Upper Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) skeleton remains from Praha-Podbaba and other lion finds from loess and river terrace sites in Central Bohemia (Czech Republic)

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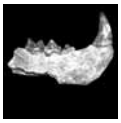

Historical finds of bone remains of *Panthera leo spelaea* (Goldfuss) from the Upper Pleistocene loess open air site at Praha-Podbaba (Czech Republic) are reviewed. The largely complete cranium from Central Bohemia and finds from other sites in Czech Republic are also described. The bone proportions of the cranial and postcranial material from Podbaba indicate them to have come from an adult male lion carcass. One foreleg and lower jaw belonged to an adult female as evidenced by their much smaller proportions. A few additional bones were found at other loess pits around Praha along the Vltava River and at open air sites along the Berounka River close to Beroun. By undertaking a preliminary overview of these finds and other bones from cave sites in Central Bohemia, a first palaeobiogeographical distribution of these extinct carnivores can be presented. The lion remains from the open air sites, were found alongside the typical glacial cold-period macrofauna consisting of a few *Mammuthus primigenius* (Blumenbach), but mainly *Coelodonta antiquitatis* (Blumenbach) bones, which were often well-chewed by Ice Age spotted hyenas. Other faunal remains were found in the loess sites, and these appeared, in most cases, to be hyena prey depots or scavenging sites. These remains included *Bison priscus* (Bojanus), *Equus ferus* Boddaert [partly *Equus przewalskii* (Poljakoff)], *Equus hemionus* (Pallas), *Rangifer tarandus* (Linnaeus), *Cervus elaphus* Linnaeus, *Capra ibex* (Linnaeus) and rarely *Rupricapra rupricapra* (Linnaeus). The latter two animals indicate that an alpine fauna existed in Central Bohemia during the early and middle Upper Pleistocene. Some lion remains and locations described here may be of Saalian Age, during which a similar fauna existed. The bone accumulations, including lion remains, are probably, in many cases, hyena prey deposits. Their presence in caves seems to have been mainly the result of hyena and lion conflicts, and lion kills which were imported, often as complete carcasses, into the hyena cave dens such as the one at Srbsko Chlum-Komín. Their carcasses seemed to have very often been imported by hyenas into their dens in loess along the Weichselian river valleys, the Vltava and Berounka Rivers. In some cases, lions may have been killed at the conflict site, and been scavenged there. The proven minimum number of individuals (MNI) lions for the Weichselian in Central Bohemia can be estimated from cave and open air sites to be about 20 compared with a provable hyena MNI of more than twice this number at about 48 individuals. • Key words: *Panthera leo spelaea* (Goldfuss, 1810), open air sites, Upper Pleistocene loess pits, Central Bohemia, bone taphonomy, palaeobiogeography.

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During the development of the city of Praha and the accompanying increase in construction work during the industrialization period (*ca* 1900) many loess pits were opened for the production of bricks. These pits which lay along the Vltava River and its tributaries were found to contain many bones of Pleistocene macromammals. These now form a large collection in the National Museum of Praha (NMP). The details of this material have not been published until now, although a first overview of the locations and some interpretations of the bone accumulations, focussing on cave sites, were recently published (Diedrich & Žák 2006, Fig. 1). The taphonomical and faunal description of non-cave locations started with the rare cave bear material (Diedrich 2006a) and continues here with a consideration of the few lion bone remains contained in the collection.

In addition to the bone material from open air sites, many bones of lions and other species were collected,

