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Steppe lion remains imported by Ice Age spotted hyenas into the Late Pleistocene Perick Caves hyena den in northern Germany

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ABSTRACT

Upper Pleistocene remains of the Ice Age steppe lion *Panthera leo spelaea* (Goldfuss, 1810) have been found in the Perick Caves, Sauerland Karst, NW Germany. Bones from many hyenas and their imported prey dating from the Lower to Middle Weichselian have also been recovered from the Perick Cave hyena den. These are commonly cracked or exhibit deep chew marks. The absence of lion cub bones, in contrast to hyena and cave bear cub remains in the Perick Caves, and other caves of northern Germany, excludes the possibility that *P. leo spelaea* used the cave for raising cubs. Only in the Wilhelms Cave was a single skeleton of a cub found in a hyena den. Evidence of the chewing, nibbling and cracking of lion bones and crania must have resulted from the importation and destruction of lion carcasses (4% of the prey fauna). Similar evidence was preserved at other hyena den caves and open air sites in Germany. The bone material from the Perick and other Central European caves points to antagonistic hyena and lion conflicts, similar to clashes of their modern African relatives.

Introduction

Hyena den caves must be identified as such in order to correctly interpret the significance of lion remains in these caves. In many caves from northwestern Germany in the Sauerland Karst (Fig. 1), evidence of hyena dens has been overlooked. Historically, this may have happened at the Perick Caves ("Sundwighöhle": Cuvier, 1805, 1806; Nöggerath, 1823, 1824; Giebel, 1849) and elsewhere because the quest was for evidence of cave bears, for example (Diedrich, 2006). During this pioneering stage of cave exploration, other faunal remains were, for the most part, only listed. This was the case for the lion bone material presented here and taken from one of the richest hyena den sites of Europe (Diedrich, 2005). This problem of poorly understood taphonomy of bone accumulation at many European caves resulted from the non-identification of hyena dens. Even in recent papers, old interpretations like "bones were washed into the cave" and that lions "fell into caves" are still being repeated. The latter does possibly happen, but rarely. One convincing example is the description of a Late Pleistocene saber tooth cat *Smilodon* which was found in a vertical shaft of the Hurricane River Cave in North America (Norman and Youngsteadt, 1980). Here it will be shown that this seems to be the exception, not the rule and doesn't explain lion remains in horizontal cave systems at all. Bone taphonomy is the key, especially the study of the palaeoecology of hyenas, to understanding why there are lion remains in caves, and even complete carcasses. Here 11 northern German caves of the Sauerland Karst recently identified as hyena den caves (Fig. 1) are presented with their faunal statistics for an initial lion and taphonomy study.

South of Münsterland Bay, the Devonian limestone in the mountainous Sauerland Karst or right Rhenish Massif contains several hundred mapped caves (e.g., Zygowski, 1988). The Perick Caves locality is in the city of Hemer, Westphalia, NW Germany and was referred to in former times as "Sundwighöhlen" (e.g., Nöggerath, 1824). One part was called "Alte Höhle" ("Old Cave"), whereas the other one, open to visitors since 1905, is called "Heinrichshöhle" ("Heinrich's Cave"; Meise, 1926; Fig. 1). Both are connected and part of the Perick Caves system (Weber, 1989). Whereas the Heinrich's Cave was clearly the main or only hyena den (Diedrich, 2005), the "Alte Höhle" was the main cave bear den (Diedrich, 2006).

Most of the lion bones described here from the Perick Caves were found in the bone dump in Heinrich's Cave; unidentified or misidentified as hyena (a lion skull in the Humboldt-University Museum Berlin) or giant deer bones (specimens in the Staatliche Naturhistorische Sammlungen Dresden). The misidentification of lion bones was typical for the historically collected Sauerland Karst lions. Therefore, they are rarely mentioned in historical publications (cf. Giebel, 1849). Another bone material was carefully studied over longer periods (Diedrich, 2005, 2006, 2009a) and further study will continue with about 2500 bones and several cave bear skeletons.

The taphonomy of the studied bone material from the Perick Caves suggests this is one of the richest hyena den caves in Central Europe with five hyena skulls and about 150 more bones. It is a horizontal cave where a large population of hyenas must have imported prey remains over generations (Diedrich, 2005). Cave bear scavenging by

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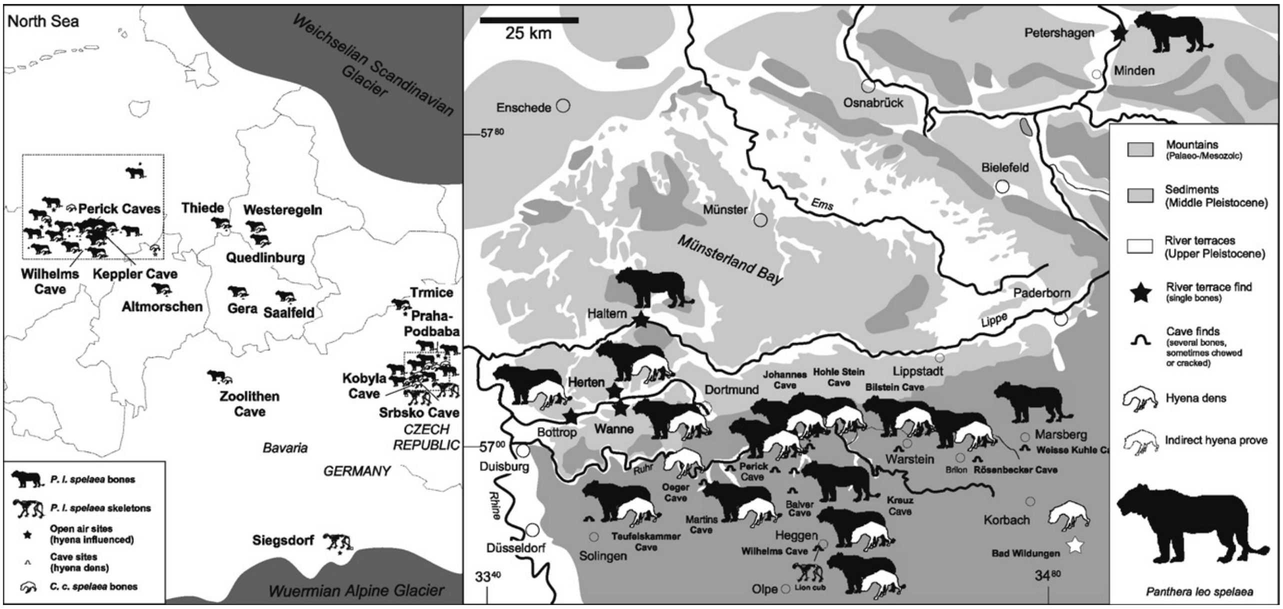

Figure 1. Studied localities. (A) in Central Europe showing the Upper Pleistocene (Weichselian/Würmian) steppe lion *Panthera leo spelaea* open air (stars) and cave (cave symbols) sites. (B) in the Sauerland Karst of north-western Germany. The distribution is mainly a result of carcass and bone protraction by the Ice Age spotted hyenas *Crocuta crocuta spelaea* to their den sites. Lion remains in nearly all cases were found in the hyena den caves of the Sauerland mountainous region, but also along the river at the bone deposit sites of the hyenas. The situation is similar at all other localities. The only lion cub skeleton was discovered in the Wilhelms Cave hyena den.

hyenas, which was previously not well understood in European caves, was described here (Diedrich, 2006). This cave has no archaeological remains and was used only by different large carnivores in the Upper Pleistocene, such as cave bears and hyenas, over many generations. Here non-human influenced bone accumulations and the bone taphonomy can be studied, which can help distinguishing in the future animal cave and human influenced cave sites.

Geology and dating

The lion bones in the Perick Caves are all similarly preserved (the same as the hyena and cave bear material) and seem to be exclusively from the "bone gravel layers" (Fig. 2). The bones of hyenas and cave bears in bioturbated sediments from these caves are dated preliminarily by the cave-bear tooth morphology and believed to be from the Upper to Middle Weichselian (75–35 ka, Diedrich, 2006). The main bones in the Perick Caves are from *Ursus spelaeus*. All other fauna seems to relate to the activities of *Crocuta crocuta spelaea* (Goldfuss), which imported *Mammuthus primigenius* Blumenbach, *Coelodonta antiquitatis* Blumenbach, *Bison priscus* Bojanus, *Equus ferus przewalskii* Poljakoff 1881, *Megaloceros giganteus* Blumenbach, *Cervus elaphus* Linné, *Rangifer tarandus* Linné, *Canis lupus* Linné, and possibly a few *Gulo gulo* Linné (Diedrich, 2006) remains. This faunal assemblage is typical of the Weichselian area of northern Germany. The less diverse reindeer fauna (*R. tarandus*, *E. ferus przewalskii*, *C. lupus*, *G. gulo*, *A. lagopus*), which is preserved differently and found above the gravel with around 10 cm of massive speleothem layer, seems to be from the high to late glacial age (Upper Weichselian). Finally, the Holocene fauna can be easily identified by its bone preservation and consists of *V. Vulpes*, *S. scrofa*, *U. arctos* and *B. primigenius*.

