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# Europe's first Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) skeleton from the Koněprusy Caves: a hyena cave prey depot site in the Bohemian Karst (Czech Republic)

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One of the Europe's most complete *Crocuta crocuta spelaea* (Goldfuss 1823) skeletons from the Koněprusy Caves, Bohemian Karst (Czech Republic) is an older pathological (hindlimb arthritis) and possibly smaller female individual. Few other cannibalistically scavenged hyena remains of older animals demonstrate a 'small population' that used the Main Dome area as a den site, which was marked well by faecal pellets. A large amount of megafauna prey was accumulated, and bones were further damaged or cracked. These hyenas hunted Przewalski horses dominantly, as has been documented all over the Bohemian Karst at several Late Pleistocene hyena den caves. The mammoth was mostly absent, instead the woolly rhinoceros was one of the meat colossi with indestructible bones also found in the Main Dome. These are the best indicators for hyena den sites identifications in general. Those massive bones found are left in repeating damaged ways and mainly as shafts and exposed best with bite marks in the bone spongiosa. Rhinoceros carcass body parts were removed by hyenas from the scavenging sites of the nearby surroundings, which they deported to the 'prey storage den'-type site in the Main Dome area of the Koněprusy Caves.

**Keywords:** *Crocuta crocuta spelaea* (Goldfuss 1823); skeleton; hyena prey storage den; paleobiology and cannibalism; Koněprusy Cave; Czech Republic

## Introduction

The 'cave hyena' was figured for the first time with teeth of 'cave animals' from the Zoolithen Cave in southern Germany by Esper (1774). The species '*Hyaena spelaea*' was described later based upon an incomplete skull from the same cave (Goldfuss 1823; Diedrich 2008c; Figure 1(A)). Similarly, Cuvier figured hyena remains from this cave (Cuvier 1805), but all remains from historic times were single bone finds. Reynolds (1902) published what he believed to be the first two 'skeletons' for the 'Wookey Hole Cave' in southern England, which are indeed from the Sandford Hill Cave, and after own studies of this material, it was not clear whether the remains were from 'individual skeletons' at all (Diedrich 2010e).

At one of the famous Bohemian cave sites, the first European 'individual skeleton' of the Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) described here was found 55 years ago in one part of the large Koněprusy Cave (Diedrich and Žák 2006). Koneprusy Cave is the cave system in the Bohemian Karst, which has a length of 2050 m and vertical extent more than 70 m (Kučera et al. 1981). The newest but not original entrance is situated on the top of Golden Horse (Zlatý Kůň) Mountain (Figure 1). The hyena remains and other bones were collected by J. Petrbok, I. Chlupác and J. Kovanda (Kovanda 2002; Diedrich and Žák 2006). After collecting the bone on the surface, some systematic excavations were carried out in the Prošek Dome shortly after the discovery of the cave (Kukla 1951; Stárka et al. 1952; Vlček 1952). The skeleton was collected with single bones and fragments not in articulation, and must have been spread unrecognised all over the Main Dome with other prey bones. The first overview about the history and prey bones as well as coprolite and hyena material was described in Diedrich and Žák (2006) who identified the cave as a Late Pleistocene hyena den site. The skeleton's den is a particularly important locality in the 'European Ice Age spotted hyena project' for understanding a special type of hyena den, the so-called 'prey depot'-den type in caves, as well as the woolly rhinoceros bone taphonomy at many dens.

## Material and methods

The complete bone collection of the Koněprusy Cave was sorted by the author in 2005. The complete megafaunal material of some hundreds of bones was sorted by its bone preservation, which allowed a well separation of Middle and Upper Pleistocene and Holocene bone assemblages. This collection management resulted in the here described overlooked hyena individual skeleton, but also another Late Magdalenian human humerus bone shaft with carnivore chewed joints was found between bone fragments. Many bones of the hyena skeleton were

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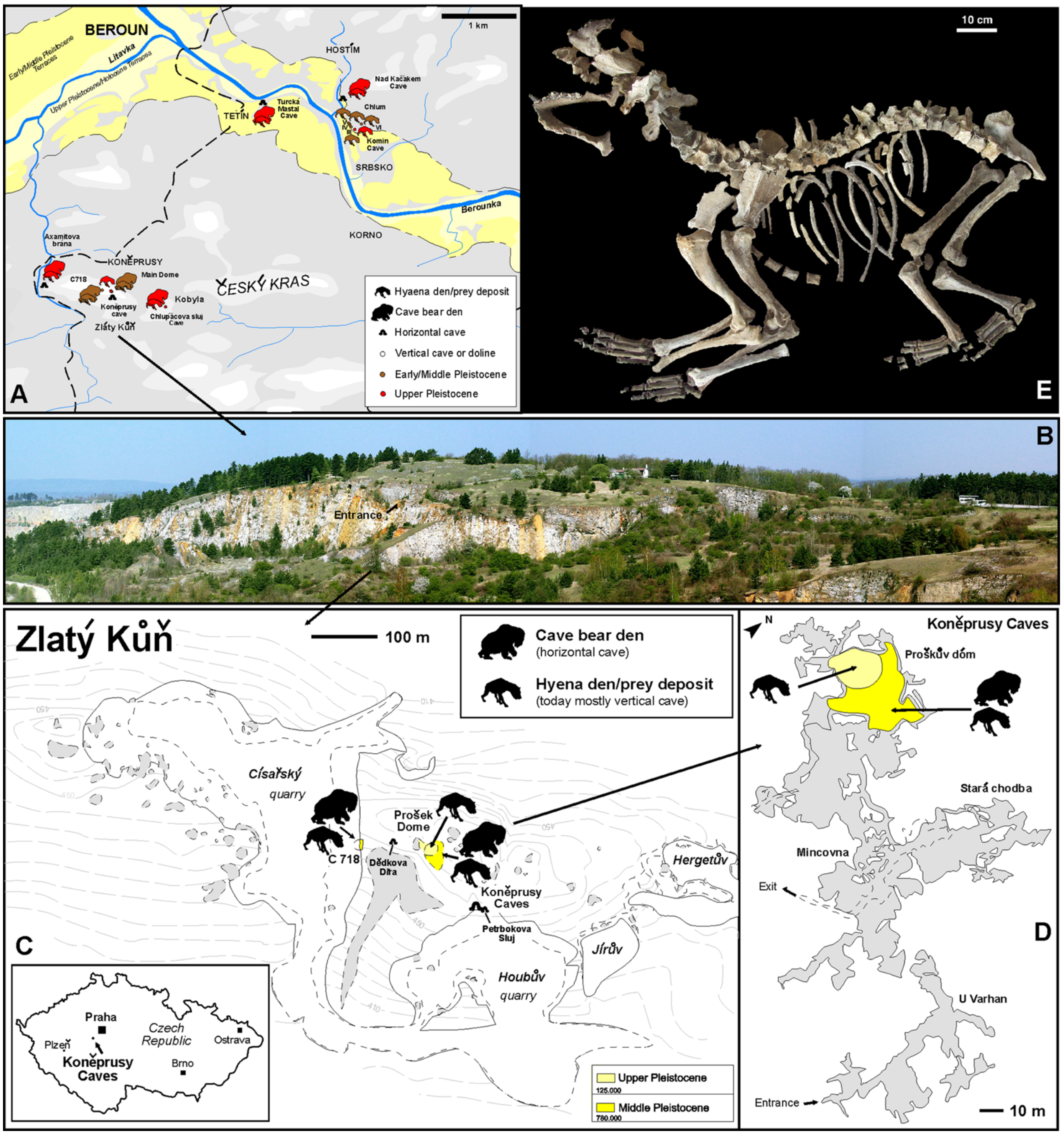


Figure 1. A–C. Positions of the hyena prey deposit and vertical cave sites in the Golden Horse (Zlatý Kůň) mountain area and hyena and cave bear cave den sites in the Bohemian Karst (after Diedrich 2006a, 2006b) with the D. Koněprusy Caves and E. Nearly, complete individual skeleton of *C. c. spelaea* (Goldfuss 1823).

fragmented and were glued. All bones of the described hyena skeleton were cleaned and partially prepared (removing parts of some speleothem encrustations). Two third of the skeleton was in 'bone fragment boxes', and the other part was already inventoried and identified as 'cave hyena *H. spelaea*' remains. Finally, the late Pleistocene material was anatomically and taxonomically identified in the bone types and by the species. This hyena material described here and prey bones and coprolites, and the other studied fauna from the Koněprusy Cave (see geology and bone taphonomy) are stored in the National Museum Prague (=NMP), and few in the Museum of the Bohemian Karst Beroun (=MBKB), Czech Republic. Comparative modern hyena den bone material was used from the Sutcliffe collection (Natural History Museum London). The bone metrics were followed by the schemes of Driesch (1976).

## Geology and bone taphonomy

The Bohemian Karst is a small karstic region located between Prague and Zdice of central Czech Republic, and is a hilly mountainous region built of Silurian and Devonian limestones. These Paleozoic sediments are folded and faulted into the Prague Synform, which outcrop about 33 km in length and up to 8 km in width. In the Bohemian Karst, there are 672 caves with total length of more than 21 km, but the caves are usually small, of complex fused vertical and horizontal cave connection morphology and are frequently filled with sediments mostly of Tertiary to Quaternary age (Diedrich and Žák 2006; Žák and Diedrich 2006), of which the most famous Miocene fossil locality was discovered with the oldest porcupine den cave of Europe in the Plešivec quarry at Suchomasty (Diedrich 2007c). Most of the known Bohemian Karst caves have been discovered in Devonian massive limestone quarries, like the largest Bohemian Karst cave system Koněprusy Cave (Figure 1(D)) on the top of the hill (Figure 1(B)). The cave surrounding of the Zlatý Kůň (=Golden Horse) Hill additionally contains numerous sediment-filled karst depressions, which are strongly damaged by limestone quarries on its southern and western slope (Figure 1(C)).

### *Early to Middle Pleistocene fauna*

The oldest Lower Pleistocene (Lower Biharian) bat fauna was found below the fallen cave roofs in NW part of the Prošek Dome (Horáček 1984). In some of the pockets nearby the Koněprusy Cave (pocket C718), a Middle Pleistocene megafauna that seem to be related again to be of hyena activities (den site) was found (Figure 1(A)). Another Middle Pleistocene *Ursus deningeri* cave bear that dominated (Lysenko 1976) megafauna cave is present in the lower layers in some parts of the Koněprusy Cave (Figure 1(D)). Only a few remains of hyena*s* and coprolites and some prey remains indicate a periodical hyena frequentation or first hyena den of a Middle Pleistocene hyena species. A few Middle Pleistocene hyenas started to store prey remains from bovid and deer which are within the collections. Many cave bear bones have chew marks or are cracked in a manner typical of hyena scavenging. This is comparable to described incomplete and cracked bones from the late Pleistocene cave bears in northern Germany (Diedrich 2009) and the Bohemian Karst (Diedrich and Žák 2006). At that time, the Main Dome must have been accessible to cave bears. These bears hibernated mostly in the Koněprusy Cave, and also in the large Main Dome chamber.

### *Upper Pleistocene fauna and human remains*

In the Upper Pleistocene, only the Main Dome was reused by hyenas with a diagonal possibly new entrance through a diagonal shaft reaching the surface of the top of the hill to the 'Dědkova Dira Cave entrance' (a part of the Koněprusy Cave, Figure 1(C))). The large 'Mohyla' stalagmite in the centre of the Main Dome (Prošek Dome) was badly damaged by freezing (see U-series dating of Mohyla in Diedrich and Žák 2006), which demonstrates that this diagonal shaft was open to the surface until the final late Pleistocene. This connection to both cave parts was finally blocked in the Holocene with larger fallen limestone blocks and sediments, which collapsed over time even into the central part of the Main Dome (Diedrich and Žák 2006).

Hyenas imported many prey remains during the Upper Pleistocene into the Main Dome, which was finally collected from the surface ('upper layer'). The Upper Pleistocene megafauna consists of *Coelodonta antiquitatis* (Blumenbach 1799), *Bison priscus* (Bojanus 1827), *Equus caballus* cf. *przewalskii* (Poliakov 1881), *Megaloceros giganteus* (Blumenbach 1799), *Cervus elaphus* Linné 1758, *Rangifer tarandus* (Linné 1758), *Capra ibex* Linné 1758, *Rupicapra rupicapra* (Linné 1758), *Panthera leo spelaea* (Goldfuss 1810) and *Canis lupus* subsp. Linné 1758 dated the surface finds into the cold period, and therefore into the Late Pleistocene. Also, *Allactaga major* (Kerr 1792), *Alopex lagopus* (Linné 1758) and *Lagopus lagopus* (Linné 1758) fit to the cold period fauna of the Early to Middle Upper Pleistocene (cf. Koenigswald 2002). Finally, the dating of the speleothems ("Mohyla" stalagmite in the centre of the Main Dome, Diedrich and Žák 2006), on which the bones were found, indicates a pre-Late Upper Pleistocene age.

### *Hyena skeleton bone taphonomy*

The hyena skeleton bones are less fossilised and include the herein described hyena skeleton in which bones have all similar bone preservations including very few mineral impregnations (green-grey to white colour). In some cases, there is a slight speleothem incrustation. One thoracic vertebra (No. Ra 4058) has two preservation colours and must have been stuck half in the sediment. On the lateral left, the vertebra is non-impregnated and nearly white, while on the lateral right side, it is mineralised by dark minerals of grey colour. This preservation also contains small pedal bones or ribs or skull remains, which must have been found on the sediment surface. One middle thoracic rib was broken in former Late Upper Pleistocene times, but the anterior part must have been deposited in the sediment or was covered later by thin speleothem layer, while the other distal part was embedded only in the sediment. The above represented examples of Late Upper Pleistocene or Early Holocene fracturing and disarticulation of the skeleton may have been caused by trampling by Holocene wolves or brown bears (skeletons found in the Main Dome). Possibly, the final Upper Pleistocene Late Magdalenian people could have disarticulated the skeleton to spread it around the Main Dome, when they used the Main Dome for a single burial purpose (cf. Kuželka 1997). The Late Magdalenian skeleton skull has strong chew marks and even crushing is documented on different coloured fitting brain case fragments which were interpreted of 'hyena origin' (cf. Kuželka 1997; Svoboda 2000), but seems to be the result of wolf scavenging; hyenas at that time were already extinct in the region. Possibly, also from this final Late Pleistocene time or the hyena den occupation, remains from a 'fox den' (fox/hare remains) are also represented, which again indicate the still open entrance via the Dědkova Dira Cave entrance.

### *Holocene fauna*

In the Holocene, a brown bear '*U. arctos* (Linné 1758)' skeleton part, and a nearly complete wolf *C. l. lupus* (Linné 1758) skeleton (see photo in Mach 1951), some *Vulpes vulpes* (Linné 1758) and many *Lepus europaeus* Pallas 1798 bones are the last animal records. Access into the cave from the diagonal chimney until the Holocene is not only documented by the non-described brown bear and wolf skeletons, but also by common fox *V. vulpes* and *L. europaeus* hare prey remains (common fox den via the Dědkova Dira Cave entrance). The brown bear has some chewed long bone joints, which seem to be the result of wolf scavenging activities.

## Systematic paleontology

Family Hyaenidae Gray, 1821
Genus *Crocuta* Kaup, 1828
*Crocuta crocuta* Erxleben, 1777
***Crocuta crocuta spelaea* (Goldfuss 1823)**
Figures 3–11

The hyena population of the Koněprusy Caves Main Dome is represented by at least three individual remains (Figure 2) and 24 coprolite pellets. The most important find is a nearly complete adult animal skeleton (Figures 3–10), on which bite and chew marks are absent. This is in contrast to some single bones of the other two cannibalistically scavenged very old animals.

A list from the Upper Pleistocene hyena bone and coprolite collection of the Main Dome catalogue is included (Tables 1–3). The main number for the individual skeleton is Ra 2434; however, each bone has its own number (Table 1).

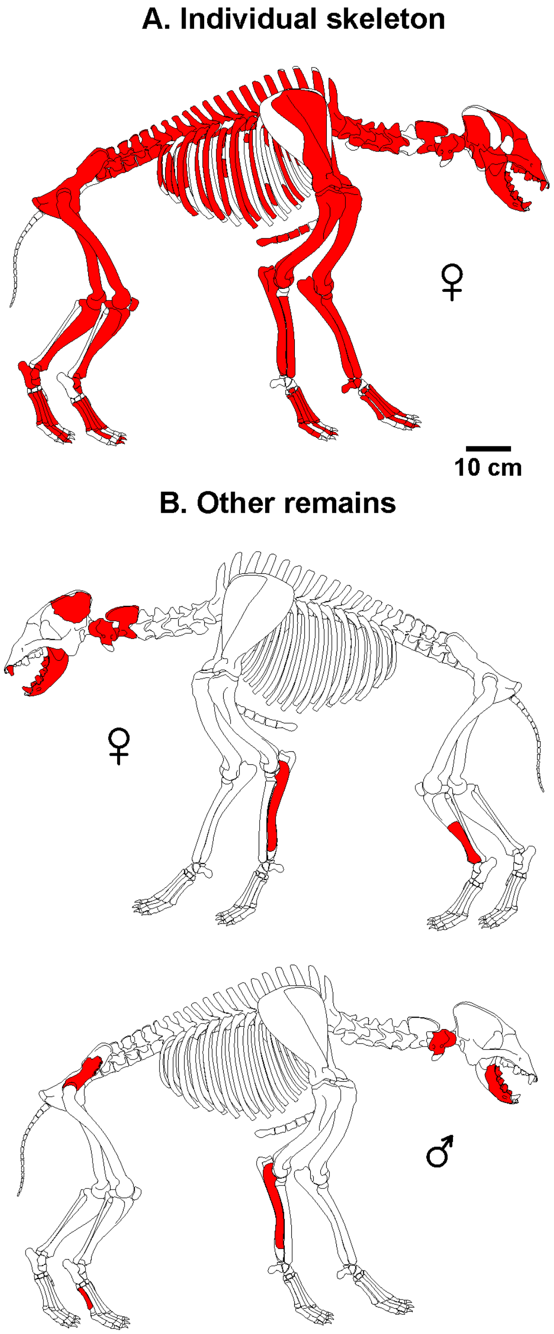


Figure 2. Present bones (marked in grey) from the A. Nearly, complete *C. c. spelaea* (Goldfuss 1823) hyena individual skeleton and B. remains of cannibalistically scavenged individuals from the hyena site Koněprusy Caves Main Dome, Bohemian Karst (Czech Republic).

