**Homotherium** from Middle Pleistocene archaeological and carnivore den sites of Germany – Taxonomy, taphonomy and a revision of the Schöningen, West Runton and other saber-tooth cat sites

Cajus G. Diedrich a, b, *, 1, Donald A. McFarlane c

a PaleoLogic, Private Research Institute, Petra Bezruce 96, CZ-26751 Zdice, Czech Republic
b University of Koblenz-Landau, IFIN, Department of Biology, Universitätsstr. 1, D-56070 Koblenz, Germany
c Keck Science Department, The Claremont Colleges, 925 North Mills Avenue, Claremont, CA 91711-5916, USA

**Abstract**

Four new saber-tooth cat (*Homotherium*) sites in Germany with new dental and postcranial bone material are different in their taphonomic context: 1. The Archaeological Middle Palaeolithic (MIS 9e-Interglacial) Schöningen Lake site with remains of a cub carcass. 2. The Middle Palaeolithic (MIS 5e-9) Archaeological/cave bear den site of Balve Cave yielding a lower canine tooth of an older individual. 3. The Zoolithen Cave (MIS 3–9) cave bear/hyena den with one distal half humerus of an adult, 4. The Ketsch open air Rhine River terrace site which has provided another distal humerus of an adult saber-tooth cat. Whereas only the Schöningen site is precisely dated as Holsteinian Interglacial (approx. 330,000–315,000 BP), all material seems to come from the same Middle Pleistocene warm period, or few younger Saalian interstadials (MIS 7a, e) deposits, and did not extend over the last MIS 7 glacial into the Late Pleistocene. *Homotherium* as hyena-like slow moving cat seems to have disappeared within the Saalian due to competition with other scavengers like Ice Age spotted and brown hyenas (*Crocuta crocuta praespelaeula/ultima* and *Pachycrocuta brunnea mosbachensis*). The juvenile saber-tooth cat cub from Schöningen might be in archaeological context or represent only a carnivore kill. At the Zoolithen Cave, the single bone must have been imported into a hyena prey bone assemblage. The situation is possibly similar at the two other sites Ketsch and Balve Cave. The formerly described Schöningen "saber-tooth cat" humerus is revised, such as other opposite as lion humeri described material from different European sites. The presence of the well-developed supracondylar ridge distinguishes *Homotherium* well from Middle/Late Pleistocene lions *Panthera leo* (e.g. *spelea, fossilis*). The Schöningen lion humerus has been chew-cut first most probably by a stripped hyena whose cutting scissor teeth produced a diagonal bite cut and P4/M1 impact marks around the trochlea. 1–2 mm small, mostly triangular-oval bite marks on the lion humerus shaft compacts results from a second scavenger and not from "Neanderthall tool use". Those bite mark sizes are produced mainly of the upper molar teeth of a the red wolf *Cuon alpinus* subsp. (or small fox *Vulpes praeacorsa*), which were present in the region within the Holsteinian/Saalian.

**1. Introduction**

The only known European saber-tooth cat *Homotherium crenatidens* (Weithofer, 1889) skeleton from the Early Pleistocene (Villafranchian) of the French site Seneze is well published in a monograph by Ballesio (1963). This specimen includes complete preserved humeri, which are compared herein for a revision of several questionable “distal humeri” described in recent years from several Central European sites often as “felid or lion humeri” (e.g. Lewis et al., 2010). The Middle Pleistocene European saber-tooth cats, which are not yet known by skeletons, are assigned to *Homotherium latidens* (Owen, 1843) (e.g. Antón et al., 2005), for which one of the most northern records comes from an English cave (Dawkins and Sandford, 1872; McFarlane and Lundberg, 2013). The “Late Pleistocene” records from the North Sea (Reumer et al., 2003) are without stratigraphic value or reliable dates because of...
their embedding in modern marine sediments: no other European finds support their survival into the last Ice Age.