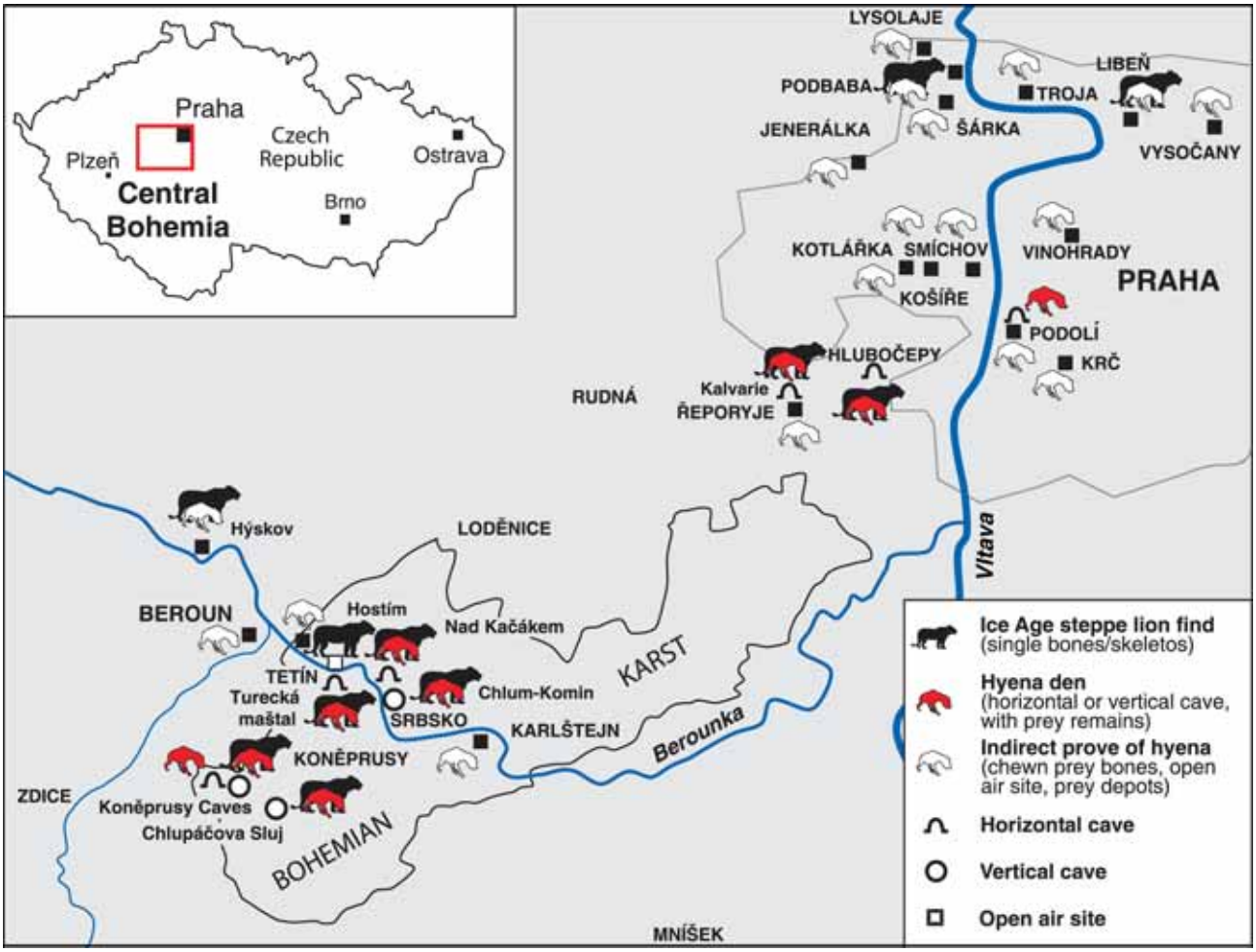


Figure 1. Geography of the Saalian to Weichselian (Late Middle to Upper Pleistocene) Ice Age lion *Panthera leo spelaea* (Goldfuss, 1810) sites in Central Bohemia (Czech Republic). Articulated skeletons were found in Srbsko Chlum-Komín and Chlupáčova Sluj vertical caves in the Bohemian Karst (hyena prey depots). Along the Moldau River valley around Praha the lion skeleton remains of Praha-Podbaba are one of the most important open air loess site finds. The lion skull from Beroun area is the most complete one from open air loess sites in this region.

mostly in the Bohemian Karst caves after 1945. Details of this material remain largely unpublished. Only material from "Chlupáčova Sluj" in the Kobyla quarry cave has been described (Zázvorka 1954). The material has generally been poorly preserved and is stored mainly in the NMP. When the management of the Pleistocene bone collection came into the author's hands in 2005/6 some of the macromammal material became available for study for the first time; some of the older material had remained in its original wrappings for decades.

