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The holotypes of the upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823: Hyaenidae) and *Panthera leo spelaea* (Goldfuss, 1810: Felidae) of the Zoolithen Cave hyena den (South Germany) and their palaeo-ecological interpretation

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The rediscovered holotype skulls of Late Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) (Felidae) and *Crocuta crocuta spelaea* (Goldfuss, 1823) (Hyaenidae) from the Zoolithen Cave at Burggeilenreuth, southern Germany, are discussed. The cave became famous mainly due to its rich cave bear bone remains from the late Saalian (OIS 6–8) to Eemian/Weichselian (OIS 3–6) including additionally a third holotype of *Ursus spelaeus* Rosenmüller, 1794 (Ursidae). The '*Felis spelaea*' holotype represents an adult male with a strong bite mark on the saggital crest, which was in an early stage of healing. Compared with other European Late Pleistocene lion skulls and skeletons, and with modern African lions, it provides evidence of intraspecific conflict between male Ice Age lions. The holotype of '*Hyaena spelaea*' is one of several hundred hyena remains from a well-frequented hyena den cave. The cave was used intensively by Late Pleistocene hyena clans, for collecting lion carcasses in addition to their accustomed prey, as happened in many caves throughout Europe. Ice Age spotted hyena clans might have killed Ice Age steppe lions for many reasons, such as fights over prey and territory, and the protection of cubs, but they did not always scavenge on their carcasses. *Zoological Journal of the Linnean Society*, 2008, **154**, 822–831.

ADDITIONAL KEYWORDS: carnivores – Europe – Late Pleistocene – skulls.

INTRODUCTION

Holotypes of both the Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) and the Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) were thought to be lost. As a result of the European Ice Age spotted hyena project, 3 years' work to rediscover the material was finally successful. During the project, many localities that had been excavated in the past were restudied from several European museum collections (these are listed in the acknowledgements). In none of them was information available on the 'Geilenreuther Cave' originals, and even these were not labelled as holotypes, but were found to have a red dot on the cranium indicating holotype identification.

Bones of the famous, animal bone-rich European 'Geilenreuther Höhle' (Fig. 1), which is presently known under the name 'Zoolithenhöhle' (= Zoolithen Cave, cave No. D 106, 455 a.s.l.) were first described (but few figured) in a large monograph by Esper (1774). Heller (1966, 1972) and Poll (1972) reported on the history of this large cave and its fossils based on a review of the literature, but without restudying the originals in different museum collections. Groiss (1972, 1978, 1979, 1983, 1996) began some new research on the geology and palaeontology of Zoolithen Cave, whereas more recently Rosendahl & Kempe (2004) dated some speleothems at the bottom of the cave and

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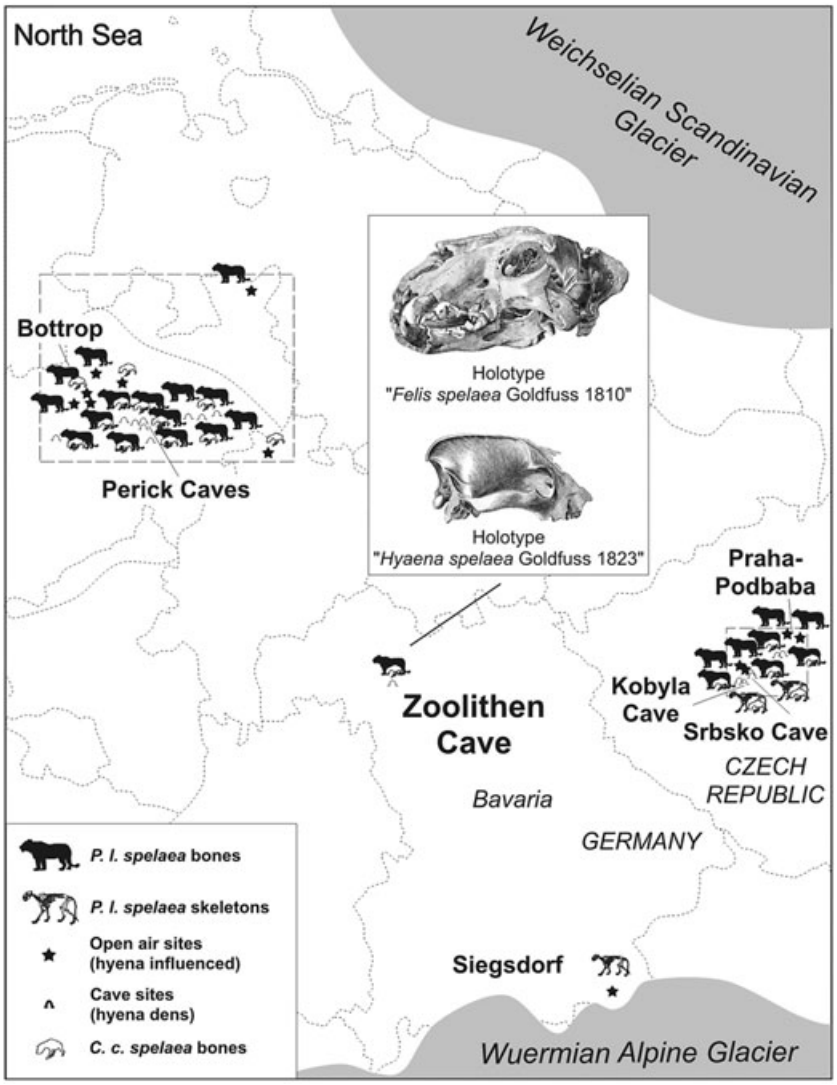