Materials and methods

The Perick Caves *P. leo spelaea* collection, one of the most important in Europe, is archieved in the Heinrich's Cave (=HC). Some bones are housed at the Staatliche Naturhistorische Sammlungen Dresden (=SNSD) and another isolated bone is in the Naturkundemuseum Bielefeld (=NMB). The only complete skull from northern Germany (Sack collection from 1850), is stored with a mandible and calcaneus at the British Museum of Natural History London (=BMNHL). The Museum für Naturkunde der Humboldt Universität Berlin (=MB) has another cranium and ulna. The Goldfuss-Museum Bonn is another institution with some postcranial bones (=GMB). The material is listed here (Supplementary Table 1) with all important details.

The bones and teeth of lions and hyenas, as well as hyena dens in general, were studied at the Nationalmuseum Prague, the Museum of the Bohemian Karst Beroun, the Geological–Paleontological Museum of the Westphalian Wilhelms-University Münster, the Felsenmeer-museum Hemer, Naturkundemuseum Gera, Stadtmuseum Saalfeld and Stadtmuseum Bad Wildungen and the Museum für Ur- und Ortsgeschichte Bottrop, where a modern African *Panthera leo* skeleton in the collection was helpful for the comparison of single Pleistocene postcranial bones. The individual age and sex determination was made by reference to the works of Smuts et al. (1978), Turner (1984) and Gross (1992).

Family *Felidae* Gray, 1821
Genus *Panthera* Oken, 1816
Panthera leo spelaea (Goldfuss, 1810).

Material

Two skulls: one lioness skull is nearly complete; the second from a male is a brain case. Another cranium fragment is a right maxillary. All together 59 bones and teeth, a few mandibles and mostly postcranial bones represent the most important material from the Rhenish Massif Sauerland Karst. The small bones, such as phalanges, are missing possibly as a result of non-sieving of sediments. This problem is also found with the hyena and cave bear material and such specimens may turn up in the old dumps in front of Heinrich's Cave. Nearly all bones belong to adult and senile animals; young juvenile material is almost completely absent. A single humerus fragment is from an adolescent animal. The presence of three metatarsi IV bones or three calcanei allows for the determination of three adult to senile animals. Using lower jaws and calcanei, two lions and one lioness can be distinguished as the smallest number of individuals. Finally, a fourth individual of adolescent age is represented by a lion fore leg. Sixty-six

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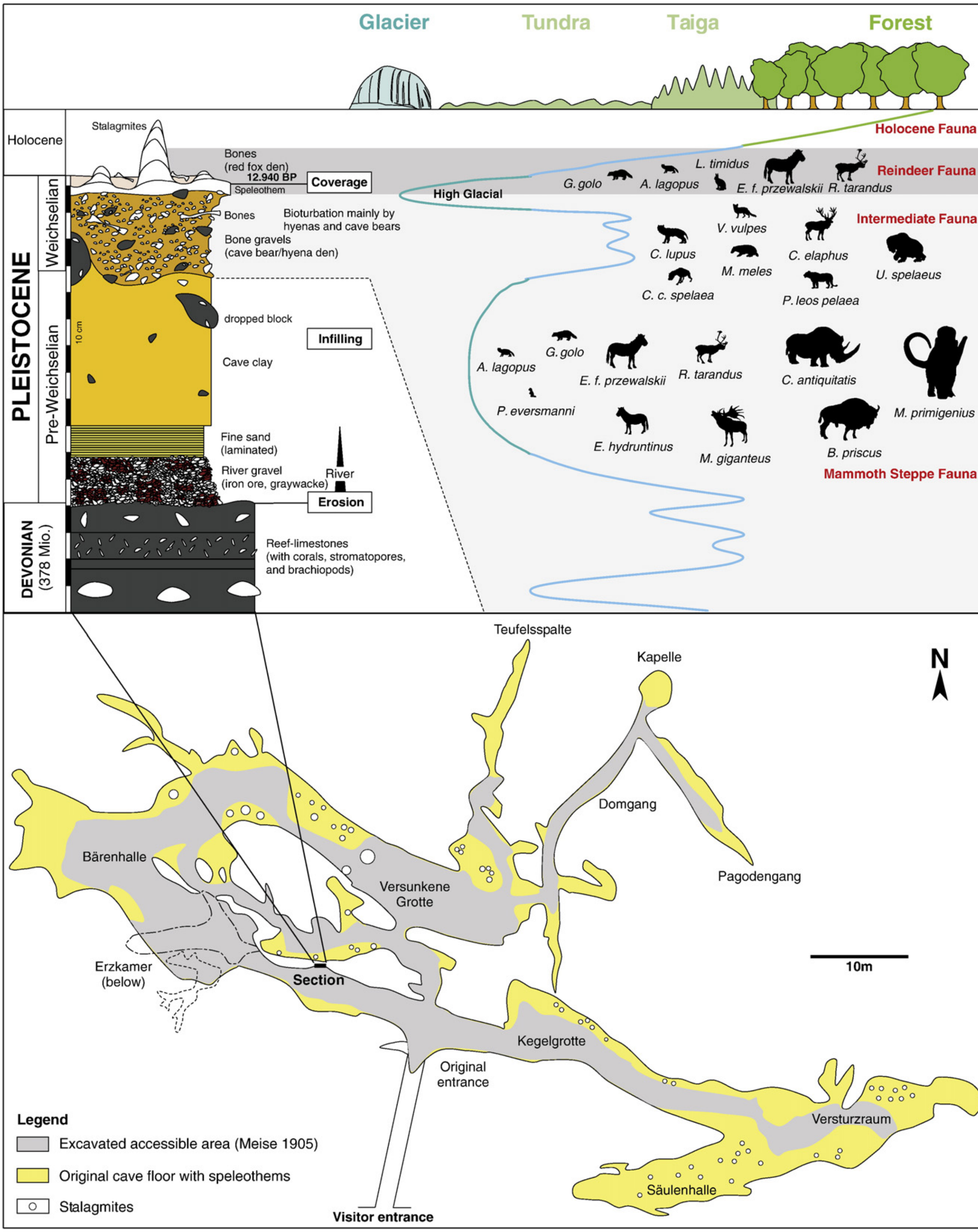


Figure 2. Dating of the Upper Pleistocene bone-bearing gravel layer in the eastern part of the Perick Caves (Heinrich's Cave), in which all three large Ice Age carnivores (*U. spelaeus*, *C. c. spelaea* and *P. leo spelaea*) and prey remains of the hyenas were found. Above and in the speleothem layer that covers the entire Perick Caves, late glacial reindeer fauna was found, and above a Holocene fauna with red fox, badger or brown bear. (after Diedrich, 2005).

percent of the bones can be referred to as males, only 33% as lionesses (only 27 determinable bones).

The first skull (Fig. 3.1) is preserved by its brain case and shows a lot of chew marks. The skull was opened by hyenas who reached the brain. The brain case is mainly comprised of the parietals, frontals and the basisphenoid. Measurements cannot be given because it is not complete. If a right maxillary fragment (Fig. 3.2) belonged to this skull, it cannot be verified. Only direct comparison to much larger male