The material from the NMP described here had been, in some cases, misidentified by previous researchers as, for example, *Rangifer tarandus* or *Ursus spelaeus*. Other pieces identified by Kafka (1903) from Praha-Podbaba as cranial bones of *Panthera* are, in fact, non-carnivore bone fragments, as verified by direct comparison with skull material from the Srbsko Chlum-Komín cave site. A large number of fragmented lion bones, especially ribs, had not been identified at all. In many cases, cave bear canines were identified as lion lower jaw canines and *vice versa*. Distinguishing between these bones is relatively straightforward (*cf.* Kafka 1903), since the lions have two parallel longitudinal groves in the enamel on the lingual and labial side. The upper canines are more flattened and are blade-like in character in lions whereas they are missing in cave bear canines. Remains of individual skeletons were not stored as such but the constituent bones were spread throughout the entire collection.

The open air site material in this collection is now presented, for the first time, more-or-less completely; the cave finds have been partially published elsewhere along with an important skeleton from the Srbsko Chlum-Komín cave. Furthermore, many of the lion bones from cave locations had been included in a palaeobiogeographical map (Fig. 1). The cave material, originating mainly from the Srbsko Chlum-Komín cave (Beneš 1970), will be studied

in the future, once it has been completely separated from the fragment bone boxes and prepared.

As well as the Praha loess pit material, a skull with a left mandible in the Museum of the Bohemian Karst Beroun (abbreviation = MBKB) was included in this study, since it is the only known substantially complete skull from an open air site in Central Bohemia. The older finds from the historical collection (found before 1945) were difficult to identify since the location was given as "surroundings of Beroun"; this will be discussed in detail later. On the skull and the mandible, some carbonate caliche-type encrustation was attached, which unfortunately could not be removed without destroying the bone surface. The material was therefore left in its original condition.

Locations and dating

The studied locations are briefly described and discussed since this is important to our understanding of the origin of some incompletely labelled lion remains (*cf.* Tab. 1).

The Praha-Podbaba Meilbek brick-yard at the Vltava River was located between the present-day streets of Podbabská and Pod Juliskou in the area of the existing Crown Plaza Hotel. In the surrounding area there were several small pits in which some Middle Palaeolithic artefacts were also found (Lutovský & Smejtek 2005). The association of human and animal remains is uncertain because of the lack of accurate bone mappings. Most of the lion bones described and analysed originate from this site. The complete macrofauna appears to be represented including *Mammuthus primigenius* (Blumenbach), *Coelodonta antiquitatis* (Blumenbach), *Bison priscus* (Bojanus), *Equus ferus* Boddaert, *Equus hemionus* (Pallas), *Rangifer tarandus* (Linnaeus), *Cervus elaphus* Linnaeus, rarely *Capra ibex* (Linnaeus) and occasionally *Rupricapra rupricapra* (Linnaeus). The carnivores *Ursus* cf. *spelaeus* (Rosenmüller), *Canis lupus* (Linnaeus) and *Gulo gulo* (Linnaeus) are also represented, whereas the presence of the Ice Age spotted hyena, *Crocuta crocuta spelaea* (Goldfuss), is indicated indirectly by the typical chewing marks and incomplete woolly rhinoceros bones, similar in preservation state, to those found in hyena cave dens of the Bohemian Karst (*cf.* Diedrich & Žák 2006). The documented loess section at the open air site at Praha-Podbaba is important for our understanding of the geological history of the region and for dating many of the other loess finds in the surrounding area. The site was described and drawn well by Kafka (1893). It is redrawn here with a more modern geological-palaeontological and climatic interpretation (Fig. 2). The Praha-Podbaba section starts with the river gravels of the Vltava River (terrace IIIc after Záruba-Pfeffermann 1943, terrace VI, or basal part of terrace V, after Záruba *et al*. 1977, see also Paluska 1976) which belong to the Saalian glacial or Eemian interglacial stages. The first thin loess of the discussed loess profile, denoted here as the "Lower Loess", is interpreted here as having been deposited during the first cold period of the Lower Weichselian. In the Lower Loess a "mammoth steppe fauna" was found, including *M. primigenius*, *C. antiquitatis*, *B. priscus*, *E. ferus*, *U. spelaeus*, and the *P. leo spelaea* skeleton remains described here as well as some remains of *G. gulo* (Kafka 1903). For the lower part of the section at Praha-Podbaba, *Alactaga saliens,* being typical for the lower and middle part of the Upper Pleistocene cold stages (Koenigswald 2002), was listed and even drawn by Kafka (1893). Most of the bone material from Praha-Podbaba and other sites which is housed at the NMP, was discovered in the so-called "Middle Loess" (second cold period) which seems to represent most of the middle part of the Upper Pleistocene (third cold period). Here, marmot and other micromammal bioturbation were frequently recognized, along with burrows of other cold-period micromammals (*cf.* Kafka 1893). The "Upper Loess", which must have been accumulated at the end of the Weichselian, has yielded no macrofauna either at this location or anywhere among the Central Bohemian open air sites. Most of the *P. l. spelaea* bones from Praha-Podbaba drawn here (17 bones, Tab. 1) were collected before 1888 in the Meilbek pit ("Meilbekova cihelna"). At that time, a large loess pit was situated in the Upper Pleistocene loess deposits on the west side of the river, from which the historical section is re-interpreted here (Fig. 2, *cf.* original in Kafka 1893). Finally Kafka (1893) dated the section according to its micromammals and larger rodents (*e.g.*, marmots) as belonging to the "Weichselian/Würmian" age, whereas the loess underlying gravels were thought to be older.