### *Skeleton individual remain*

One hundred and fourteen bones (Table 1) from the hyena individual were fragmented in many cases by the collecting activities and later during improper collection handling or transport. The individual origin is demonstrated also by the presence of only one of each bone type, and by those in mirror symmetrically similar proportions. The postcranial material is represented by 112 bones. The vertebrae are present with only one each, except the atlas or axes in which the additional ones of other individuals are strongly chewed. The ribs were heavily fragmented recently, as well as the scapulae and other bones. Half of the very small manus and pedal bones, especially phalanges and sesamoid, carpal and tarsal bones are missing, most probably not being collected. Osteoporosis is symmetrically present on the limb long bones (femora, tibiae), as well.

### *Cranium*

The skull (Figure 3) was originally complete and has recent fractures. One larger piece consists of the right part of

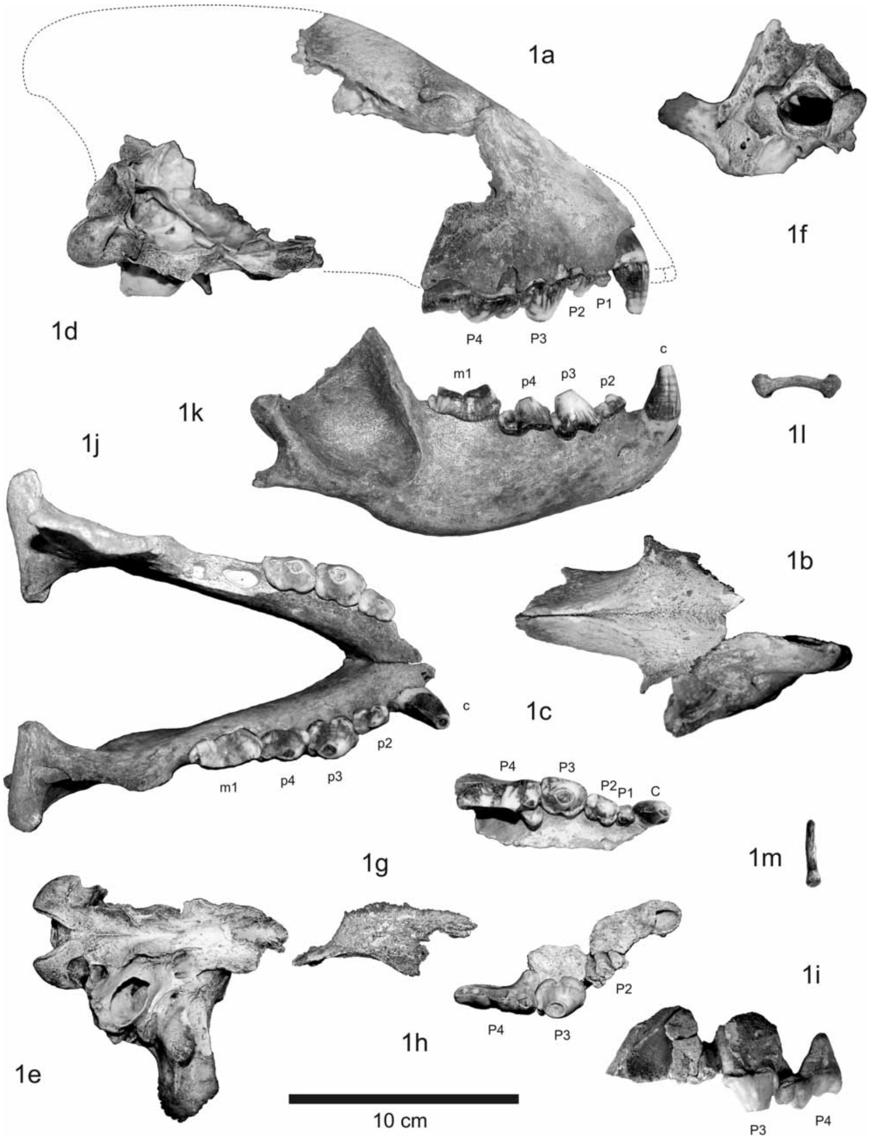


Figure 3. Cranial bones from an older adult female *C. c. spelaea* (Goldfuss 1823); crushed skull from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst) (No. R 2434). 1.A, Right maxillary and frontals, lateral right. B, Right maxillary and frontals, dorsal. C, Left maxillary dentition C–$P^4$, ventral. D, Occipital, lateral. E, Occipital, ventral. F, Occipital, caudal. G, Right palatine, ventral. H, Left maxillary with roots of $P^{3-4}$, and $P^4$–$M^1$ teeth, ventral. I, Left maxillary with roots of $P^{3-4}$, and $P^4$–$M^1$ teeth, lateral. J, Lower jaws, dorsal. K, Right mandible, lateral. L, Ceratohyoid (No. Ra 4065), ventral. M, Right upper jaw $I^2$ (No. Ra 4100), lingual.

maxilla (Figure 3.1(a)) with the C and $P^{1-4}$ dentition. The teeth are semi-worn. The heavily fragmented left part of maxilla has teeth in similar wear stages and is dissolute in parts from dripping water. Only the $P^{3-4}$ is preserved almost completely. The $P^{1-2}$ is present only with its roots; the enamel was newly broken. The left canine and all incisor teeth are missing in the lower jaw. One maxillar incisor (right $I^2$) is present loosely and matches the tooth use stage of the skull dentition. The right mandible is well preserved, including the C and $P_{2-4}$, $M_1$ (Figure 3.1(j–k)). The left mandible has only the $P_{2-4}$ left; from the $M_1$, the root bases. The bone and tooth preservations of the maxillae and mandibles indicate that the skull must have been embedded on its right side in the sediment, whereas the left side was partially eroded by dripping water. Other skull remains and fragments are the right palatal and the jugal fragment. Another larger piece is represented by the occipital and connected with left skull bone parts. A tongue bone seems to be a ceratohyoid and is nearly complete (Figure 3.1l). Main measurements of the fragmented skull in mm are length of right maxillary $P^{2-4} = 82$, length of right maxillary $P^{1-4} = 90$, width of right maxillary canine $= 18$, occipital

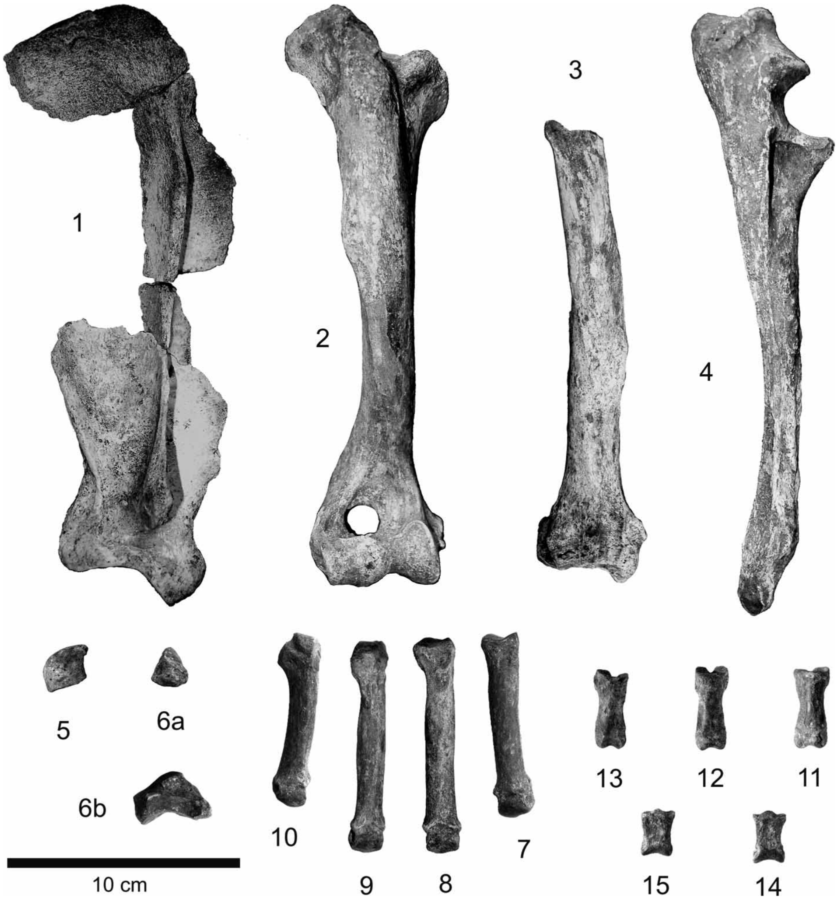


Figure 4. Right forelimb bones from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). 1, Right incomplete scapula (No. Ra 2447), lateral. 2, Right humerus (No. R 2437), cranial. 3, Right proximally incomplete radius (No. R 2438), craniolateral. 4, Right Ulna (No. R 2440), craniolateral. 5, Right ulnar (No. Ra 4035), cranial. 6, Right intermedium (No. Ra 4010), cranial. 7, Right Mc II (No. Ra 4000), cranial. 8, Right Mc III (No. R 6144), cranial. 9, Right Mc IV (No. R 6145), cranial. 10, Right Mc V (No. Ra 4001), cranial. 11, Right phalanx II of ?digit III (No. R 6138), dorsal. 12, Phalanx I of ?digit IV (No. Ra 4021), dorsal. 13, Phalanx I of ?digit V (No. Ra 4022), dorsal. 14, Phalanx II of ?digit III (No. Ra 4025), dorsal. 15, Phalanx II of ?digit V (No. Ra 4026), dorsal.

condyle width = 52, length of total mandible = 200, length of right maxillary $P^2 - M^1 = 90$, length of right mandible $M_1 = 33$, right mandible c basal length = 17.

### *Forelimbs*

The forelimb bones (Figures 4 and 5) are preserved with both incomplete scapulae, nearly complete humeri, both complete ulnae, one complete and one proximally incomplete radii, some carpals such as the left scapholunatum, left pisiform, right ulnar, both intermedia and all eight metacarpals. The small reduced first metacarpal and many carpals are missing. Four first phalanges seem to be from the manus and some are larger than the ones from the pedal skeleton. Only one of them (No. Ra 4022) has a diagonal proximal articulation surface and is from the right digit V. Two other phalanges (No. Ra 4019, 4021) are similar in size and have straight proximal articulation surfaces, which are typical for digits III and IV. The last phalanx (No. Ra 4024) has the same characteristics, but is a little larger in size. This one might also be from the left digit III or IV. Measurements in mm are: total length of right humerus = 253, distal width right humerus = 59, smallest width humerus shaft = 21. Total length of right ulna = 260, smallest width right ulna (lower third of shaft) = 16, largest width right ulna (basis proximal joint) = 50.

### *Hindlimbs*

From the hindlimbs, both femora (Figure 6.2–3) and tibiae (Figure 6.5–6) are more or less complete. Caudally, they are slightly pathological because of arthritic bone growth (Figure 6, arrows). One patella (Figure 6.4) and one left calcaneus (Figure 6.7), both astragali (Figure 6.8–9), none of the tarsals and all of the large eight metatarsals II–V (Figure 6.10–17) are preserved. The first phalanges of the

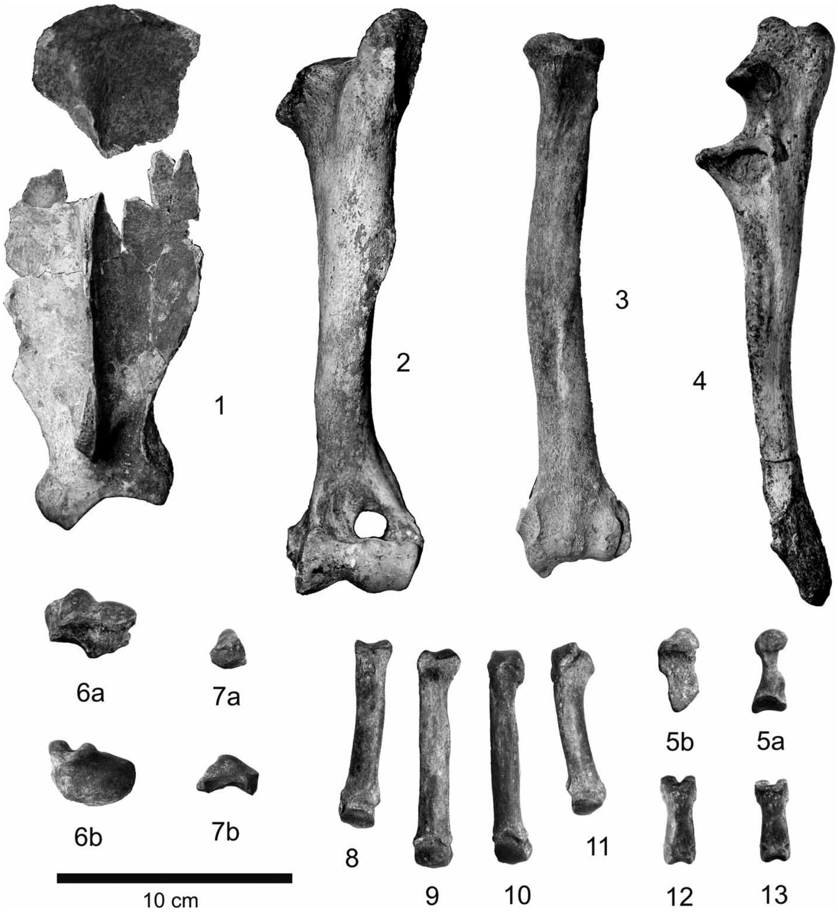


Figure 5. Left forelimb bones from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). 1, Left scapula (No. Ra 4036), lateral. 2, Left proximally incomplete humerus (No. Ra 4037), cranial. 3, Left radius (No. R 2439), craniolateral. 4, Left distally incomplete ulna (No. R 2441), craniolateral. 5, Left pisiform (No. Ra 4017), dorsal. 6, Left scapholunatum (No. Ra 4003), cranial. 7, Left intermedium (No. Ra 4011), lateral. 8, Left Mc V (No. R 6146), cranial. 9, Left Mc III (No. R 6148), cranial. 10, Left Mc IV (No. Ra 4002), cranial. 11, Left Mc II (No. R 6147), cranial. 12, Phalanx I, ?digit III (No. Ra 4024), dorsal. 13, Phalanx I, ?digit IV (No. Ra 4019), dorsal.

hindlimbs (Figure 6.18–19) are generally a little shorter and smaller in size as those of the manus. Three of them seem to be from the right and one from the left pedal skeletons. One phalanx (No. Ra 4020, Figure 6.19) has a straight proximal articulation surface and must be from digit II or IV, possibly from the right pes. This bone additionally has some pathological bone growth axially on the left side. The two other phalanges (No. Ra 4018, 4023) have a diagonal proximal articulation surface and are quite similar in shape, but one must be from the right and the other from the left pes. Both seem to be from digit V. The second phalanxes (Figure 6.22–25) of the pes, like the first phalanxes, are generally smaller in size, as the ones from the manus. Their exact position cannot be given, and is estimated based on modern hyena skeleton material. Thus, for phalanx III, it is impossible to determine its exact position. The figured five bones (Figure 6.26–30) can belong to either the manus or the pes. Even their right or left position can be only estimated at the different basal angles, but they are even with one pedal skeleton which is opposite to the II and V digits.

### *Vertebral column*

The vertebral column (Figures 7 and 8) is incomplete, and the cervical vertebra C5 and all caudal vertebrae are missing. The lateral and especially dorsal spines of the thoracic vertebrae were broken in modern times. The centre of the thoracic vertebrae T11 and T12 is missing. The determination of the cervical vertebrae is clearer from the cranial and dorsal views, whereas the thoracic vertebra is figured in cranial and lateral view, such as the lumbar vertebrae, to show the most important characteristics.