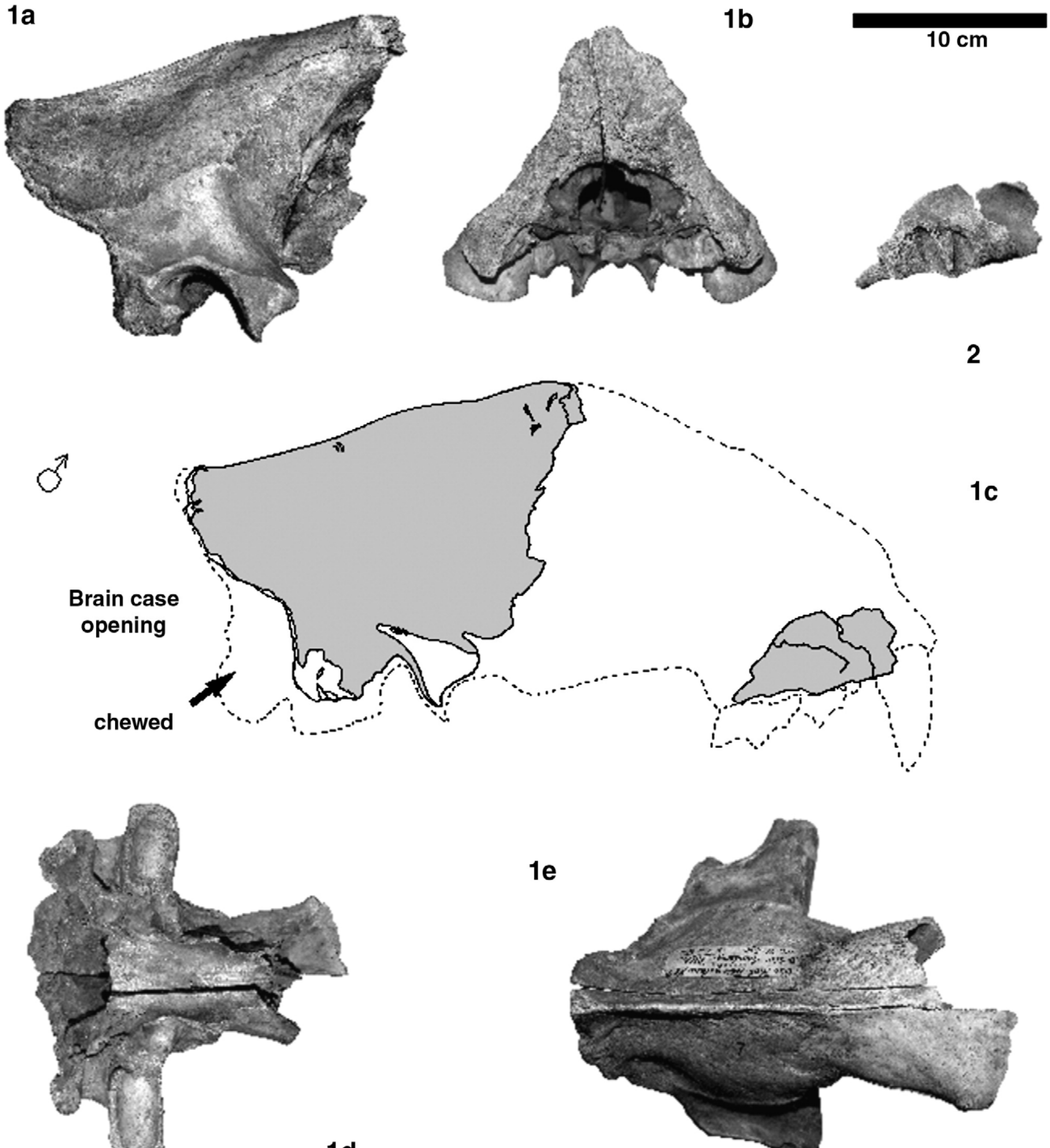


Figure 3. *Panthera leo spelaea* (Goldfuss, 1810) from the Perick Caves hyena den. 1. Scavenged skull brain case of an older adult to senile male lion (MB No. Ma.30353). This was cut for brain case castings in former times, a. lateral right, b. occipital, c. redrawing (grey — bone, white — chew marks), d. ventral, e. dorsal. 2. Right maxillary fragment with P3 and C alveoli (HC No. Hemer-740), lateral.

skulls from the Siegsdorf open air site (Gross, 1992), Zoolithen Cave (Diedrich, 2008), Arrikrutz (Altuna, 1981) or Grotte d' Aze (Argant, 1988) could prove the male lion is adult to senile in age. Finally the skull was recently cut in two pieces for use in brain studies, whereas it was incorrectly believed at the time to be a hyena skull (cf. Klinghardt, 1931).

The second skull (Fig. 4), with its short length of 30.1 cm and small proportions, is from a lioness and could be compared to skulls from the Srbsko Cave (Diedrich and Žák, 2006) and Beroun open air site (Diedrich, 2007b). The right dentition consists of the I1, I3, C and P4 whereas the left is represented by the I1-2, C and P4. The left canine is freshly broken; while the right canine is well-used and indicates an older adult animal. The incomplete fused sutures match this individual age determination. The jugals and temporal arches were chewed off by hyenas in order to break the lower jaw articulation. This is typical for hyena scavenging on other carnivores. Even within their own species, this type of cannibalistic damage can be observed on skulls. A modern spotted hyena skull from an African cave hyena den (BMNHL, Sutcliffe collection) is similarly preserved.

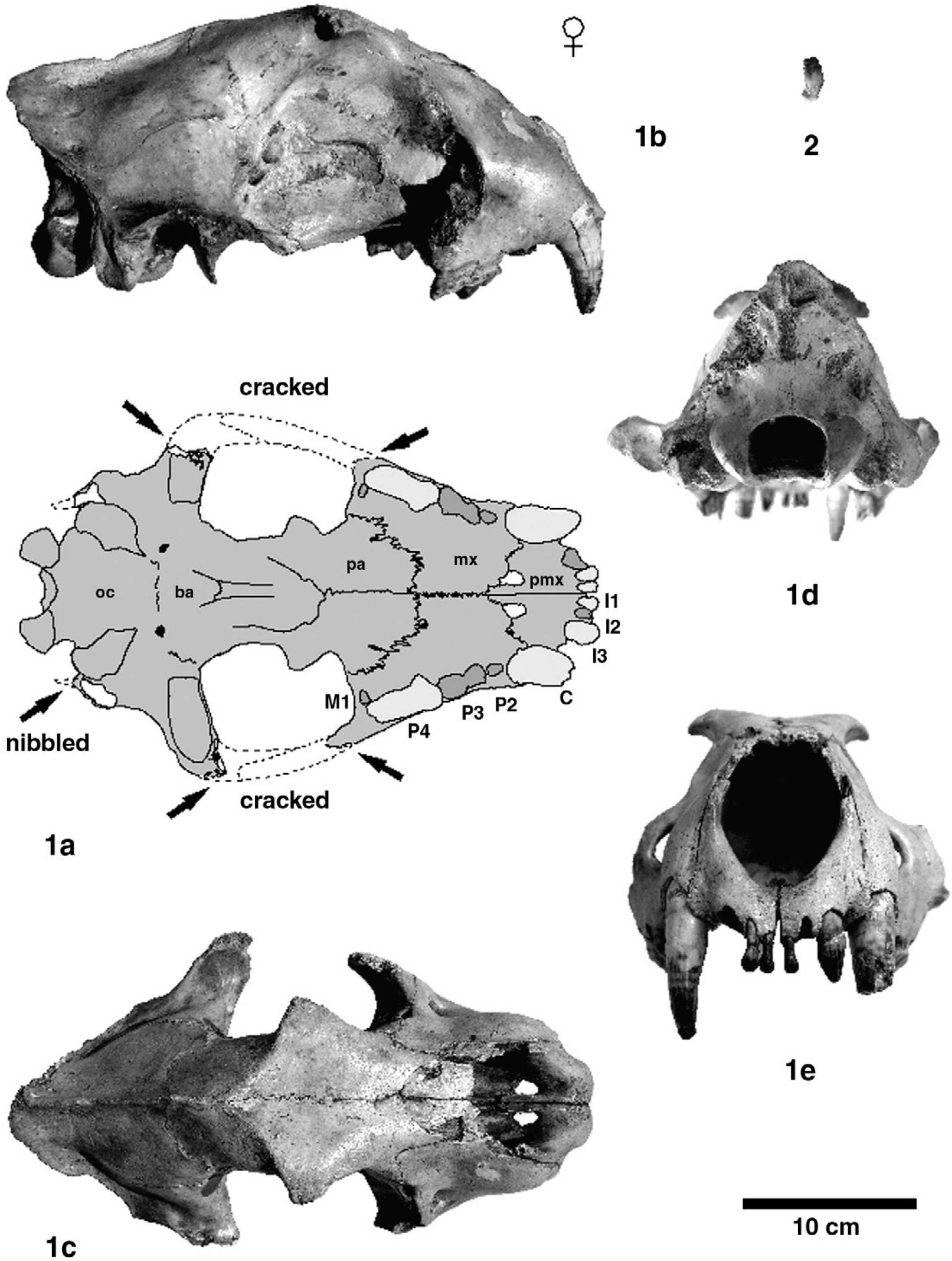


Figure 4. *Panthera leo spelaea* (Goldfuss, 1810) from the Perick Caves hyena den. 1. Skull of an older adult lioness which was chewed (BMNHL No. 28553). For removing the lower jaw from the skull, hyenas had to destroy the jugal arches, a. ventral redrawing (grey — bone, white — chew marks), b. lateral right, c. dorsal, d. occipital, e. frontal. 2. Upper jaw I2 tooth (Hemer-1709), lateral.

Four mandibles are all incomplete and again, must have been cracked by hyenas. To remove the jaws out of the skull, hyenas had to break the ramus from the skull in order to crack the lower jaws. Therefore the jaws are in the same incomplete condition and lack all the rami. Three of the mandibles can be considered adult to older adult lions (Figs. 5.1–3), whereas one is much smaller and most likely from a lioness (Fig. 5.4). The first two figured have the C to M1 teeth, the third male one is missing the P3. The right mandible of the lioness has only the three P3 to M1 teeth. Additionally a lower canine (Fig. 5.5) and a lower incisor (Fig. 5.6) are both from adult animals, as are all the lower jaws.

The long fore limb bones are not well-represented with only two complete ulnae (Figs. 6.2–3), which are different in size. The roughly six cm longer right one is from a lion, the second left one is from a lioness. This was discovered by comparing it to the lioness skeleton from Srbsko Chlum-Komin, Czech Republic (Diedrich and Žák, 2006).

Eight metacarpals (Figs. 6.4–9) from the right and left sides are recorded. Four of them can be considered males as a result of their much larger size. One must be from a female; the other ones are intermediate in their proportions which makes it more difficult to determine the sex. At least one mc II, two mc III, three mc IV and two mc V are represented.