The Praha-Šťáhlavka brick pit was situated at a slightly higher position, NW of the Meilbek brick yard loess pit. Only one lion femur fragment was found here along with other Pleistocene macromammal bones.

Another important Pleistocene macromammal loess site was found in Praha-Libeň Báně, where remains of a lion skull were collected (6 fragments of teeth and jaw).

Hostim sand pit near Beroun (see Fig. 1) was operated until the 1960s and is located east of the Berounka River. It was left partially open having been later incompletely refilled. It is unique in terms of its bone preservation among all the open air sites along the Berounka River, because the Pleistocene bones must have been found directly in sand/gravel, and not in loess. Here the bone material was found directly in the river terrace sediments and, in some cases, shows signs of abrasion and surface polishing (see later, Figs 10I, 11A). The sand pit was named as "Berounka Terrace III (Rissian)" on some labels by J. Petrbok (it is located between 4 and 12 m above present-day river level, it equals to part of terraces VI and VII after Balatka & Loučková 1992). It seems from the bone preservation that

Table 1. Bone remains of *Panthera leo spelaea* (Goldfuss, 1810) from open air sites in Central Bohemia and other regions of the Czech Republic deposited in the Quaternary Mammal collection of the National Museum Prague (NMP), Museum of the Bohemian Karst Beroun (MBKB) and Museum für Naturkunde der Humboldt-Universität in Berlin (NMB), BM – Bite marks, O – Original.

