. Based on the large number of hyena bite marks, especially on the mammoth, it is clear that a part of the cadaver lay exposed, at least for a certain period. The extremely well-preserved bones in the find deposits nevertheless indicate that embedding must have taken place relatively quickly. The sediment, which tightly enclosed the bones, would also have contributed to the good state of preservation.

The skeletal remains found originate either from older (e. g., *Mammuthus primigenius*, *Panthera spelaea* and *Canis lupus*), or from juvenile individuals (*Coelodonta antiquitatis*, *Megaloceros giganteus* and *Bison priscus*).

After the bones were embedded, the waterhole was covered with thick layers of gravel (**Fig. 7**) that were deposited during the Last Glacial Maximum (LGM). During the LGM, the area was not directly affected by the advancing ice, as the Weißtraun glacier moving northward from the Alpine mountains did not reach the Gerhartsreiter Graben. Its northernmost Würmian moraine is located

Species	element	inv. no.	lab. no.	^{14}C-Age [BP]	± [BP]	Age [cal BP] *	C:N	C [%]	collagen [%]	references	original figures	endogenous DNA [%]	reference
Panthera spelaea	femur, dex.		KIA 14406	47,180	+1190 -1040	49,369-45,989			19.4	Rosendahl & Darga, 2002	Gross, 1992	3.3	Stanton et al., 2020
Mammuthus primigenius	bone		KIA 14407	45,180	+1130 -990	47,922-44,694			17.1	Rosendahl et al., 2005	Ziegler, 1994: Plate 7, Fig. 1		
Megaloceros giganteus	scapula	NKM522	MAMS 45184	42,260	390	45,914-45,208	3.3	42.9	7.6	this paper	Ziegler, 1994: Plate 9, Fig. 3		
Bison priscus	tibia	NKM523	MAMS 45185	43,270	450	46,921-45,953	3.3	42.9	4.1	this paper	Ziegler, 1994: Plate 9, Fig. 4		
Coelodonta antiquitatis	mandibula	NKM526/2	MAMS 45186	36,540	460	41,615-40,739	3.3	43.3	2.1	this paper	Ziegler, 1994: Plate 8, Fig. 2		

Tab. 1 Radiocarbon dates from the Siegsdorf fauna. * 1-sigma.

to the south of Eisenärzt near Neustadl, 2 km south of Siegsdorf (Ebers, 1939). It is due to this circumstance that the movement of ice did not strip off the find-bearing layers during the LGM.
During the Late Glacial and Holocene rivers eroded the glacial gravel deposits, and cut into the site.

ARCHAEOLOGY

Traces of cut-marks on several bones of the preserved cave lion skeleton were discovered as far back as its first analysis in 1992 (Gross, 1992). They are located on the insides of several ribs, on the pelvic bones, and on both femora (**Fig. 5**; **Fig. 8**). Comparisons undertaken during these investigations revealed that the cut-marks produced on the Siegsdorf lion remains were most certainly the work of humans. The find complex, however, has not yielded any stone artefacts or human bone remains, making these cut-marks the only indications for human presence at the site. Combined with the ^{14}C-date of the cave lion's right femur one has to conclude that (a) Neanderthal(s), *Homo neanderthalensis*, produced the cut-marks (Rosendahl et al., 2005). Hence, the Siegsdorf site provides the first confirmation for the presence of Neanderthals in the Alpine foothills of Upper Bavaria. At the same time, it is the earliest proof for the presence of humans in this region (Rosendahl and Darga, 2004).
Even if a general consensus exists on the fact that Neanderthals did not hunt cave lions to obtain their meat, the position of the cut-marks on the skeletal remains of the Siegsdorf cave lion (e. g., on the inside of several ribs and the pelvic bone) nevertheless show that the cadaver was gutted. It is doubtful that the animal was also skinned, as typical bones that would otherwise be missing (e. g., phalanges) are still present. Cut-marks that would clearly confirm that the animal was skinned are also missing (e. g., on the outside of the ribs). Neither the skeleton nor the location of the find provides any indication as to how or if the animal had been hunted.

Fig. 7 Excavators clear the soil and rocky material above the site in 1985. The dark grey clay of the bone bearing layer is cut at a depth of approximately 2 m below the person standing in the centre of the picture. – (Photo: Natural History and Mammoth Museum Siegsdorf).