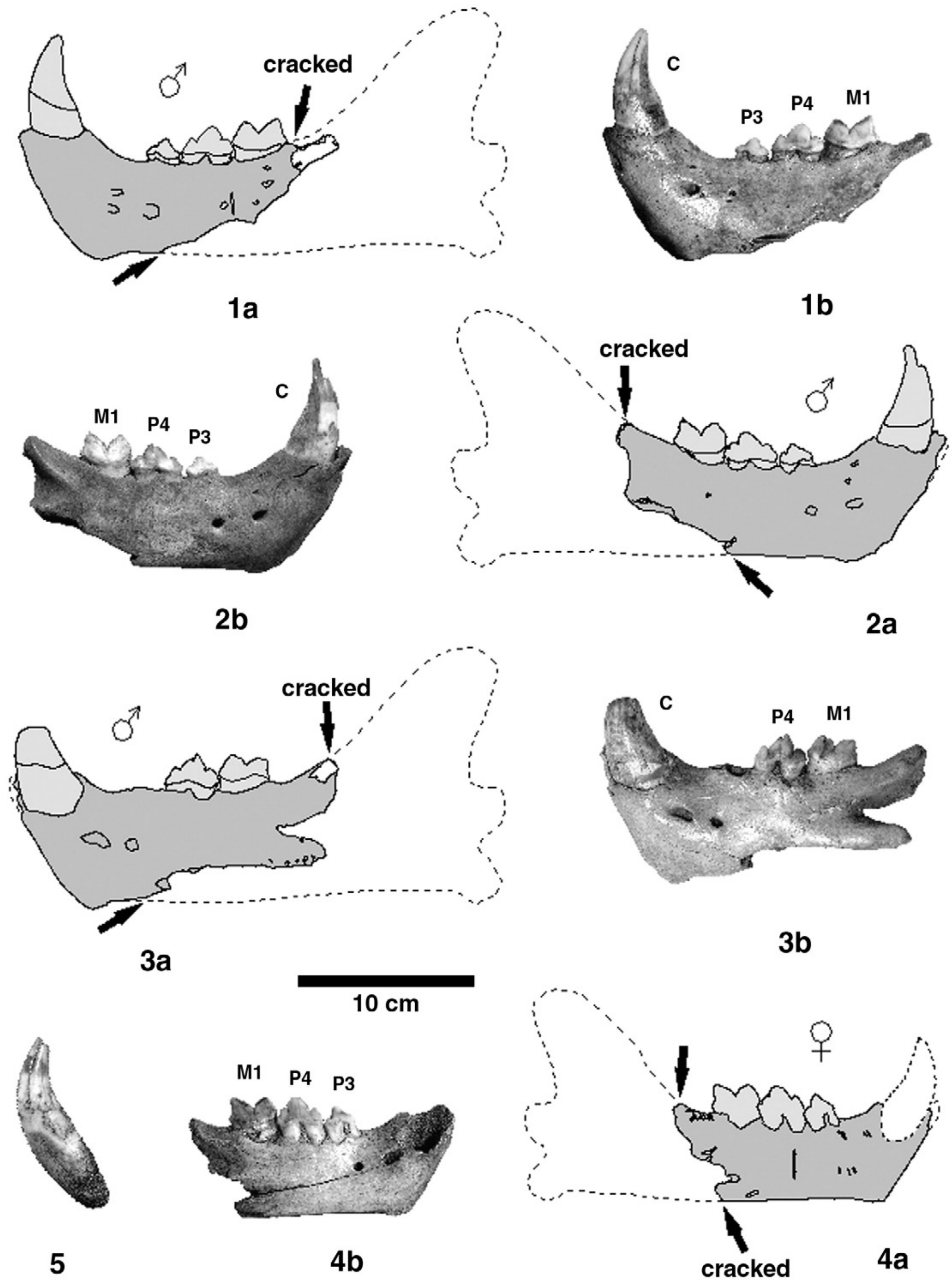
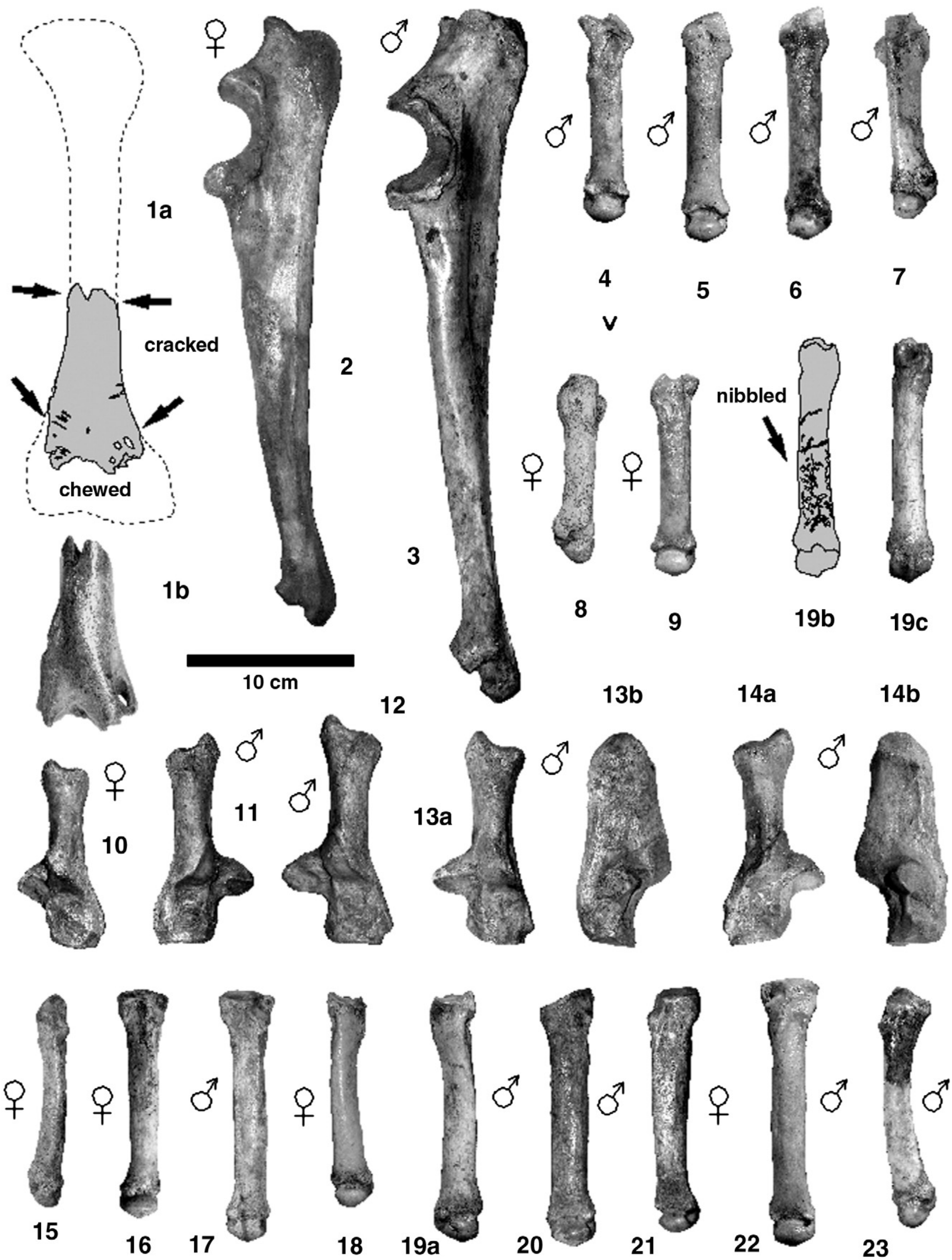


Figure 5. *Panthera leo spelaea* (Goldfuss, 1810) lower jaws and teeth from the Perick Caves hyena den. 1. Left cracked mandible of an adult male lion (SNSD No. Sundwig-59), lateral. 2. Right cracked mandible of an adult male lion (BMNHL No.28554), lateral. 3. Left cracked mandible of an adult male lion (with questionable implanted cave bear canine) (SNSD No. Sundwig-58), lateral. 4. Right cracked mandible of an adult female lion (SNSD No. Sundwig-60), lateral. 5. Left mandible canine of an adult animal (SNSD No. Sundwig-61), labial. 6. Incisor of an older adult lion (HC No. Hemer-1709), lateral. a. redrawing (grey — bone, white — chew marks).

Figure 6. *Panthera leo spelaea* (Goldfuss, 1810) fore and hind limb bones from the Perick Caves hyena den. a. redrawing (grey — bone, white — chew marks). 1. Left cracked humerus shaft fragment (HC No. Hemer-726), caudal. 2. Left ulna of a lioness (MB No. Ma.48284a), lateral. 3. Right ulna of a male lion (GMB No. M2469), lateral. 4. Right metacarpus III of a male lion (SNSD No. Sundwig-68), dorsal. 5. Left metacarpus IV of a male lion (SNSD No. Sundwig-69), dorsal. 6. Left metacarpus IV of a male lion (SNSD No. Sundwig-81), dorsal. 7. Left metacarpus V of a male lion (SNSD No. Sundwig-65), dorsal. 8. Left metacarpus V of a lioness (SNSD No. Sundwig-64), dorsal. 9. Left metacarpus III of a lioness (SNSD No. Sundwig-67), dorsal. 10. Left calcaneus of a lioness (GMB No. M3152), dorsal. 11. Right calcaneus of a fairly strong male lion (GMB No. M2562), dorsal. 12. Left calcaneus of a strong male lion (GMB No. M2564), dorsal. 13. Left calcaneus of a male lion (HC No. Hemer-1708), a. dorsal, b. lateral inner view. 14. Left calcaneus of a male lion (BMNHL No. M449), a. dorsal, b. lateral inner view. 15. Right metatarsus V (SNSD No. Sundwig-71), dorsal. 16. Right metatarsus IV of a lioness (NB No. Heinr-8), dorsal. 17. Right metatarsus IV of a male lion (SNSD No. Sundwig-73), dorsal. 18. Left metatarsus II of a lioness (Sundwig-76), dorsal. 19. Left metatarsus II of a male lion (SNSD No. Sundwig-75), a. dorsal, b–c. ventral. 20. Left metatarsus III of a male lion (GMB No. M459a), dorsal. 29 21. Left metatarsus III of a lioness (GMB No. M459b), dorsal. 22. Left metatarsus IV of a lioness (SNSD No. Sundwig-72), dorsal. 23. Left metatarsus V of a male lion (Sundwig-70), dorsal.

