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Cracking and nibbling marks as indicators for the Upper Pleistocene spotted hyaena as a scavenger of cave bear (*Ursus spelaeus* ROSENMÜLLER 1794) carcasses in the Perick caves den of Northwest Germany

Zusammenfassung:

Viele Skelette und Einzelknochen von Höhlenbären wurden im 19. und 20. Jahrhundert in den Perick-Höhlen von Hemer bei Iserlohn (Sauerland, NW-Deutschland) gefunden. 2.404 Knochen wurden taxonomisch und taphonomisch untersucht. Der größte Teil (1.893) stammt vom Höhlenbären. Die Anwesenheit von 14 verschiedenen pleistozänen Großsäugern in der Heinrichshöhle, besonders 140 Knochen und drei Schädel der Fleckenhyäne, deuten jedoch darauf hin, daß das Perick-Höhlen-System ein typischer Hyänenhorst war. Dieser wurde im Mittel-Weichsel (Oberpleistozän) genutzt, nach Datierungen an Höhlenbärenzähnen und dem Schnitt. Die meisten Beutetierknochen aller pleistozänen Tiere weisen Biß- und Nagespuren auf. 778 Höhlenbärenknochen sind angeknabbert, angenagt oder gebrochen (41% der Höhlenbärenknochen). Die starke Zerstörung der *Ursus spelaeus*-Knochen durch *Crocuta crocuta spelaea* sieht man an jedem Knochentyp, qualitativ besonders an dem adulten Knochenmaterial, aber auch an juvenilen Knochenresten. Der massive Knochenschaft war in vielen Fällen zerbrochen worden, um an das Knochenmark zu kommen. Zum Schluß wurden Fragmente zu „Knabbersticks" zerknabbert. Die Knochenzerstörung ist wichtig für das Verständnis der taphonomischen Erscheinungen in Höhlenbärenhöhlen, in denen weder Hyänenknochen noch Beutereste von Hyänen gefunden werden. Der Vergleich der Knochen aus den Perick-Höhlen mit Material aus anderen Höhlen im nördlichen Sauerland und aus weiteren europäischen Höhlen verweist auf das regelmäßige Auftreten der Fleckenhyäne in vielen Höhlenbärenhöhlen. Hier müssen sie sich regelmäßig von Höhlenbären-Kadavern ernährt haben, wobei sie in vielen Fällen die Skelette völlig zerstörten. Die fünf Hyänenhorste, besonders die Perick-Höhlen, zeigen eine Beute-Spezialisierung der Hyänenclans auf Höhlenbären-Kadaver. Hier machen die Beute-Knochen der Höhlenbären 66% aller Beute-Knochen aus. Dieses Fressen von Höhlenbären-Kadavern muß hauptsächlich während des Frühjahrs in den

Höhlenbärenhöhlen stattgefunden haben, wenn sehr alte Höhlenbären nicht mehr aus der Winterruhe erwachten. *Ursus spelaeus*-Knochen zeigen in diesen Höhlen typische Zerkauungsspuren und sind meist in hunderte von kleinen Stücken zerbrochen. Auch in anderen Höhlen des Sauerlandes, in denen keine Hyänenknochen gefunden wurden, wurden Höhlenbären-Kadaver oft durch Hyänen zerstört. Das Vorhandensein typischer Biß-merkmale verweist auf die periodische Anwesenheit von Fleckenhyänen, die als pleistozäne Gesundheitspolizei die Mammutsteppe und die Höhlen reinigten.

Summary:

Many skeletons and isolated bones of cave bears were found in the 19. and 20. Century at the Perick caves, Hemer near Iserlohn (Sauerland, NW Germany). 2.404 bones were studied taxonomically and taphonomically. Most of them (1.893) are cave bear bones, but the presence of 14 different large Pleistocene mammals in the Heinrichscave, especially 140 bones and three skulls of the spotted hyaena, indicate a typical hyaena den at the Perick cave system. This was used in the Middle Weichsel (Upper Pleistocene) dated by cave bear teeth and the section. Most prey bones of all Pleistocene animals expose bite and gnaw marks. 778 cave bear bones are nibbled, gnawn or cracked (41% of the cave bear bones). The strong destruction of *Ursus spelaeus* bones by *Crocuta crocuta spelaea* is shown for each bone type qualitatively especially at adult bone material, but also at juvenile bone remains. The massive bone shaft was cracked in many cases for getting the bone marrow. Finally fragments were nibbled to „nibble sticks". The bone destruction is important to understand the taphonomy in cave bear caves, in which no hyaena bones or preys of hyaenas occur. The comparison of the Perick caves bones to material of other caves in the northern Sauerland and other European caves indicate the periodical presence of the spotted hyaena in many cave bear dens. Here they must have feeded on the carcasses of cave bears periodically, destroying skeletons in many cases completely. The five hyaena dens, especially the Perick caves, show a prey specialization of hyaena clans feeding onto cave bear carcasses. Here the prey bones of cave bears counts 66% of all prey bones. This cave bear feeding must have happened primary during spring time in the cave bear dens, when senile cave bears did not wake up out of the winter rest period. In these caves *Ursus spelaeus* bones possesses typical chewing marks and are mostly cracked into hundreds of small pieces. In other caves in the Sauerland, in which no hyaena bones were found, cave bear carcasses were also often destroyed by hyaenas. The presence of typical bite structures indicates the periodical presence of spotted hyaenas, being the Pleistocene health police cleaning the mammoth steppe and the caves.

Résumé:

De nombreux squelettes et ossements isolés d'ours des cavernes ont été trouvés dans le courant des 19^{e} et 20^{e} siècles dans les grottes de Perick

d'Hemer non loin d'Iserlohn (Sauerland, nord-est de l'Allemagne). 2404 ossements ont été étudiés d'un point de vue taxonomique et taphonomique. La plus grande partie (1893) provient de l'ours des cavernes. La présence de 14 espèces différentes de grands mammifères pléistocènes dans la grotte de Heinrich (Heinrichshöhle), en particulier de trois crânes et de 140 ossements d'hyène tachetée, indiquent que le système karstique de Perick était un refuge d'hyènes typique. La plupart des ossements des proie ont été mordus et rognés. 778 ossements d'ours des cavernes (41%) présentent des morsures et des cassures. La destruction intensive des restes d'*Ursus spelaeus* par *Crocuta crocuta spelaea* est présente sur tous les éléments du squelette, particulièrement sur les ossements d'adultes, mais les restes d'individus juvéniles n'ont pas été épargnés. Les os longs sont brisés, probablement pour accéder à la moelle. Ces fragments ont été à leur tour rongés. L'observation de la destruction des ossements est importante pour permettre de comprendre les phénomènes de taphonomie dans les grottes à ours dans lesquelles aucuns restes, ni d'hyènes ni de leurs proies, n'ont été découverts. La comparaison des ossements provenant des grottes de Perick avec du matériel provenant d'autres grottes du Sauerland et d'Europe indique que l'hyène tachetée a visité régulièrement de nombreuses grottes à ours. Elles se sont probablement nourries périodiquement des cadavres d'ours, détruisant souvent complètement le squelette. Les cinq refuges d'hyènes étudiés, en particulier les grottes de Perick, montrent une spécialisation de l'hyène sur les cadavres d'ours des cavernes, car les ossements d'ours représentent 66% de tous les restes des proie. La consommation des cadavres a du avoir lieu principalement durant le printemps, après l'hibernation dont certains animaux ne se réveillèrent pas. Dans d'autres grottes du Sauerland, dans lesquelles aucuns restes d'hyènes ne furent découverts, les cadavres d'ours ont souvent été détruits par des hyènes. La présence de marques de morsure typiques indique une présence périodique des hyènes tachetées.