No.	Coll.-No.	Location	Bone type	Commentary	left	right	Age	BM	O	Collection
1	P 363a, b	Beroun area	Cranium	Cranium with left mandible, incomplete with canines and P^{3-4}, and lower jaw with C, P_4–M_1			High adult		x	MBKB, Coll. before 1945
2	R 5	Praha-Podbaba	Cranium	Maxillary fragment with P^3		x	Adult, male		x	NMP, Coll. Museum 1888
3	R 3	Minice near Kralupy nad Vltavou	Cranium	Maxillary, and temporal	x		Adult, female		x	NMP, Coll. Hlánaček 1954
4	R 2425	Zechovice near Volyně	Cranium	Premaxillary, maxillary, and temporal	x		Adult, female		x	NMP, Coll. Želízko 1960
5	R 1292	Praha-Libeň, Báně	Tooth	Canine without root, upper jaw					x	NMP, Coll. Museum 1880
6	R 6156	Praha-Libeň, Báně	Tooth	P4, upper jaw		x	Adult		x	NMP, Coll. Museum 1893
7	R 1288	Praha-Libeň, Báně	Tooth	I^3, upper jaw	x		Adult		x	NMP, Coll. Museum 1880
8	R 2630/2640	Praha-Podbaba	Lower jaw	Incomplete, teeth damaged, rami not original	x	x	Adult		x	NMP, Coll. Museum, (Original Kafka 1901)
9	R 1	Praha-Podbaba	Lower jaw	Without all incisives and ramus	x		Adult, female		x	NMP, Coll. Museum 1888
10	R 6157	Praha-Libeň, Báně	Lower jaw	Fragment with P_{3-4}		x			x	NMP, Coll. Museum 1893
11	R 67	Trmice	Lower jaw	Symphyseal fragment with canine			Adult	x	x	NMP, coll. Museum
12	R 2	Svobodné Dvory near Hradec Králové	Lower jaw	Without all incisivi and ramus		x	Adult		x	NMP, Coll. J. Soukup 1941
13	MB.Ma.30092	Trmice (= Türmitz)	Radius	Complete	x		Adult, male		x	NMB, Coll. Nehring 1894
14	R 65	Praha-Podbaba	Tooth	Canine, incomplete, ?lower jaw			Adult		x	NMP, Coll. Museum 1888
15	R 1289	Praha-Libeň, Báně	Tooth	Canine without root, lower jaw					x	NMP, Coll. Museum 1880
16	R 4	Praha-Libeň, Báně	Tooth	M_1	x		Adult		x	NMP, Coll. Museum 1893
17	R 121	Holedeč near Žatec	Tooth	Canine			Adult		x	NMP, Coll. Museum 1928
18	R 2310	Praha-Podbaba	Scapula	Fragment, proximal part	x		Adult, male		x	NMP, Coll. Museum 1888
19	R 6	Praha-Podbaba-Štáhlavka	Humerus	Without proximal joint	x		Adult, male		x	NMP, Coll. Museum 1888
20	R 8	Praha-Podbaba	Humerus	Without proximal joint	x		Adult, female		x	NMP, Coll. Museum 1888
21	R 9	Praha-Podbaba	Humerus	Without proximal joint		x	Adult, female		x	NMP, Coll. Museum 1888
22	R 6208	Hostim	Humerus	Without proximal joint		x	Adult, female		x	NMP, Coll. Petrbok 1959
23	Ra 859	Ústí nad Labem	Ulna	Fragment			Adult		x	NMP, coll. Museum
24	R 1279	Praha-Podbaba	Ulna	Without distal joint	x		Adult, ? female	x	x	NMP, Coll. Museum 1888
25	R 1278	Praha-Podbaba	Radius	Without proximal joint	x		Adult, female		x	NMP, Coll. Museum 1888
26	R 6207	Hostim	Metacarpus	III		x	Adult		x	NMP, Coll. Petrbok 1959
27	R 7377	Hostim	Femur	Largely complete	x		Adult, female		x	NMP, Coll. Petrbok 1959
28	R 1277	Praha-Podbaba	Tibia	Largely complete	x		Adult, male		x	NMP, Coll. Museum 1888
29	R 5505	Holedeč near Žatec	Phalanx	I			Adult		x	NMP, Coll. Beneš 1904
30	K207	Unclear, Praha-Podbaba?	Cervical vertebra	No. 7, incomplete			Adult, male		x	NMP, Coll. Museum 1888
31	R 1286	Praha-Podbaba	Thoracic vertebra	No. 9, incomplete			Adult, male		x	NMP, Coll. Museum 1888
32	R 1287	Praha-Podbaba	Thoracic vertebra	No. 10, incomplete			Adult, male		x	NMP, Coll. Museum 1888
33	R 7360	Hostim	Thoracic vertebra	Incomplete			Adult		x	NMP, Coll. Petrbok 1958
34	R 1280	Praha-Podbaba	Lumbar vertebra	No. 1, incomplete			Adult, male		x	NMP, Coll. Museum 1888
35	R 1284	Praha-Podbaba	Lumbar vertebra	No. 2–3, incomplete			Adult, male		x	NMP, Coll. Museum 1888
36	R 1283	Praha-Podbaba	Lumbar vertebra	No. 6, incomplete			Adult, male		x	NMP, Coll. Museum 1888