Figure 1. Geographical position of the Zoolithen Cave (Bavaria, southern Germany) with both originals and compared regions with Ice Age spotted hyena den sites, at which Late Pleistocene lion remains were found in northern Germany and central Czech Republic.

suggested the presence of a mixed fauna ranging in age from OIS 3 to 8 (late Middle to Upper Pleistocene or Saalian to Weichselian). They discussed the possibility of different bone layers, as already mentioned by Goldfuss (1823), who distinguished an 'upper layer' with different coloured bones that were 'clean on the surface' (mainly non-cave bear bones, including the hyena holotype skull described here) and bones from the 'lower layer', the 'Knochenbrekzie' (= bone breccia). The latter bones are stained slightly yellow, and often speleothems, sediment and bone fragments are attached to the non-cleaned bones, especially cave bear skulls. In these characteristics the Geilenreuther cave bear bones are clearly distinguished from those of other European cave localities.

Zoolithen Cave is one of the most famous European Pleistocene mammal bone localities owing to thousands of bone finds, mainly of cave bears, which are widespread in European museums. Some mammals were described in more detail (e.g. *Lynx lynx*: Groiss, 1983, Mustelidae: Eberlein, 1996, *Gulo gulo*: Goldfuss, 1818; Döppes, 2001, *Ursus spelaeus*: Weinstock, 2001), specimens other than bears are still poorly described, and the interpretation of the cave as a hyena den has not previously been revealed. In the present study, hyena remains including several skulls, and the presence of prey remains and lion material, support the theory that hyenas used the cave as a den over a longer period and even introduced many lion carcasses. Detailed studies of Zoolithen Cave will be

carried out in future with regard to its hyena population and taphonomy to get a clearer picture of the use of the cave by animals other than cave bears.

All three holotypes of the late Pleistocene large 'carnivores', cave bear '*Ursus spelaeus* Rosenmüller, 1774', 'cave lion *Felis spelaea* Goldfuss, 1810' and 'cave hyena *Hyaena spealea* Goldfuss, 1823' were found in the Zoolithen Cave at Geilenreuth (Bavaria, southern Germany) in the Wiesent valley (Fig. 1), which makes this cave unique in Late Pleistocene mammal research in Europe.

The first description of the 'Hölen Hyäne' (= 'cave hyena') was made by Goldfuss (1810), but the cave hyena was named much later in the Linnean zoological systematics in 1823, because the skull described by Goldfuss was too incomplete. In the Goldfuss-Museum of the University of Bonn, the original cave hyena specimen could be identified based on the original figure of Goldfuss (1823). In addition, he illustrated a lower jaw, also from Zoolithen Cave, which could not be found or identified until recently. On the ventral side of the skull written in red ink is '*Hyaena spelaea* Goldfuss', and there is also a red dot, both supporting the holotype identification. The incomplete skull was figured and described by Goldfuss for the first time in 1810 (Fig. 2), but the skull in his sketch lacks the left maxilla and nearly all teeth, although the saggital crest is complete. Therefore, it was unclear if the skull depicted here was the original, as the damage was fresh and must have occurred much later. Another problem was that Goldfuss sketched the holotype later in 1823 as a 'hybrid'. The holotype is the mentioned and figured one in 1810, but as a result of its incompleteness he used another skull from the 'Sundwig Caves' (today Perick Caves, Sauerland, northern Germany, cf. Diedrich, 2005), as mentioned in Reynolds (1902), which he studied in material of the British Museum of Natural History, London. Here both skulls were compared (BMNHL No. 28558, 28557), but the holotype must be designated as the first described and pictured one, because clearly neither of the two skulls in the British Museum of Natural History are similar to the drawings of Goldfuss (1823). Therefore, the holotype is the incomplete one from Zoolithen Cave. All other features, especially the presence of just the roots of the right P^2, clearly identify the original as figured in 1810.