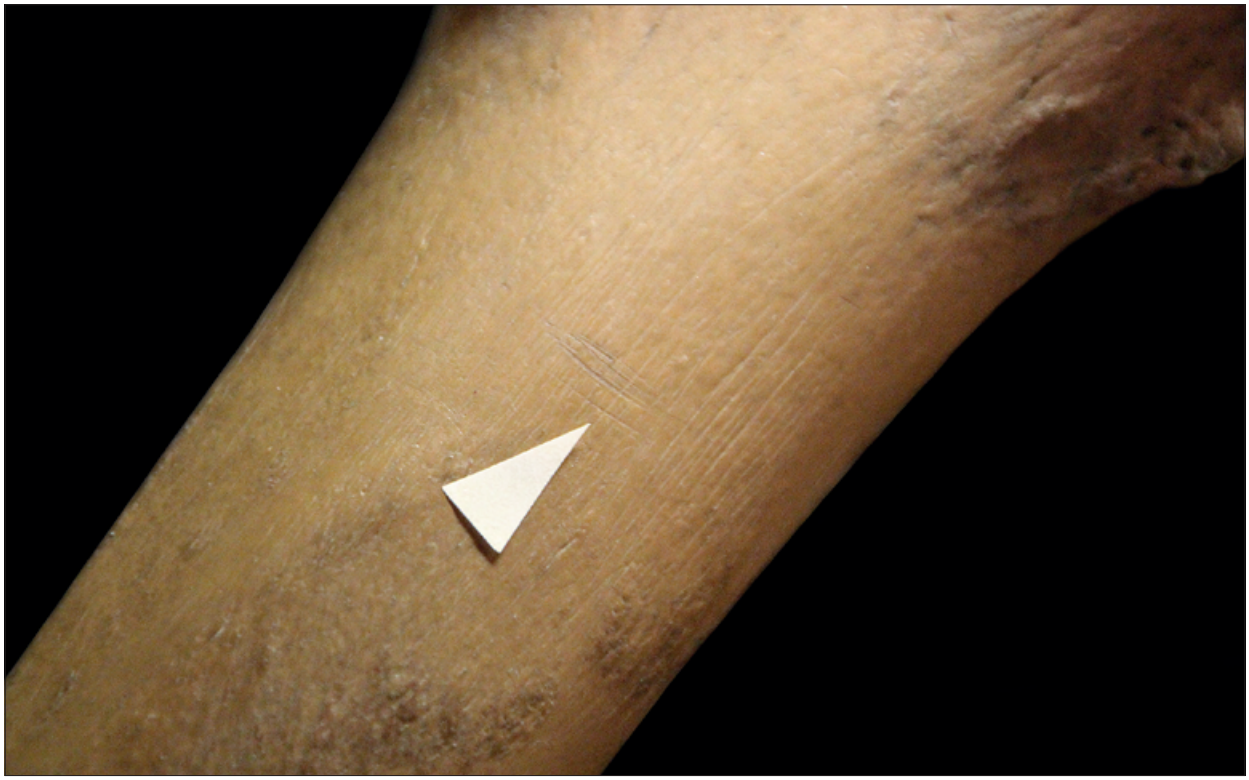


Fig. 8 Cut-marks (arrow) on the left femur of Siegsdorf cave lion. – (Photo: Natural History and Mammoth Museum Siegsdorf).

It is certain, however, that the lion's cadaver was very quickly embedded in the clay-like sludge of the waterhole, once the Neanderthals had used stone tools to eviscerate the lion carcass. This is confirmed by the extremely good preservation of the osseous substance, and the lack of any gnawing marks, such as those exhibited by numerous other bone remains found at the site (**Fig. 9**).

GENETIC ANALYSES

Due to the excellent depositional conditions the faunal remains of Siegsdorf are characterised by their outstanding bone preservation. This led to their suitability for various aDNA studies, which are summarized here. Relevant literature has discussed a variety of different variations, with respect to the taxonomic designation of Upper Pleistocene cave lions (Hemmer, 1974). Besides a sister species to *Panthera spelaea* (e. g., Barnett et al., 2009), the genus is also recorded as subspecies *Panthera leo spelaea* (e. g., Burger et al., 2004) or even as *Panthera tigris fossilis* or *Panthera tigris spelaea* (Groiss, 1996).
For the first molecular genetic analyses (Burger et al., 2004), a sample was taken from the left femur of the cave lion at the same time as the dating samples were taken; this sample was used to conduct aDNA analysis. A comparison with recent bones showed that the aDNA of the Siegsdorf lion is in extraordinarily good condition for preservation of aDNA and, in places, is of comparable preservation as with that of modern bones (Burger et al., 2004). A second aDNA sample of the Siegsdorf lion, taken from a tooth root, was compared with 31 mitochondrial genome sequences (Stanton et al., 2020). The results support previous hypotheses that at least two different subspecies of cave lions existed during the Pleistocene, and that lions

Fig. 9 The Siegsdorf ice age fauna ~45,000 to ~50,000 years ago in the Weißtraun valley south of Siegsdorf, Bavaria. This view from Rudhart (a hamlet near the contemporary place of discovery) to the west shows the ancient river Traun much less incised into the ground than today, the alpine foothills and the summit of the mountain Hochfelln on the horizon. The bones of the Siegsdorf ice age animals were preserved in a marshy depression similar to the waterhole in the foreground. – (Photo: Natural History and Mammoth Museum Siegsdorf).

and cave lions represent distinct species. The ca. 47,600 cal years-old Siegsdorf cave lion perfectly matches Clade C, the only lineage known from Europe (Stanton et al., 2020), that is continuously documented on the continent until the LGM.

A further molecular genetic study was conducted in 2005, using residue from a tibia, which until then had only been identified within the Siegsdorf fauna spectrum as *Bos vel Bison* (aurochs or wisent, i. e., European bison). The aDNA analysis conducted in the Institute of Anthropology at the University of Mainz (Palaeogenetic Research Group under Prof. Joachim Burger) resulted in its species attribution to the steppe wisent (*Bison priscus*) (Bollongino, 2006).

The mammoth was also sampled as part of a large-scale international study on the reconstruction of the gene pool of *Mammuthus primigenius* (Chang et al., 2017). One purpose of this study, among others, is to find out more about the genetic diversity found among mammoths. Near the end of the Pleistocene epoch, populations of woolly mammoth (*Mammuthus primigenius*) were distributed across parts of three continents, from Western Europe and northern Asia through Beringia to North America. The Eurasian range of the woolly mammoth confirms that the Late Pleistocene mammoth populations comprised three distinct mitochondrial lineages. The Siegsdorf mammoth matches to clade 3 (haplogroup B2), documented from European and Siberian sites (Chang et al., 2017).

The excellent depositional conditions of the faunal remains of Siegsdorf and their outstanding bone preservation led to their suitability for various aDNA studies. The Siegsdorf site provides also the first confirmation

for the presence of Neanderthals in the Alpine foothills of Upper Bavaria and it is the earliest proof for the presence of humans in this region. Therefore the Siegsdorf site is one of the best investigated *Mammuthus-Coelodonta* faunal complex in the SE of the German Pre-Alps.

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