Key words: *Ursus spelaeus*, *Crocuta crocuta spelaea*, scavenging, Pleistocene, Perick caves

1. Introduction

Cave bears were known since the 18th century from Northwest-German caves of the Sauerland (cf. Zygowski 1988, Hammerschmidt et al. 1995, Rosendahl & Marks 2002, Diedrich 2005c). A few cave bear material was listed by Siegfried (1983) from more than ten caves. Outcave remains were first described from river gravel deposits north of the Sauerland caves in the Münsterland Bay at three localities (Diedrich 2004a). The cave hyaenas are studied now for the first time in northern Germany systematically where the main hyaena den sites in the northern Sauerland mountainous region are known yet (Diedrich 2004b). Indirect proof of these ice age carnivores was shown by nibbled and gnawn prey bones also at many open-air sites, where no hyaena bones were found (Fig. 1, and Diedrich 2004b). The

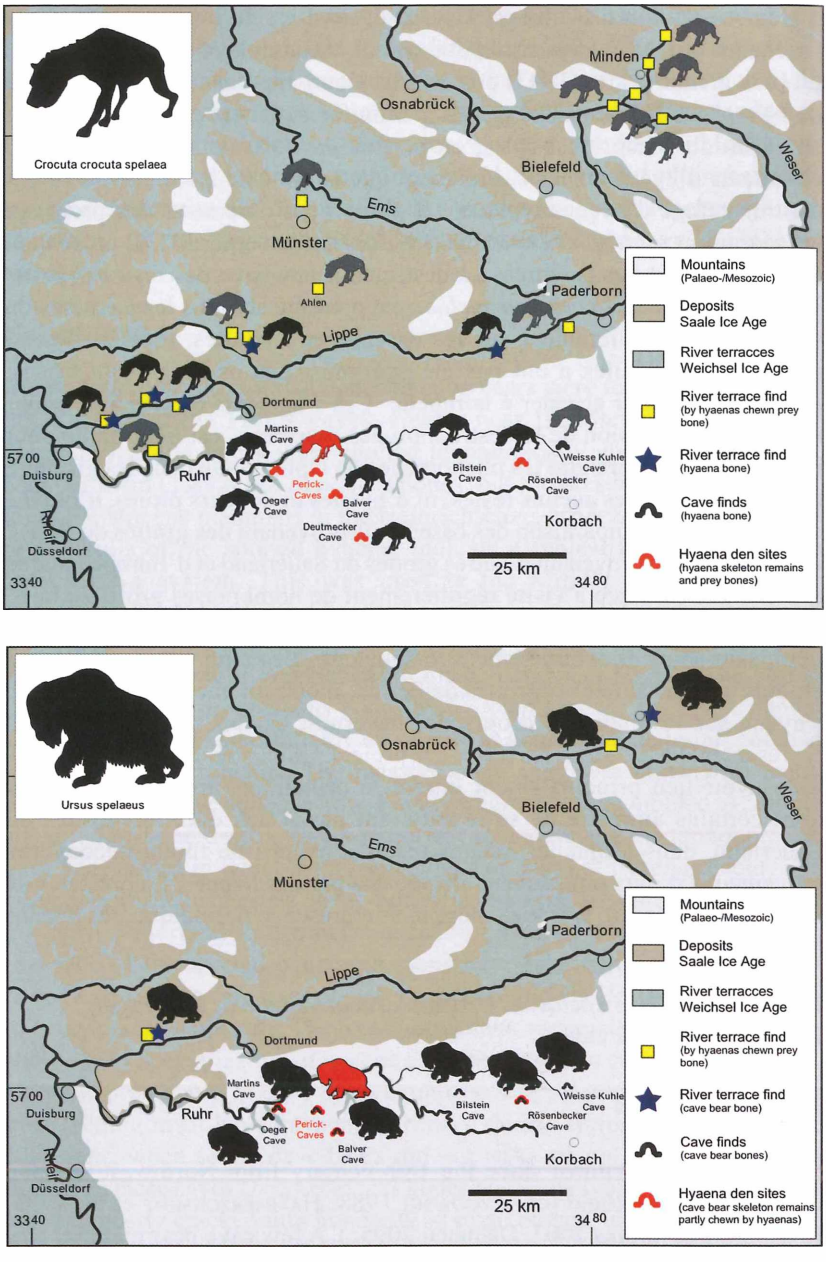


Figure 1. Position of the Upper Pleistocene hyaena and cave bear den caves (Heinrichscave, Martins cave, Deutmecker cave, Roesenbeck cave, Balve Cave etc.) and other open-air sites at the Emscher and Lippe river. Hyaena gnawn bones of *Coelodonta antiquitatis* and *Mammuthus primigenius* were found at many free land sites being an indirect proof of theses animals in the Münster Basin and northern the Wiehengebirge during the mammoth steppe period of the late Weichsel. In the Perick caves and Martins cave e.g. hyaenas feeded strongly on the cave bear carcasses.

subdividing hyaena from cave bear dens is of importance to understand the palaeoecology of both extinct animals in detail. Especially the question of the feeding habits or specialization of the hyaenas onto a few ice age animals and the possible use of caves of both animals at the same time or even period will become clearer.

In the 19th century the well known French biologist CUVIER described 1805 the first Pleistocene spotted hyaena bones (old name = cave hyaena) and in

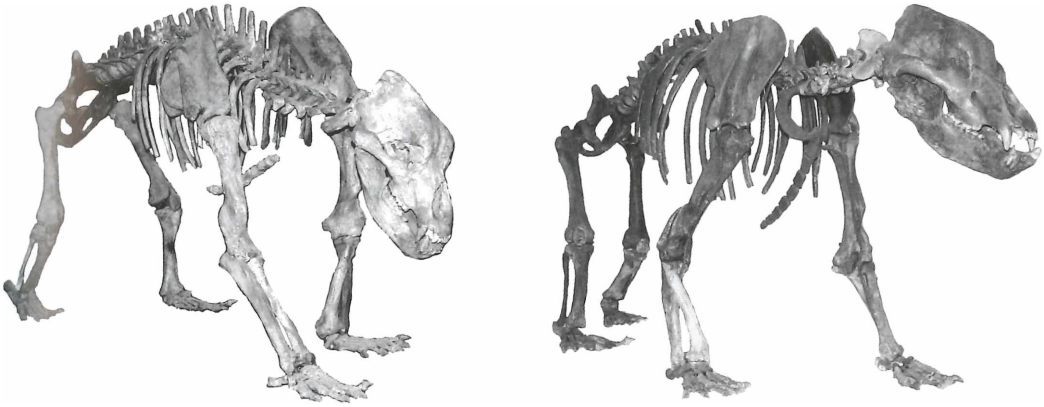


Figure 2. A. Skeleton of the cave bear *Ursus spelaeus* ROSENMÜLLER 1794 created of bones from different individuals of the Perick caves, Sauerland. Exposed in the permanent exhibition of the Geologisch-Paläontologisches Museum of the Westphalian Wilhelms-University Münster. **B.** Another skeleton of *Ursus spelaeus* ROSENMÜLLER 1794 mounted by bones of different individuals from the Perick caves, Sauerland. Presented in the permanent exhibition of the Emschertalmuseum Schloß Strünckede Herne.

1806 cave bear remains from the „Sundwigcave" near Iserlohn. With many spade digs in the 19th century by NÖGGERATH (1823, 1824), SACK (described by GIEBEL 1842), KLAATSCH (1904) and later by MEISE (1926) many bones were found in the Sundwig- and the Heinrichscave building the connected Perick caves system (Cave Kataster No. 4612/001-4, cf. WEBER 1989). Most of the material was sold to museums in Europe (e.g. London, Berlin, Dresden). More than five skeletons were mounted of the cave bear bones. These are recently in the collections of the British Museum of Natural History London, in the Humboldt-Museum Berlin, the Geologisch-Paläontologisches Museum of the Westphalian Wilhelms-University Münster (Fig. 2A), the Felsenmeermuseum Hemer, Emschertalmuseum Schloß Strünckede Herne (Fig. 2B) and finally in the Heinrichscave itself.

The rediscovery of additional 2.404 bones in six different collections from both cave parts (Sundwig-, Heinrichscave), allowed a first detailed study of a combined spotted hyaena and cave bear den in the Sauerland. Here for the first time a typical ice age fauna of the late Weichsel period with *Mammuthus primigenius* BLUMENBACH 1799, *Coelodonta antiquitatis* BLUMENBACH 1807, *Rangifer tarandus* LINNÉ 1758, *Megaloceros giganteus* (BLUMENBACH 1799), *Cervus elaphus* LINNÉ 1758, *Bison priscus* BOJANUS 1827, *Equus ferus przewalskii* POLJAKOFF 1881, *Ursus spelaeus* ROSENMÜLLER 1794, *Panthera leo spelaea* (GOLDFUSS 1810), *Crocuta crocuta spelaea* (GOLDFUSS 1823), *Canis lupus* LINNÉ 1758, *Alopex lagopus* (LINNÉ 1758), and *Gulo gulo* (LINNÉ 1758) can be listed.