The material found in Germany (Fig. 1A) is quite sparse and lacks even complete skulls. A few single teeth and postcranial elements have been published. The Early Pleistocene records are from the river terrace site Untermässfeld (cf. Hemmer et al., 2011). Some material comes from the Mosbach Sands Neckar River terrace (Schütt, 1970), which are revised by the actual stratigraphy of this site (cf. Stephan, 2014) now into the early Middle Pleistocene Cromerian Complex. Further Middle Pleistocene material was found in the “Heppenloch” also being called Gutenberg Cave (Adam, 1975).

In this contribution, Middle Pleistocene material from three new German sites can be added (Figs. 1–3). It is not intended to be a full review of German, or revision of Eurasian Pleistocene saber-tooth cat sites, but it is of urgent need because material has been confused. Some saber-tooth cat remains are figured (only 0.1%, in each publication) in lion publications (cf. Diedrich, 2011a,b; Diedrich and Rathgeber, 2012). Opposite, some lion remains have been misidentified as saber-tooth cat remains. For example, the newest “saber-tooth cat” records described by Serangeli et al. (2015) represent only one saber-tooth cat cub dentition and to its age class fitting humerus such as few other bone fragments of a cub (not two individuals as discussed therein). We revise the figured humerus determined in their study as “Homotherium” (second individual) here. Furthermore, the well-known taphonomy of European Late Pleistocene lion carcasses caused mainly by hyena feeding (Diedrich, 2011a) can be extended with more details of hyena feeding strategies on their felid competitors, lions and saber-tooth cats.

2. Material and methods

The carnivore material of the Paleon - Schöningen Spear Museum (= Pal) was only screened and is partly exposed in the permanent exhibition, which needs further detailed work in future. The humerus discussed herein was checked by the tooth mark forms and sizes. The studied saber-tooth cat and other bone material of the Balve Cave is stored in the Geologisch-Palaontologische Museum of the Westphalian Wilhelms-University Münster (= GPIM). The Zoolithen Cave material is in the collection of the Fränkische Höhlen und Karstforscher Club (= FHKF). One humerus fragment is stored in the Staatliche Museum für Naturkunde Stuttgart (= SMNS). One complete lion humerus is stored in the Landesamt Sachsen Anhalt collection (= LDA). The upper jaw saber-tooth cat canine from the Czech C718 Cave site is in the Nationalmuseum Prague (= NMP). The compared damaged lion humerus from the Neander Valley is in the Goldfuss-Museum of the Rheinische Wilhelms-University Bonn (= GMB). A single tooth cusp from Sanderhausen is kept in the collection of the Spenglermuseum Sangerhausen (= SPM).

2.1. Geology and dating

All new German sites are of Middle Pleistocene (Cromerian-Saalian, = MIS 21-7) in age according to the updated German
The H. latidens remains from Schöningen are dated according to the newest work on the Middle to Late Pleistocene stratigraphy in northern Germany, in which the Holsteinian Interglacial is dated into the MIS 9e isotope stage (330.000–315.00 BP) (Müller, 1974). It is characterized by the development in general of temperate mixed forests in central and...
northwestern Europe and seasonality (e.g., Nitychoruk et al., 2005; Koutsodendris et al., 2010). The Zoolithen Cave has been recently revised and its bone remains are thought to have been accumulated not only in Late Pleistocene times, but instead since the Elsterian/Holsteinian (Diedrich, 2014). The long-term multiple use of this cave as a cave bear, hyena and wolf den within different climatic periods explains the large amount of bones (mainly different cave bear species/subspecies of Middle Pleistocene: Ursus deningeri, Late Pleistocene: Ursus spelaeus eremus/spelaeus, Ursus ingressus) and the presence of the “largest amount of lion remains ever excavated in a European cave”, which also includes Middle Pleistocene P. l. fossilis remains (Diedrich, 2011a, 2014). All material, including the rare saber-tooth remains, are in secondary/tertiary positions within the cave system due to predator activities and later floods and can not be dated exactly in many cases, except using biostatigraphy (e.g. C. alpinus spelaeus and H. latidens are such as U. deningeri Middle Pleistocene species: Diedrich, 2014). The third site discussed here, Ketsch, is a Rhine River Valley gravel pit terrace site, which has mixed Middle to Mainly Late Pleistocene megafauna elements (Diedrich and Rathgeber, 2012).