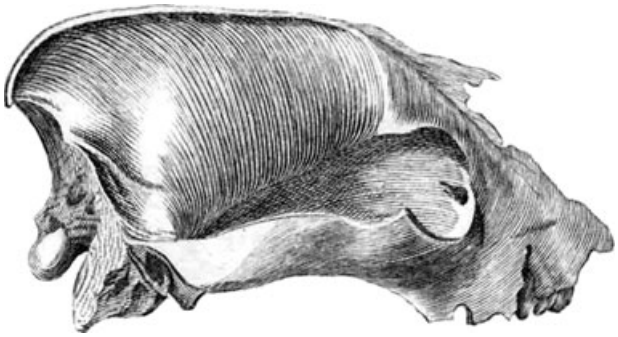

Figure 2. Original figure of the holotype of '*Hyaena spelaea* Goldfuss, 1823' from Goldfuss (1810) from Zoolithen Cave, southern Germany. Skull is damaged on the left side and lacks most teeth (cf. Fig. 3).

Goldfuss (1810) depicted the original '*Felis spelaea*', but gave no indication of where it was stored. At that time he worked at the University of Erlangen, but an attempt to find his pictured skull there was unsuccessful, because parts of this collection went via Leipzig and finally to Berlin (Bundesamstalt für Rohstoffe Berlin, Humboldt-Museum Berlin). When Goldfuss became Professor at the Rheinische Friedrich Wilhelms-University in Bonn in 1823, he finally named and depicted the originals of the 'Hölen-Hyäne *Hyaena spelaea*', but again, he gave no depository for the finds of the Zoolithen Cave. The skull of the lion was recently found by chance in the Museum für Naturkunde Berlin at Humboldt University. Here there are four skulls from the Zoolithen Cave, which were all studied and compared with the holotype illustration. Additionally, postcranial lion material is mixed with cave bear bones, especially vertebrae. None of the skulls was labelled as the '*Felis spelaea*' original of Goldfuss (1810, 1821). A red dot on the palatinal supported the holotype identification. Only one of the four skulls from the Humboldt-Museum Berlin collection has lower jaws, and a very characteristic feature, a V-shaped notch in the middle of the saggital crest, which is described in detail in the pathology section herein. This saggital crest damage did not result from excavation: it is a strong bite mark, visible only on that skull. Finally, the left side of the skull has a modern large hole below the frontal, and the left jaw is missing the ramus in Goldfuss' (1810) figures, which was damaged in historical times by the excavations, all characteristics seen in the lion skull.

MATERIAL AND METHODS

Under the European Ice Age spotted hyenas project, hyena den sites, caves and open air or gypsum karst sites are being studied taphonomically to understand large bone accumulations and the palaeoecology of the Late Pleistocene carnivore *Crocuta crocuta spelaea* (Goldfuss, 1823). Studies have focused on hyena dens in two main regions: the Sauerland cave-rich region of northern Germany (Diedrich, 2004), and the Central Bohemia region of the Czech Republic (Diedrich & Žák, 2006; Diedrich, 2007c; Fig. 1). More than 1200 hyena bones and about 800 lion bones have been studied. During these studies a few

Late Pleistocene skeletons of hyena and lion individuals were rediscovered in old collections which had been subsequently repaired (cf. Diedrich & Žák, 2006). Here a report is given of both holotype Late Pleistocene hyena and lion skulls, including their identification, sex and the question of whether they originate from one individual or are composed of several. For this, many other skulls were compared from hyena den caves of Germany, England and the Czech Republic. Also, interspecific variation among the four studied lion skulls and four hyena skulls from the Zoolithen Cave in the collections of the Goldfussmuseum Bonn, and Humboldt-Museum Berlin were important for sex identification. Systematic descriptions and systematic comparisons are not given here, and not all metric data are given in detail. These would be of little help in modern Late Pleistocene phylogenetic identifications (see metric misidentification to *P. tigris spelaea*, 'cave tiger' by Groiss (1996), because DNA analyses have recently shown the close relationship of *Panthera leo spelaea* to *Panthera leo* subspecies of Africa (Burger *et al.*, 2004). The 'cave tiger' described from the Zoolithen Cave (Groiss, 1996) is therefore a *P. leo spelaea*. Metrics were used here only to identify the skulls of the two carnivores as regards sex or individual age.

SYSTEMATIC PALAEONTOLOGY

FAMILY HYAENIDAE GRAY, 1821

GENUS *CROCUTA* KAUP, 1828

CROCUTA CROCUTA SPELAEA (GOLDFUSS, 1823) (FIGS 2, 3)

1810 'Hölen Hyäne'. – Goldfuss: 280–281, table V, figs 2a, b.
1823 *Hle*. LVI, figs 1–3.

Holotype: Hyaena spelaea Goldfuss, 1823. Incomplete cranium (Goldfuss-Museum Bonn No. M2609).