First P4-observations at some cave bear teeth from the Heinrichscave date into the maximum glaciations during the late Weichsel/Würm period (cf. DIEDRICH 2005c) and correspond to the mammoth steppe fauna found in the caves which were deposited by the ice age spotted hyaena *Crocuta crocuta spelaea* (GOLDFUSS 1823).

The most important refinds are 140 bones and three skulls of the Pleistocene spotted hyaena studied for the first time (DIEDRICH 2005a). Especially hyaenas from Westphalian Sauerland caves were poorly mentioned and analyzed with a few remains by HELLER (1960) and SIEGFRIED (1961, 1983). This and many new rediscovered material in the collections material was studied

new and the few important outcave bones were still published (DIEDRICH 2004b). A new study of more than 400 rediscovered hyaena bones and teeth from many caves of the northern Sauerland (NW Germany), also the Perick caves, is in progress. This is very important for the understanding of the bone taphonomy in the Sauerland caves, always only described as „cave bear dens". Only a few spotted hyaena dens were mentioned and are not well analyzed in south and East Germany by the old publications of LIEBE (1876), SOERGEL (1937), and EHRENBERG et al. (1938). Modern digs and studies are lacking.

The *U. spelaeus* population from the Perick caves is recently studied by DIEDRICH (2005c). A short list and some photos of other well preserved material from Berlin can be found in LASS (1998). This selected bone material has primary no gnaw marks, typical of many museums collections. Here only jaws, skulls, skeletons and a few complete bones were sold from Mr. Meise in 1905 and 1906 to the Museum in Berlin. The „bad preserved bones and fragments" were selected and left fortunately on a „bone dump" in the visitor Heinrichscave about 100 years. The remixing of the well preserved and gnawn and cracked bones of different collections allow for the first time a qualitative and quantitative statistical analysis, 1.893 of them representing cave bear bones. The total bone percentage of the ice age mammals found in the Perick-caves is shown in Fig. 10.

The studied collections are the following: Staatliche Naturhistorische Sammlung Dresden (SNSD), Naturkundemuseum Bielefeld (NB), Geologisch-Paläontologisches Institut der Westfälischen Wilhelms-Universität Münster (GPIM), Eiszeithalle Quadrat Bottrop (EQB), and Heinrichscave (HC). All studied collections were thankfully loaned by the museums for a new permanent exhibition in the Heinrichscave opening in 2005/6.

2. Taphonomy

First detailed gnaw marks of the spotted hyaenas at bones from Upper Pleistocene mammals such as woolly rhinoceros or mammoth were figured by ZAPFE (1939), THENIUS (1961), and HELLER (1962). The latter discussed the „Osteodontoceratic Culture". In former times scientists believed the presence of humans that caused the nibbling marks. This old interpretation can be disproved not only here. In a new study of the taphonomy of *M. primigenius* bones the massive impact of ice age spotted hyaenas was shown for carcasses and isolated bones of German sites.

The most material (cave bears, 18 skulls were mentioned) were found in the western Perick caves system, the "Sundwigcave" or today named "Alte Höhle" (cf. NÖGGERATH 1823, 1824). Another proof for a cave bear den are polished edges (Fig. 3). The close connected Heinrichscave seems to be the hyaena den in which most prey bones and many gnawn cave bear and other prey bones were rediscovered on the bone dump in the cave of which the cave bear bones are described here.

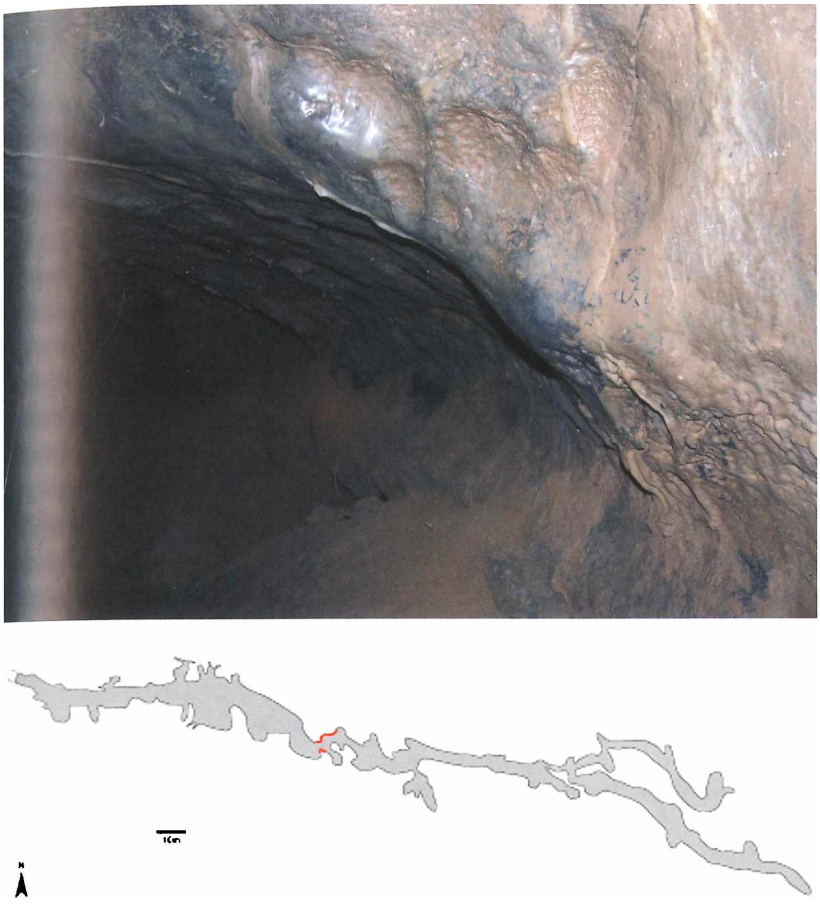


Figure 3. *Ursus spelaeus* polished edge („cave bear polish") in the Sundwigcave (= „Old cave", part of the Perick caves at Hemer, 150 m far away from the cave entrance). During the Upper Weichsel/ Würm period the distance between the floor and the roof measured only 1,2 m. Therefore the adult *Ursus spelaeus* scratched along the edge built of Devonian reef limestones. In this 50 m in length and at many places polished part of the cave winter beds of the bears must have been existed also indicated by in situ bone material. Below: Plan of the main part of Alte Höhle (Höhlenkataster No. 4612/001), Part of the Perick cave system.

The specialized dentition of the hyaenas was used for different feeding activities (cf. also SUTCLIFFE 1970). The teeth left different tooth marks on bones depending on their activity (Fig. 4). All these types of marks were found extensively on the Perick caves bones. The most effective part of the jaws was on the one hand the jaw-cracking scissor built by the last huge teeth (upper jaw P4, lower jaw M1). With this meat, cartilage and even soft bone joints were cut and eaten. On the other hand the bone cracking took place in between the lower jaw P3-4 and upper jaw P3. With these triangular positioned teeth an effective bone cracker jaw was produced to break massive bones and reach their marrow. Bone fragments also were swallowing because the hyaenas could digest the bone collagen.

Normally three stages of the bone destruction can be observed at long bones. At first the soft joints were gnawn off. After this, some bone fragments were cracked from the bone shaft that was finally cracked completely. In some cases, the bones were cracked directly before gnawing. Many bone fragments were rounded at their ends and points out in a tip as a result of intensive nibbling. Such bones are named here "nibbling sticks".