Six of the seven cervical vertebrae are preserved. The atlas (Figure 7.1) has missing parts on the lateral processes due to recent breakages. The axes (Figure 7.2) also have

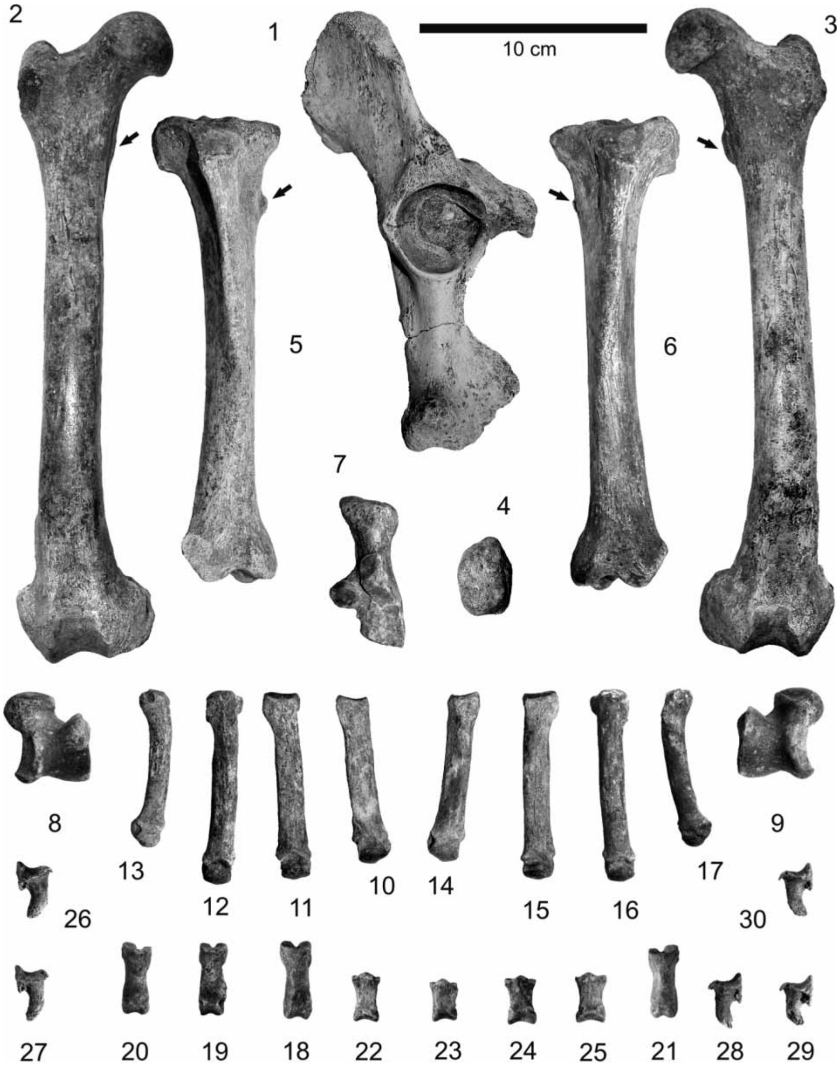


Figure 6. Hindlimb bones from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). Arrows indicate arthritic pathological bone growth. 1, Right pelvis remains (No. R 2442), acetabular. 2, Right femur (No. R 2447), cranial. 3, Left femur (No. R 2443), cranial. 4, Patella (No. Ra 4012), cranial. 5, Right tibia (No. R 2445), cranial. 6. Left tibia (No. Ra 2446), cranial. 7, Left calcaneus (No. R 2448), dorsal. 8, Right calcaneus (No. Ra 4008), dorsal. 9, Left calcaneus (No. Ra 4009), dorsal. 10, Right metatarsal II (No. R 6141), cranial. 11, Right metatarsal III (No. R 6142), cranial. 12, Right metatarsal IV (No. Ra 4006), cranial. 13, Right metatarsal V (No. R 6143), cranial. 14, Left metatarsal II, (No. R 6139), cranial. 15, Left metatarsal III (No. R 6140), cranial. 16, Left metatarsal IV (No. Ra 4007), cranial. 17, Left metatarsal V (No. Ra 4004), cranial. 18, Right phalanx I, ?digit III (No. Ra 4019), dorsal. 19, Right phalanx I, ?digit IV (No. Ra 4020), dorsal. 20, Right phalanx I, ?digit V (No. Ra 4023), dorsal. 21, left phalanx I, ?digit V (No. Ra 4018), dorsal. 22, ?Left phalanx II, ?digit II or IV (No. Ra 4029), dorsal. 23, Left Phalanx II, ?digit II or IV (No. Ra 4027), dorsal. 24, Right Phalanx II, ?digit III or IV (No. Ra 4028), dorsal. 25, Right Phalanx II, ?digit II (No. Ra 4030), dorsal. 26, ?Right Phalanx III digit? (No. Ra 4115), dorsal. 27, ?Left Phalanx III digit ? (No. Ra 4031), dorsal. 28, ?Right Phalanx III, digit ? (No. Ra 4032), dorsal. 29. ?Left Phalanx III, digit ? (No. Ra 4033), dorsal. 30, ?Right Phalanx III digit ? (No. Ra 4034), dorsal.

incomplete lateral processes. In the incomplete cervical vertebra C3 (Figure 7.3), the width of the prezygapophyses is smaller in size, versus the quite large and flat postzygapophyses. In the complete cervical vertebra C4 (Figure 7.4), the zygapophyses width is opposite, the distance in between the prezygapophyses is less than in the postzygapophyses. This feature is also present in all the following incomplete cervical vertebrae (Figure 7.5–6). The C4 is the largest and the neural arch is the longest. This length is reduced from C5 to C7. Only the cervical vertebra C6 possesses the large wing-like lateral and ventrally oriented spines. On vertebra C6, these are broken. Finally, the C7 can be easily identified by the lack of lateral foramina and also the shorter neural arch length.

All 15 thoracic vertebrae are more or less present, but most of them were damaged recently and are missing parts.

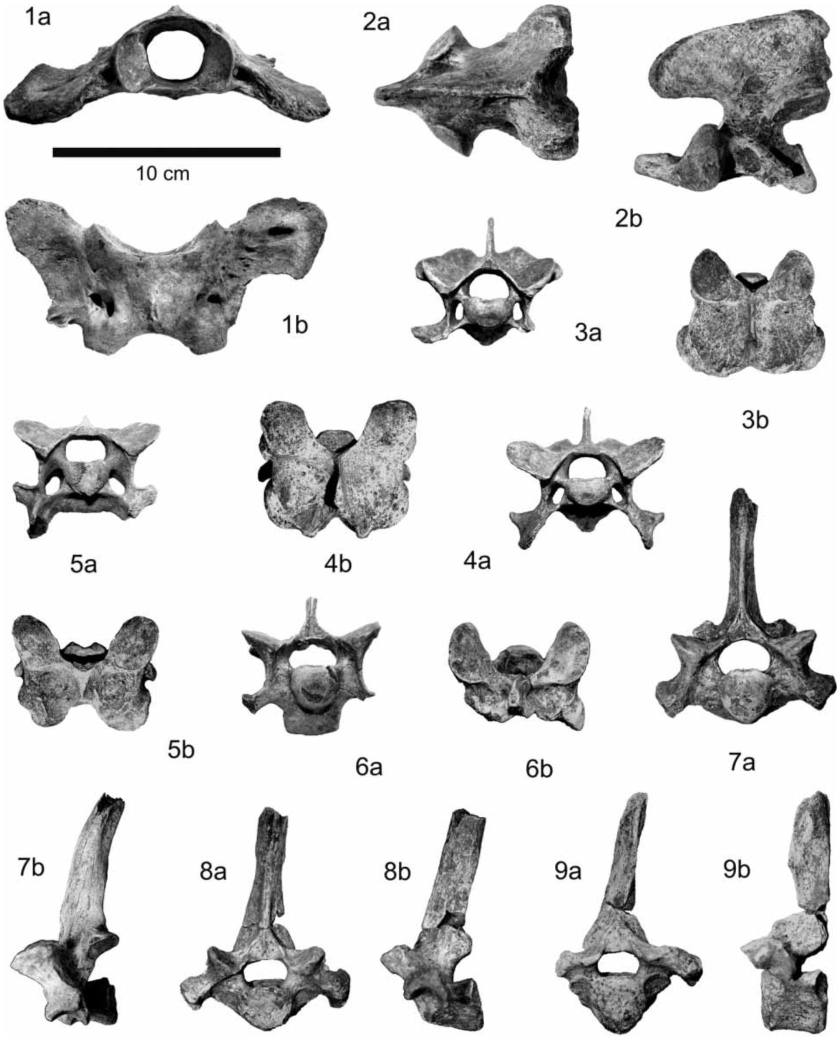


Figure 7. Vertebral column (first cervical to third thoracic vertebrae) from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). 1, Atlas (No. Ra 4038), cranial and dorsal. 2, Axes (No. Ra 4039), a. cranial and b. dorsal. 3, C3 (No. Ra 4040), cranial and dorsal. 4, Fourth cervical vertebra (No. Ra 4041), cranial and dorsal. 5, C6 (No. Ra 4042), cranial and dorsal. 6, C7 (No. Ra 4043), cranial and dorsal. 7, T1 (No. Ra 4054), cranial and lateral. 8, T2 (No. Ra 4055), cranial and lateral. 9, T3 (No. Ra 4056), cranial and lateral.

The first (Figure 7.7) and the last thoracic vertebrae (Figure 8.12) are preserved the best. The first three thoracic vertebrae differ from the others mainly in the very large width of the prezygapophyses, which decreases from the first to the third thoracic vertebra (Figure 7.7–9). The foramen vertebral also changes its form from a more oval to a triangular shape in the frontal view. Finally, the first thoracic vertebra has a large lateral processus which is directed ventrally, and the prezygapophyses' articulation surface is strongly concave. The processi are smaller in size at the second thoracic vertebra. In the third thoracic vertebra, the prezygapophyses articulation surfaces are now convex and the postzygapophyses are much smaller in width. The middle thoracic vertebrae are very similar and can be distinguished only by complete dorsal spines which change their angles. The spines become shorter in height and are caudally more angled backwards. The spines also decrease in width up to the tenth thoracic vertebra. With the eleventh thoracic vertebra, the dorsal spines have more width in the centre and are short, being similar in shape to the lumbar vertebrae, but they do have slenderer dorsal spines. All five lumbar vertebrae (Figure 8.13–17) are incompletely preserved. The processi transverses are nearly all missing from recent damage. The neural canal changes its outline from the first to the last lumbar vertebra and shifts from high oval to flat oval. The processi transverses of the first lumbar vertebra are ventrally oriented at an angle of about 110°, which changes to the last lumbar vertebra that has nearly straight processi transverses. The pre- and postzygapophyses increase in

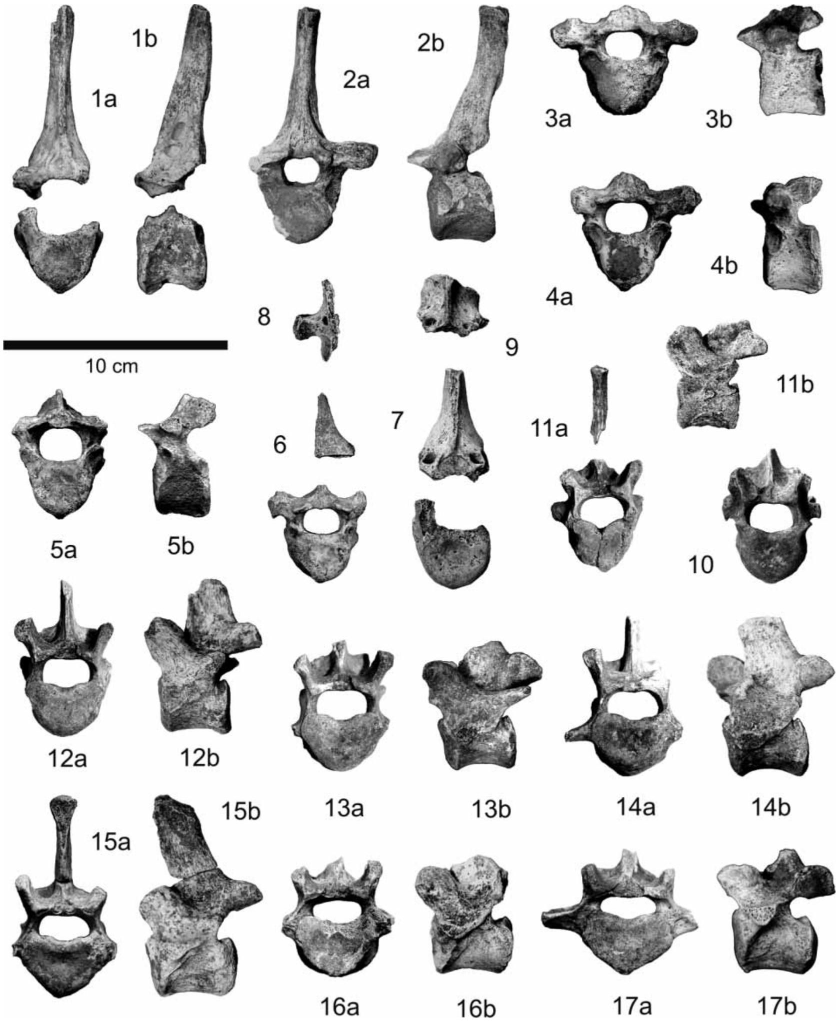


Figure 8. Vertebral column (fourth thoracic to last lumbar vertebrae) from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). 1, T4 (No. Ra 4065), a. cranial and b. lateral. 2, T5 (No. Ra 4057), a. cranial and b. lateral. 3, T6 (No. Ra 4060), a. cranial and b. lateral. 4, T7 (No. Ra 4062), a. cranial and b. lateral. 5, T8 (No. Ra 4064), a. cranial and b. lateral. 6, T9 (No. Ra 4063), cranial. 7, T10 (No. Ra 4061), cranial. 8, ?T11 (No. Ra 4059), dorsal. 9, ?T12 (No. Ra 4101), a. cranial and b. lateral. 10, T13 (No. Ra 4097), a. cranial and b. lateral. 11, T14 (No. Ra 4097), cranial. 12, T15 (No. Ra 4098), a. cranial and b. lateral. 13, L1 (No. Ra 4096), a. cranial and b. lateral. 14, L2 (No. Ra 4095), a. cranial and b. lateral. 15, L3 (No. Ra 4094), a. cranial and b. lateral. 16, L4 (No. Ra 4093), a. cranial and b. lateral. 17, L5 (No. Ra 4092), a. cranial and b. lateral.

their width from the first to the last lumbar vertebra. None of the 18 caudal vertebrae are present, however.

*Ribs and sternum*

The other thoracic bones are ribs and sternal bones (Figure 9). The costae of the Main Dome individual were broken (in most recent cases) into many pieces. At least half of the ribs are represented. Possibly 10 are left and seven right ribs of each of the 15 are preserved, but in most cases they are largely incomplete. Only the first (Figures 9.1–2, 11–12) and the last rib (Figure 9.9) can be given their exact position. Most of the ribs can be distinguished as anterior, middle and posterior. Complete ribs of the skeleton are only the right first (Figure 9.1) and ninth (Figure 9.4) costa. The rib heads are normally two, except at the last two, 14–15 costae (see No. 15th, Figure 9.9), which is typical not only in carnivores, but also in other animals as well. The first short costa has two strong separated heads (Figure 9.1), which has an angle of about 95°. This angle declines to the middle of the thorax (Figure 9.3–4, 7) and decreases again to the posterior ribs (No. ?13th, Figure 9.8). While the separation of the two rib heads is clear in the anterior ribs, it is less subdivided in the posterior ribs, whose first head is rounded, and second head is flat (Figure 9.9). In the anterior ribs both heads are rounded (Figure 9.2). There is not much curving in the anterior ribs, which have a flatter cross section in the middle. The central ribs are more oval in