Locus typicus: Zoolithen Cave, Geilenreuth (cave No. D 106) Franconian Alb, Wiensent Valley, Bavaria, southern Germany, Central Europe.

Stratigraphy: 'Upper layers above the main cave bear bone gravels' after Goldfuss (1810, 1823). Weichselian/Würmian, Upper Pleistocene (probably OIS 3). OIS 3–6 after Rosendahl & Kempe (2004). A radiocarbon date on cave bear teeth is given as 28.905 ± 255 BP (Poll, 1972).

Collection: Goldfuss-Museum of the Rheinische Friedrich Wilhelms-Universität Bonn, Germany.

Figure 3. Original skull of the holotype of '*Hyena spelaea* Goldfuss, 1823' from Zoolithen Cave, southern Germany (Goldfuss-Museum Bonn No. M2609). A, lateral right; B, ventral; C, occipital; D, dorsal.

Short description and discussion: The holotype was described as an incomplete cranium (Fig. 2A), which is missing the left maxilla and premaxilla (cf. Goldfuss, 1810). The right maxilla has the alveoli of the P^{3-4}. The P^2 is represented by its roots and indicates a mature to very old individual. The gender of the hyena is not yet clear as a result of lack of premaxillaries and total length measurements. The Late Pleistocene hyenas often show clear sexual dimorphism, clan-leading females being slightly larger with skull length of 30–32 cm (e.g. Diedrich, 2005, 2007b); the general sexual dimorphism in *C. c. spelaea* is present in the modern African spotted hyena *C. c. crocuta* (cf. Rohland, 2003). Recently, parts of the saggital crest have been damaged (compare Figs 2 and 3A); this damage was not present in 1810, when the skull was figured in a lithography. One additionally figured lower jaw in 1810 could not be found recently and it be shown to belong to the skull. Many mandibles were found in this cave, and it is thus not possible to prove that both parts are from one individual. In contrast, the skull must be from a very old animal. The P^2 is represented by rounded roots; both M^1s are missing and their alveoli were already completely closed. The historically figured mandible was from an adult animal and has much less worn teeth.

Figure 4. Original figure from Goldfuss (1810) of the holotype of '*Felis spelaea* Goldfuss, 1810' from Zoolithen Cave, southern Germany. The skull has a strong bite mark and pathology in the middle of the saggital crest (cf. Figs 6, 7).

FAMILY FELIDAE FISCHER, 1817

GENUS *PANTHERA* OKEN, 1816

PANTHERA LEO SPELAEA (GOLDFUSS, 1810)
(FIGS 4–8)

1810 *Felis spelaea*. – Goldfuss: 277–280, table V, fig. 1.

Holotype: Felis spelaea Goldfuss, 1823. Skull (Figs 4–8) of an adult male individual (Museum für Naturkunde der Humboldt-Universität Berlin No. MB.Ma.50948).

Paratype: Lower jaw composed of two different individuals and of different sexes. At least one mandible clearly does not belong to the cranium because of its smaller size; the other has a strongly used canine, which indicates a very old individual, and would also not fit with the adult male skull (No. MB.Ma.50948).

Locus typicus: Zoolithen Cave, Geilenreuth (cave No. D 106), Franconian Alb, Wiensent valley, Bavaria, southern Germany, Central Europe.

Stratigraphy: 'Upper layers above the main cave bear bone gravels' after Goldfuss (1810, 1823). Weichselian/Würmian, Upper Pleistocene (most probably OIS 3–6). OIS 3–6 after Rosendahl & Kempe (2004). Radiocarbon date on cave bear teeth 28.905 ± 255 BP (Poll, 1972).

Collection: Museum für Naturkunde of the Humboldt-Universität Berlin.

Short description and discussion: The nearly complete skull (Figs 5–8) and lower jaws cannot all be derived from one individual. The left mandible is about 3 cm shorter and more slender in its proportions. This half mandible would fit better with a lioness. The right mandible has a very heavily used canine, which again