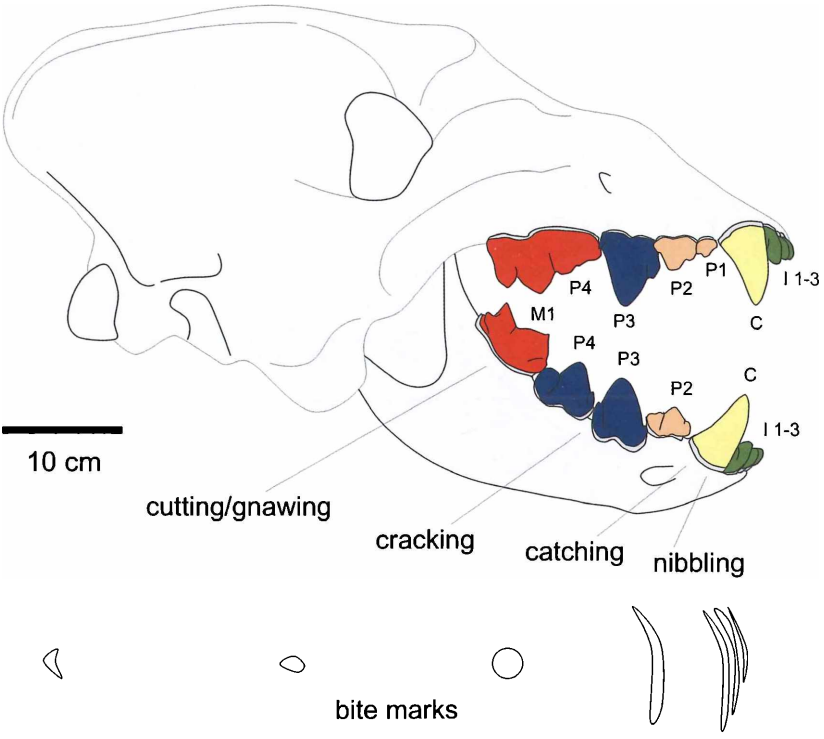
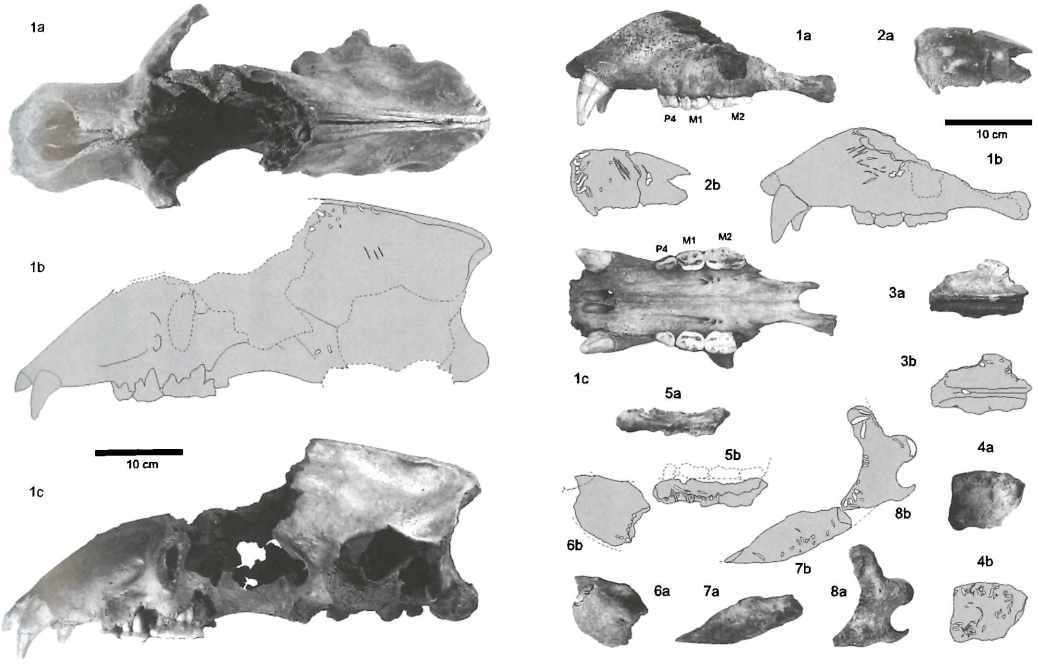


Figure. 4. Specialized bone cracker and nibbler jaws of the Upper Pleistocene spotted hyaena *Crocuta crocuta spelaea* (GOLDFUSS 1823). The lower jaw M1 and Upper jaw P4 were used for cutting meat and soft bone joints. Where these chewn off, the massive middle bone shafts were cracked between the UJ P3 and the LJ P3-4 to reach the bone marrow. Meat and bones were nibbled by the incisive.

In the following the different bone types and their nibbling and gnawing marks are described and figured:

Cranium:
A typical skull in the middle stage of gnawing destruction of a female cave bear represents the lacking of the frontal region and the jugals (Fig. 5A). There are more skull fragments of adult and young cave bears that resulted of the skull cracking (Fig. 5B.1-4). Naturally the brain was mainly of interest for the hyaenas. A clear system of skull destructions can not be observed yet. Some skull fragments of the parietal, frontal and other skull elements of adult and juvenile cave bears with bite marks proof the skull destruction by hyaenas. Also the break of the bow like jugals seems to be the result of massive cracking activities. The same hyaena bite and gnaw structures were remembered at cave bear cranium material from the Martins cave hyaena den (coll. GPIM).

Mandible:
Many lower jaws were cracked into pieces. It is not clear, if they were broken out of the top skull first, but in some cases it seemed to be. There are some jaws lacking the posterior part with the jaw joint and the ramus. This mandible preservation is typical for other carnivores such as the ice age wolf, hyaena or lion, too. It is the result of strong pressure by breaking the lower jaws out of the top skull. By the cracking of isolated jaws some

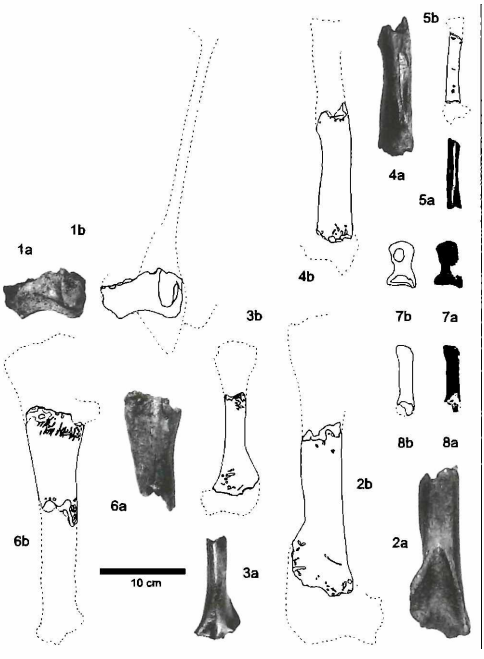


typical fragments were produced by hyaenas. The different fragment types of the mandible are figured here (Fig. 5B.5-8). In many cases the ramus and jaw joint (Proc. articularis) were gnawn or cracked off (Fig. 5B.8). Other fragment types are the basal mandible (Fig. 5B.7), a middle upper part of the central (Fig. 5B.5) with the teeth and finally the symphyseal area (Fig. 5B.6). In some cases the lower jaws were cracked in the middle into two pieces. Only the successful cracking into many pieces have brought the interesting bone marrow for the hyaenas. The bite and cracking structures were compared to cave bear cranium material from the Martins cave hyaena den (coll. GPIM), that show the same cracking and chewing structures.

Scapula:

The fragile and in most parts thin or soft scapula was destroyed in most cases nearly completely. Only the Fossa articularis was left in most cases (Fig. 6A.1). This bone part is also soft; therefore it must have been articulated to the humerus joint during the carcass destruction. It proves that hyaenas disrupted sometimes the foreleg out of the body carcass, after eating parts bone tendons, cartilage and musculature of the shoulder girdle. The same preservations of hyaena eaten scapulae and their remains

Figure 5. A. By spotted hyaenas gnawn top skull of a high adult to senile female cave bear from the Perick caves. Especially the frontal was eaten completely; also the jugals were broken off (SNSD No. Sundwig-316). a. Dorsal, b. Lateral, redrawing, c. Lateral. Grey: Bone position, White: gnawn off parts. **B.** By Upper Pleistocene spotted hyaena's gnawn and cracked skulls and lower jaws of early juvenile and adult individuals. **1.** Anterior skull remains (maxillas, praemaxillas etc.) of an adult cave bear (SNSD No. Sundwig-314), a-b. lateral, c. ventral. **2.** Right parietal and frontal of an individual less then 5 months of age with bite scratches and bite holes (HC No. Hemer-714), lateral. **3.** Fused parietal crest fragment of an adult to senile individual with cracking and bite marks (HC No. Hemer-715), dorsal. **4.** Left parietal of an individual of less then one year of age with bite marks (HC No. Hemer-707), lateral. **5.** Upper middle part with alveolars of the premolars and molars of an adult animal (HC No. Hemer-709), lateral left. **6.** Anterior fragment with canine's alveolar of an adult animal (HC No. Hemer-873). **7.** Posterior lower part of an adult animal (HC No. Hemer-545), lateral left. **8.** Jaw joint and ramus fragment of an adult animal (HC No. Hemer-67), lateral left. Grey: bone position, White: Nibbling notches and imprints.