the Pleistocene material is from the Weichselian age. Following recent observations it now appears that the pit includes layers from different terraces of Late Saalian to Weichselian ages. Many bones of *B. priscus* (Bojanus), *C. antiquitatis* (Blumenbach), *E. ferus* and *R. tarandus* (Linnaeus) and even most of the pieces of lion material are white-yellow in colour and resemble non-fossilized bones. There are also Holocene bones mixed in with the collection which can be easily distinguished. No loess seems to be present in this sand pit and no caliche-type encrustation was found on any of the bones. This pit was certainly not the location of the MBKB lion skull drawn here, since this was discovered before the Hostim sand pit started to operate. At least four bones found here (Tab. 1) may have belonged to a single female lion.

Pleistocene lion sites outside Central Bohemia are mentioned here only to complete the study of the NMP collection. Their history and geology cannot be discussed without studying the locations more in detail and considering further local reports. Non-carnivore bones were present at all the sites suggesting that they date from the Late Saalian to Weichselian ages and glacial faunas.

In the Holedeč near Žatec sand pit one *P. leo spelaea* canine and one phalanx I must have been collected from loess deposits in around 1904 and 1928, respectively, and these were stated as being "Würmian" in age. This is also indicated by the impressions of grass roots on the phalanx bone surface, which are generally very abundant on bones found in loess.

Minice near Kralupy nad Vltavou and Zechovice near Volyně (Ve vopuce quarry) have each yielded cranium fragments in more recent times (1954 and 1960).

In Trmice (= Türmitz in Kafka 1903, = Aussig in Woldřich 1888) a mandible fragment was found by H. Seehars, the position of which was given in the generalized section of Kafka (1903), that included the macrofauna *Felis Leo spelaeus* (= *P. leo spelaea*), *Hyena crocuta* (= *Crocuta crocuta spelaea*), *Elephas primigenius* (= *Mammuthus primigenius*), *Rhinoceros tichorhinus* (= *Coelodonta antiquitatis*) and *Equus caballus fossilis* (= *Equus ferus* Boddaert). Recently another undescribed radius was found in the Naturkundemuseum Berlin, which originates from the A. Nehring collections (Fig. 11A). This section is not drawn here again because it has already been compared with former descriptions with similar sequences and stratigraphy to the Weichselian/Würmian section of Praha-Podbaba (*cf.* Fig. 2). The faunal content, which includes *Spermophilus refuscens* Keyser & Blasius, in the middle part of the section (Loess 2), and especially *Alactaga saliens foss*. Nehring [= *Alactaga saliens* (Gmelin)], date the fauna of the Middle Loess to the middle Weichselian (*cf.* Jacobshagen 1963, Koenigswald 2002, Diedrich 2006c). Furthermore, the typical glacial steppe micromammal, *Arvicola gregalis foss*. Nehring [= *Microtus gregalis* (Pallas)], and other micromammals mentioned by Kafka (1893) are widely acknowledged to have existed during the Early to Middle Weichselian of Europe (*cf.* Koenigswald 2002).

At Svobodné Dvory near Hradec Králové another mandible fragment of *P. leo spelaea* was collected. Various other macrofaunal specimens in the NMP collections including *Coelodonta antiquitatis*, *Bison priscus* and *Equus* sp. were found to have come from this site, but the association of the historical collected material with particular archaeological horizons (*cf.* Šída *et al*. 2006) is unclear. None-the-less, the dating of the Upper Paleolithic site would support the dating of the lion and bone material described here as being Late Weichselian had the bones been found in their archaeological context.

Finally, at Ústí nad Labem, a lion ulna fragment seems to have originated from another gravel and sand pit, but it may have also been found in loess sediments. The accompanying fauna was identified as *Coelodonta antiquitatis*, *Bison priscus*, *Rangifer tarandus*, and *Equus ferus* Boddaert. An interesting find was the partial skeleton of a woolly rhinoceros bearing obvious chewing and scavenging marks, similar to those found at the German hyena loess site at Bad Wildungen-Biedensteg (Diedrich 2006c). This provides further indirect evidence for hyena activity at a location containing lion remains and lends further support for the presence of hyenas outside Central Bohemia in the Czech Republic at open air locations. In Central Bohemia lion remains also have chewing marks for which no taphonomic explanation or other important information can be concluded at the moment.