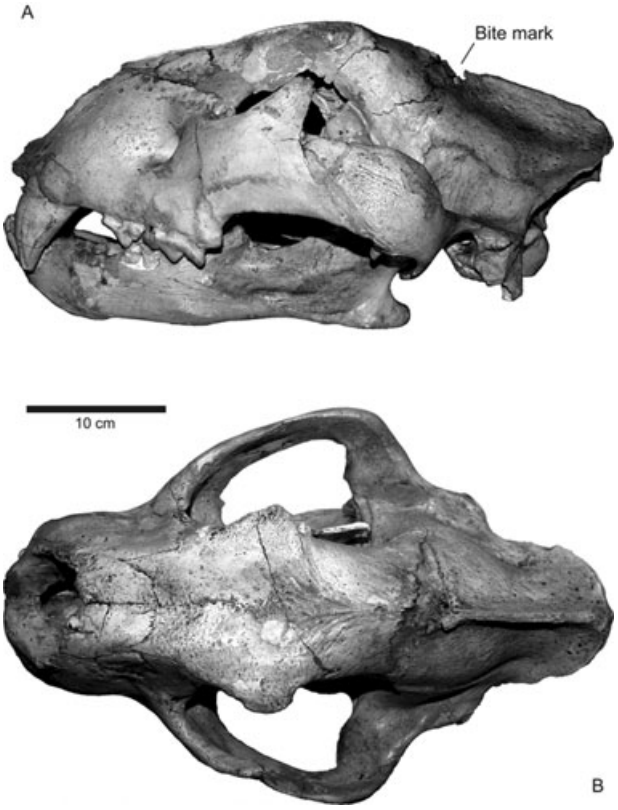

Figure 5. Original skull of the holotype of '*Felis spelaea* Goldfuss, 1810' from Zoolithen Cave, southern Germany (Museum für Naturkunde der Humboldt-Universität Berlin No. MB.Ma.50948). Skull with bite mark and pathology on the middle of the saggital crest (cf. Figs 4, 9). A, lateral left with lower jaws; B, dorsal view with lower jaws. The bite mark on the right parietal and pathology is characteristic of this skull.

would not fit with the adult male skull. Several crania and even some lower jaws are present from this cave. The original skull has unique saggital crest damage. This is the result of a strong bite mark on the right parietal bone. This damage had undergone healing for a short time. The deep bite left a V-shaped notch in the centre of the crest. Only this skull of four possible candidates has these characteristics. Additionally, on the left side there is a modern hole damage in the skull, and the lower left jaw is missing most of the ramus, which must have occurred during the excavations. All these characteristics can be found only in one skull in the collection of the Museum für Naturkunde Berlin. The skull is 40.2 cm in total length and fits the description of skulls of male Late Pleistocene lions, which had skulls about 10 cm longer than those of female lions (cf. Altuna, 1981; Argant, 1988; Gross, 1992). The dentition was shown to be more complete in Goldfuss (1810). The lower jaw is now missing the right P_3 and all incisors have been

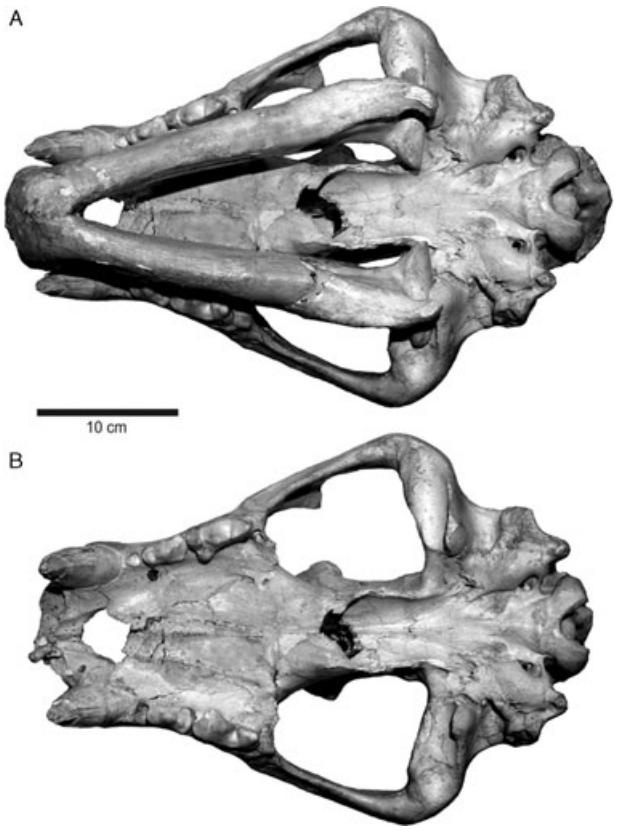

Figure 6. Original skull of the holotype of '*Felis spelaea* Goldfuss, 1810' from Zoolithen Cave, southern Germany (Museum für Naturkunde der Humboldt-Universität Berlin No. MB.Ma.50948). A, ventral with lower jaws; B, ventral without lower jaws.