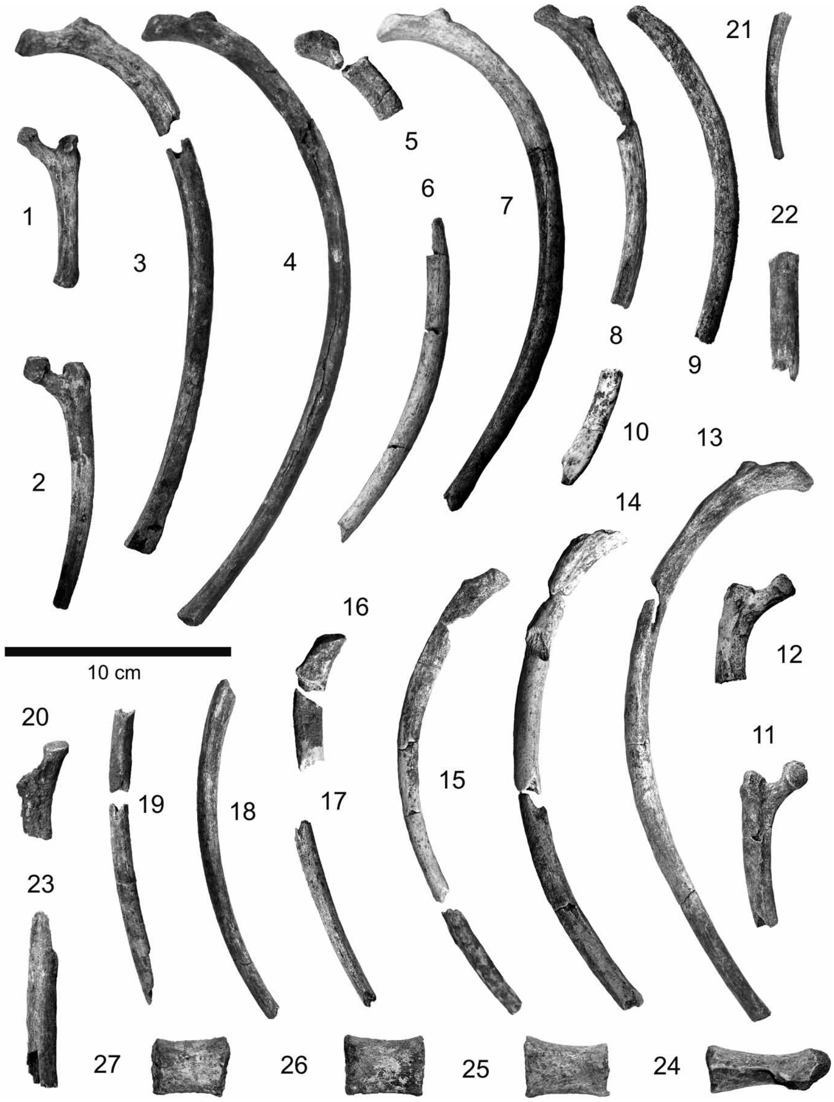


Figure 9. Thoracic bones from an older adult female *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). 1, First left costa (No. Ra 4108), cranial. 2, Second left costa (No. Ra 4107), cranial. 3, 5–6 left costa (No. Ra 4104), cranial. 4, ?ninth left costa (No. Ra 4105), cranial. 5, Middle left costa fragment (No. Ra 4119), cranial. 6, Posterior left costa fragment (No. Ra 4036), cranial. 7, 11th left costa (No. Ra 40106), cranial. 8, ?13th left costa (No. Ra 4103), cranial. 9, Last fifteenth left costa (No. Ra 4102), cranial. 10, costa fragment (No. Ra 4120), cranial. 11, Second right costa (No. Ra 4117), cranial. 12, 3–4 right costa fragment (no. Ra 4116), cranial. 13, ?ninth right costa (No. Ra 4114), cranial. 14, Middle to posterior costa (No. Ra 4113), cranial. 15, ?13th right costa (No. Ra 4111), cranial. 16, Middle to posterior right costa fragment (No. Ra 4118), cranial. 17, Middle to posterior costa fragment (No. 323/77 (62). 18, Middle to posterior costa fragment (No. Ra 4110), cranial. 19, Middle to posterior costa fragment (No. Ra 4121), cranial. 20, ?14th right costa fragment (No. Ra 4112), cranial. 21, Middle to posterior costa fragment (No. Ra 4109), cranial. 22, Middle to posterior costa fragment (No. Ra 4122), lateral. 23, Middle to posterior costa fragment (No. Ra 4123), lateral. 24, First sternal bone (No. Ra 4013), lateral. 25, ?Second sternal bone (No. Ra 4014), lateral. 26, ?Third sternal bone (No. Ra 4015), lateral. 27, ?Fifth or sixth sternal bone (No. Ra 4016), lateral.

cross section, but are well curved. The posterior ribs are again less incurved and centrally nearly round in the cross section.

Four sternal bones (Figure 9.24–27) were found. The first sternal bone is more elongated and anteriorly flat (Figure 9.24). The middle sterna bones (Figure 9.24–26) are very similar in shape and it seems as if the sternal bones 2, 3 and 5 are present. The last sternal bone, which has a rounded posterior, is not in the material.

### *Other hyena bone remains*

From two adult to elderly male and female individuals (see Figure 2), one skull fragment, two lower jaws, one

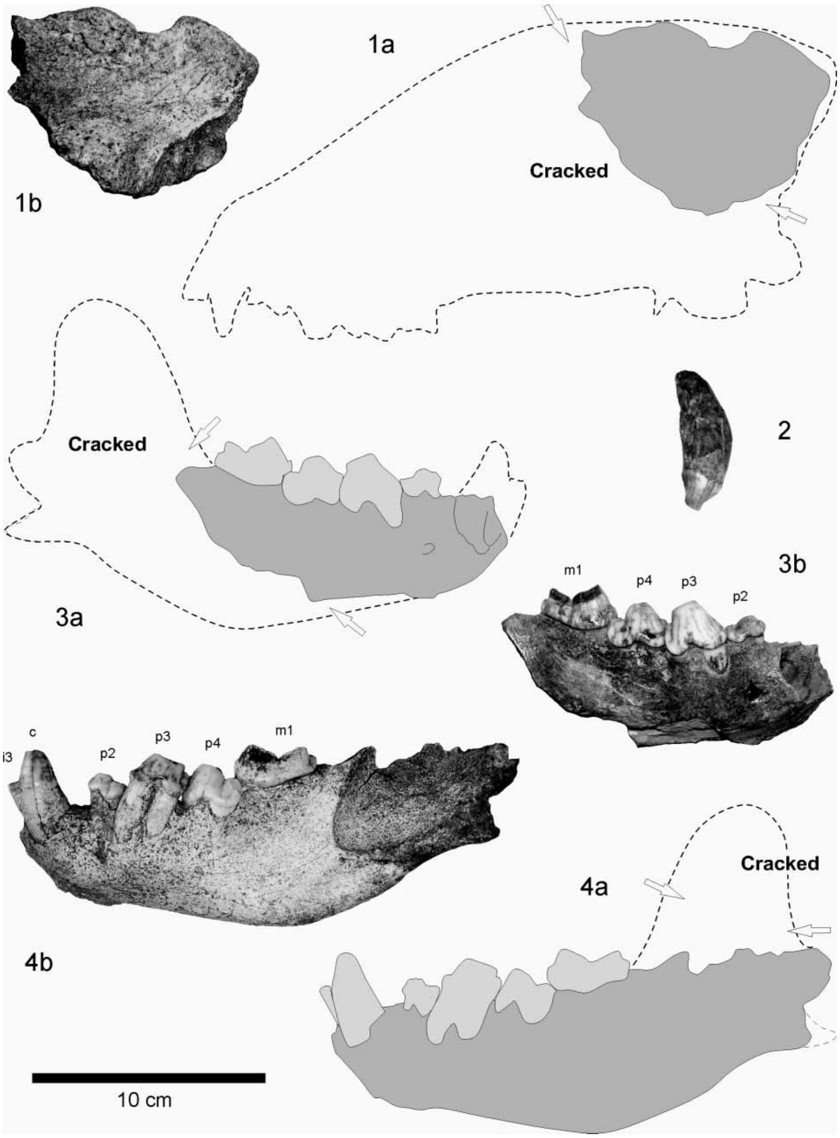


Figure 10. Cranial cracked bones from other older adult *C. c. spelaea* (Goldfuss 1823) individuals from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst); redrawing (white = bite marks). 1, Skull fragment (No. Ra 4051), lateral. 2, Canine (No. R 3318), lateral. 3, Right mandible (No. Ra 4037), lateral. 4, Left mandible (No. R 2433), lateral.

tooth and a few postcranial bones are listed (Table 2) and figured (Figures 10 and 11). They are mostly preserved in the same way as half of the bones from the individual skeleton must have been found in the upper sediment layers or on the surface. These bones include almost only large bone material, except one metapodial which can be separated from the individual skeleton remains by its smaller proportions. All bones can be separated from the individual skeleton because of different bone preservations, proportions and presence of scavenge marks, such as finally individual age differences. The incomplete postcranial bones all have gnawing and chewing marks resembling those from cannibalistically scavenged animals. Two mandibles from adult to elderly animals (Figure 10.3–4), one from a male and one from a female, are incomplete and both are missing the rami. Also, the braincase fragment (Figure 10.1) is from a cracked skull of an adult to an elderly animal. In the Main Dome material, two single incomplete cervical vertebrae (atlas/axes) are represented (Figure 11.1–2). Long bones are represented by the ulnae and one half tibia (Figures 11.3–4 and 6), but are cracked or are missing both the distal parts due to chewing. The fifth metatarsal (Figure 11.7) is cracked, and is the only pedal remains from other individuals. The proportions of a second right pelvic bone remains are larger than the skeleton remains and do not match the proximal femora joints of the skeleton. The nibbling and chewing on this hip bone (Figure 11.5) are easily visible.

Table 1. Bones of the *C. c. spelaea* (Goldfuss, 1823) skeleton from the hyena site Main Dome of the Koněprusy Caves site (Czech Republic, Bohemian Karst).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Original | Collection |
|---|---|---|---|---|---|---|---|---|
| 1 | R 2434 − 1-3 | Cranium | Incomplete, right maxillary and frontals, and lower jaws | | | High adult | x | NMP |
| 2 | Ra 4100 | Dens | $I^2$ | | x | High adult | x | NMP |
| 3 | Ra 4065 | Ceratohyoid | Complete | | | High adult | x | NMP |
| 4 | R 2447 | Scapula | Incomplete | | x | High adult | x | NMP |
| 5 | Ra 4036 | Scapula | Incomplete | x | | High adult | x | NMP |
| 6 | R 2437 | Humerus | Nearly complete, length: 232 mm distal width: 56 mm | | x | High adult | x | NMP |
| 7 | Ra 4037 | Humerus | Nearly complete, length: 232 mm distal width: 56 mm | x | | High adult | x | NMP |
| 8 | R 2440 | Ulna | Complete, length: 260 mm distal width: 50 mm | | x | High adult | x | NMP |
| 9 | R 2441 | Ulna | Complete, length: 260 mm distal width: 50 mm | x | | High adult | x | NMP |
| 10 | R 2438 | Radius | Without proximal joint | | x | High adult | x | NMP |
| 11 | R 2439 | Radius | Complete, length: 220 mm distal width: 46 mm | x | | High adult | x | NMP |
| 12 | Ra 4017 | Pisiform | Complete | x | | High adult | x | NMP |
| 13 | Ra 4003 | Scapholunatum | Complete | x | | High adult | x | NMP |
| 14 | Ra 4035 | Ulnar | Complete | | x | High adult | x | NMP |
| 15 | Ra 4011 | Intermedium | Complete | x | | High adult | x | NMP |
| 16 | Ra 4010 | Intermedium | Complete | | x | High adult | x | NMP |
| 17 | R 6147 | Metacarpal | II | x | | High adult | x | NMP |
| 18 | R 6147 | Metacarpal | II | | x | High adult | x | NMP |
| 19 | R 6148 | Metacarpal | III | x | | High adult | x | NMP |
| 20 | R 6144 | Metacarpal | III | | x | High adult | x | NMP |
| 21 | Ra 4000 | Metacarpal | IV | | x | High adult | x | NMP |
| 22 | Ra 4002 | Metacarpal | IV | x | | High adult | x | NMP |
| 23 | Ra 4001 | Metacarpal | V | | x | High adult | x | NMP |
| 24 | R 6146 | Metacarpal | V | x | | High adult | x | NMP |
| 25 | Ra 4021 | Phalanx | I, Manus, Digit III or IV | | x | High adult | x | NMP |
| 26 | R 6138 | Phalanx | I, Manus, Digit III or IV | | x | High adult | x | NMP |
| 27 | Ra 4019 | Phalanx | I, Manus, Digit III or IV | x | | High adult | x | NMP |
| 28 | Ra 4024 | Phalanx | I, Manus, Digit III or IV | x | | High adult | x | NMP |
| 29 | Ra 4022 | Phalanx | I, Manus, Digit V | | x | High adult | x | NMP |
| 30 | Ra 4026 | Phalanx | II, Manus, ?Digit V | | ? | High adult | x | NMP |
| 31 | Ra 4025 | Phalanx | II, Manus, ?Digit III | | ? | High adult | x | NMP |
| 32 | R 2442 | Pelvis | Ilium and ischium, incomplete | | x | High adult | x | NMP |
| 33 | R 2444 | Femur | Complete, pathological, length: 262 mm distal width: 55 mm | | x | High adult | x | NMP |
| 34 | R 2443 | Femur | Complete, pathological, length: 262 mm distal width: 55 mm | x | | High adult | x | NMP |
| 35 | R 2445 | Tibia | Complete, pathological, length: 204 mm distal width: 42 mm | | x | High adult | x | NMP |
| 36 | R 2446 | Tibia | Complete, pathological, length: 204 mm distal width: 42 mm | x | | High adult | x | NMP |

Table 1 – *continued*

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Original | Collection |
|---|---|---|---|---|---|---|---|---|
| 37 | Ra 4012 | Patella | Complete | | | High adult | x | NMP |
| 38 | R 2448 | Calcaneus | Complete | x | | High adult | x | NMP |
| 39 | Ra 4008 | Astragalus | Complete | | x | High adult | x | NMP |
| 40 | Ra 4009 | Astragalus | Complete | x | | High adult | x | NMP |
| 41 | R 6141 | Metatarsal | II | | x | High adult | x | NMP |
| 42 | R 6139 | Metatarsal | II | x | | High adult | x | NMP |
| 43 | R 6140 | Metatarsal | III | x | | High adult | x | NMP |
| 44 | R 6142 | Metatarsal | III | | x | High adult | x | NMP |
| 45 | Ra 4007 | Metatarsal | IV | x | | High adult | x | NMP |
| 46 | Ra 4006 | Metatarsal | IV | | x | High adult | x | NMP |
| 47 | Ra 4004 | Metatarsal | V | x | | High adult | x | NMP |
| 48 | Ra 6143 | Metatarsal | V | | x | High adult | x | NMP |
| 49 | Ra 4020 | Phalanx | I, Pes, ?Digit III or IV | | x | High adult | x | NMP |
| 50 | Ra 4018 | Phalanx | I, Pes, ?Digit V | x | | High adult | x | NMP |
| 51 | Ra 4019 | Phalanx | I, Pes, ?Digit III or IV | | x | High adult | x | NMP |
| 52 | Ra 4023 | Phalanx | I, Pes, ?Digit V | | x | High adult | x | NMP |
| 53 | Ra 4028 | Phalanx | II, Pes, ?Digit III or IV | | x | High adult | x | NMP |
| 54 | Ra 4027 | Phalanx | II, Pes, ?Digit III or IV | x | | High adult | x | NMP |
| 55 | Ra 4030 | Phalanx | II, Pes, ?Digit II | | x | High adult | x | NMP |
| 56 | Ra 4029 | Phalanx | II, Pes, ?Digit II or IV | x | | High adult | x | NMP |
| 57 | Ra 4031 | Phalanx | III | x | | High adult | x | NMP |
| 58 | Ra 4115 | Phalanx | III | | x | High adult | x | NMP |
| 59 | Ra 4034 | Phalanx | III | | x | High adult | x | NMP |
| 60 | Ra 4032 | Phalanx | III | | x | High adult | x | NMP |
| 61 | Ra 4033 | Phalanx | III | x | | High adult | x | NMP |
| 62 | Ra 4038 | Cervical vertebra | Atlas, incomplete | | | High adult | x | NMP |
| 63 | Ra 4039 | Cervical vertebra | Axes, incomplete | | | High adult | x | NMP |
| 64 | Ra 4040 | Cervical vertebra | C3, incomplete | | | High adult | x | NMP |
| 65 | Ra 4041 | Cervical vertebra | C4, incomplete | | | High adult | x | NMP |
| 66 | Ra 4042 | Cervical vertebra | C6, incomplete | | | High adult | x | NMP |
| 67 | Ra 4043 | Cervical vertebra | C7, incomplete | | | High adult | x | NMP |
| 68 | Ra 4054 | Thoracic vertebra | T1, incomplete | | | High adult | x | NMP |
| 69 | Ra 4055 | Thoracic vertebra | T2, incomplete | | | High adult | x | NMP |
| 70 | Ra 4056 | Thoracic vertebra | T3, incomplete | | | High adult | x | NMP |
| 71 | Ra 4065 | Thoracic vertebra | T4, incomplete | | | High adult | x | NMP |
| 72 | Ra 4057 | Thoracic vertebra | T5, incomplete | | | High adult | x | NMP |
| 73 | Ra 4060 | Thoracic vertebra | T6, incomplete | | | High adult | | NMP |
| 74 | Ra 4062 | Thoracic vertebra | T7, incomplete | | | High adult | x | NMP |
| 75 | Ra 4065 | Thoracic vertebra | T8, incomplete | | | High adult | x | NMP |
| 76 | Ra 4063 | Thoracic vertebra | T9, incomplete | | | High adult | x | NMP |
| 77 | Ra 4061 | Thoracic vertebra | T10, incomplete | | | High adult | x | NMP |
| 78 | Ra 4059 | Thoracic vertebra | T11, neural arch | | | High adult | x | NMP |
| 79 | Ra 4101 | Thoracic vertebra | T12, neural arch | | | High adult | x | NMP |
| 80 | Ra 4058 | Thoracic vertebra | T13, incomplete | | | High adult | x | NMP |
| 81 | Ra 4097 | Thoracic vertebra | T14, incomplete | | | High adult | x | NMP |
| 82 | Ra 4098 | Thoracic vertebra | T15, incomplete | | | High adult | x | NMP |