3. Results and discussion

3.1. Saber-tooth cat Homotherium versus lion Panthera humerus osteology

In most previous accounts of Middle Pleistocene H. latidens, the distal humeri were figured, but in no case was the most important defining character discussed, although it was also used in soft tissue fore limb reconstructions by Antón et al. (2009). Based on the complete and well-preserved Plio-/Early Pleistocene H. crenatidens humerus figured by Ballesio (1963) (Fig. 3.1), the supracondylar ridge is absent in this genus, which does not allow a rotation of the paw (cf. Antón et al., 2009). Here, in one example figured (Fig. 4A), for a small lion (most probably female) from the Late Pleistocene of the Hermann’s Cave (Harz Mountain Range), the ridge is strong and about 2–3 mm wide – a level of development similar to that seen in modern and Middle to Late Pleistocene lions (P. l. leo, P. l. spelaeus, P. l. fossilis: cf. Dietrich, 1968; Diedrich, 2011a,b). On this ridge, the rotator musculature (Brachiaridialis) for the lower forelimb is attached to the radius (e.g. Frewein and Vollmerhaus, 1994; Antón et al., 2009) (Fig. 4A). This allows lions to catch its prey with the forelimb paws (Antón et al., 2009). It is much different in the saber-tooth cat Homotherium (as in hyenids, canids), where absence of the supracondylar ridge does not allow the forelimbs to be rotated and used in prey capture (Antón et al., 2009). Also, based on this osteological character, it is likely that the gait of Homotherium was “hyena-like” (Antón et al., 2005, 2009, 2014). The supracondylar ridge is also absent in the two distal humeri from the Zoolithen Cave and Ketsch river terrace site (Fig. 3). Using this very important osteological character, the felid humerus from Schöningen figured by Serangeli et al. (2015) (Fig. 4A) is a typical lion humerus by comparison to the H. crenatidens holotype humerus (cf. Ballesio, 1963; Fig. 3). Interestingly, the length of the supracondylar ridge is 5–10 mm shorter in the Schöningen specimen than in other Middle-Late Pleistocene lions, is some such as the Late Pleistocene Hermann’s Cave lion humerus (Fig. 4A). The Middle/Late Pleistocene lions from Germany are still in revision about this theme of “three different sized” forms (not variability nor sexual dimorphism) are not discussed herein further.

3.2. The humeri osteologic and biostratigraphic differences in H. crenatidens/latidens

The material from Germany is few and most is incomplete, but the humeri allow a new discussion to the validities of the Early H. crenatidens and Middle Pleistocene H. latidens species (Figs. 1 and 3). The humerus differences of both biostratigraphic relevant species seem not to relate to sexual dimorphism or variability in sizes, as thought to have been demonstrated for Pliocene saber-tooth cat mandibles of Europe and Northern America (Antón et al., 2014). As a simple fact of a strong faunal turnover between the Early/Mid-Pleistocene, it must be expected, that there was also a species change/evolutionary trend within Homotherium, similar as for other felids (e.g. Hemmer, 2004).

The Early Pleistocene holotype skeleton of H. crenatidens is recently under new studies, and original material was not possible include. The most obvious character to distinguish the humeri of H. crenatidens and H. latidens lies in the difference of the complete, and especially the distal shaft width, which is about 5 mm larger and more robust in the older H. crenatidens (Fig. 3). Based on the Early Pleistocene Senizee skeleton H. latidens humerus, the Early Pleistocene Homotherium humerus figured from the Spanish site Incarcal described as “H. latidens” (cf. Galobart et al., 2003; Antón et al., 2005) must be revised herein to belong to H. crenatidens, also correlating then with the biostatigraphy (Fig. 1B). Also Italian finds (cf. Sardella and Iurino, 2012) seem to belong to this older species.