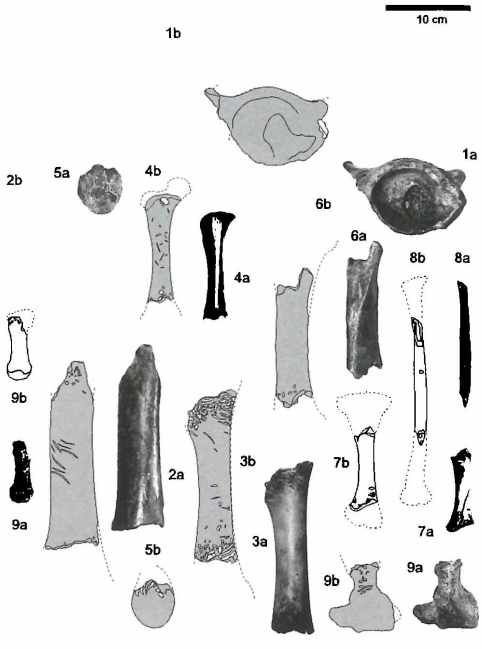


Figure 6. A. By Upper Pleistocene spotted hyaenas gnawn and cracked foreleg bones of some individuals. **1.** Joint of the left scapula (HC No. Hemer-695), lateral. **2.** Middle shaft of a left humerus of an adult animal (HC No. Hemer-226), caudal. **3.** Middle shaft of a left humerus of an about two months old animal (Hemer-887), cranial. **4.** Middle shaft of a left radius of an adult animal (HC No. Hemer-30), cranial. **5.** Middle shaft of a left radius of an about two months old animal (Hemer-886), cranial. **6.** Middle shaft of a left ulna of an adult animal (HC No. 324), lateral. **7.** Right pisiform of an adult animal (HC No. Hemer-711), lateral. **8.** Right metacarpal IV of an adult animal (HC No. Hemer-702), cranial. Grey: bone position, White: Nibbling notches and imprints. **B.** By Upper Pleistocene spotted hyaenas gnawn and cracked hind leg bones of some individuals. **1.** Left acetabulum of the pelvis of an adult animal (HC No. Hemer-354), lateral. **2.** Central shaft of a left femur of an adult animal (HC No. Heinr-274), cranial. **3.** Central shaft of a right femur from an about six months old animal (Hemer-851), cranial. **4.** Central shaft of a right femur from an about two months old animal (Hemer-883), cranial. **5.** Patella of an adult animal (HC No. Hemer-694), cranial. **6.** Central shaft of a left tibia of an adult animal (HC No. Hemer-63), cranial. **7.** Central shaft of a right tibia of an about two months old animal (Hemer-1478), cranial. **8.** Central shaft of a right fibula of an adult animal (HC No. Hemer-692), cranial. **9.** Right calcaneus of an adult animal (HC No. Hemer-691), dorsal. **10.** Left metatarsus I of an adult animal (HC No. Hemer-693), dorsal. Grey: bone position, White: Nibbling notches and imprints.

were found in the cave bear material from the Martins cave (coll. GPIM).

Humerus:

Most of the humeri of adult (but also of juveniles) cave bears lack their joints and the distal shaft parts as a result of gnawing (Fig. 6A.2-3). The non-fused very soft joints at juvenile bones were eaten completely and easily by the hyaenas. Therefore in most cases only the shaft of the foreleg bone is preserved, even if it is not cracked into some pieces for getting the bone marrow (Fig. 8A). Sometimes the bone shaft was not cracked into pieces and bite marks at the ends indicate the gnawing of the joints and softer shaft parts. In a few cases humerus fragments were used finally as "nibbling sticks" (Fig. 9.1-2). Some humeri from the Martins cave hyaena den (coll. GPIM) are absolutely similar to the described Heinrichscave material.

Radius:

In most cases both joints are gnawn off completely (Fig 6A.4-5). In a few cases the proximal joint head is preserved, the distal lacks generally. Also at this bone type it is obvious, that the radius

was cracked sometimes immediately before gnawing, also indicated by many bone fragments (Fig. 8C). The radius proves together with the ulna by gnawn of distal joints the separation or eating of the manus and pes of the cave bear carcasses by the hyaenas. This happened also in the Martins cave den, where many radii expose similar preservation types (coll. GPIM).

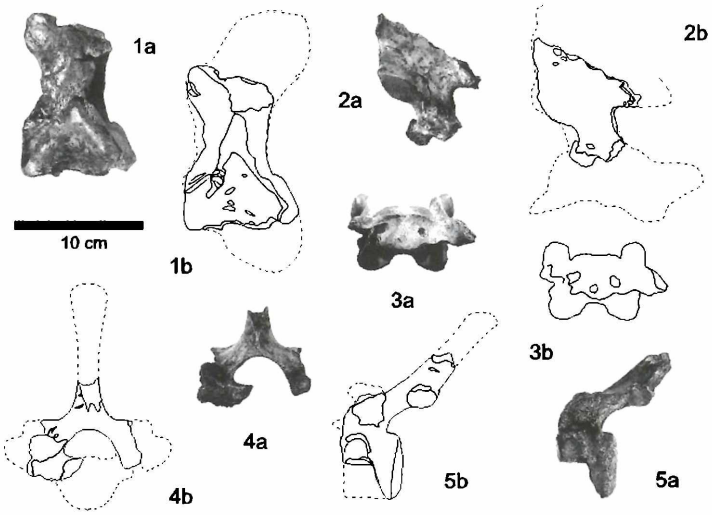


Figure 7. By Upper Pleistocene spotted hyaenas gnawn and nibbled vertebrae of early adult to senile individuals. **1.** Atlas with gnaw lateral wing like Proc. transverse (HC No. Hemer-699), dorsal. **2.** Proc. spinosus of the axes, the centrum, Proc. transverse and top of the Proc. spinosus are gnawing of (HC No. Hemer-697), lateral. **3.** Cervical vertebra with round to oval canines imprints in the soft centrum (HC No. Hemer-836), ventral. **4.** Proc. spinosus and fragments of the transverse of an anterior thoracic vertebra, the centrum was eaten completely (HC No. Hemer-689), cranial. **5.** Middle thoracic vertebra with lacking of the distal points of the Processes, one fourth of the centrum was bitten away whereas the imprint of canines is remarkable (HC No. Hemer-361), lateral left. Grey: bone position, White: Nibbling notches and imprints.

Ulna:
From this bone type the hyaenas normally left parts of the proximal joint, whereas the distal one lacks commonly. In some cases the proximal joint was eaten completely (Fig. 6A.6). Cracked and gnawn off distal joints prove the direct bone cracking of the long bone and the separation (or even eating) of the feet of the cave bear carcasses. The bone cracking of the shaft is not surprising, because the bone marrow was of interest to the hyaenas. Therefore many of these bones were crushed into pieces (Fig. 8B). The typical bone rests that left hyaenas were also found in the Martins cave hyaena den (coll. GPIM).

Pisiform:
At one of this manus bones some laterally chewn parts could be recognized (Fig. 6A.7).

Metacarpus:
Sometimes metacarpals have round to oval bite marks, being similar to the ones at metatarsals, vertebra centra, and the pelvis bone or rarely in skull fragments. Only in a few cases the distal joint was gnawn off (Fig. 6A.8). The biting marks could be the result of separating and pulling of the manus from the bear carcasses, but there are not enough bones for an exact analysis and interpretation at the moment.