Table 1 – *continued*

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Original | Collection |
|---|---|---|---|---|---|---|---|---|
| 83 | Ra 4096 | Lumbar vertebra | L1, incomplete | | | High adult | x | NMP |
| 84 | Ra 4095 | Lumbar vertebra | L2, incomplete | | | High adult | x | NMP |
| 85 | Ra 4094 | Lumbar vertebra | L3, incomplete | | | High adult | x | NMP |
| 86 | Ra 4093 | Lumbar vertebra | L4, incomplete | | | High adult | x | NMP |
| 87 | Ra 4092 | Lumbar vertebra | L5, incomplete | | | High adult | x | NMP |
| 88 | Ra 4013 | Sternal bone | First proximal, incomplete | | | High adult | x | NMP |
| 89 | Ra 4014 | Sternal bone | Second, complete | | | High adult | x | NMP |
| 90 | Ra 4015 | Sternal bone | Third, complete | | | High adult | x | NMP |
| 91 | Ra 4016 | Sternal bone | Fifth or sixth, complete | | | High adult | x | NMP |
| 92 | Ra 4108 | Costa | First, incomplete | x | | High adult | x | NMP |
| 93 | Ra 4107 | Costa | Second, incomplete | x | | High adult | x | NMP |
| 94 | Ra 4104 | Costa | Middle, No. 5-6, incomplete | x | | High adult | x | NMP |
| 95 | Ra 4105 | Costa | Middle No. ?9, complete | x | | High adult | x | NMP |
| 96 | Ra 4119 | Costa | Middle, fragment | x | | High adult | x | NMP |
| 97 | Ra 4036 | Costa | Middle, incomplete | x | | High adult | x | NMP |
| 98 | Ra 4106 | Costa | Posterior, No. ?11, incomplete | x | | High adult | x | NMP |
| 99 | Ra 4103 | Costa | Posterior, No. ?13, incomplete | x | | High adult | x | NMP |
| 100 | Ra 4102 | Costa | Last, No. 15, incomplete | x | | High adult | x | NMP |
| 101 | Ra 4120 | Costa | Posterior, fragment | x | | High adult | x | NMP |
| 102 | Ra 4117 | Costa | Second, incomplete | | x | High adult | x | NMP |
| 103 | Ra 4116 | Costa | Anterior, No. 3-4, fragment | | x | High adult | x | NMP |
| 104 | Ra 4114 | Costa | Middle, No. ?9, incomplete | | x | High adult | x | NMP |
| 105 | Ra 4113 | Costa | Middle, incomplete | | x | High adult | x | NMP |
| 106 | Ra 4118 | Costa | Middle, fragment | | x | High adult | x | NMP |
| 107 | Ra 4111 | Costa | Posterior, No. ?13, incomplete | | x | High adult | x | NMP |
| 108 | Ra 4110 | Costa | Posterior, incomplete | | ? | High adult | x | NMP |
| 109 | Ra 4112 | Costa | Posterior, No. ?14, fragment | | x | High adult | x | NMP |
| 110 | Ra 4121 | Costa | Posterior, incomplete | | ? | High adult | x | NMP |
| 111 | 323/77 (62) | Costa | Fragment | | | ? | x | MBKB |
| 112 | Ra 4109 | Costa | Fragment | | | ? | x | NMP |
| 113 | Ra 4122 | Costa | Fragment | | | ? | x | NMP |
| 114 | Ra 4123 | Costa | Fragment | | | ? | x | NMP |

NMP and MBKB collections.

Table 2. Other *C. c. spelaea* (Goldfuss, 1823) bone remains from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Original | Collection |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Ra 4051 | Cranium | Fragment | | | High adult | x | x | NMP |
| 2 | R 2433 | Mandible | Without ramus, C and all I | x | | High adult | x | x | NMP |
| 3 | Ra 4037 | Mandible | Without ramus, and all I | x | | High adult | x | x | NMP |
| 4 | R 3318 | Dens | Canine | | | High adult | | x | NMP |
| 5 | Ra 4044 | Ulna | Without joints | x | | High adult | x | x | NMP |
| 6 | Ra 4045 | Ulna | Without joints | x | | High adult | x | x | NMP |
| 7 | Ra 4046 | Tibia | Half, distally | x | | High adult | x | x | NMP |
| 8 | Ra 4005 | Metatarsal | V, without proximal joint | | x | High adult | x | x | NMP |
| 9 | Ra 4047 | Pelvis | Fragment | | x | High adult | x | x | NMP |
| 10 | Ra 4048 | Atlas | Incomplete | | | High adult | x | x | NMP |
| 11 | Ra 4049 | Atlas | Incomplete | | | High adult | x | | NMP |
| 12 | Ra 4050 | Axes | Incomplete | | | High adult | x | x | NMP |

NMP collections.

### *Hyena excrements*

About 24 nearly complete coprolite pellets and 11 fragments Table 3 were found, as listed in Table 3. These were rediscovered between the bone material of the ‘bone fragment’ boxes of the 1950/51 collected material of Petrbok (Diedrich and Žák 2006), and are presented herein with more pellet figurations. Here, all the complete well–preserved ones are figured (Figure 12) to demonstrate the variability of single pellets, which were originally mostly attached to others in excrement aggregates. These single pellets are compared to an African modern spotted hyena excrement, which consists of three main pellet shape types (Figure 12.14), to which the pellets of the Koněprusy Cave can be attributed well. In one case, only three single pellets could be reaffixed (Figure 12.6). On this pellet aggregate, more pellets must have been attached, which can be seen on the large flat surface of pellet No. C (Ra 4068). Typically, in between the attached pellets, radial wrinkle marks are present (Figure 12.2 and 4). These pellets especially, which built larger oval aggregates, often vary in shape and have edges and mostly flat sides (Figures 12.2 and 4–5). Long oval-shaped pellets (Figure 12.3 and 10–11), oval pellets (Figure 12.8) and also drop-shaped pellets with one flat side

Table 3. Coprolites of *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst).

| **No.** | **Coll.-No.** | **Material type** | **Commentary** | **Original** | **Collection** |
|---|---|---|---|---|---|
| 1 | Ra 4052 | Coprolites | 11 fragments | | NMP |
| 2 | Ra 4069 | Coprolite | Single pellet | x | NMP |
| 3 | Ra 4085 | Coprolite | Single pellet, half | | NMP |
| 4 | Ra 4077 | Coprolite | Single pellet | | NMP |
| 5 | Ra 4086 | Coprolite | Single pellet | | NMP |
| 6 | Ra 4088 | Coprolite | Single pellet, half with prey bone | | NMP |
| 7 | Ra 4066 | Coprolite | Single pellet, with prey bone | x | NMP |
| 8 | Ra 4082 | Coprolite | Single pellet | | NMP |
| 9 | Ra 4067 | Coprolite | Single pellet | x | NMP |
| 10 | Ra 4068 | Coprolite | Three articulated pellets | x | NMP |
| 11 | Ra 4071 | Coprolite | Single pellet | x | NMP |
| 12 | Ra 4073 | Coprolite | Single pellet | x | NMP |
| 13 | Ra 4076 | Coprolite | Single pellet | x | NMP |
| 14 | Ra 4072 | Coprolite | Single pellet, with prey bone | x | NMP |
| 15 | Ra 4089 | Coprolite | Single pellet, with prey bone | x | NMP |
| 16 | Ra 4070 | Coprolite | Single pellet | | NMP |
| 17 | Ra 4083 | Coprolite | Single pellet | | NMP |
| 18 | Ra 4075 | Coprolite | Single pellet, with prey bone | | NMP |
| 19 | Ra 4084 | Coprolite | Single pellet, incomplete | | NMP |
| 20 | Ra 4080 | Coprolite | Single pellet | | NMP |
| 21 | Ra 4079 | Coprolite | Single pellet, incomplete | | NMP |
| 22 | Ra 4078 | Coprolite | Single pellet, incomplete | | NMP |
| 23 | Ra 4074 | Coprolite | Single pellet, incomplete | | NMP |
| 24 | Ra 4087 | Coprolite | Single pellet, | | NMP |
| 25 | Ra 4081 | Coprolite | Single pellet, incomplete | | NMP |

NMP collections.

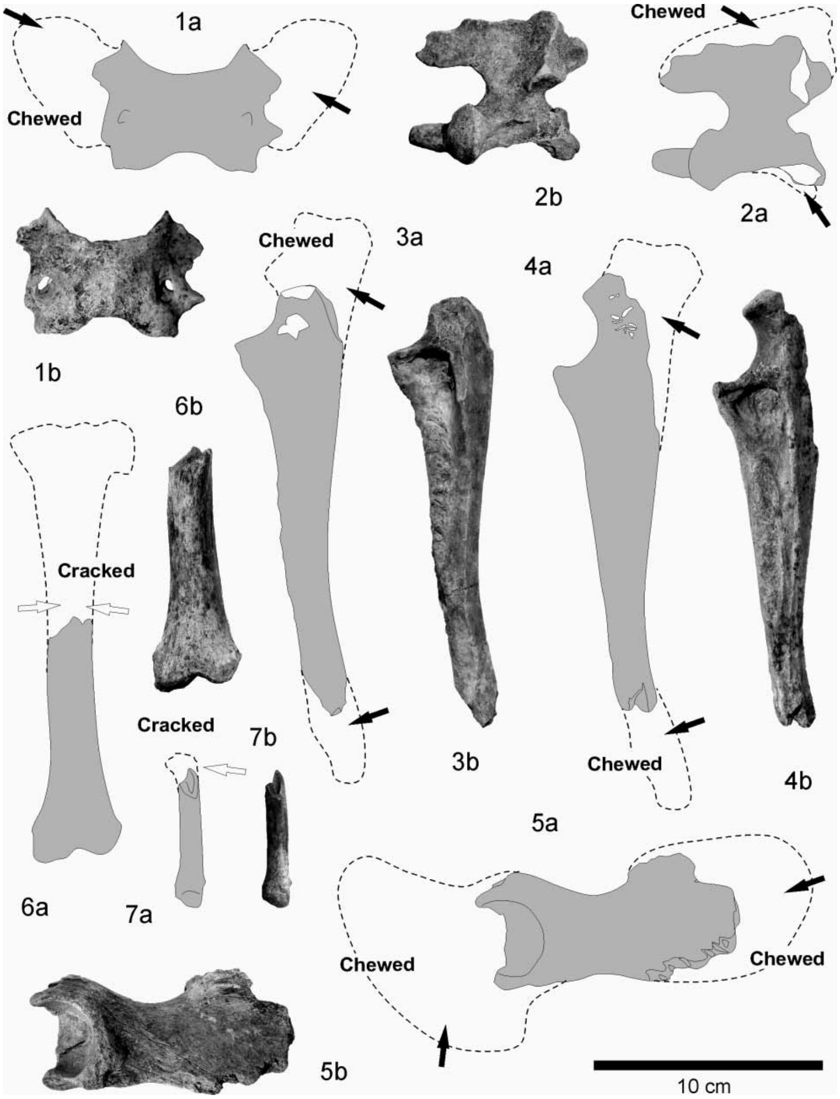


Figure 11. Postcranial cracked and chewed bones from other older adult *C. c. spelaea* (Goldfuss 1823) individuals from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst); redrawing (white = bite marks). 1, Atlas (No. Ra 4048), dorsal. 2. Axes (No. Ra 4050), lateral. 3, Left ulnar of a male (No. Ra 4045), lateral. 4, Left ulnar of a female (No. Ra 4044), lateral. 5, Right pelvis fragment (No. Ra 4047), lateral. 6, Left tibia (No. Ra 4046), lateral. 7, Right Mt V (No. Ra 4005), dorsal.

(Figure 12.9) are more common in elongated sausage-like pellet aggregates (Figure 12.14). Especially, at the ends, the last pellet type can be found. In quite a few pellets from the Main Dome, small prey bone fragments of bone compacta and spongiosa are visible on the coprolite surface (Figure 12.7–8) or at parts that have been newly broken (Figure 12.9). In five pellets from the Main Dome, such small bone remains (cf. Table 3) are visible.

## Discussion

### *Individual skeletons or single bones*

Skeleton remains of the Late Pleistocene *C. c. spelaea*, a close relative of the modern African spotted hyena, *C. c. crocuta* Erxleben 1777 (Rohland et al. 2005), were not known from Europe. The only records of Upper Pleistocene hyena skeletons were believed to be from a cave locality in south-western England, described in the monograph of Reynolds (1902) as 'two skeleton remains' from the late Pleistocene hyena den site 'Wookey Hole Cave' (= Sandford Hill Cave: Diedrich 2010e). Following this study and own comparisons to the original material, the bone material of the 'individual skeletons' was actually from more than three sites and not only from two individuals. The Reynolds cranial material in the British Museum of Natural History was compared, as was the described and rediscovered 'skeleton' material in the Summerset collection, in which both original skulls are recently refigured (Diedrich 2010e). Partial skeletons from a juvenile and older adult animal were recently described

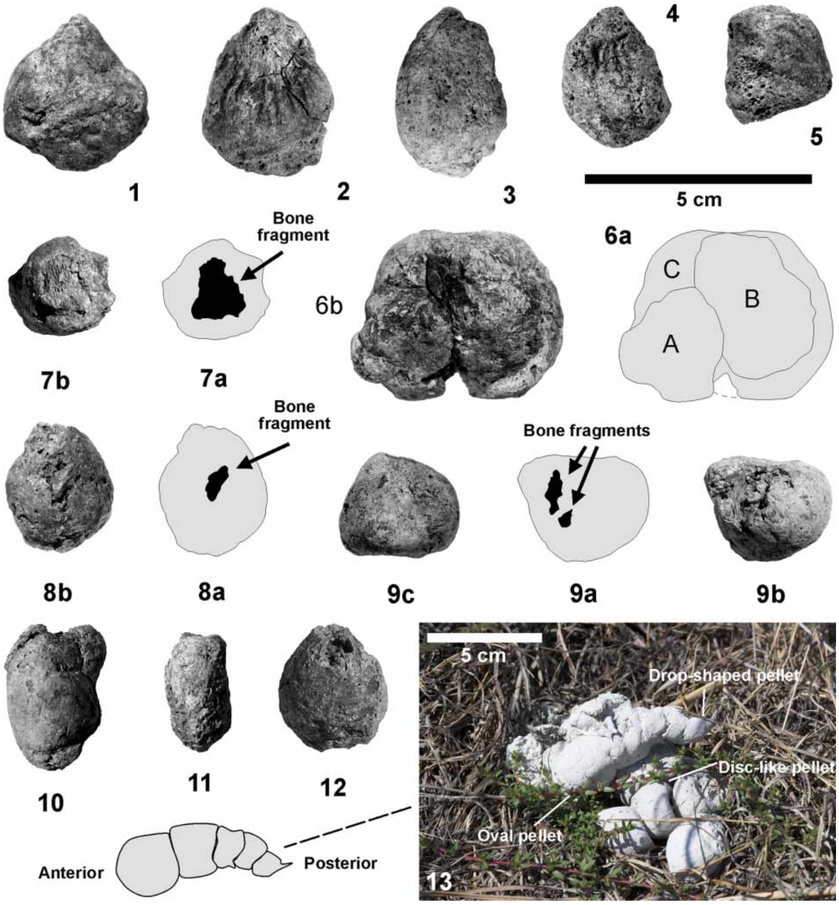


Figure 12. Coprolites from *C. c. spelaea* (Goldfuss 1823) from the hyena site Main Dome of the Koněprusy Caves (Czech Republic, Bohemian Karst). a. redrawing (bone fragments in black), b. photo. 1, Large, single, drop-shaped pellet (No. Ra 4071). 2, Irregular-shaped pellet with radial wrinkles, which was attached to other pellets (No. Ra 4069). 3, Long oval-shaped pellet (No. Ra 4073). 4, Irregular-shaped pellet with radial wrinkles, which was attached to other pellets (No. Ra 4076). 5, Irregular-shaped pellet (No. Ra 4067). 6, Three (A-C) articulated pellets (No. Ra 4068). 7, Single round-shaped pellet with bone fragment (No. Ra 4089). 8, Single oval-shaped pellet with bone fragment (No. Ra 4072). 9, Single drop-shaped pellet, which was attached to other pellets, with bone fragments (No. Ra 4066). 10. Single oval-shaped pellet (No. Ra 4070). 11. Single oval-shaped pellet (No. Ra 4083). 12. Single, drop-shaped pellet (No. Ra 4080). 13. Modern African spotted hyena pellet aggregate composed of different pellet shapes (photo from: www.predatorconservation.com/spotted%20hyena.htm).

from the Perick Caves, an Upper Pleistocene northern German hyena den site (Diedrich 2005). These are the only incomplete skeletons, even though single bones and teeth are mentioned in many publications about the European late Pleistocene (e.g. Liebe 1876; Kafka 1903; Musil 1962; Miracle 1991; Fosse et al. 1998; Baryshnikov 1999; Böttcher et al. 2000; Diedrich 2006a, 2008b, 2011a). The incorrectly mounted 'skeleton' in the Geological-Paleontological Museum of the University of Münster is not from one individual skeleton as incorrectly mentioned by Humpohl et al. (1997). Bones from different large males and females and from three different cave sites (Martins Cave, Balve Cave and 'Biggetal Cave' = Wilhelms Cave) were indeed integrated, in which material from the Balve Cave was recently published (Diedrich 2010c). What is interesting is the presence of rare complete hyena skeletons, which were found in the Bohemian Karst even at two vertical cave sites, the Main Dome of the Koněprusy Caves and possibly also in the Srbsko Chlum-Komin Cave (cf. Diedrich and Žák 2006), the latter of which are not yet published in detail. Another third unpublished skeleton has recently been mentioned from the Czech Moravian Karst Výpustek Cave hyena den of which only the skull was figured preliminary (Diedrich 2010c). Normally, hyena carcasses seem to have been scavenged in most cases cannibalistically, and therefore, only single bone remains are typical at late Pleistocene hyena dens in Europe.