Long hind limb bones (femur, tibia, and fibula) are absent or were cracked into pieces. These cannot yet be separated from cave bear long bone fragments. Luckily, the calcanei and metatarsi are in the anthropogenous selected material. As in the case of the manus, the phalanges of the pes seem to be absent, a primary result of non-sieving of the sediment.



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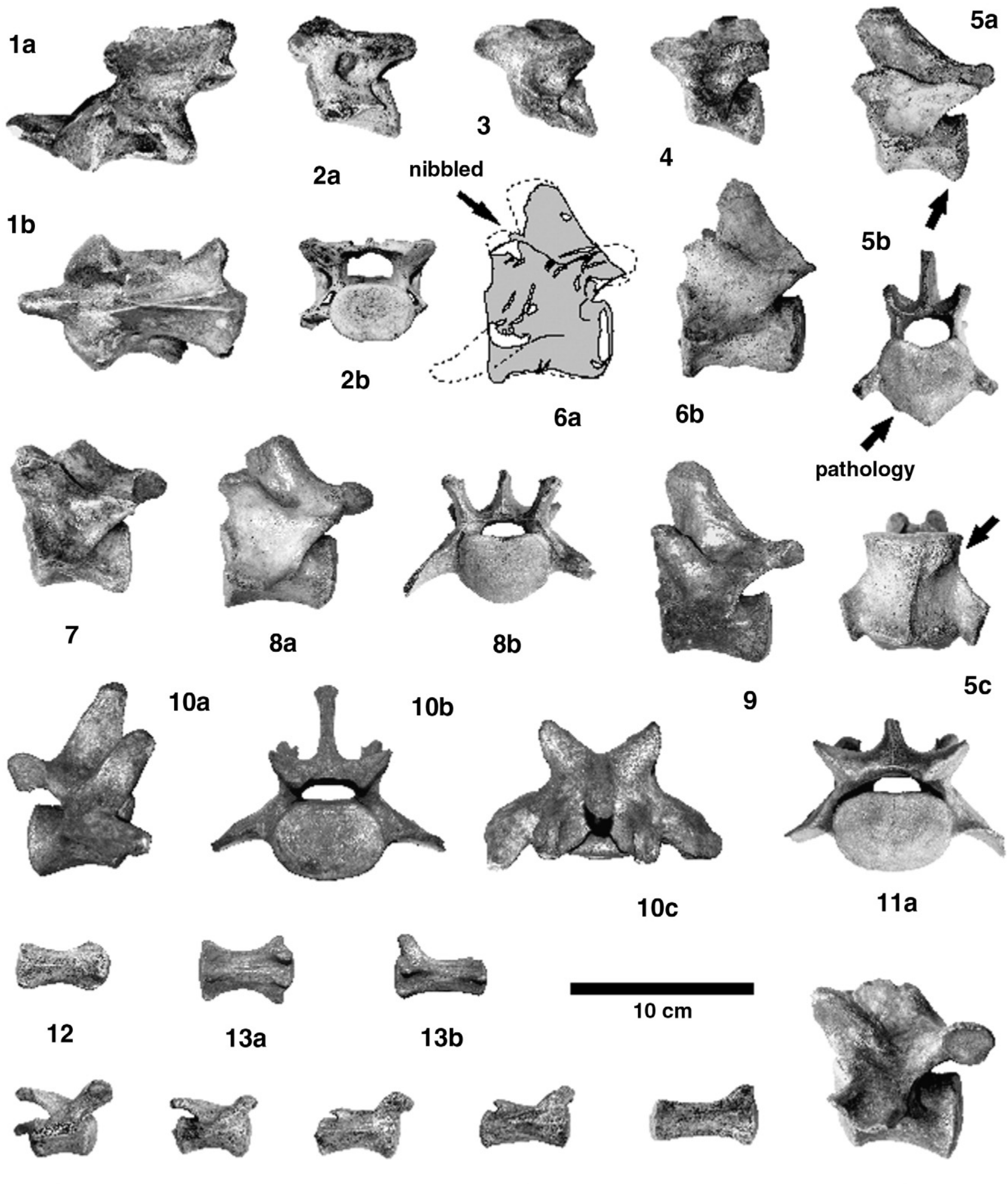

Figure 7. *Panthera leo spelaea* (Goldfuss, 1810) vertebrae, all of adult to senile animals, from the Perick Caves hyena den. a. redrawing (grey — bone, white — chew marks). 1. Axes (HC No. Hemer-831), a. lateral, b. dorsal. 2. Second or third cervical vertebra (HC No. Hemer-830), a. lateral. b. caudal. 3. Cervical vertebra (HC No. Hemer-829), lateral. 4. Cervical vertebra (HC No. Hemer-828), lateral. 5. First to second lumbar vertebra (osteoporosis) (SNSD No. Sundwig-106), a. lateral, b. cranial, c. ventral. 6. Middle lumbar vertebra (SNSD No. Sundwig-104), a–b. lateral. 7. Middle lumbar vertebra (HC No. Hemer-263), lateral. 8. Third or fourth lumbar vertebra (SNSD No. Sundwig-103), lateral. 9. Middle lumbar vertebra (SNSD No. Sundwig-105), lateral. 10. Fifth to seventh lumbar vertebra (GMB No. M2558), a. latera, b. caudal, c. dorsal. 11. Sixth lumbar vertebra (SNSD No. Sundwig-291), a. caudal, b. lateral. 12. Lower caudal vertebra (SNSD No. Sundwig-63), dorsal. 13. Middle caudal vertebra (MB No. Ma.3553), a. dorsal, b.lateral. 14. Upper caudal vertebra (HC No. Hemer-452), lateral. 15. Upper caudal vertebra (SNSD No. Sundwig-200), lateral. 16. Upper caudal vertebra (SNSD No. Sundwig-201), lateral. 17. Middle caudal vertebra (HC No. Hemer-207), lateral. 18. Lower caudal vertebra (SNSD No. Sundwig-63), lateral.

Twelve metatarsals (Figs. 6.15–23) are all from grown animals, as are the metacarpals. Four of them can be considered males; two, represent females. The sex of the others cannot be positively identified. Represented in the material are four mc II, one mc III, five mc IV and finally two mc V. Twenty vertebrae from all positions were found in the collections. All of them were mislabeled as giant deer or cave bear or were not identified as lion vertebrae at all. The vertebral column (Fig. 7) is almost fully represented by cervical, lumbar and caudal vertebra. Thoracic vertebra cannot be selected. If they are damaged, they are difficult to distinguish from female cave bear thoracic vertebra. Here one axis (Fig. 7.1), three more cervical vertebrae (Figs. 7.2–4), nine lumbar vertebrae (Figs. 7.5–11) and