The sections of the Praha-Podbaba Meilbek loess pit (*cf.* Kafka 1893), Trmice loess pit (Woldřich 1888, Kafka 1903) and the Bad Wildungen Biedensteg loess pit (Huckriede & Jacobshagen 1963, Jacobshagen 1963, Semmel 1968, Storch 1969, Diedrich 2006c) are very similar in their sedimentary sequences and micro- to macrofaunal content. They represent the complete Weichselian/Würmian climatic history including two warmer periods which resulted in palaeosoil horizons. All sites contained a hyena-influenced macrobone accumulation and chewed prey bones, representing, in most cases, hyena prey depots in loess deposits. Pleistocene hyenas appear to have cached prey remains in muddy loess, especially during the summer, when the permafrost soil allowed effective storage of prey body parts. Such prey accumulations have already been described for German sites (*cf.* Wernert 1968, Diedrich 2006a–c), but have not been well-studied. The loess sediments were optimal for the storage of prey remains, similar to the clays in hyena cave den sites. Modern spotted hyenas do store similar prey remains in muddy soil to keep them fresh (*cf.* Kruuk 1972).

As a result of these descriptions and comparisons most of the loess sites along the Vltava and Berounka Rivers described here, along with their faunal finds, seem to be of

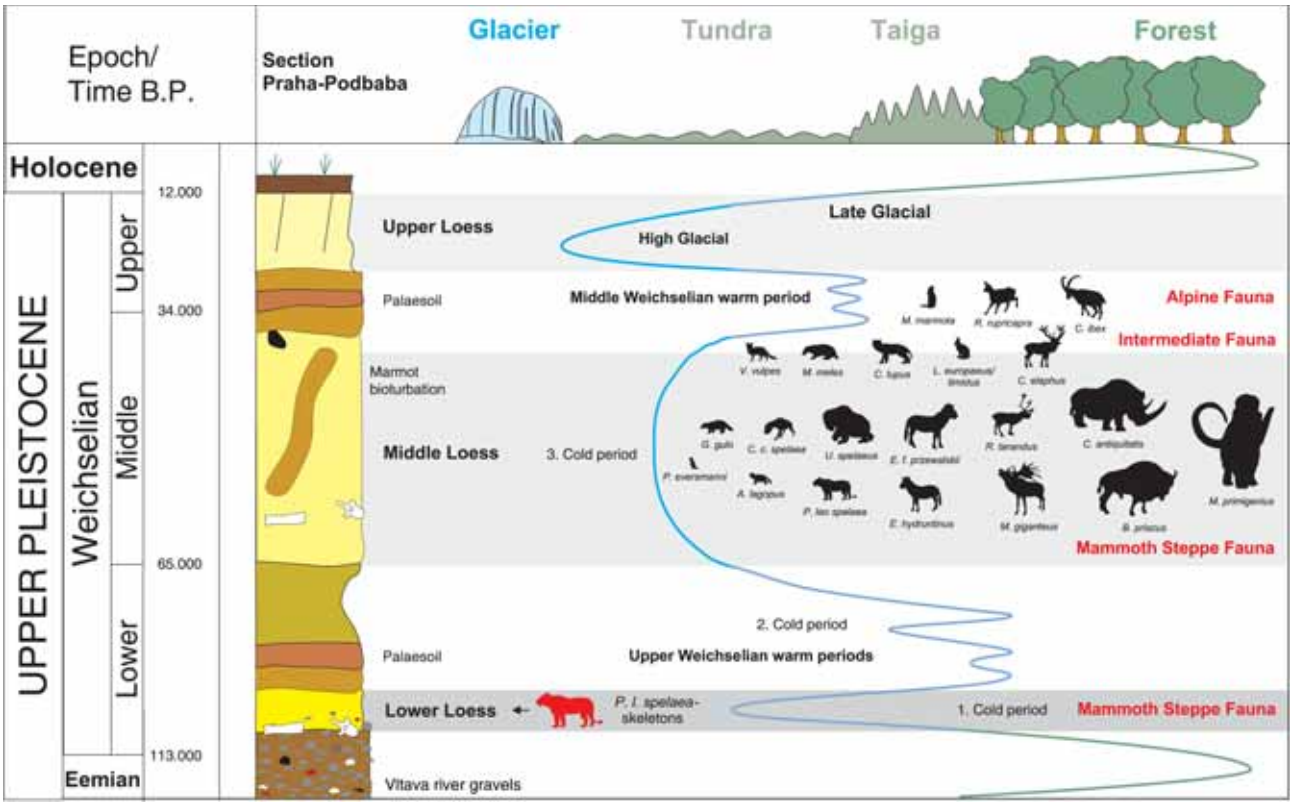


Figure 2. Geological-palaeontological and climatologic history of the section at the Upper Pleistocene bone locality Praha-Podbaba, Czech Republic (generalized section redrawn after Kafka 1893, with new interpretation). The remains of the lion skeletons were found in the Lower Loess that is interpreted as being of Lower Weichselian age. Bones from other loess pits around Praha were probably found in the same or younger Middle Weichselian loess deposits. At these sites an enormous amount of macromammals were collected during the 19th century and beginning of the 20th century as a result of manual working methods in the pits.

Weichselian age, although it is possible that some of the macrofaunas are of Saalian age.

The most complete *Panthera leo spelaea* skeleton from the Central Bohemia was put together by the author from NMP bone material collected in 1960s, 1970s, and 2006 (Beneš 1970, Diedrich & Žák 2006) from the cave locality Srbsko Chlum-Komín. This important find representing almost complete skeleton (see Diedrich & Žák 2006) is used here for comparison and will be published in detail independently in future.