However, compared to clan sizes of modern African hyenas (e.g. Hofer and East 1995), the Main Dome 'population' consists of only about 'three individuals'. This is quite a low number, especially for 'commuting den' sites, and lends itself to the interpretation of a 'prey storage site' that was only used for a short time. Possibly, the last animal of the 'clan' died in the cave itself, leaving its skeleton untouched.

### *Hyena cannibalism*

The postcranial chewed bones from other hyena individuals of the Main Dome were compared with those of other Bohemian Karst cave sites (Srbsko Chlum-Komin Cave, Nad Kačákem Cave, Turská Maštal Cave), the German Zoolithen Cave with its holotype and paratype specimens and large 'population', Perick Caves and the Bad Wildungen Biedensteg open-air site, where hyena cannibalism was demonstrated at all mentioned den sites several times (Diedrich 2005, 2006b, 2011a; Diedrich and Žák 2006). At den sites, only the skulls, lower jaws and typically the first two cervical vertebrae (atlas/axes) are over-represented in the bone material (cf. Perick Caves; Diedrich 2005), such as in the Main Dome. Typically, the long bones are all cracked or are missing both the distal parts (Figure 11) as a result of hyena activities. Such cracking of long bones in the cave itself has even been singularly documented at the Srbsko Chlum-Komin hyena den cave site by fitting bone fragments (Diedrich and Žák 2006). The massive pelvic bone remains again show bite marks. Cannibalism in modern spotted hyenas is not highly common, but may appear (Kruuk 1972; Bateman 1987; East at al. 1989; Frank 1994).

### *Hyena den marking with pellets*

Coprolite pellets are typical of modern (Kruuk 1972; Bearder and Randall 1978) and fossil Late Pleistocene spotted hyena den sites (Musil 1962; Miracle 1991; Fosse et al. 1998; Tournepiche and Couture 1999; Diedrich 2006b; Diedrich and Žák 2006) in general. Only from the Koněprusy Cave and Srbsko Chlum-Komin cave of the Bohemian Karst, a small amount of pellets survived such as from the Nad Kačakem Cave (Diedrich and Žák 2006). Such comparative behaviour of faecal marking of den sites in Africa by modern spotted hyenas *C. c. crocuta* was described by Kruuk (1972) and Bearder and Randall (1978). They are figured in similar shapes for modern African spotted hyenas (Diedrich and Žák 2006), and can be distinguished here in three main forms: a. oval pellets (from posterior), b. disc-like pellets (from middle) and c. drop-shaped pellets (from anterior to middle), according to modern spotted hyena excrements (Figure 12.14). Bone fragments such as those found in the Main Dome (Figure 12.7–9) and coprolites are also recorded in the hyena pellets from the open-air site Biedensteg (Diedrich 2006b) or the Sloup Cave den (Diedrich 2011c).

### *Sex and individual ages*

The long bones from the Czech Koněprusy Cave Main Dome hyena individual skeleton were compared in the metrics not only to the published material from the most important holo- and paratype Zoolithen Cave collection (Diedrich 2011a), the population of the Perick Caves (Diedrich 2005), but also to the rediscovered, unpublished material from the Martins Cave and Wilhelms Cave (Sauerland Karst, Germany) and even to other German open-air gypsum karst hyena den sites such as Westeregeln or Sevecken-Berge and finally to the large Rösenbecker Cave 'population' (Diedrich 2010e; Figure 13). Other compared material is from the Srbsko Chlum-Komin, another very important Bohemian Karst Upper Pleistocene hyena den site (Diedrich and Žák 2006).

The nearly complete mandible of the Main Dome individual and parts of the damaged skull are very massive, similar to the ones figured for female skulls from the Perick Caves and one individual from the Srbsko Chlum-Komin Cave (see Diedrich and Žák 2006). The average worn teeth usage gives an older adult individual age of the Main Dome individual compared to skulls from the Perick Caves (cf. Diedrich 2005).

Sexual dimorphism or variation in the size of *Crocuta* during warm and cold periods in the Late Pleistocene was described (Turner 1984; Klein and Scott 1989), but is not well confirmed or rediscussed yet, whereas sexual dimorphism was recently figured for *C. c. spelaea* from Perick Caves, Teufelskammer Cave, Rösenbecker Cave and Zoolithen Cave (Diedrich 2005, 2007b, 2010e, 2011a). Similar to modern African spotted hyenas (cf. Kruuk 1972; Lynn 2009), the males are also few and smaller in their size as in glacial Late Pleistocene spotted hyenas (Diedrich 2010e, 2011a). There is most likely an overlap of small females and large males, such as demonstrated on the skulls (Lynn 2009), but modern spotted hyena postcranial skeletons have not been studied yet(East and Hofer 2002). This obvious sexual dimorphism can be seen fairly well not only on the long bone material, but also on the skull and lower jaws. The teeth proportions are also smaller in size, but more variable, and are not that useful for sex determination with the exception of the $M_1$.

The long bones were compared to the populations of the Martins Cave, Wilhelms Cave and Perick Caves, in which all males are again reported to be smaller than the females (cf. Diedrich 2010e). The Main Dome skeleton humerus distal joints are both about 59 mm in width and length is about 232 mm. The largest humerus from the Perick Caves measures 56 mm in width, and was believed to be from a female animal when compared to recently published material from other hyena den sites (cf. Diedrich 2005, 2007a–b). The ulnae are both 260 mm long and have the largest width of 50 mm. The one complete radius of the Main Dome animal is 220 mm long and distally 46 mm in width, this again matches more to female hyenas. The femora of the Main Dome hyena, with proportions of 262 mm in total length and 55 mm distal width, matches a large female femur from the Perick Caves (262 mm length

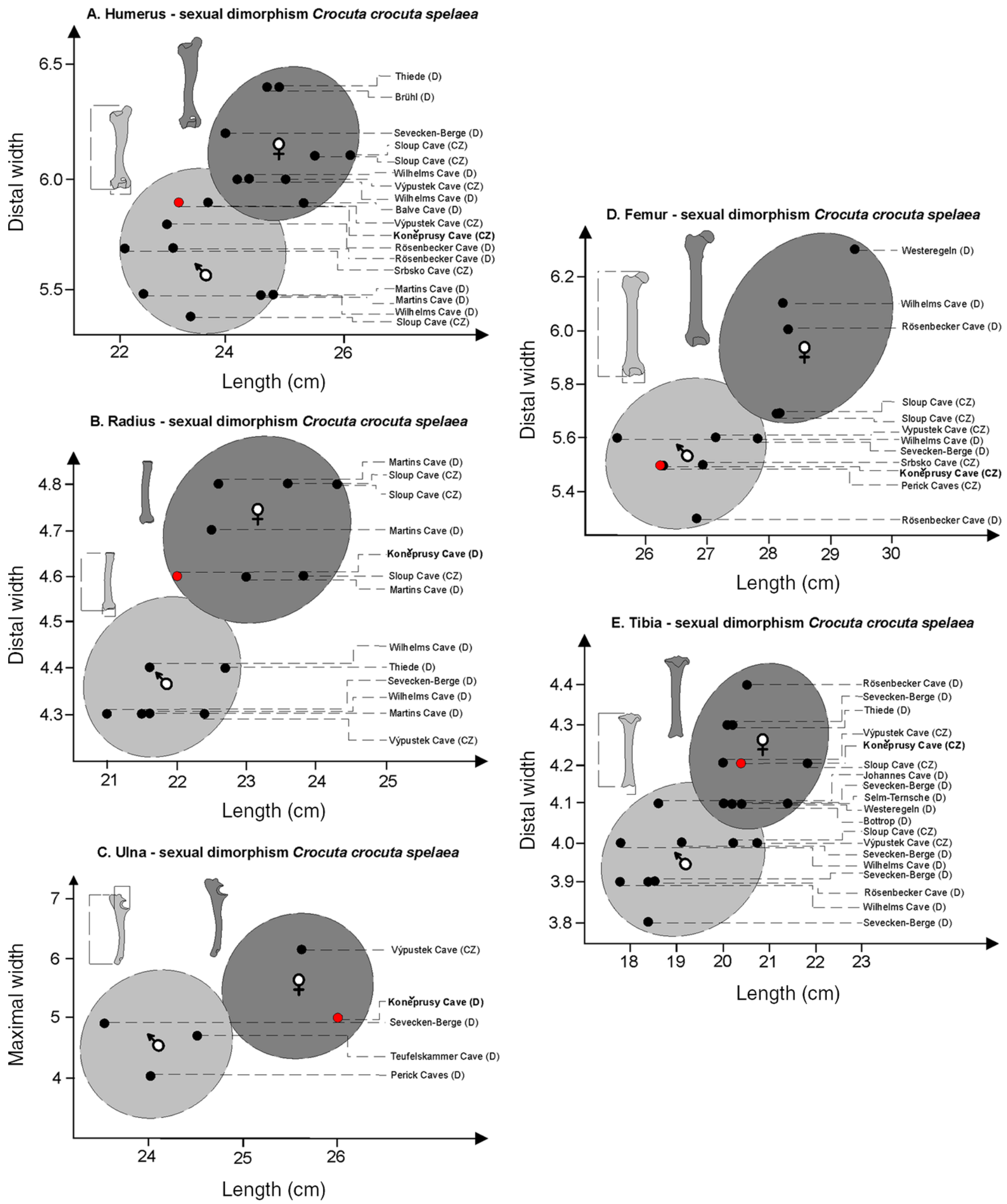


Figure 13. Sexual dimorphism in glacial cold period Upper Pleistocene *C. c. spelaea* (Goldfuss 1823), in the A. Humerus, B. Radius, C. Ulna, D. Femur, E. Tibia (other data from Diedrich 2011a) compared to the Koněprusy Caves Main Dome individual skeleton long bones.

and 55 mm width). Finally, the tibiae of the Main Dome animal (length: 204, distal width: 42 mm) is again larger than that of the male ones (Wilhelms Cave, length: 178, distal width: 39 mm).

All the postcranial bone metrics of the Koněprusy Cave Main Dome individual skeleton (Figure 13) range with most postcranial long bones (humerus/ulna/radius/tibia) in the clusters of smaller females. Only the femorae, which are pathological (and possibly therefore even shortened), are out of this range in the clusters of medium-sized males (Figure 13). Therefore, a clear sex identification cannot be given for the pathological individual skeleton, but the metrics at all correspond more to a smaller-sized female, which had possibly shortened upper hind legs as a result of illness (arthritis).

### *Woolly rhinoceros remains: taphonomy and den indicators of important prey*

In many cases, the hyena prey bones from the Main Dome have typical chew and gnaw marks (Figure 15(A)) or are

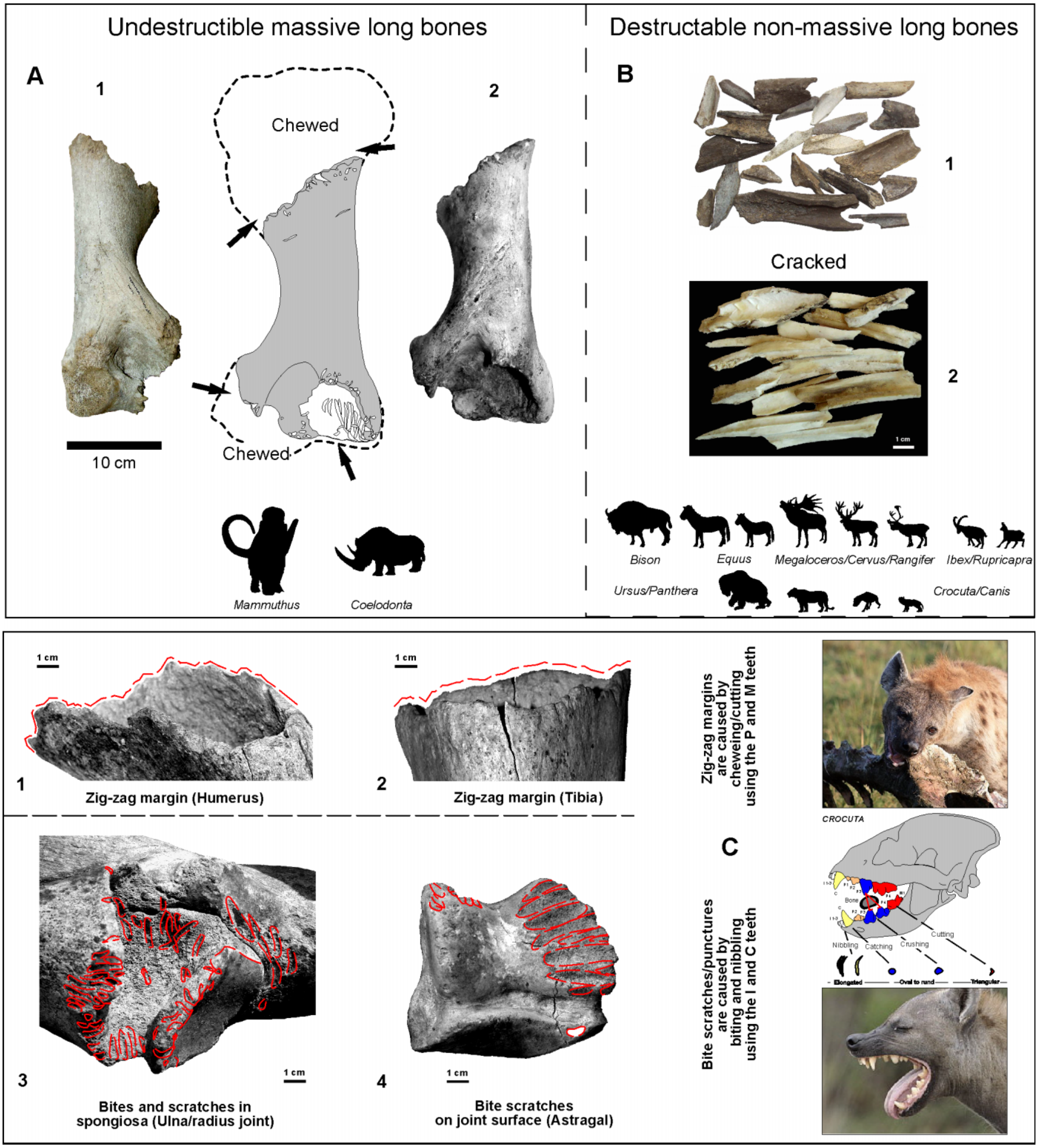


Figure 14. Bone taphonomy at spotted hyena dens. A. Comparison of modern and Late Pleistocene rhinoceros humerus, both similar chewed. 1. Modern Kayanya Cave hyena den (Tanzania) (Sutcliffe coll. BMNHL), 2. Late Pleistocene Srbsko-Chlum-Komin hyena den Cave (Czech Republic). B. Hyena long bone cracking results. The main reason for the cracking activity is the bone marrow as nutrition. 1. Late Pleistocene Cracked bones of *R. tarandus*, *E. c. przewalskii*, *M. giganteus* and other animals from the Koněprusy Caves Main Dome hyena den, Czech Republic (NMP No. Ra 4213). 2. Modern cracked zebra and antelope and other long bone fragments from a recent hyena den in the Ngorongoro Crater, Tanzania (Sutcliffe coll. BMNHL). C. Main hyena bone damage and bite mark types on Late Pleistocene *C. antiquitatis* bones. 1–2. Zig-zag margins at the woolly rhinoceros humerus and tibia from the Koněprusy Caves Main Dome hyena den (cf. Figures 15.3 and 6). 3. Bites in the spongiosa of the woolly rhinoceros ulna/radius from the Koněprusy Caves Main Dome hyena den (cf. Figure 15.4). 4. Bite scratches on the joint surface of an woolly rhinoceros astragal from the Axamitová Brana Cave hyena den, Czech Republic (NMP No. R 1631). Spotted hyena photo: T. Heald.

cracked into pieces (Figure 15(B); Diedrich 2005, 2006b; Diedrich and Žák 2006). Typical zigzag margins and elongated bite marks on large woolly rhinoceros bones (Figure 15(C)) are typical for hyena activities and can be attributed to different teeth that had different functions in the bone-crushing jaw function of *Crocuta* (cf. Figure 15(C)). While rhinoceros bones are nearly indestructible because of their completely filled spongious structure (similar in mammoths), bones of all other megafauna were often crushed into pieces which were found commonly in the Main Dome (Figure 15(B1)).

The largest prey for the Bohemian hyenas and the 'population' of the Koněprusy Caves was the woolly rhinoceros *C. antiquitatis* (Figure 15; Diedrich and Žák 2006), and not the woolly mammoth, such as known from many other European hyena den sites which are situated at the margin or in the middle high mountainous regions (cf. Figure 17), such as German Perick Caves (Diedrich 2008d), Balve Cave (Diedrich 2010c), Teufelskammer Cave in the Neander Valley (Diedrich 2010f), the open-air site Bad Wildungen-Biedensteg (Diedrich 2006a) or Czech Republic Sloup Cave (Diedrich 2011c). At all dens, bones of the rhinoceroses are similarly damaged and incomplete such as figured for other Bohemian Karst caves and open-air sites around Prague (Diedrich and Žák 2006), or recently at the open-air site Bottrop in the north-western German lowlands (Diedrich 2011b).