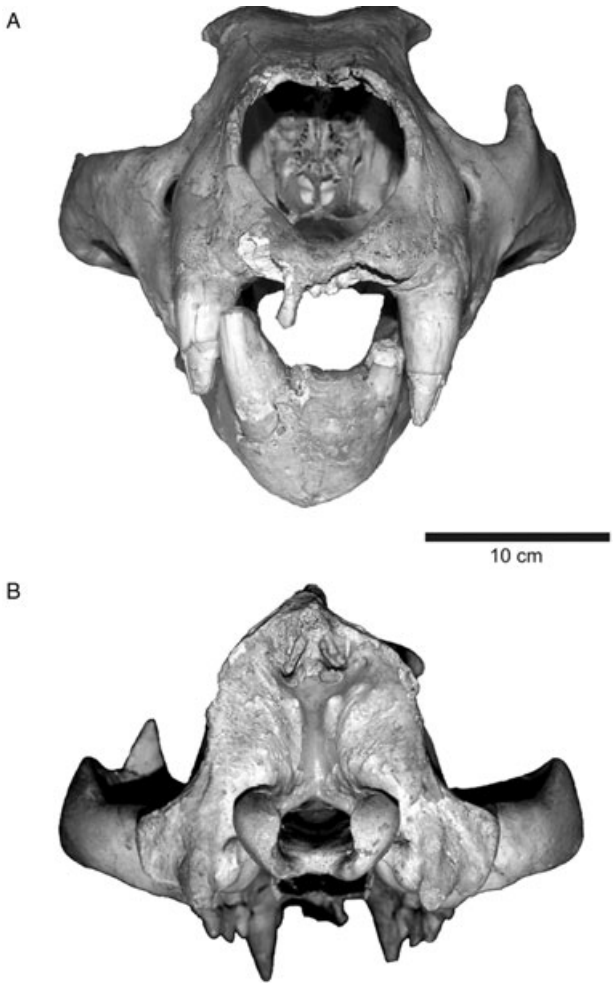

Figure 7. Original skull of the holotype of '*Felis spelaea* Goldfuss, 1810' from Zoolithen Cave, southern Germany (Museum für Naturkunde der Humboldt-Universität Berlin No. MB.Ma.50948). A, frontal; B, occipital.

lost. Similar losses can be observed in the upper incisors. Only the right I^2 now remains. It appears that the nasal bones have lost some anterior parts. The skull probably sustained modern frontal damage during which it unfortunately lost many teeth and other parts. Additionally, some parts in the symphyseal region of the mandible have been filled with plaster, especially around the canines.

Palaeopathological observations: The skull of the male lion from Zoolithen Cave obviously had been severely bitten. The saggital crest was punctured up to 2 cm depth by the bite of another carnivore, and a large piece of bone must have been removed. Thus, the characteristic V-shaped notch in the middle of the saggital crest (Figs 8.2, 9A), which was clearly drawn by Goldfuss in 1810, can be clearly seen and is unique in all known lion skulls of the Zoolithen Cave. Additionally, a deep groove, 2 mm wide and about 5 cm long, starts from the V-shaped depression. This braincase damage must have been caused by the incisor of an attacking large carnivore. The bite was deep, and therefore it is possible that parts of the brain were damaged. The motor cortex (area motoria) is situated in this area (Fig. 9). The deep cut was in an early stage of the healing process with some callus production, but the animal cannot have survived for more than a couple of days. Even if the area motoria was not directly damaged, the callus healing process would have had an influence on the behaviour of the animal. The injured lion was possibly not able to move properly, having lost some of its motor capacity, but detailed palaeopathological studies, possibly with tomography, will need to be made to understand the exact injury and its impact.

CONCLUSIONS

In both cases of the 'lost holotypes' of '*Hyaena spelaea*' (= *Crocuta crocuta spelaea* Goldfuss, 1823) and '*Felis*