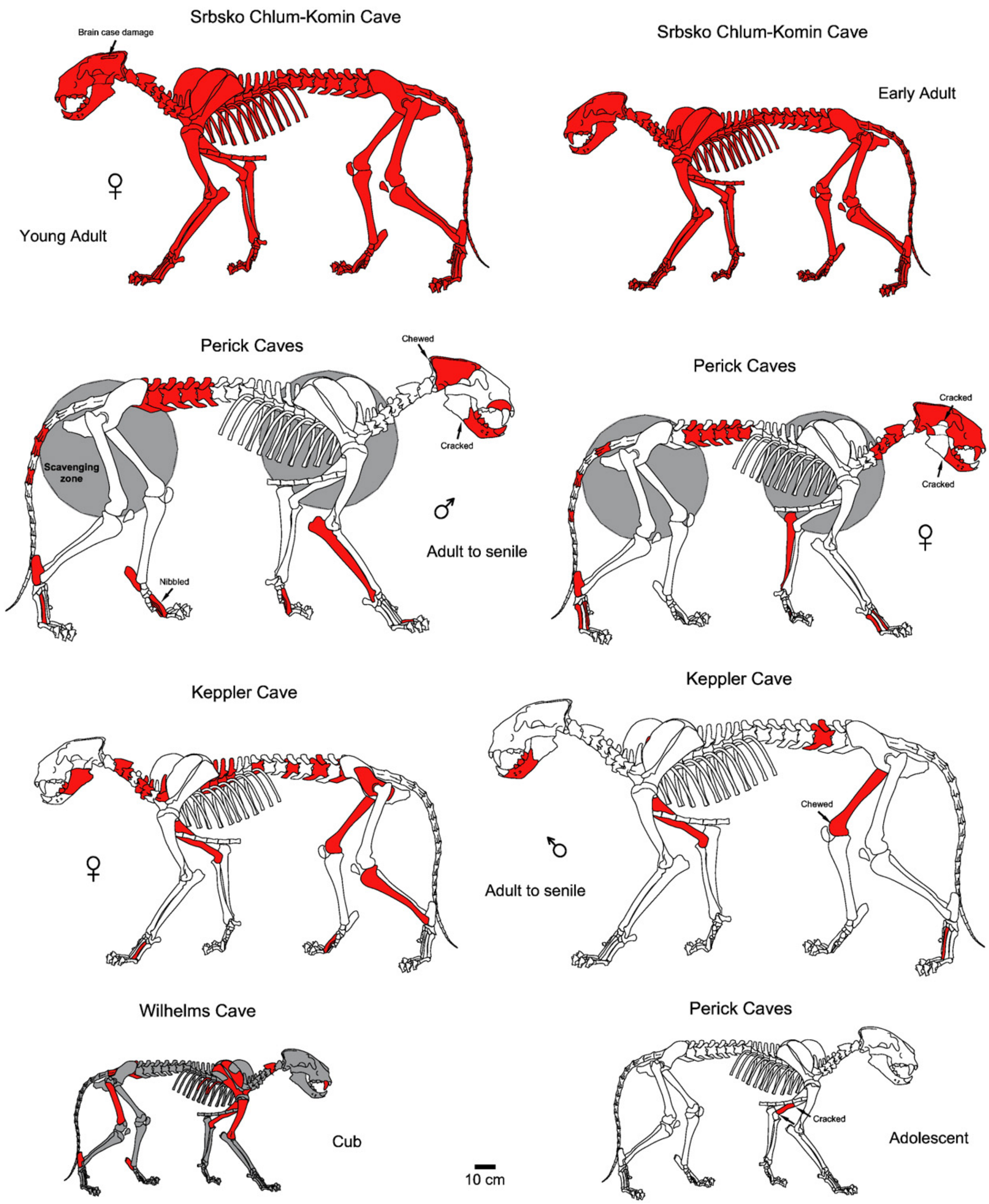

Figure 8. Lion skeletons and remains nearly all from hyena den caves. In the Srbsko Chlum-Komin Cave diagonal to vertical hyena prey depot, a complete skeleton of a brain case damaged young lioness and a young adult animal were found. These were not scavenged. The incomplete bone remains of adult males and females from the Perick Caves hyena den and prey depot might reflect scavenging stages, at which imported carcasses were further eaten by hyenas in the cave itself. Main scavenging zones were around the meat-rich shoulder and pelvic and thorax (intestines). Single cracked bones seem to be remains from imported body parts such as a front leg. In the Keppler Cave, a cave bear den with a periodical hyena scavenging impact; lioness bones from different body areas are present, possibly from an originally complete lioness that was not scavenged. The few male remains have, in two cases, hyena bite marks and might again represent imported body parts. In the Wilhelms Cave hyena den, bones are preserved from an originally complete cub carcass; the only lion remains are mingled with other prey bones. In this cave neonate hyena remains are typical for den sites, which were rarely used as prey storages.

finally six caudal vertebrae (Figs. 7.12–18) are all from adult to senile animals. Generally they are all incomplete as a result of scavenging, except for the tail vertebrae, which generally has no bite marks. The processes of other vertebrae are for the most part missing.

Two anterior lumbar vertebrae have osteoporosis growths on the ventral side (Figs. 7.5ac) and seem to be from a senile animal; probably a male lion after being compared to the Siegsdorf skeleton. The exact position of nearly all vertebrae is difficult, as a result of their incompleteness and the lack of complete Pleistocene lion vertebral columns for comparison. Even the comparison to a modern lion skeleton in the collections of the Eiszeithalle Quadrat Bottrop did not always make the position clear.

Phalanges and sterna are absent, so too are pelvic remains, humeri, femora and tibiae. In some cases, possibly long bone fragments are

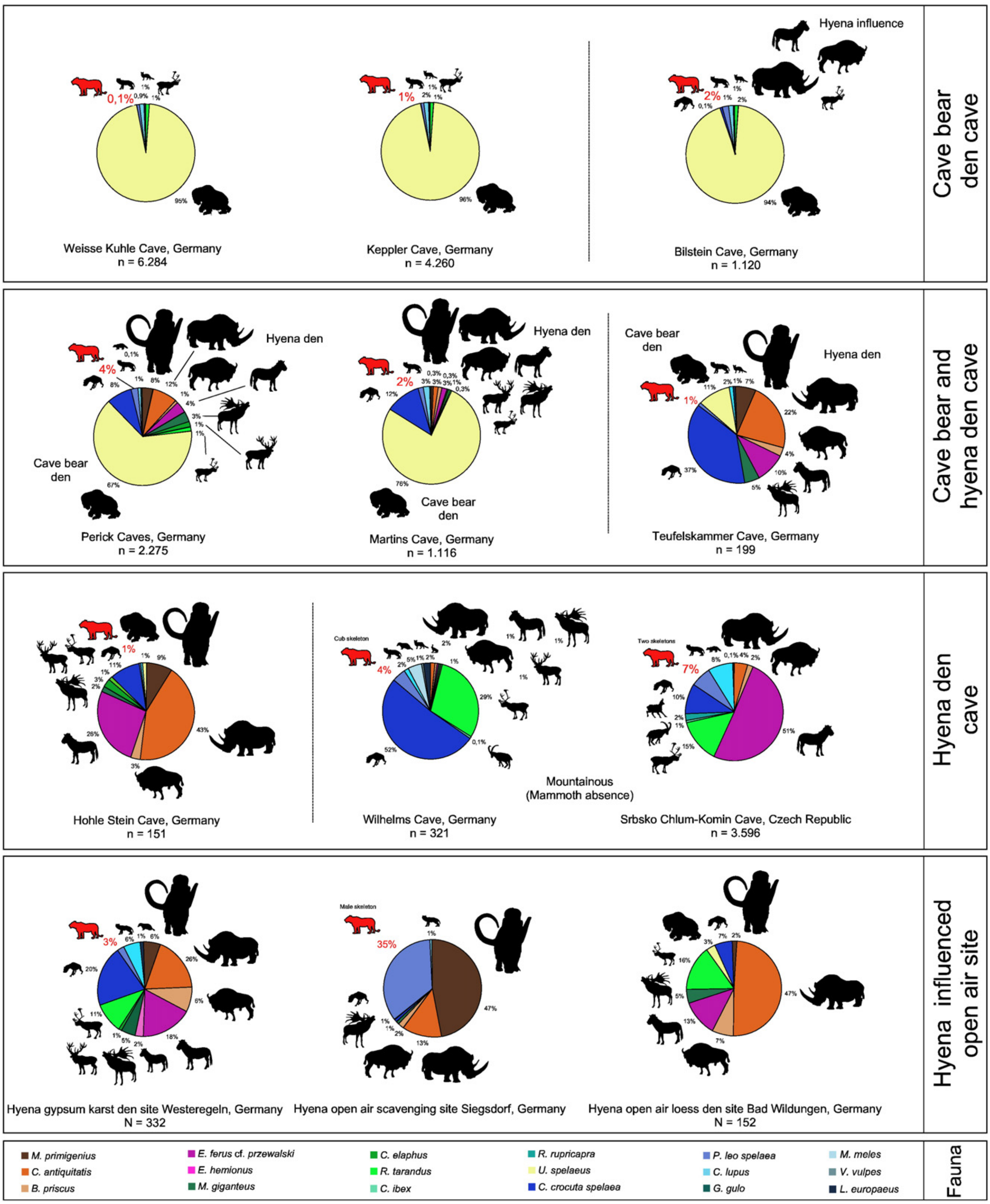

Figure 9. Percentages of lion bones in hyena dens and prey depot sites of Central Europe. Normally the lion bone percentage is about 1–7%. Where skeletons are represented, the percentage can increase to 35%.

from lions, but cannot be clearly separated from the cracked cave bear long bones.

Discussion

C. crocuta spelaea was relatively common in the Sauerland Karst region during the Late Pleistocene and is represented by more than 80 individuals (>600 bones) from the Teufelskammer Cave, Martins Cave, Oeger Cave, Perick Caves, Grürmanns Cave, Balve Cave, Wilhelms Cave, Hohler Stein Cave, Johannes Cave and Rösenbecker Cave (Figs. 1, 9, Diedrich, 2006, 2009a). The existence of their antagonists, the lions, in this region can be estimated by the finding of at least 26 *P. leo spelaea* individuals (223 bones, Diedrich, 2009b). These bones came from the Teufelskammer Cave (two bones, one individual), Martins Cave (16 bones, 1 individual), Perick Caves (59 bones, 4 individuals), Grürmanns Cave (2 bones, 1 individual), Balve Cave (48 bones, 4 individuals), Wilhelms Cave (15 bones, 1 cub individual), Hohler Stein Cave (1 bone, 1 individual), Johannes Cave (2 bones, 1 individual), Kreuz Cave (3 bones, 1 individual), Bilstein Cave (39 bones, 5 individuals), Pfefferburg Cave (3 bones, 1 individual), and Keppler Cave (33 bones, 4 individuals); all have recently undergone more detailed descriptions. A similar situation with a slightly larger amount of hyena remains was recently published for the Bohemian Karst (Diedrich and Žák, 2006).