Pelvis:
This bone type is completely spongios and soft. The hyaenas started gnawing and eating the bone from all sides without a clear system, like they did with the vertebral column. Ilium, Ischium and Pubis were gnawn from their distal parts. Often round and deep bite mark impressions of the hyaena canine are well preserved in the soft bones. After pulling out the pelvis out of the carcass and intensive gnawing at least the hyaenas left only the most central joint articulation

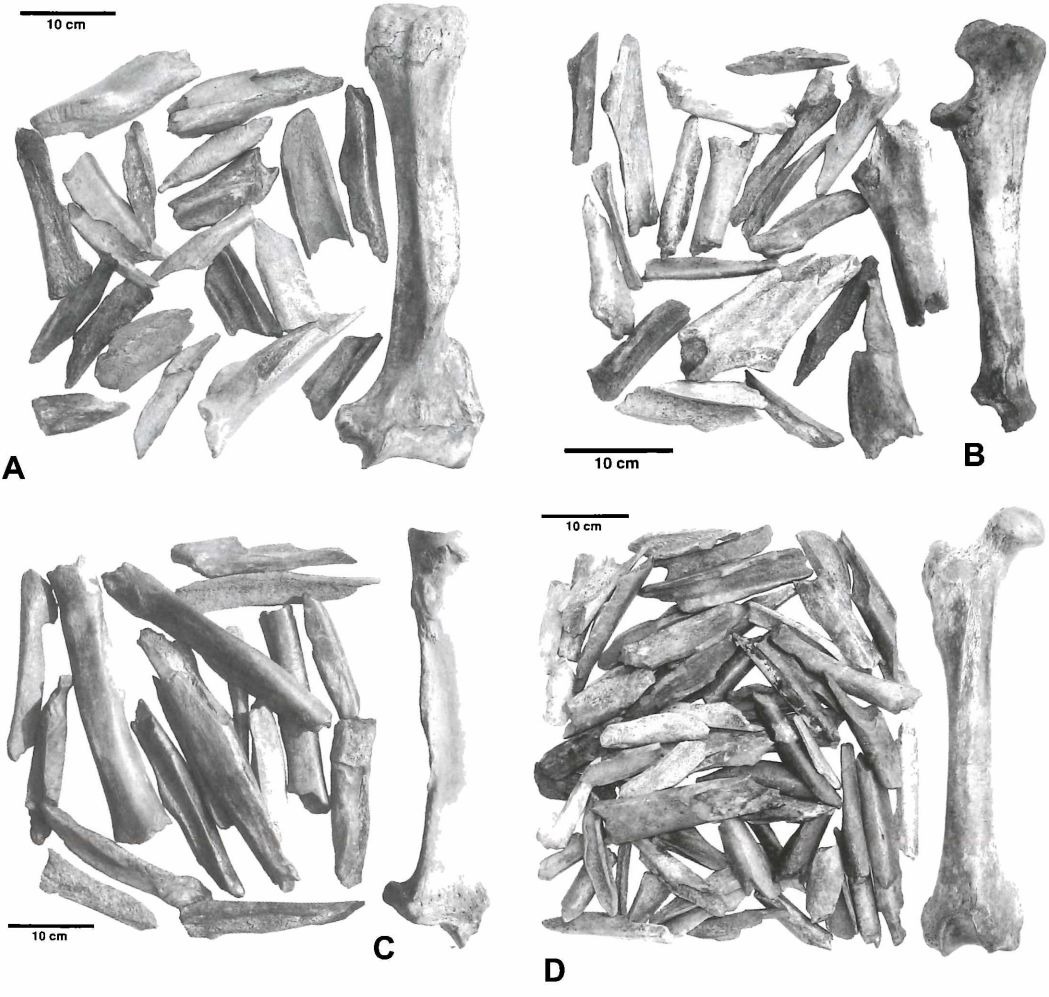


Figure 8.
By Upper Pleistocene spotted hyaenas cracked cave bear bones from the Heinrichscave den.
A. Humeri (right complete) of adult to senile individuals. Complete right humerus (right) (HC No. Sundwig-478), bone fragments (left) (HC No. Hemer-1362-1364, 1366, 1508-1523).
B. Ulnae (right complete) of adult to senile individuals. Complete right ulna (right) (HC No. Heinr-32), bone fragments (left) (HC No. Hemer-1440-1459).
C. Radii (right complete) of adult to senile individuals. Complete right radius (right) (HC No. Heinr-33), bone fragments (left) (HC No. Hemer-1524-1540).
D. Femora of adult to senile individuals from the Heinrichscave eyrie. Complete right femur (right) (HC No. Sundwig-469), bone fragments (left) (HC No. Hemer-1372-1439).
E. Tibiae of adult to senile individuals from the Heinrichscave. Complete left tibia (right) (HC No. Hemer-229), bone fragments (left) (HC No. Hemer-1460-1507).

area (Fig. 6B.1). It also might be the result comparable to the shoulder girdle. The hyaenas tried to pull out the hind limb from the pelvic girdle, where they sometimes had to destruct the pelvis. One articulated femur proximal joint connected with the pelvic acetabulum prove the technique of isolating the hind limb from the carcass by destroying first the pelvic girdle.

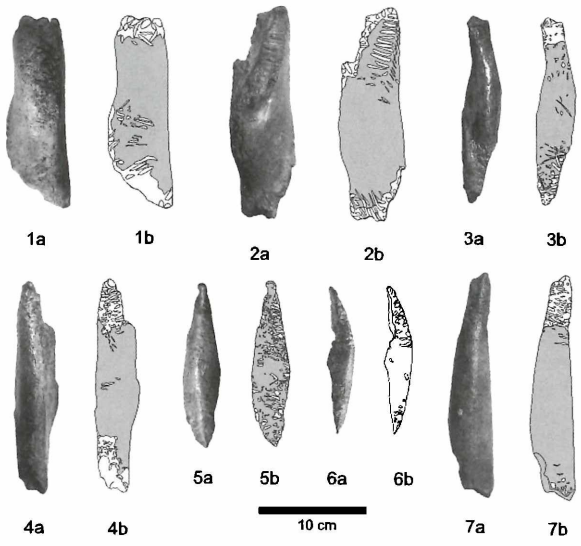


Figure 9. Nibbling sticks of bones from adult animals. a. Photo, b. Redrawing (grey - bone, white - bite marks).
1. Humerus shaft nibbling stick, Sundwig-485.
2. Humerus shaft nibbling stick, Hemer-1366.
3. Humerus shaft nibbling stick, Hemer-1363.
4. Radius shaft nibbling stick, Hemer-1364.
5. Humerus shaft nibbling stick, Hemer-1362.
6. Mandibula Humerus ? nibbling stick, Hemer-696.
7. Femur shaft nibbling stick, Hemer-1356.

Femur:
The hyaenas used mostly other ways to isolate hind limbs from cave bear carcasses by cutting the musculature between femur and pelvis and pulling out the femur out of the acetabulum. After the successful hind limb or even femur isolation both joints were almost gnawn off. Therefore in many cases only short central bone shafts were found in the cave and are comparable to material found in the Martins cave hyaena den (coll. GPIM). Many of these are from the lower shaft (Fig. 6B.2-4), because of its thicker bone walls and more stable round cross section. In the upper bone shaft the femur is more oval in cross section and the bone thinner, that means more easier to crack. Hundreds of bone fragments are the result of cracked femora shafts, which contained the most bone marrow, than any other bone (Fig. 8D). It is interesting, that these splitters only rarely were finally used by the hyaenas as "nibbling sticks" (Fig. 9.7). The very rare use of cave bear bones as such nibbling sticks is obvious. Bone fragments of all other hyaena preys of the studied Heinrichscave bone material show more intensive gnawing and a higher percentage of nibbling sticks. Only whoolly rhinoceros bones show the same rare use as nibbling sticks, but this is more the result of the different bone structure of *C. antiquitatis* bones. They are more spongios filled and do not crack easily into fragments. The reason for the low number of cave bear nibbling sticks is unclear at the moment. It is maybe a result of the different bone collagen or the use of more fresh carcasses of non-bear preys, and a use of old meatless cave bear skeletons?

Patella:
Only one patella of the few material exposes well preserved nibbling marks (Fig. 6B.5). These completely spongios bones were easily destroyed by the hyaenas. A systematic nibbling at this bone type was surely not present and bite marks seems to be more lucky circumstances. Surely they must have happened by the separation of the femur and the tibia.