### *Prey faunal composition*

The accumulation of macromammal prey and bones by the modern spotted hyena *C. c. crocuta* has been well documented at African open-air sites (Sutcliffe 1970; Kruuk 1972; Henschel et al. 1979; Behrensmeyer and Boaz 1980; Brain 1980; Scott and Klein 1981; Skinner et al. 1986; Cooper 1993; Brugal et al. 1997; Di Silvestre et al. 2000). For the Late Pleistocene, this has rarely been studied, but only at a few cave localities in France (e.g. Brugal et al. 1997), in Germany at Zoolithen Cave (Diedrich 2011a), Perick Caves (Diedrich 2005), at the open-air site Bad Wildungen-Biedensteg (Diedrich 2006a) and most recently more extensively not only in the Bohemian Karst (Diedrich and Žák 2006; Diedrich 2010a) but also in the Moravian Karst like the Sloup Cave (Diedrich 2011c).

The percentage of the hyena prey remains (NISP = 585) in the Main Dome of the Koněprusy Caves (Figure 16) was estimated using the number of identified specimens by species (NISP) of 711 bones including the hyena remains (Diedrich and Žák 2006). Typical at den sites is the large amount of hyena remains (Ehrenberg 1966; Fosse et al. 1998; Diedrich 2005; Figure 16), which is also high at the Koněprusy Caves at 15%. The most abundant hyena prey in the Main Dome, besides the woolly rhinoceros (Figure 16), was *E. c. przewalskii*. Other large animals such as *B. priscus*, *M. giganteus*, *C. elaphus* and *R. tarandus* are represented additionally by only a small amount of *P. l. spelaea* remains. Remarkable is the fragmented skull from a steppe bison, of which the hyenas left cracked mandibles and many parts of the skull are fragmented into many pieces. All bones found seem possibly to belong to a single large male bison individual (Figure 16). *C. ibex* and *R. rupicapra* as alpine animals were common during the Late Pleistocene in the Bohemian Karst (Diedrich and Žák 2006). There are only a few represented in the bone record (0.1–1%); possibly also as a result of their fragile bones and less as a result of prey selection. Because of the mountainous position of the hyena den in the Bohemian Karst, the lack of *Mammuthus primigenius* (Blumenbach 1799) in the prey composition seems to be the result of topography (Figure 17). In this mountainous region of the Bohemian Karst, generally the mammoth is nearly absent or barely represented with bone material only along the Berounka River Valley; the same can be said for other Late Pleistocene hyena den and prey deposit sites in the Bohemian Karst (Diedrich and Žák 2006). The absence of the largest prey was the reason to hunt medium-sized animals in larger amounts – especially horses (Diedrich 2010a). In general, at all Bohemian Karst cave sites, especially at the Srbsko Chlum-Komin Cave, a specialisation on this horse hunting was recently published and is compared to modern spotted hyena zebra hunting (Diedrich 2010a); such abundant horse remains are also represented at the Koněprusy Caves hyena prey fauna (39% of the NISP). Such behaviour of accumulating prey remains in communal and less in birth/natal den sites can be observed in the modern spotted hyena *C. c. crocuta* from Africa (Mills and Mills 1977; Cooper 1993; Boydston et al. 2006; Pokines et al. 2007).

### *Hyena den types in the Bohemian Karst*

Many Late Pleistocene bone sites in Bohemia were recently identified as hyena dens (Diedrich and Žák 2006), but there are differentiations in the biological sense into a. birth/natal den, b. commuting den (cf. Holekamp and Smale 1990; East and Hofer 2002; Figure 16) and c. prey depot den in which latter is more possible to be distinguished within the European Ice Age spotted hyena site studies (cf. Diedrich 2005, 2006a, 2006b, 2007a, 2007b, 2010a–2010f, 2011a–2011c). Whereas hyenas, especially cubs, are raised modern in smaller caves (birth/natal dens sensu East et al. 1989), in the Late Pleistocene at open-air sites, hyena dens are concluded to have been present at the German Bottrop and Bad Wildungen hyena open-air sites (Diedrich 2011c), but these can be found better preserved in smaller cave branches of larger caves or smaller caves (Diedrich 2005, 2011a, 2011c; Diedrich and Žák 2006). In such birth/natal dens, hyena cubs left typical 'nibbling sticks,' bone

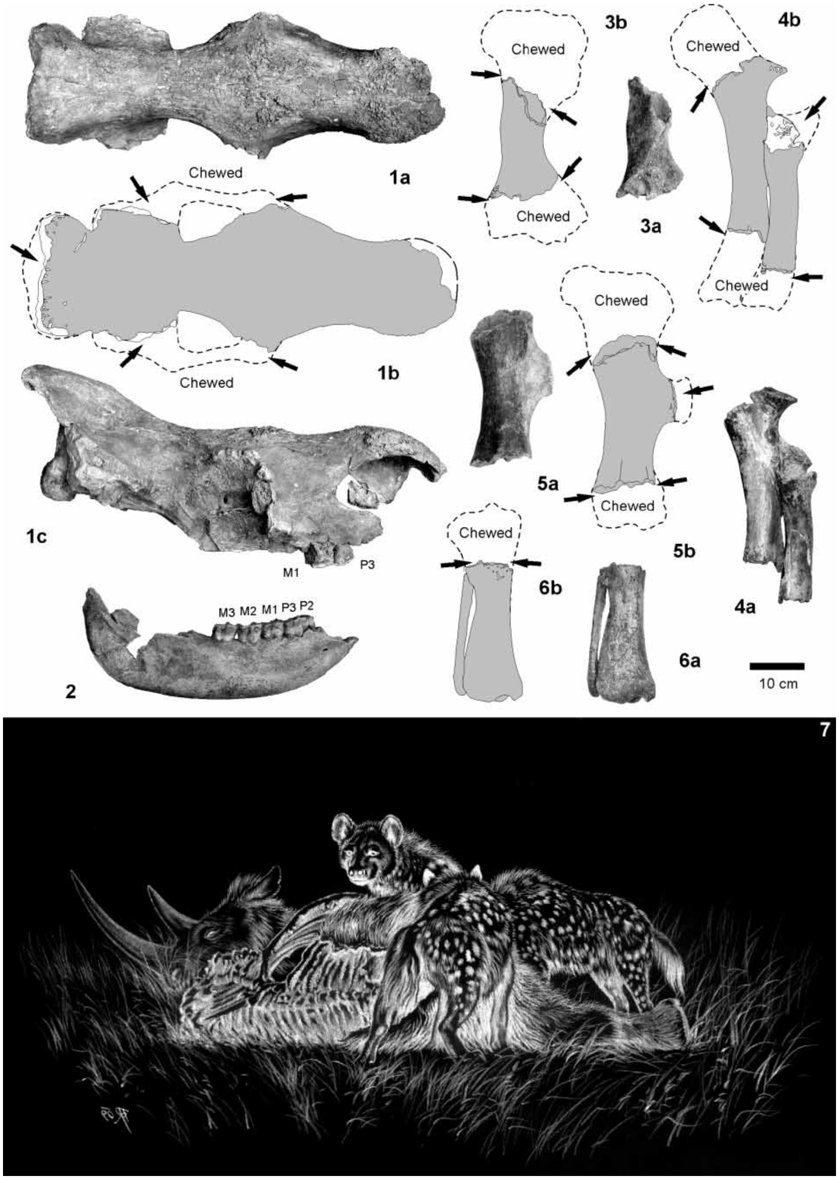


Figure 15. Into the cave imported woolly rhinoceros *C. antiquitatis* hyena prey from Koněprusy Caves Main Dome with typical chew and bite damages on the large bones. 1. Skull which was chewed at the occipital and zygomatic/jugals (NMP No. R 2054), a-b. dorsal, c. lateral. 2. Possibly to the skull belonging to right mandible (NMP No. R 2054), lateral. 3. Right humerus (NMP No. Ra 4194), cranial. 4. Articulated right ulna/radius (NMP No. Ra 4153-radius/4152-ulna), lateral. 5. Left femur (NMP No. Ra 4193), cranial. 6. Articulated right tibia/fibula (NMP No. Ra 4192), cranial. 7. Late Pleistocene hyena clan scavenging on a woolly rhinoceros carcass nearby their prey depot Main Dome of the Koněprusy Caves on the hill of the Golden Horse (=Zlatý KÜň), Bohemian Karst, Czech Republic (Nightvision-google-Illustration: "Rinaldino" G. Teichmann 2010).

fragments which are strongly chewed on one or two sides (Diedrich and Žák 2006; Diedrich 2011a), which are obviously absent in the Koněprusy Caves bone fragment material. In caves with difficult access, such as the Koněprusy Caves, prey remains must have been stored such as in the Main Dome to avoid conflicts with clan members and especially lions. Hyenas fed on the stored material only partly in bad feeding times, but left even complete woolly rhinoceros or other prey fauna remains in abundant prey times. The Main Dome was not a den site in which hyenas gave birth and raised their young (natal/birth den); therefore, it lacks any cub and even adolescent remains. It can also not be attributed to a 'commuting den', because of further absence of young animal lack. In both fossil and modern records, bone remains of cub/juvenile cannibalistically scavenged hyenas can be found in and mostly around the modern commuting dens (Mills and Mills 1977) similar as at Late Pleistocene ones (Diedrich 2005, 2006b, 2010f, 2011a; Diedrich and Žák 2006). Such prey storage den sites are less known in Africa, but there in

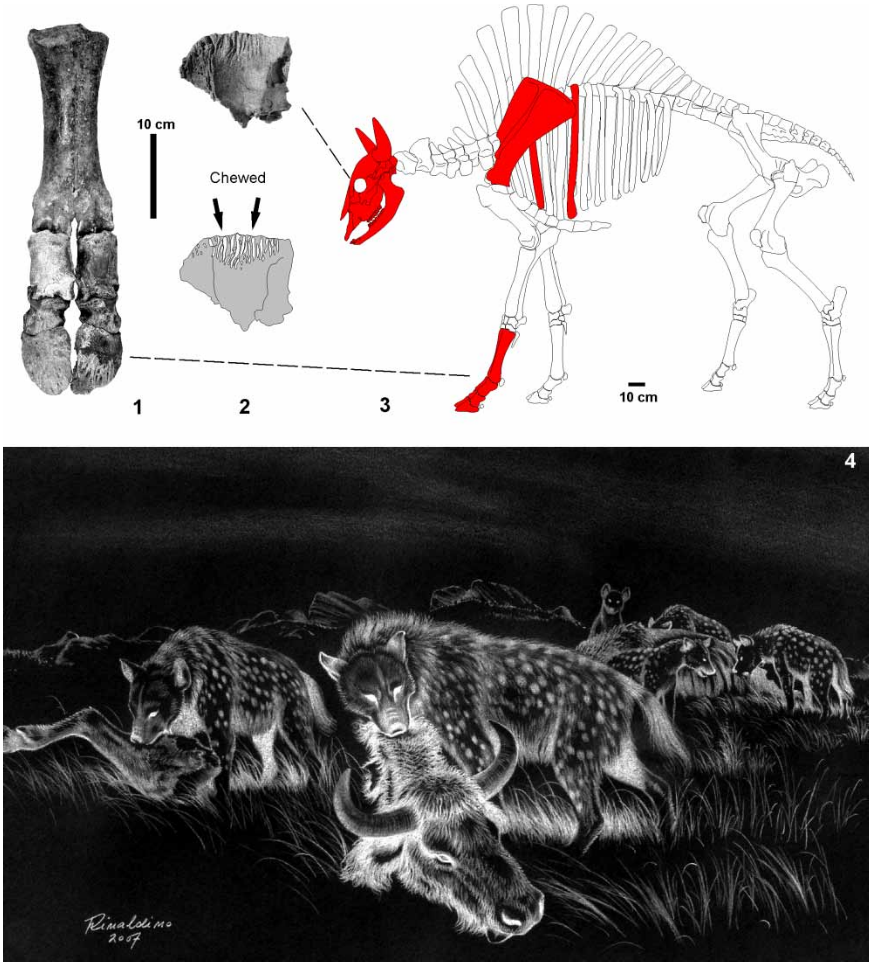


Figure 16. A. Steppe bison *B. priscus* articulated left distal forelimb (left metacarpal NMP No. R 2450, right phalanx 1 NMP No. R 2450, left phalanx 1 MBKB No. Ra 4216, right phalanx 2 NMP No. R 3296, left phalanx 2 NMP No. Ra 4217), right phalanx 3 NMP No. R 3317, left phalanx 3 NMP No. R 3316. 2-3.), cranial. B. Frontal fragment with 3-5 mm wide bite scratch marks only on the orbit side (NMP without No.), ventral. C. Present bones of *B. priscus* of probably a single adult individual found in the Main Dome of the Koněprusy Caves. D. Late Pleistocene hyena clan scavenging and importing steppe bison carcass pieces (skull and legs) into the Main Dome of the Koněprusy Caves (Nightvision-google-Illustration: "Rinaldino" G. Teichmann 2007).

open-air sites body pieces are stored in mud along lakes/rivers (Kruuk 1972). The Koněprusy Cave has a new to distinguish 'prey depot site' character. The small difference about such sites in the Late Pleistocene might be explained by the climatic differences mainly. Caves in the Late Pleistocene cold climate were certainly optimal storage sites, where the temperature was always above the freezing point (outside partly permafrost), and the caves were humid and under similar temperatures all year long. These circumstances are best to hide and conserve prey carcass remains, and especially flesh and bones. In Africa, higher temperatures and less cave availabilities do not allow that much prey storage (Avery et al. 1984; Holekamp and Smale 1990). In Czech Republic (Diedrich and Žák 2006) and Germany (Diedrich 2006a, 2011b), several bone accumulation sites in loess (around Prague, Bad Wildungen) and river terrace deposits (Bottrop) must also be referred to such hyena prey depot den sites at least in some parts. Only a few 'clan members' or small 'population' seem to have had access to the Koněprusy Cave, the theory of which is supported by the absence of cubs/juvenile remains.

## Conclusion

The only known European Upper Pleistocene Ice Age spotted hyena *C. c. spelaea* (Goldfuss 1823) individual skeleton from the Koněprusy Cave, Bohemian Karst (Czech Republic) displays arthritis on both hindlimbs of the smaller-sized most probably female individual. Remains from two additional older individuals show damage most likely due to cannibalism. Faecal pellets were used to mark the 'prey

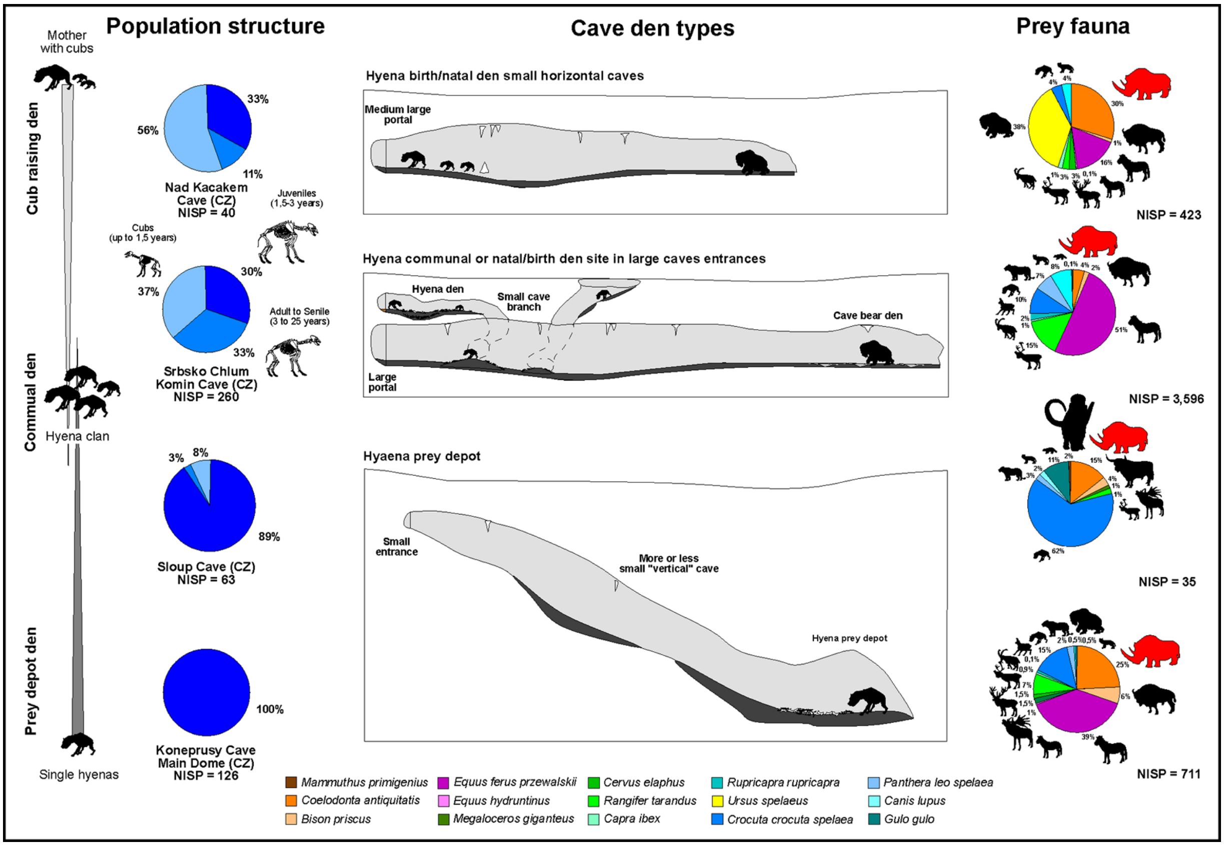


Figure 17. Specialised woolly rhinoceros hunters and bone accumulators in different cave den type situations in mountainous regions of the Bohemian and Moravian Karst of Czech Republic (composed from Diedrich and Žák 2006, Diedrich 2011c).

storage site' restricted to one diagonal surface connected chamber, the Main Dome. Indicators for such a den type, a third one besides 'natal/birth dens', and 'communal dens' (compared to modern African spotted hyena den types) are the full absence of cub and juvenile hyena remains, dominance of older to senile hyenas and presence of non-scavenged hyena carcasses, absence of nibbling sticks and a high amount of prey remains. In this large room, about 585 additional prey bones of the middle mountainous Late Pleistocene megafauna which lacks mammoth were found, including a cracked skull from a steppe bison *B. priscus* (Bojanus 1827). *E. caballus przewalskii* (Poliakov 1881; 40%, NISP) horses were the main prey source. Hyenas also chased *R. tarandus* (Linné 1758), alpine-influenced Central Bohemian *C. ibex* Linné 1758 and *R. rupricapra* (Linné 1758). Many bovid and cervid bones are crushed into pieces. Other important remains of the prey bone assemblage are from the woolly rhinoceros *C. antiquitatis* (Blumenbach 1799; 25%, NISP). Some whole legs of this animal were imported as well as a complete skull. In many cases, these bones have typical hyena chew and gnaw mark damage. The dominance at several hyena den sites in the Bohemian Karst does not reflect the real prey fauna individual amount (MNI), because the bone damages and consumption of medium-sized megafauna are much higher, whereas the rhinoceroses which had massive and fully spongious-filled bones were too cumbersome to be destroyed. Hyenas were unable to crush even the *Coelodonta* bones; therefore, the "high amount" of their prey bones reflects a taphonomic selection influence.