With a growing knowledge of the taphonomical situation of European hyena dens and prey depot caves; and their comparison to modern African lions and spotted hyenas (cf. Sutcliffe, 1970; Kruuk, 1972; Schaller, 1972; Brain, 1981; Henschel and Tilson, 1988; Lam, 1992; Grzimek, 1997; Estes, 1999), the presence of lion material in caves and bone rich sites became clearer after the first more detailed taphonomic and palaeoecological studies in the Bohemian Karst hyena den sites (Diedrich and Žák, 2006). Even for the type locality of *P. leo spelaea* and *C. crocuta spelaea*, the Zoolithen Cave at Geilenreuth (southern Germany) was recently described as a very important Late Pleistocene hyena den cave, too (Diedrich, 2008). In the Zoolithen Cave, many lion carcasses were found and after the initial study of the rich lion material, the carcasses of adult to senile male lions dominate. In the Perick caves 66% of the lion bones are from males, only 33% are from lionesses. Comparative data is not currently available because the bone taphonomy of "cave lions" was not critically studied, and the old models of a cave-adapted lion (e.g. Boule, 1906; Dietrich, 1968) are still in the minds of Pleistocene palaeontologists.

The presence of an ill lioness and another adolescent lion approximately 1 to 2 years old in the Srbsko Chlum-komin Cave hyena den (Fig. 8) demonstrated for the first time the feeding habits of, and conflicts between, lions and hyenas in the Ice Age (cf. Diedrich and Žák, 2006). *Crocuta c. spelaea* clans could easily have hunted down a sick lioness and young lions or cubs, as is done by modern spotted hyenas and lions in Africa. Currently, 50% of the kills of each carnivore can be ascribed to the other predator. In many cases hyenas do kill lions, but do not always scavenge on them (in the film by Joubert and Joubert, 2003). The main purpose of the killing of a lion by a hyena is not for feeding; instead it is about antagonism, the protection of their cubs, or conflict over prey and even territory (Schaller, 1972; Joubert and Joubert, 2003).

The proof for the thesis, that Late Pleistocene hyenas scavenged and imported lion remains such as African spotted hyenas rarely do, can be obtained from the report on the African spotted hyena den in Amboseli National Park (Hill, 1989; Lam, 1992). Here the lion remains were given in the statistics as well as remains of a hyena individual. In the African sites, as in the Pleistocene record at the Perick Caves and many other mentioned Caves in Germany/Czech Republic, hyena and lion remains can both be present at hyena dens in the bone record. In the comparisons of spotted hyena dens by Lam (1992), the site with the largest amount of bones (56 prey animal individuals) included one individual lion remain. Other dens with less material (46 prey animal individuals) such as the Syokimau spotted hyena den near Nairobi in Kenya (Bunn, 1983), included at least one hyena remains, but no lions. In a smaller and more shortly used den such as the KFHD 1 spotted hyena den near Koobi Fora in Kenya (Lam, 1992) even hyena remains are missing (MNI = 31 prey animal individuals, NISP = 872 bones).

The presence of lion bones correlates in nearly all well-known cases to hyena dens and prey depots in the studied Czech and German cave sites (Diedrich and Žák, 2006, Diedrich, 2007a, Fig. 2) such as the here-presented Sauerland Karst hyena cave dens (Figs. 8, 9), including the Perick Caves. Some lion carcasses were scavenged but they are more often found in readily accessible horizontal hyena cave den sites. Interestingly, here at the Perick Caves the skeletons lack the bones from the main scavenging zones (Fig. 8), where most of the meat can be taken by carnivores. The hyenas of the Perick Caves have scavenged in the shoulder and upper leg zones and the pelvic to hind leg part (Fig. 8), which are well-known regions for larger motor muscles. Also here they started removing the extremities, which is typical for the Late Pleistocene spotted hyenas and carnivores in general. The hyena clans seemed not to have imported only lion carcass body parts, but also all kinds of non-carnivore prey remains (Diedrich, 2005). There is additional proof of the scavenging of lions by hyenas. The holotype of the Zoolithen Cave steppe lion is another example proving conflicts between lions and possibly hyenas. This lion was a male with strong bite damage on the middle saggital crest. As a result of its illness it was an easy prey for a hyena clan, just like the lioness from Srbsko Chlum-Komín Cave. Both cases involved damaged brain cases and ill lions survived only for a couple of days if their injury was visible during the healing processes. The question if they were eventually killed by the hyenas, or if they were only imported into their dens as "animals found dead" has not been answered.

However, the taphonomical situation at the studied sites proves that the steppe lions clearly were never cave-adapted "cave lions." *P. leo spelaea* must have lived on the extensive Mammoth Steppe or in taiga forest environments and did not use caves for the protection of their cubs. This is in contrast to other ice-age carnivores, like the cave bear, the spotted hyena or wolves, which occupied caves for different reasons. Cave bears initially raised their cubs and hibernated for several months in caves in the Sauerland region, including the Perick Caves, Keppler Cave, Weiβe Kuhle Cave, Martins Cave and others (e.g. Diedrich, 2006, Fig. 9). Spotted hyenas used the caves in this region, either for protection of their cubs, or as prey food storage sites (Fig. 9), which is found also in other regions such as the Bohemian Karst (Diedrich and Žák, 2006).

For this reason, the amount of cub bone and tooth remains, especially abundant milk teeth and tooth cusps, in cave bear and hyena den caves is relatively high (e.g. Diedrich, 2006). Lion remains in hyena dens do not show this high percentage of juvenile bones at all (e.g. Srbsko Chlum-Komin, Perick Caves), and consist mainly of a few adolescent and more common adult animal remains (Diedrich and Žák, 2006). Milk teeth from lions were not found in any of the collections from the studied localities, in contrast to the cave bears and hyenas. This important difference provides additional evidence that Late Pleistocene lions did not use caves to raise their cubs (Diedrich, 2007a) being similar to African lions who are adapted to open grassy terrain (Grzimek, 1997). Modern lions do not use caves for food storage, not only because they are generally occupied by hyena clans (cf. Kruuk, 1972; Estes, 1999). Modern African lions move their prey into trees to protect it from hyenas (Estes, 1999).

In contrast to the vertical cave dens and prey depots, the lion bone and carcass materials from the Weichselian in horizontal cave dens such as the Perick Caves are more incomplete and often cracked and strongly chewed. Such caves were more easily accessible; in addition the hyena cubs grew up here and played with the prey and bones. They chewed strongly and tried to crack the bones during the changes of dentition (Diedrich and Žák 2006). But even adults had access to these large dens, which were perfect hiding and food storage places.

Hyenas left typical “nibbling sticks” there (Diedrich, 2006; Diedrich and Žák 2006). In such caves, lion carcass and body parts or single bones are generally incomplete, missing their joints or have strong bite and scratch marks on their surfaces (Diedrich, 2006; Diedrich and Žák, 2006).

The few adolescent lion bones in hyena den caves presented here for the Sauerland Karst (Fig. 9) are important for the comparison with modern spotted hyenas and their lion kills as well as to demonstrate that spotted hyenas in the Late Ice Age had similar habits to modern hyenas. Even modern spotted hyenas often kill young lions and also try to kill the cubs, which they eat directly at the killing place (cf. Joubert and Joubert, 2003). Rarely do they move them to their dens to scavenge them at a distance from the lions (Schaller, 1972; Estes, 1999; Ford, 2005). Even if they imported such lion cubs to the dens such as in the Wilhelms Cave in the Pleistocene, the bones are usually too soft to be preserved after a scavenging by hyenas.

Lion carcasses or body parts appear to have been frequently imported by hyenas not only into their cave dens but also into mud pits in loess along the Weichselian rivers; the pre-Moldau and pre-Berounka in the Czech Republic (Diedrich, 2007b). Possibly they were killed directly at the prey scavenging sites where the conflict between hyenas and lions was most intense. Such a scenario could have occurred at the mammoth carcass site at Siegsdorf (cf. Ziegler, 1994; Darga, 1998), where hyenas scavenged heavily on a mammoth carcass. They must have been responsible for the skull destruction and have left many typical deep bite and chew marks mainly on the long bones. They also left their coprolites to mark their territory. A skeleton of an Ice Age steppe lion was found there (dated from the Middle Weichselian by ^{14}C analyses, Rosendahl and Darga, 2004), which was most probably a victim of a hyena clan attack. However, hyena scavenging could not be proved by bite marks on this incomplete skeleton, but possibly by its incompleteness, because hyenas often remove body parts. At the Siegsdorf scavenging site the lion skeleton was interpreted to have been left by Neanderthals which “slaughtered the lion” (Rosendahl and Darga, 2004), but the cut marks appear to be the product of modern excavations in which metal tools were used, but not mentioned (Rosendahl and Darga, 2004). The analyses did not identify the age of the cut marks. In addition, the site is clearly a hyena scavenging area, most probably an open-air prey depot and at least a mammoth carcass feeding site, at which no stone tools or artifacts of human origin have been found. Instead, the typical Late Pleistocene macrofauna prey composition, chewed bones of different mammals, and even hyena coprolites, are present (Ziegler, 1994). The mammoth site was dominated by hyena activity, scavenging a mammoth carcass, and most probably in conflict with lions over this giant prey. A similar situation between African modern spotted hyenas and lions in a heavy battle over an African elephant carcass was impressively documented by Joubert and Joubert, 2003. Here, finally, the lions were chased away by a large hyena clan. During these struggles, a lion could have easily been killed, if it was outnumbered. The hyenas, again, did not scavenge on the male lion carcass because the predator was killed during the conflict — not as prey to feed on; ample food was available from the elephant carcass. This may explain the “completeness” of the steppe lion of Siegsdorf. Additionally, hyenas stored prey remains of other large mammals here because all the bones show bite or chew marks, especially those of the woolly rhinoceros and steppe bison.