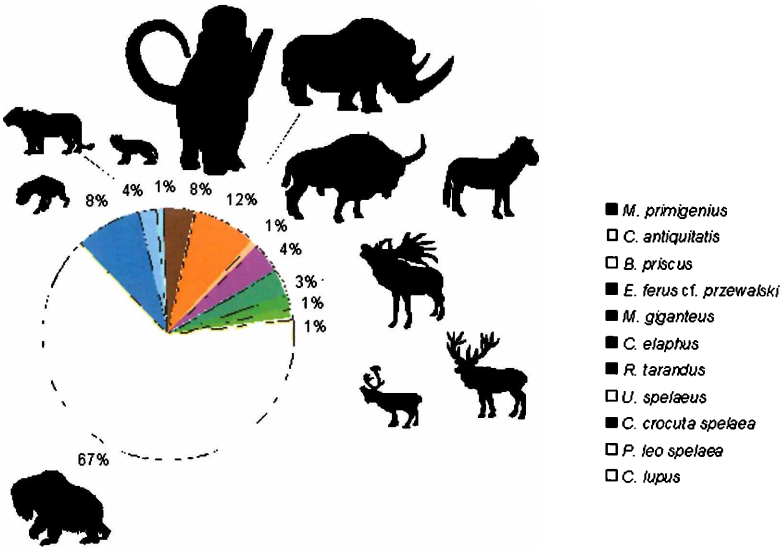


Figure 10. Percentage of the 1.169 ice age mammal bones including only the 778 cave bear bones with biting and cracking structures from the Perick-cave system. These percentages are typical for cave bear den sites that were also used by ice age spotted hyaenas as their den. In the Sauerland cave and cave bear rich region hyaenas were specialized on the feeding onto bear carcasses, which they destroyed normally in the caves (Graphics PALEOLOGIC).

Tibia:

Many tibia shafts from juvenile to senile individuals are present in the bone material of the Heinrichscave (Fig. 6B.6-7), and also of the Martins cave hyaena den (coll. GPIM). Typically is the lack of both soft bone joints. This may result on the one hand of the gnawing of the pes, and on the other hand the separation of the tibia from the femur bone. Normally after the separation the bone shaft was mostly cracked. More than hundred bone fragments from the tibia were found in the Heinrichscave (Fig. 8E) indicating the strong tries to get the bone marrow.

Fibula:

These bones are thin but massive in the shaft. They seemed to be cracked often by the hyaenas into pieces, when they were eating the lower hind limb. Therefore joints are often preserved at fibula fragments. In some cases, in which the bone was isolated, only the joints were gnawn away and the middle shaft was left (Fig. 6B.8). Such bone shafts are also present at the Martins cave hyaena den (coll. GPIM).

Calcaneus:

In most cases the distal part of this pedal bone was gnawn (Fig. 6B.9). Such preservations were observed at two other hyaena den sites, the Martins cave and the Balver cave (coll. GPIM). Maybe this is the result of the non-feeding of the pes, because of its sharp claws. Similar phenomena are visible at the manus and pes bones of the ice age lion, wolf, and spotted hyaena itself in the Heinrichs cave bone material. Phalanges and metapods were found mostly in good non-nibbled conditions. Maybe manus and pes of other carnivores, but surely also of horses were not very attractive food for the hyaenas and therefore separated in the middle-hand and -foot area from the limbs.

Metatarsus:
In a few cases there are also metapods from the manus in the Heinrichscave, the Martins cave and the Balver cave material. Mostly the distal joint at the bones of adult individuals is missing, in some cases there are some nibbling marks preserved at the proximal joints (Fig. 6B.10).

Vertebra:
Some hundred vertebrae of the Heinrichscave were studied, and compared with similar preserved ones from the Martins cave and the Balver cave hyaena den sites. Most of the ones from the Heinrichscave are cervical, thoracic and lumbar vertebra; small caudal ones are very few. The thoracic vertebra is mostly more fragmented in contrast to the cervical and lumbar ones. In some cases it is difficult to decide weather the processes are gnaw or bitten of by hyaenas or not. At the first vertebra (atlas) commonly the wing like transversal processes are disappeared completely (Fig. 7.1). The second vertebra (axes) has commonly a nibbled Proc. spinosus, and lateral processes. Sometimes the vertebra centrum was entirely eaten by the hyaenas (Fig. 7.2). Normally the vertebra centrum is the most soft part of the bones, but generally first the Processes show biting structures. This is in contrast to the long bones, where first the soft part was gnawed. This indicates that the vertebral column was in most cases in connection when hyaenas feeded on the cave bear carcasses. In some vertebra centra clear bite holes from the hyaena canine can be observed (Fig. 7.3). In another case only the vertebra centra were eaten completely and the Proc. spinosus was left (Fig. 7.4). As shown for the different vertebrae a typical scheme can not be identified, in contrast to long bones. It seems to be the result that articulated vertebral column parts were erupted out of the carcasses. Not isolated vertebrae were nibbled or gnawn and were not very of interest because of lacking bone marrow. Therefore no specialized strategy was developed by the hyaenas to eat or crack vertebrae.

3. Discussion

The ice age spotted hyaenas were distributed in Eurasia during the last Upper Pleistocene (e.g. Reynolds 1902, Diedrich 2004b) but are one of the poorly studied ice age mammals. This is surprising, because these animals had the most important impact on every other living or dead ice age mammal, especially at cave sites.
The ice age carnivores must have lived such as recent African spotted hyaenas in clans with about 25 animals in different ages that were leaded by females (cf. Kruuk 1966). There were two different main habitats of the ice age spotted hyaenas in northern Germany, the open mammoth steppe (e.g. Münsterland Bay, Fig. 1) and the cave den sites (Sauerland caves, Fig. 1). It is not clear, if there were seasonal migrations or connections between these close connected areas. The protraction of steppe animal bones of mammoth, woolly rhinoceros and other mammals into some caves in

the northern Sauerland (DIEDRICH 2005a, National Geographic 2005) could let think about a special position of the Sauerland hyaena den sites. It seems that the caves were used more in the spring and early summer, especially by the growing up of young hyaenas. The hunting radius from these sites reached into the Münsterland Bay. This would not surprise, if compared the action radius of recent African spotted hyaenas reaching up to 400 square kilometres for each family-clan (cf. KRUUK 1966), but the size is variable depending on the season and offer of the prey number (cf. GRZIMEK 1997). Some bones of very young mammoth and woolly rhinoceros found in the Perick caves could let think about successful hunts, but they also could be imported by the hyaenas as carcass remains.

The detailed qualitative and quantitative study of prey bones is presented for the Perick caves den at which bones of 14 different Upper Pleistocene mammal preys shows the bright spectrum (Fig. 10). All huge ice age mammals were hunted or even carcass remains were imported into the cave den sites or were deposited in wet mud close to the old river systems or lakes in the Münsterland Bay (Fig. 1). Gnaw, nibbled, chewn and cracked bones of *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Megaloceros giganteus*, *Cervus elaphus*, *Bison priscus*, *Equus ferus przewalskii*, *Panthera leo spelaea*, *Crocuta crocuta spelaea*, *Canis lupus*, and *Alopex lagopus* were found in the Perick caves. For the first time it becomes very obvious, that in the hyaena den sites Martins cave and Perick caves hyaenas intensively feeded on cave bear carcasses and bones in the mountainous zones (cf. also National Geographic 2005). In the open mammoth steppe cave bears were rare and hyaenas surely never hunted on grown up cave bears to risk their life. Therefore a specialization onto cave bear carcasses can be proved for the hyaena and cave bear den Perick caves.

About 40% of all cave bear bones in the Perick caves exposes bite, gnaw, nibbling, and chewing marks or are even cracked into hundreds of pieces. The find of these bone fragments prove the cave bear carcass destruction and intensive feeding by the hyaenas directly in the dark caves. Bones were not imported by the hyaenas in contrast to other prey bones. Therefore the main food sources for hyaenas in the Perick caves, and surely other caves in the Sauerland, were cave bear carcasses. When hyaenas did not hunted outside on cave bears, or even rarely on their cubs, there is only one interpretation. Hyaenas feeded mainly on dead cave bears, that did not survive the winter rest. This must have happened primary in late winter and early spring time. It might be, that cave bears respected the short presence of the hyaenas to "clean up" the cave and stinky decaying carcasses. Maybe also dead born or died young cave bears were eaten rapidly in that period, where cave bears where not very active in their caves. But maybe the cave bears did not respected the presence of hyaenas. In this case hyaenas must have smelled the periodically non-presence of the living bears and the decaying carcasses inside the caves. The bone preservation of many cave bears and the high number of cracked long bones seems to be an argument for this theory. Surely old cave bear bones could have been also

used by hyaenas after cave bears had left their den for longer times. The rare number of cave bear bone nibbling sticks, bones hyaenas needed time to nibble on, could be an argument for more rapid cleaning activities in most of the caves.