The humeri from the Middle Pleistocene H. latidens are slimmer or gracile in their shafts in all herein figured English and Middle Pleistocene specimens (Fig. 2). The comparison between the humeri figured herein (Fig. 3) includes the “P. leo” humerus from the Cromerian West Runton interglacial MIS 19 (Stuart and Lister, 2010) site in England (cf. Lewis et al., 2010). This humerus is, compared to the H. crenatidens holotype humerus in same size and shape in the distal shaft width to the German finds (Fig. 2). The English West Runton site also delivered a calcaneus of H. latidens (Lewis et al., 2010), which finally supports the humerus identification.

3.3. Hyena bone damage versus human “bone tools”

The taphonomy of carnivore bone damage for the Schöningen site is misinterpreted in both papers of Berkholst (2015) and Serangeli et al. (2015). Furthermore, the carnivores were not yet well determined (c.f. Kolschoten, 2014), but are well known now in most cases (see Table 1). Older literature and important material has been overlooked, for example the only complete stripped hyena ancestor skull of Parahyaena brunnea mosbachensis (cf. Reichenau, 1906; Schütz, 1971), to which material another partial skull can be added from the Middle Pleistocene of the Upper Rhine Graben herein as very rare record in Central Europe (Fig. 3). The spotted and brown hyenas are still to be discussed, if those are late Early Pleistocene Parahyaena brunnea mosbachensis (in some cases Pachycrocuta: e.g. Palmqvist et al., 2011) or Crocuta crocuta praespeleae/ultima (cf. Schütz, 1971; Tseng and Chang, 2007) forms in the Middle-Pleistocene. Whereas Berkholst (2015) identified bite damage on a distal bovid tibia as “rodent bite marks”, those should have been compared to the larger rodent bite marks of species such as Pleistocene porcupines, which are completely different (cf. Diedrich, 2009). The bite marks on this bovid guilt bone (see Fig. 4B) are in fact typical large predator bite marks, based on bite mark analysis of large prey (e.g. elephants, rhinoceroses and even bisons: Diedrich, 2005, 2012, 2013b). Instead of classical “bite mark metric” analyses, the much more successful direct digital-projection test of the “bite-fit” into the bite marks of different predator candidates was applied to the lion humerus and the bovid tibia from Schöningen (Fig. 4B). The test of the largest predators Homotherium, Panthera, Hyaena and Crocuta dentitions demonstrates that in both cases only hyenas account for all the bite damage (see Fig. 4). Most convincing is the fit of the cutting scissor...
Fig. 4. A. Comparison of small-sized Middle-Late Pleistocene lion humeri (most probably females) and their taphonomic damage stages caused by different hyena species. The “non-Homotherium” distal humerus (modified from Serangeli et al., 2015) from the archaeological site Schöningen lake in comparison to similar sized lion humeri from Late Pleistocene German caves (1. Hermann’s Cave cave bear den, 2. Teufelskammer Cave hyena den). The typical lion character (Supracondylar ridge) and also much thicker and not oval shaft (cf. differences in Homotherium humeri Fig. 3) let identify this humerus fragment as a lion subspecies. Furthermore, the taphonomic felid humeri comparison demonstrate the chew/cut damage stages made by hyenas – most probably the Middle Pleistocene Parahyaena brunnea mosbachensis (new unpublished record added herein from the Rhine Graben, C.G. Diedrich, D.A. McFarlane / Quaternary International 436 (2017) 76–83.)