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## References

Avery G, Avery DM, Braine S, Loutit R. 1984. Bone accumulation by hyenas and jackals a taphonomic study. S Afr J Sci. 80:186–187.
Bateman G. 1987. Raubtiere der Welt. München: Orbis-Verlag. p. 159.
Baryshnikov G. 1999. Chronological and geographical variability of *Crocuta spelaea* (Carnivora, Hyaenidae) from the Pleistocene of Russia. Deinsea. 6:155–174.

Bearder SK, Randall RM. 1978. The use of fecal marking sites by spotted hyaenas and civets. Carnivore. 1:32–48.

Behrensmeyer AK, Boaz D. 1980. The recent bones of Amboseli Park Kenya in relation to east African paleoecology. In: Behrensmeyer AK, Hill AP, editors. Fossils in the making – vertebrate taphonomy and paleoecology. Chicago (IL): University of Chicago Press. p. 72–92.

Böttcher R, Cep B, Kind C-J, Mörike D, Pawlik A, Rähle W, Steppan K-H, Torke R, Torke W, Ziegler R. 2000. Kogelstein – eine paläolithische Fundstelle bei Schelklingen-Schmiechen. Fundberichte Baden–Württemberg. 24:1–76.

Boydston EE, Kapheim KM, Holekamp KE. 2006. Patterns of den occupation by the spotted hyaena (*Crocuta crocuta*). Afr J Ecol. 44:77–86.

Brain CK. 1980. Some criteria for the recognition of bone collecting agencies in African caves. In: Behrensmeyer AK, Hill AP, editors. Fossils in the making – vertebrate taphonomy and paleoecology. Chicago (IL): University of Chicago Press. p. 107–130.

Brugal JP, Fosse P, Guadeli JP. 1997. Comparative study of bone assemblages made by recent and Plio-Pleistocene Hyaenids (*Hyena, Crocuta*). Hot Springs South Dakota Occasional Publications. 1(1): 158–187.

Cooper SM. 1993. Denning behavior of spotted hyaenas (*Crocuta crocuta*) in Botswana. Afr J Ecol. 31:178–180.

Cuvier JLNF. 1805. Sur les ossements fossiles des Hyènes. Annales du Musée Histoire Naturelle Paris. 6:127.

Diedrich C. 2005. Eine oberpleistozäne Population von *Crocuta crocuta spelaea* (Goldfuss 1823) aus dem eiszeitlichen Fleckenhyänenhorst Perick-Höhlen von Hemer (Sauerland, NW Deutschland) und ihr Kannibalismus. Philippia. 12(2):93–115.

Diedrich C. 2006a. By ice age spotted hyenas protracted, cracked, nibbled and chewed skeleton remains of *Coelodonta antiquitatis* (Blumenbach 1799) from the Lower Weichselian (Upper Pleistocene) freeland prey deposit site Bad Wildungen-Biedensteg (Hesse, NW Germany). J Taphon. 4(4):95–127.

Diedrich C. 2006b. The *Crocuta crocuta spelaea* (Goldfuss, 1823) population from the early Upper Pleistocene hyena open air prey deposit site Biedensteg near Bad Wildungen (Hess, NW Germany) and contribution to their phylogenetic position, coprolites and prey. Cranium. 23(1):1–15.

Diedrich C. 2007a. The Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) population and its prey from the gypsum karst den site Westeregeln near Magdeburg (Middle Germany). Abhandlungen und Berichte für Naturkunde Magdeburg. 30:57–83.

Diedrich C. 2007b. *Crocuta crocuta spelaea* (Goldfuss 1823) remains from the Upper Pleistocene hyaena Teufelskammer Cave den site near Hochdahl in the Neander valley (NRW, NW Germany). Cranium. 24(2):39–44.

Diedrich C. 2007c. Porcupines in the Bohemian Karst – excavation results of the first known Miocene *Hystrix* (*Hystrix*) *parvae* (Kretzoi 1951) cave den in Central Europe. Scripta Facultatis Scientiarum Universitatis Masarykianae Geology. 35(2005):129–134.

Diedrich C. 2008b. Bone accumulators between the Scandinavian and Alpine ice shields of central Europe – the last ice age spotted hyenas: mammoth scavengers, woolly rhino killers, horse hunters and cave bear/lion antagonists. Abstract 33rd International Geoscience Conference Oslo, Norway.

Diedrich C. 2008b. Late Pleistocene hyenas *Crocuta crocuta spelaea* (Goldfuss 1823) from Upper Rhine valley open air sites and the contribution to skull shape variability. Cranium. 25(2):31–42.

Diedrich C. 2008c. The rediscovered holotypes of the Upper Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) and the steppe lion *Panthera leo spelaea* (Goldfuss, 1810) and taphonomic discussion to the Zoolithen Cave hyena den at Geilenreuth (Bavaria, South-Germany). Zool the Linn Soc Lond. 154:822–831.

Diedrich C. 2008d. Eingeschleppte und benagte Knochenreste von *Coelodonta antiquitatis* (Blumenbach 1807) aus dem oberpleistozänen Fleckenhyänenhorst Perick-Höhlen im Nordsauerland (NW Deutschland) und Beitrag zur Taphonomie von Wollnashornknochen in Westfalen. Mitteilungen der Höhlen- und Karstforscher. 2008(4):100–117.

Diedrich C. 2009. Cave bear killers, scavengers between the Scandinavian and Alpine Ice shields – the last hyenas and cave bears in antagonism – and the reason why cave bears hibernated deeply in caves. Stalactite. 58(2):53–63.

Diedrich C. 2010a. Specialized horse killers in Europe – foetal horse remains in the Late Pleistocene Srbsko Chlum-Komín Cave hyena den in the Bohemian Karst (Czech Republic) and actualistic comparisons to modern African spotted hyenas as zebra hunters. Quat Int. 220(1–2):174–187.

Diedrich C. 2010b. Die späteiszeitlichen Fleckenhyänen und deren Exkremente aus Neumark-Nord. In: Meller H, editor. Elefantenreich – eine Fossilwelt in Europa: Archäologie in Sachsen-Anhalt Ausstellungs-Begleitband [Elephant kingdom – a fossil life in Europe: archaeology in Saxony-Anhalt accompanying exhibition]. Halle/Saale: LDA. p. 445–451.

Diedrich C. 2010c. Periodical use of the Balve Cave (NW Germany) as a Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) den – hyena occupations and bone accumulations versa human Middle Palaeolithic activity. Quat Int (in press).

Diedrich C. 2010d. Rare Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) remains from northern Czech Republic open air loess sites along the Elbe River. Cranium (accepted).

Diedrich C. 2010e. One of Europe's last glacial *Crocuta crocuta spelaea* (Goldfuss 1823) clans from the Rösenbeck Cave hyena den (Germany) and contribution to cranial shape variability. Biol J Linn Soc Lond (in press).

Diedrich C. 2010f. The *Crocuta crocuta spelaea* (Goldfuss 1823) population and its prey from the Upper Pleistocene Teufelskammer Cave hyena den site in the Neandertal (NRW, NW Germany). Hist Biol. 23(2–3):237–270.

Diedrich C. 2011a. The Late Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) population with its type specimens from the Zoolithen Cave at Gailenreuth (Bavaria, South Germany) – a hyena cub raising den of specialized cave bear scavengers in boreal forest environments of Central Europe. Hist Biol (accepted).

Diedrich C. 2011b. The Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) population from the Emscher River terrace hyena open air den Bottrop and other sites in NW-Germany – woolly rhinoceros scavengers and their bone accumulations along rivers in lowland mammoth steppe environments. Quat Int (in review).

Diedrich C. 2011c. The Ice Age spotted *Crocuta crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the Late Pleistocene hyena den Sloup Cave in the Moravian Karst; Czech Republic. Bull Geosci (accepted).

Diedrich C, Žák K. 2006. Prey deposits and den sites of the Upper Pleistocene hyena *Crocuta crocuta spelaea* (Goldfuss 1823) in horizontal and vertical caves of the Bohemian Karst (Czech Republic). Bull Geosci. 81(4):237–276.

Di Silvestre I, Novelli O, Bogliani G. 2000. Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal. Afr J Ecol. 38:102–107.

East ML, Hofer H, Türk A. 1989. Functions of birth dens in spotted hyaenas (*Crocuta crocuta*). J Zool Lond. 219:690–697.

East ML, Hofer H. 2002. Conflict and co-operation in a female-dominated society: a re-assessment of the 'hyper-aggressive' image of spotted hyenas (*Crocuta crocuta*). Adv Study Behav. 31:1–30.

Ehrenberg K. 1966. Die Teufels- oder Fuchsenlucke bei Eggenburg (NÖ.). Denksch Österr Akad Wissensch math-naturwissensch Klasse. 112:1–158.

Esper JF. 1774. Ausführliche Nachricht von neuentdeckten Zoolithen unbekannter vierfüssiger Thiere und denen sie enthaltenden, so wie verschiedenen anderen, denkwürdigen Grüften der Oberbürgischen Lande des Marggrafthums Bayreuth. Nürnberg. p. 148.

Fosse P, Brugal JP, Guadelli JL, Michel P, Tournepiche JF. 1998. Les repaires d' hyenes des cavernes en Europe occidentale: presentation et comparisons de quelques assemblages osseux. In: Economie Prehistorique, Les comportements de substance au Paleolithique, XVIII Rencontres internationales d' Archeologie et d' Historie d' Antibes. Editions APDCA, Sophia Antipolis. p. 44–61.

Frank LG. 1994. When hyenas kill their own. New Sci. 141:38–41.

Goldfuss GA. 1823. Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt. VI. Ueber die Hölen-Hyäne (*Hyaena spelaea*). Nova Acta Physico-Medica Academiea Caesarae Leopoldino-Carolinae Naturae Curiosorum. 3(2):456–490.

Henschel JR, Tilson R, Von Blottnitz F. 1979. Implications of a spotted hyaena bone assemblage in the Namib Desert. S Afr Archaeol Bull. 34:127–131.

Hofer H, East M. 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: Sinclair ARE, Arcese P, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. Chicago (IL): University of Chicago Press. p. 332–363.

Holekamp KE, Smale L. 1990. Provisioning and food-sharing by lactating spotted hyenas (*Crocuta crocuta*). Ethology. 86:191–202.

Horáček I. 1984. Obratlovčí mikrofauna z fosilních výplní Koněpruských jeskyní (Review of the vertebrate microfauna from the Koněprusy Caves). Český Kras. 9:68–75.

Humpohl G, Kroniger M, Lambers K. 1997. Skelettmontage einer pleistozänen Höhlenhyäne *Crocuta crocuta spelaea* (Goldfuss, 1823) im Geologisch-Paläontologischen Museum Münster. Coral Res. 5:5–69.

Kafka J. 1903. Fossile und Recente Raubthiere Böhmens (Carnivora). Archiv der Naturwissenschaftlichen Landesdurchforschung Böhmens. 10(6):1–120.

Klein RG, Scott K. 1989. Glacial/interglacial size variation in fossil spotted hyenas (*Crocuta crocuta*) from Britain. Quat Res. 32:88–95.

Kovanda J. 2002. Jaroslav Petrbok a objev Koněpruských jeskyní. Český Kras. 28:19–26.

Kruuk H. 1972. The spotted hyena. In: A story of predation and social behavior. Chicago (IL): The University of Chicago Press. p. 335.

Kučera B, Hromas J, Skřivánek F. 1981. Jeskyně a propasti v Československu. Praha: Academia. p. 252.

Kukla J. 1952. Zpráva o výsledcích výzkumů jeskyní na Zlatém koni u Koněprus v roce 1951, prováděných Krasovou sekcí Přírodovědeckého klubu v Praze. Československý Kras. 5:49–68.

Kuželka V. 1997. The postcranial skeletal remains of pleistocene Man from Zlatý kůň near Koněprusy (Bohemia). Anthropologie. 35(3):247–249.

Liebe KT. 1876. Die Lindentaler Hyänenhöhle und andere diluviale Knochenfunde in Ostthüringen. Archäologisch-Anthropologische Organ der Deutschen Gesellschaft für Anthropologie Ethnographie und Urgeschichte. 9:1–55.

Lynn T. 2009. Morphological variation in a durophagous carnivore, the spotted hyena *Crocuta crocuta* [Dissertation]. Michigan: Michigan University UMI 3381299.

Lysenko V. 1976. Příspěvek ke stratigrafii sedimentů v Koněpruských jeskyních. Český Kras. 1:8–27.

Mach V. 1951. Objev nejkrásnější české krápníkové jeskyně v pražském okolí. Vesmír. 29(5):114–115.

Mills MGL, Mills M. 1977. An analysis of bones collected at hyaena breeding dens in the Gemsbok National Parks. Ann Transvaal Mus. 30:145–155.

Miracle P. 1991. Carnivore dens or carnivore hunts? A review of Upper Pleistocene mammalian assemblages in Croatia and Slovenia. Rad Hrvatske akademije znanosti I umjetnosti. 458(25):193–219.

Musil R. 1962. Die Höhle 'Sveduv stul', ein typischer Höhlenhyänenhorst. Anthropos New Series. 5(13):97–260.

Pokines JT, Kerbis J, Peterhans CK. 2007. Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. J Archaeol Sci. 34:1914–1931.

Reynolds SH. 1902. A monograph of the British Pleistocene Mammalia. Volume II, Part II. The Cave Hyena. Palaeontographical Society Monographs. 1902:1–25.

Rohland N, Pollack JL, Nagel D, Beauval C, Airvaux J, Pääbo S, Hofreiter M. 2005. The population history of extant and extinct hyenas. Mol Biol Evol. 22(12):2435–2443.

Scott L, Klein RG. 1981. A hyena accumulated bone assemblage from Late Holocene deposits at Deelpan, Orange Free State, South Africa. Ann S Afr Mus. 86:217–227.

Skinner JD, Henschel JR, van Jaarsveld AS. 1986. Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. S Afr J Zool. 21:303–308.

Stárka V, Prošek F, Hrdlička L, Hokr Z, Lož V, Dohnal Z. 1952. Výzkum jeskyně Zlatého koně u Koněprus. Zpráva za I. výzkumné období r. 1951. 2. část. Československý Kras. 5:161–179.

Sutcliffe AJ. 1970. Spotted Hyena: crusher, gnawer, digester and collector of bones. Nature. 227:110–113.

Svoboda J. 2000. The depositional context of the Early Upper Paleolithic human fossils from the Koněprusy (Zlatý kůň) and Mladeč Caves, Czech Republic. J Hum Evol. 38:523–536.

Tournepiche JF, Couture C. 1999. The hyena den of Rochelot Cave (Charente, France). Monographien des Römisch-Germanischen Zentralmuseums. 42:89–101.

Turner A. 1984. The interpretation of variation in fossil specimens of spotted hyena (*Crocuta crocuta* Erxleben 1777) from Sterkfontein Valley sites (Mammalia: Carnivora). Ann Transvaal Mus. 33:399–418.

Vlček E. 1952. The Pleistocene man (Zlatý Kůň). Československý Kras. 5:180–191.

von Driesch A. 1976. Das Vermessen von Tierknochen aus vor- und frühgeschichtlichen Siedlungen. München: Tiermedizienische Fakultät Universität. p. 114.

von Koenigswald W. 2002. Lebendige Eiszeit [Living ice]. Darmstadt: Thorbecke-Verlag. p. 190.

Žák K, Diedrich C. 2006. Sedimenty krasových výplní v lomu Plešivec u Měňan - předběžná zpráva o Výzkumu (Sediments of karst fillings in the Plešivec Quarry - preliminary research report). Český Kras. 32:27–32.