Literature

CUVIER, G. L. C. F. D. BARON DE (1805): Sur les ossements fossiles des Hyènes.- Annales du Museé Histoire Naturelle, 6, 127, Paris.

CUVIER, G. L. C. F. D. BARON DE (1806): Sur les ossements du genre de l'ours, qui se trouvent en grande quantité dans certaines cavernes d'Allemagne et de Hongarie.- Annales du Musée histoire naturelle, 8, 325, Paris.

DIEDRICH, C. (2004a): Seltene Freilandfunde des Höhlenbären *Ursus spelaeus* ROSENMÜLLER 1794 aus den oberpleistozänen Emscher- und Weserkiesen (Norddeutschland).- Philippia, 11 (3), 201-209, Kassel.

DIEDRICH, C. (2004b): Oberpleistozäne Fleckenhyänenreste (*Crocuta crocuta spelaea* GOLDFUSS 1823) aus Flussterrassenablagerungen in der Münsterländer Bucht (NW Deutschland).- Philippia, 11 (3), 227-234, Kassel.

DIEDRICH, C. (2005a): Eine oberpleistozäne Population von *Crocuta crocuta spelaea* (GOLDFUSS 1823) aus dem eiszeitlichen Fleckenhyänenhorst Perick-Höhlen von Hemer (Sauerland, NW Deutschland) und ihr Kannibalismus.- Philippia, Kassel (in press).

DIEDRICH, C. (2005b): Reste von *Mammuthus primigenius* (BLUMENBACH 1799) aus den oberpleistozänen Weserkiesen bei Petershagen (Norddeutschland) und Beitrag zur Taphonomie von Mammutknochen.- Philippia, Kassel (in press).

DIEDRICH, C. (2005c): Die oberpleistozäne Population von *Ursus spelaeus* ROSENMÜLLER 1794 aus dem eiszeitlichen Fleckenhyänenhorst Perick-Höhlen (Sauerland, NW Deutschland).- Philippia, Kassel (in press).

EHRENBERG, K., SICKENBERG, O., STIFFT-GOTTLIEB, A. (1938): Die Fuchs- oder Teufelslucken bei Eggenburg, Niederdonau. 1. Teil.- Abhandlungen der Zoologisch-Botanischen Gesellschaft, 17 (1), 1-130, Wien.

GIEBEL, C. G. (1842): Über Säugethier-Knochen aus der Sundwich-Höhle.- Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1842, 56-68, Berlin.

HAMMERSCHMIDT, E., NIGGEMANN, S., GREBE, W., OELZE, R., BRIX, M. R., RICHTER, D. K. (1995): Höhlen in Iserlohn.- Schriften zur Karst- und Höhlenkunde in Westfalen, 1, 1-153, Iserlohn.

HELLER, F. (1960): Höhlen-Hyänen-Reste aus jungdiluvialen Ablagerungen Westfalens.- Abhandlungen des Landesmuseums für Naturkunde Münster, 22 (3), 3-8, Münster.

HELLER, F. (1962): Hyänenfraß-Reststücke von Schädeln des Wollhaarigen Nashorns *Coelodonta antiquitatis* BLUMENBACH.- Quartär, 14, 89-93, Bonn.

KLAATSCH, H. (1904): Eine Sammlung fossiler Knochen aus der Heinrichshöhle bei Sundwig.- Zeitschrift für Ethologie. Organ der Berliner Gesellschaft für Anthropologie, Ethologie und Urgeschichte, 36, 117-119, Berlin.

KRUUK, H. (1966): Clan-system and feeding habits of spotted Hyaenas (*Crocuta crocuta* Erxleben).- Nature, 209 (5029), 1257-1258, London.

LASS, R. (1998): Der Höhlenbär *Ursus spelaeus* von Hemer-Sundwig, ein interessantes Fossil aus der Diluvialzeit.- Der Antiberg, 67, 2-16, Hemer.

LIEBE, K. T. (1876): Die Lindentaler Hyänenhöhle und andere diluviale Knochenfunde in Ostthüringen.- Archiv für Anthropologie des Organs der deutschen Gesellschaft für Anthropologie, Ethnologie und Urgeschichte, 9, 155, Braunschweig.

MEISE, H. (1926): Heinrichshöhle zu Sundwig in Westfalen.- 8 S., Hemer/Westf. (Selbstverlag von Heinrich Meise, Gebrüder Burris).

National Geographic (2005): Eiszeithyänen: Mit Bisonknochen in die Kühlkammer.- National Geographic Deutschland, Mai 2005, Geographica Deutschland, 9.

NÖGGERATH, J. (1823): Das Gebirge in Rheinland-Westphalen nach mineralogischem und chemischem Bezuge. Zweiter Band.- x + 387 + 3 S., Bonn (Eduard Weber).

NÖGGERATH, J. (1824): Das Gebirge in Rheinland-Westphalen nach mineralogischem und chemischem Bezuge. Dritter Band.- viii + 291 + 1 S., Bonn (Eduard Weber).

REYNOLDS, S. H. (1902): A monograph of the British Pleistocene Mammalia. Volume II, Part I. The Cave Hyaena.- Palaeontographical Society Monographs, 1902, 1-25, London.

ROSENDAHL, W., DÖPPES, D., JOGER, U., LASKOWSKI, R., LÓPEZ CORREA, M., NIELBOCK, R., WREDE, V. (2005): New radiometric datings of different Cave Bear sites in Germany - results and interpretations.- Bull. Soc. Hist. Nat. de Toulouse et de Midi-Pyrénees, 141, 10 pp., Toulouse (in press.).

ROSENDAHL, W., MARKS, S. (2002): Bibliographie zu Benno Wolf, Fauna fossilis cavernarum I. Abt. II, die Höhlen der Rheinprovinz und Westfalens.- Speläolog. Jb. - Verein f. Höhlenkunde in Westfalen, 1998-2000, 101-105, Iserlohn.

SIEGFRIED, P. (1961): Pleistozäne Säugetiere in Westfälischen Höhlen.- Jahrbuch für Karst- und Höhlenkunde, 2, 177-191, Hagen.

SIEGFRIED, P. (1983): Fossilien Westfalens. Eiszeitliche Säugetiere. Eine Osteologie pleistozäner Großsäuger.- Münstersche Forschungen zur Geologie und Paläontologie, 60, 1-163, Münster.

SOERGEL, W. (1937): Die Stellung der *Hyaena spelaea* GOLDF. aus der Lindentaler Hyänenhöhle bei Gera.- Beiträge zur Geologie von Thüringen, 4 (5), 171-189, Jena.

SUTCLIFFE, A. J. (1970): Spotted Hyaena: crusher, gnawer, digester and collector of bones.- Nature, 227, 110-1113, London.

THENIUS, E. (1961): Hyänenfraßspuren aus dem Pleistozän von Kärnten. Ein Beitrag zur Frage der sog. „osteodontokeratischen Kultur" der Australopithecinen (Hominidae).- Carinthia II, 71(151), 88-101, Klagenfurt.

WEBER, H.-W. (1989): Höhlenkataster Westfalen 1987.- Antiberg, 31/32, 1-73, Hemer.

ZAPFE, H. (1939): Lebensspuren der eiszeitlichen Höhlenhyäne. Die urgeschichtliche Bedeutung der Lebensspuren knochenfressender Raubtiere.- Palaeobiologica, 7(2), 111-146, Stuttgart.

ZYGOWSKI, D. W. (1988): Bibliographie zur Karst- und Höhlenkunde in Westfalen (unter Einschluss des Bergischen Landes).- Abhandlungen aus dem Westfälischen Museum für Naturkunde, 50 (Beiheft), 1-295, Münster.

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