P4 tooth impact mark at the trochlea, which fits exactly to a H. h. mosbachensis bit into the lion humerus (Fig. 4A). The production of a very typical hyena-like diagonal cut, due to cutting the joint for dismembering the lower leg, can be compared to a Late Pleistocene spotted hyena (C. c. spelaea) cut on a steppe lion humerus (P. l. spelaea) (cf. Diedrich, 2011c). The same stripped hyena breaking scissor dentition fits then again (another possible candidate is the spotted hyena C. c. praespelaea/ultima) into the diagonal cut of the distal bovid tibia (Fig. 4B), which would be the second indirect prove for its short-time scavenging presence at the Schöningen site. In addition to the typical large hyenid bite marks on both, the bovid tibia and the felid humerus, the lion humerus also has very small 1–2 mm sized triangular bite impacts over larger parts of its shaft. Those were interpreted as anthropogenic “hit marks” as result of its use as a “Neanderthal bone tool” by Serangeli et al. (2015). In fact, these small triangular impacts are only marks of the molar teeth of medium-sized to smaller carnivores, especially their upper jaw M1–3 triangular coned teeth (Fig. 4C). The best candidates for these small bite impacts on the humerus shaft includes especially the Middle Pleistocene Cuon alpinus spelaeus, which is well known by bone material from the nearby Holsteinian to Saalian Complex dated Baumann’s Cave bear and Cuon den site (Diedrich, coll. Menger) which Upper jaw M1/P4 fits exactly in outline, morphology and size into the tooth bite marks of the of the trochlea. This makes sense, because hyenas use the breaking scissor teeth (see bite mark types and dentition in B) to dismember the leg parts and to cut of the joints. The Middle Pleistocene hyena most probably was the initial scavenger of a lion carcass which cracked the bone and chew damaged it on the distal lateral joint. The small triangular impact marks of the shaft “believed to be hit marks” are indeed well to identify as tooth impact marks of the red wolf Cuon alpinus subsp. (or small fox Vulpes praecorsac), which is found even in the Middle Pleistocene cave fauna of the Baumann’s Cave 30 km far from the Schöningen archaeological Neanderthal camp/hunting site. B. Distal tibia of a bovid from the Middle Pleistocene (MIS 9e) Schöningen lake site (from Berkholst, 2015), which shows B. The same diagonal cut and even better as the lion humerus (cf. Fig. 3A) more complete breaking scissor dentition impact tooth marks (outlines and tooth tips) of a hyena herein used the C. Dentition and bite marks of brown extinct hyena P. h. mosbachensis.
In any case, there is no reason to believe that the “Homotherium” humerus is from a sabre-tooth cat, nor are its triangular impact marks caused due to “tool use” by humans. This lion humerus is simply the product of interaction between carnivores (Fig. 5). A possible scenario is illustrated herein: a lion carcass – perhaps killed by hyenas (it can not be excluded that it have been killed by Neanderthals with spear weapons) – as a result of competing with humans over the remains of hunted horses, which was possible scenario is illustrated herein: a lion carcass from Schoningen, which can be attributed only to Panthera leo subsph. at the moment (most probably female), but not to the much larger Panthera onca fossilis (cf. Dietrich, 1968). This humerus is also far too large for P. o. gombaszoegensis. We can only speculate on the presence of this jaguar (e.g. Hemmer et al., 2013c; Cherin et al., 2014; Antron et al., 2014). Lions were present in the late Middle Pleistocene MIS 9e as demonstrated herein by the small-sized lion humerus from Schoningen, which can be attributed only to Panthera leo subsph. at the moment (most probably female), but not to the much larger P. l. fossilis (cf. Dietrich, 1968).