Spotted hyena predation on lions and importation of their carcasses into their dens seems to be the reason for the early taphonomical differences in male/female sex ratios at Late Pleistocene lion bone sites in general. Modern spotted hyenas generally do not hunt stronger adult male lions but there are always exceptions, especially if the lion is young, separated, or an older weaker animal (Schaller, 1972; Estes, 1999). Normally the male lion is the “hyena killer” and elects to kill the leading female to disperse the clan, in some cases even for months (Joubert and Joubert, 2003). Carcasses of male steppe lions may have been left mostly outside the caves such as in Praha-Podbaba (Diedrich, 2007b), or at the open-air site at Siegsdorf in Germany (Gross, 1992). The importation of male lion carcasses can be reported for hyena den caves, such as the Perick Caves, Keppler Cave, Bilstein Cave, and Balve Cave as well as for several Sauerland Karst caves.

In contrast to the male steppe lions, lionesses appear to have been killed more often by spotted hyenas (this is also reported in Africa: Schaller, 1972; Estes, 1999; Ford, 2005), who imported the carcasses into the cave den sites, such as at Srbsko Chlum-Komín.

When no articulated skeletons are present at the hyena den caves, lion bones generally represent only 0.1–4% of the Pleistocene megafauna remains in the studied regions (Fig. 9). In cave bear den sites, lions are represented with very few bones such as in the Keppler Cave and the Weiβe Kuhle Cave (Fig. 10). The presence at hyena den sites seems to be mainly dependent on the prey faunal assemblage, the hunting season, hyena clan size and even the presence or absence

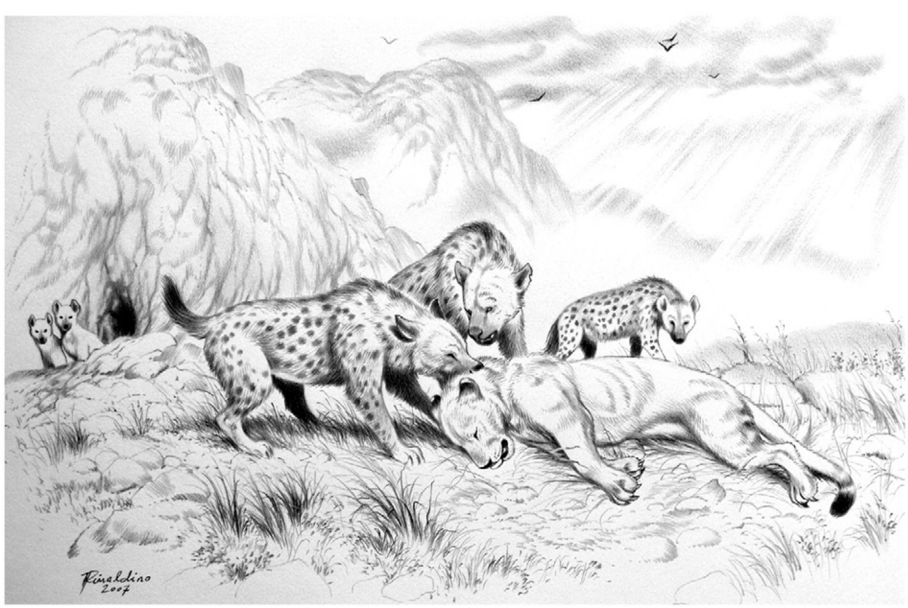

Figure 10. Illustration at the Perick Caves in the Upper Pleistocene: hyena importation of a lioness carcass (Illustration: George “Rinaldino” Teichmann).

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of large prey and of cave bears as a special food source (cf. Diedrich, 2006, Fig. 9). Compared with the Perick Caves of Germany, where hyenas specialized in scavenging of cave bear carcasses (Diedrich, 2006, Fig. 9) and additionally fed on a Mammoth Steppe fauna (Diedrich, 2005), the prey percentages are quite different at the hyena cave of Srbsko Chlum-Komín (cf. Fig. 9). There two complete lion skeletons from a young lioness with a pathologically damaged brain case and an adolescent animal were found as complete skeletons (Fig. 8). Were they imported and killed outside the cave, or were they trapped and killed while stealing hyena prey in the cave itself? Here in Late Glacial Central Bohemia, hyena predation focused on Przewalski horses (Diedrich, 2007a, Fig. 9). The mammoth was absent here, woolly rhinoceros and giant deer were rare, but reindeer and even alpine animals such as chamois and ibex were on the prey list. At Siegsdorf, the bone numbers are difficult to compare (Fig. 9) as a result of the mammoth and lion carcasses and relatively few other faunal remains. Here, the lion material of one individual skeleton comprises 35% of the faunal remains. Normally, at open-air sites, carnivore bones, including lion bones, are rare and comprise $<1\%$ of the bone material (Fig. 9).

However, the taphonomy of lion remains at different hyena cave and open-air sites, and its integration with the Late Pleistocene hyena research, give a clearer picture of antagonistic Ice Age carnivores, which routinely fought for territory and prey, as their descendants still do (cf. Joubert and Joubert, 2003). Each had completely different ecological habits concerning the use of caves. Spotted hyenas had dens and used caves; steppe lions did not live in those caves, but must have entered them to steal hyena prey and possibly to kill and scavenge cave bears, especially young ones. The conflicts and intra-species killing among mammalian carnivores such as modern spotted hyenas and lions in Africa are well known (Schaller, 1972; Grzimek, 1997; Estes, 1999; Palomares and Caro, 1999). The behavior of the steppe lions seems to be similar that of modern species, as reported by Joubert and Joubert (2003) and Ford (2005) for the extant species. More and more lion remains can be identified to have originated from hyena den or prey depot sites; an obvious coincidence which indicates the antagonistic conflicts between Late Pleistocene lions and spotted hyenas in Europe (Diedrich, 2007b). Additionally in the Sauerland Karst caves such as the Keppler Cave or Weiβe Kuhle Cave, which are typical cave bear dens with few lion remains, there are new ideas about cave bear predation by lions and the conflicts of both.

Finally this intensive study of non-archaeological hyena and cave bear den sites in the Sauerland Karst was important for the comparisons to the famous Balve Cave Middle Palaeolithic (Neandertalians to modern Aurignacian humans) site situated near the Perick Caves. At the Balve Cave, lion remains were found in different layers and archaeologists referred to those bones as “archaeological horizons” (Günther 1964). This cave site was most recently also identified to have been periodically used by cave bears and also by hyenas as a den site (Diedrich, 2009b). It was proven that many megafaunal bone remains did not resulted from human import, in contrast, quite a few large bones (e.g. from the woolly rhinoceros) were identified because of their typical incompleteness and chew marks as being hyena prey. A large amount of bones at this cave site is not human “kitchen rubbish” scavenged later by hyenas. Large bones were mostly used by humans as bone coal. The comparison to the hyena dens with no human impact, especially here in the Perick Caves, explains well the hyena den site proof of lion carcass remains as prey import by hyenas. Even the Balve Cave lion material is possibly in all cases not the result of human activity. This is important because the fact is hunting of cave bears, hyenas and lions by humans is still unclear and not convincingly proven. Here it can therefore be shown that bones, especially carnivore impact, have to be carefully studied at cave sites before attributing all bones to human activities. Caves are often multi-use and highly complex in their taphonomy and bone assemblages and the main megafaunal bone accumulator in caves was the Ice Age spotted hyena (Diedrich and Žák, 2006).

Conclusions

The material from the Perick Caves demonstrates lion scavenging and importation of their carcasses into hyena den caves. The presence of lion skeletons, body parts and single bones in hyena den caves and not only in many northern Germany Sauerland Karst caves, is not coincidental. Different models for the presence of lion remains in caves can be presented, which shows the complexity of the lion taphonomy story:

1. Lions were killed outside the caves by their strongest antagonists, the spotted hyenas, and imported as complete carcasses. Lion cubs and juveniles especially, but also outnumbered lionesses and weak males, might have been easily killed outside the caves by hyena clans. Mostly the lion bodies were scavenged there, if hyenas did scavenge on it. Cub carcasses were rarely imported to the hyena den (possible in Srbsko Chlum Komin Cave and Wilhelms Cave).
2. Hyenas imported dead lions or lion carcass body parts from killing sites. These were further scavenged by hyenas after importation into their dens, which is proven by the chew, bite and crack marks (Perick Caves and possibly Keppler Cave).
3. Lions, especially weak or ill individuals, penetrated the prey storage caves because food was easy to steal from hyenas. Hyena clans may have killed an antagonist in the cave itself; in other cases the lions may have fallen into vertical parts of the den caves where they died naturally (Srbsko Chlum Komin Cave).
4. Lions went into the front parts of the caves to kill the herbivorous cave bears. There they might have been killed, but not scavenged, by adult cave bears (Keppler Cave).
5. Lions occasionally may have fallen down vertical shafts, where they were trapped and died naturally (not provable in northern Germany, but this scenario is suspected for a *Smilodon* cat in the North American Hurricane Cave).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yqres.2008.12.006.

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