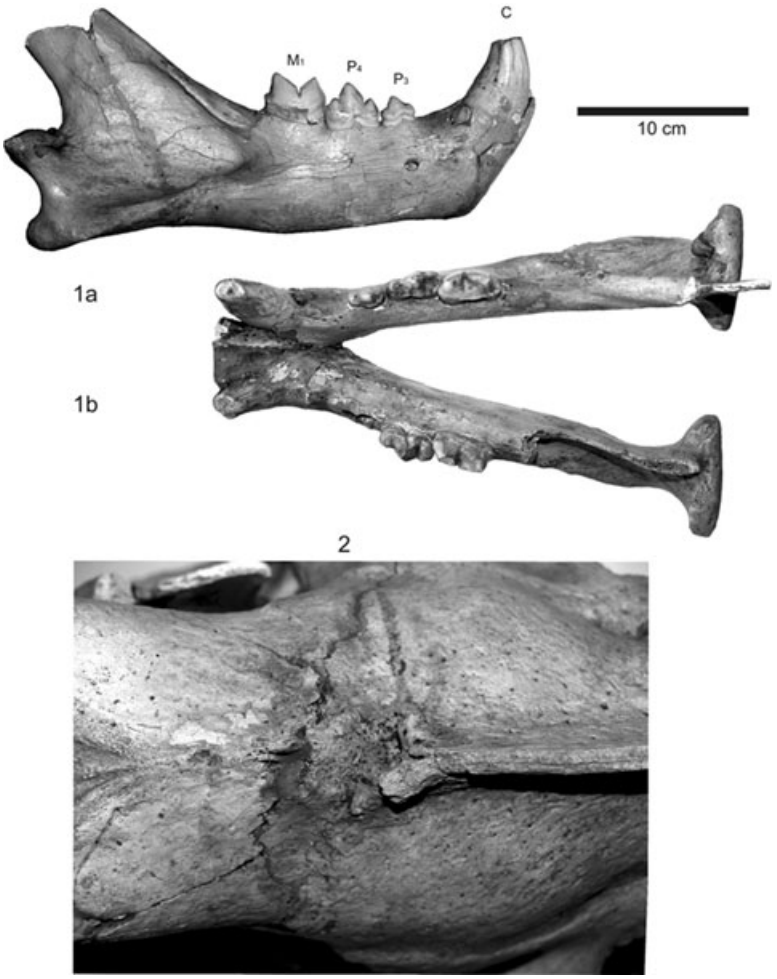

Figure 8. Original skull of the holotype of '*Felis spelaea* Goldfuss, 1810' from Zoolithen Cave, southern Germany (Museum für Naturkunde der Humboldt-Universität Berlin No. MB.Ma.50948). Skull with bite mark and pathology on the middle of the saggital crest (cf. Figs 6, 7). 1. lower jaw composed of two different individuals. The right mandible is much larger and from a very old male, whereas the smaller left one seems to be from a lioness. A, right mandible, lateral; B, jaws, dorsal. 2, bite mark in the saggital crest and long scratch groove on the right parietal. The callus indicates that the animal survived for a short time after the bite.

spelaea' (= *Panthera leo spelaea* Goldfuss, 1810), the identification of today's skulls is clear, but in both cases the originals have lost parts after their description and depiction by Goldfuss (1810, 1823). All information pertaining to them is newly described and figured here, including the remarkable pathology of the lion skull, which is compared with other pathological lion skulls of Central Europe.

It is important to understand the coincidence of hyena dens and lion remains, which are mainly present in den caves or hyena open-air sites. More and more lion remains are being found to originate from hyena den or prey sites, which indicate conflicts between Late Pleistocene lions and Ice Age spotted hyenas. In cave bear dens lion remains are extremely rare, and this supported evidence for the introduction of lions into hyena dens (Diedrich, 2007a). Lions did not use caves even for the protection or raising of their young, as shown by the general absence of neonate to early juvenile teeth and postcranial bone material in the caves, in contrast to hyena and cave bear dens. In the latter, many juvenile remains demonstrate raising of cubs and use of the caves by these large Pleistocene carnivores. No modern large cats, such as African lions, use caves (Bateman, 1987; Grzimek, 1997).

The rediscovery of both originals fits into this taphonomic and palaeoecological scheme of Late Pleistocene steppe lions and Ice Age spotted hyenas as published recently (Diedrich, 2007a). I have suggested here that the lions brought into hyena den caves were often ill or injured. It is unclear whether