The carnivores of the Middle Pleistocene in Germany and Europe are in need of a larger-scaled taxonomic, taphonomic and ethologic revision, but at least five larger felids were in competition like Panthera leo fossils, Panthera onca gombazsogenises, Panthera pardus sickenbergi, Acinonyx pardensis intermedius, and Homotherium latidens (cf. Hemmer, 2004; Hemmer et al., 2011; Diedrich, 2013c; Cherin et al., 2014; Antron et al., 2014). Lions were present in the late Middle Pleistocene MIS 9e as demonstrated herein by the small-sized lion humerus from Schoningen, which can be attributed only to Panthera leo subsph. at the moment (most probably female), but not to the much larger P. l. fossilis (cf. Dietrich, 1968). This humerus is also far too large for P. o. gombazsogenises. We can only speculate on the presence of this jaguar (e.g. Hemmer et al., 2003) and the cheetah Acinonyx pardensis intermedius (e.g. Hemmer et al., 2011) at this time in the Schoningen/Harz Mountain forest region. Similar in size as modern forms were the early spotted hyenas described from a skull and scat material from the early Middle Pleistocene Mosbach site (Reichenau, 1906; Schütt, 1971). A new find of an incomplete skull from the Middle Pleistocene of the Rhine Graben (Fig. 4C) has similar dentition to the early brown hyena Parahyaena brunnea mosbachensis (Schütt, 1971). Possibly, an undescribed scapula from Schoningen of an older individual (with pathology) belongs to H. h. mosbachensis, which improves directly the carnivore biodiversity and presence of those striped hyenas at Schoningen (Table 1). Another hyena of this time is an early spotted hyena Crocuta crocuta praespelaea (Schütt, 1971) which was also found in the Mosbach carnivore fauna. Those two hyenids from the Middle Pleistocene of Europe must have competed with all felids, especially Homotherium. At Schoningen, the presence of striped hyena is indirectly proven by their bite marks on prey bones, which are also found at modern striped hyena den site bone accumulations (cf. Owens and Owens, 1979; Skinner and Van Aarde, 1991; Fourvel et al., 2015). An open air hyena den site (striped or spotted hyena) along the Mid-Pleistocene Schoningen Lake is not yet known, but at least some coprolites have been found (pers. com. Serangeli), which are the third indicator for short-time presence. Spotted hyenas C. c. praespelaea/ultima seem to have occupied during the late Mid-Pleistocene (Holsteinian/ Saalian) a former entrance at the 30 km nearby Baumann’s Cave (Diedrich, 2013a).

4. Conclusions

In Germany, there are few sites with isolated tooth and post-cranial bone remains of the Early Pleistocene Homotherium crenatisdens sabre-tooth cat (e.g. Untermassfeld), and the Middle Pleistocene Homotherium latidens with new records recorded herein: Balve Cave in the Sauerland Karst, Zoolithen Cave in the Frankonian Karst, Ketsch Rhine Terrace Upper Rhine Graben. The new Mid-Pleistocene H. latidens humeri are discussed along with the northern German Harz foreland Schoningen lake site incomplete felid humerus, which is revised to a smaller-sized lion or female due to absence of the supracondyliar ridge. The German saber-tooth cat H. latidens records seem to reflect “dispersal events” within interglacials, several times in the Cromerian Complex MIS during the MIS 19 Interglacial (Mosbach, West Runton), the MIS 15 and 11 as shown for Czech cave (Sluj IV) records, and in the MIS 9e Holsteinian Interglacial, (Schoningen). Possibly, sabre-tooth cats appeared again in the early Late Saalien two warm periods, the Wackenian and Lietian Interstadials (MIS 7a, c), but they reached not into the final Saalian (MIS 6) nor survived into the Late Pleistocene in Europe. No sabre-tooth cat is proven from an archaeological “killing” context. All known sabre-tooth cat remains are found in hyena den cave/open air sites or in carnivore conflict contexts, including the Schoningen Lake site. Bite marks on a bovid tibia and lion humerus from the Schoningen site can be demonstrated to have the same hyena breaking scissor tooth impact marks on their distal joints. Hyenas produced similar “diagonal cuts” at any gullies between joints for dismembering large body pieces (e.g. legs) of many those from the site to avoid further carnivore or even human conflicts. Those bone damages were left most probably at Schoningen and other Mid-Pleistocene sites by the early brown hyena Parahyaena brunnea mosbachensis (or spotted hyena Crocuta crocuta praespelaea/ultima), which is indirectly proven by its bite marks, and coprolites, and possibly directly by a scapula.

References


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