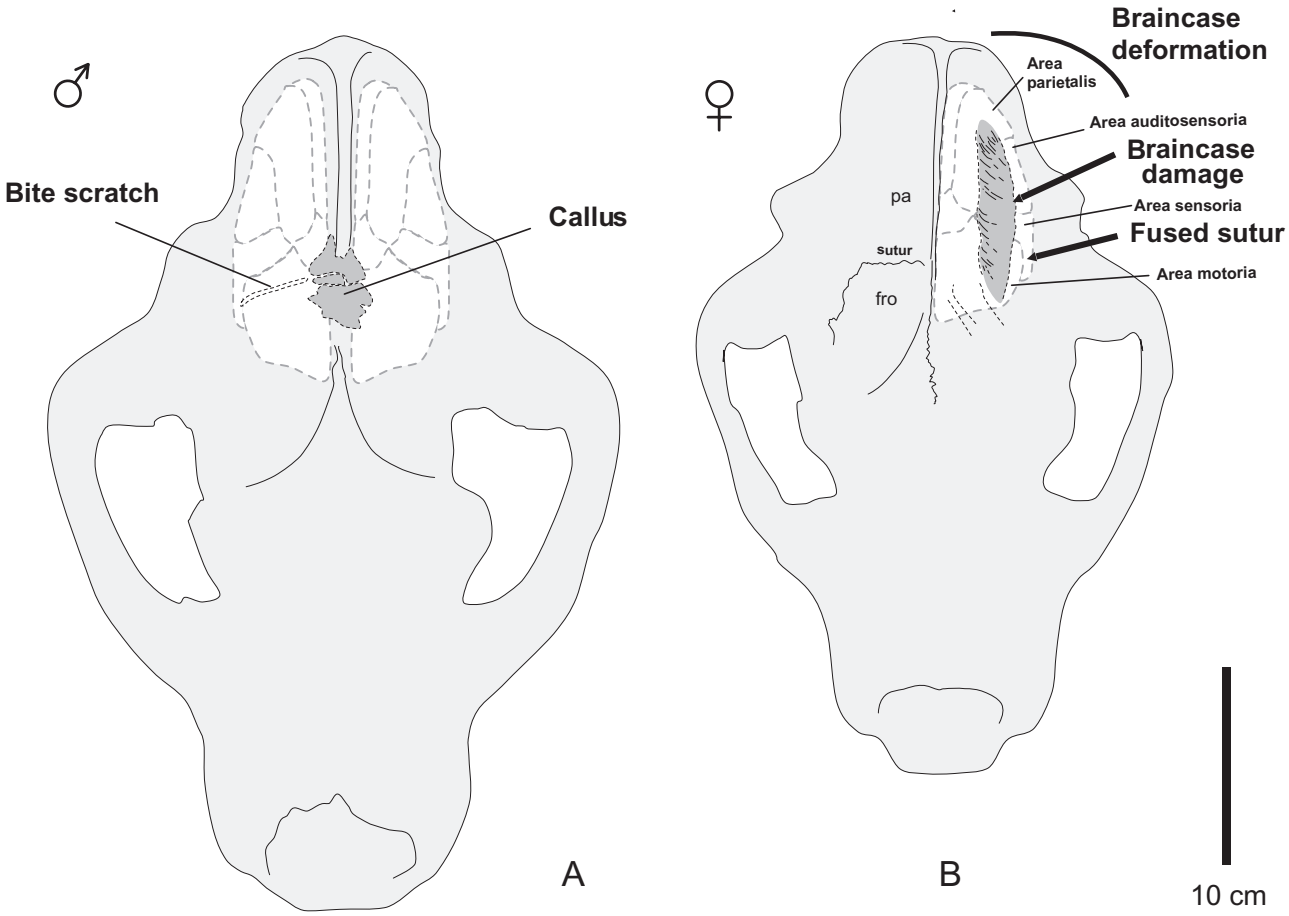

Figure 9. A, male lion with strong bite damage, which died in an early stage of the callus-healing process [holotype of *P. l. spelaea* (Goldfuss, 1810) from Zoolithen Cave, southern Germany]. B, skull of a lioness with a partially healed bite scratch or braincase fracture [original lioness skeleton of *P. l. spelaea* (cf. Diedrich & Žák, 2006) from Srbsko, central Czech Republic].

hyenas killed the lions or if they were introduced as carcasses of already dead animals discovered outside the cave (Fig. 10). Sick or injured lions, either male or female, would have been an easy kill for hyena clans, as can regularly be seen in conflicts between modern African lions and hyenas (Kruuk, 1972; Grzimek, 1997; Estes, 1999; Joubert & Joubert, 2003; Ford, 2005). In this injured state the lion would have been easy prey for other carnivores. The damage was probably caused by intraspecific conflicts, which are impressively documented in modern African male lions (Schaller, 1972; Joubert & Joubert, 2003). During such fights for territory, clan order or females, lions bite intensively into each other's heads and injure each other severely. Their sharp upper incisors are lethal weapons and can cause wounds so severe that lions can sometimes die during or after fights (Schaller, 1972; Grzimek, 1997; Estes, 1999; Joubert & Joubert, 2003). Bites are mainly above the eyes, and therefore the ears often show bite marks, and missing pieces can be used to identify individuals (Estes, 1999; Joubert & Joubert, 2003).

The same seems to have been the case for the Late Pleistocene Geilenreuth lion, providing evidence for similar behaviour in Ice Age steppe lions and their modern relatives. Perhaps a hyena clan attacked the male lion, although modern African hyenas do not normally attack a strong male lion, whereas they can sometimes kill lionesses (Schaller, 1972; Grzimek, 1997; Estes, 1999; Joubert & Joubert, 2003). Such a lioness kill might be represented in the Late Pleistocene record for the Srbsko Cave hyena den (Central Bohemia). Here a complete articulated skeleton was found amongst thousands of other remains of hyena prey (Diedrich and Žák, 2006).

In former times, Goldfuss (1810, 1821, 1823) and other scientists believed that the Late Pleistocene lions lived in the caves (e.g. Rosenmüller, 1794; Goldfuss, 1810, 1823; Boule, 1906; Heller, 1972; Groiss, 1979, 1996), and this belief permeates modern literature.

Figure 10. Ice Age spotted hyenas hauling injured male steppe lion carcass into their cave den (Zoolithen Cave, southern Germany) (Illustration: Rinaldino, 2007).

This early palaeoecological interpretation has been and can again be revised based on the study of forgotten 'cave hyenas', which were mainly responsible in non-cave bear den caves and even at open-air sites all over Europe for large mammal prey bone accumulations as a result of import of carcass body parts (e.g. Diedrich & Žák, 2006; Diedrich, 2007c).

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