Paleontology

The biogeographic distribution, within Europe, of *Panthera leo spelaea* has been mentioned by various authors (*e.g.*, Heller 1953, Fischer 1994). Many systematic discussions based on osteometric data from *P. leo spelaea* have been published (*e.g.*, Dietrich 1968; Schütt 1969, 1978; Hemmer 1974; Ballesio 1975; Sotnikova & Nikolskiy 2005). Recently more specific molecular DNA analyses by Burger *et al*. (2004) have shown that the Upper Pleistocene *P. leo spelaea* skeleton remains from Siegsdorf in southern Germany (*cf*. Gross 1992) is closely related to the African lion, *Panthera leo* subspecies. Single bone finds from Upper Pleistocene deposits have been recorded from many European cave and open air sites (*e.g.*, Dawkins & Sandfort 1900; Klähn 1922; Hilzheimer 1927; Riedel 1982; Siegfried 1983; Tichy 1985; Koenigswald & Schmitt 1987; Argant 1988; Fischer 1994; Guzvica 1998; Currant 2004; Diedrich 2004, 2007a, b) including remains from the sea floor of the North Sea Basin (Erdbrink 1983). Bone remains from further east have also been described from Yakutia in Russia (Baryshnikov & Boeskorov 2001). In contrast to these single bones, a very few articulated skeletons from Europe have been described (Altuna 1981, Tichy 1985, Gross 1992, Fischer 2001).

Some bones from Central Bohemia were mentioned and drawn for the first time by Kafka (1903) in his monograph about extinct and extant carnivores of Bohemia. Today, identification of bones using his descriptions is difficult, as a result of missing collection numbers of the specimens. He drew only the lower jaw of a Praha-Podbaba open air site lion in the form of an idealized drawing (Fig. 3, newly figured here in Fig. 8A), and a metapod from the Turská Maštal cave near Tetín. In the intervening years, the Pleis-

tocene loess site lion material has been forgotten and has lain unidentified. In some cases it has been stored undescribed, or labelled in some cases as not belonging to *P. leo spelaea*. The only complete skull with lower jaws he presented was in the form of a bad photograph from "Neudorf near Bakov" (= Nová Ves u Bakova, Central Bohemia, given by Kafka 1903, Fig. 9, as stored in the NMP collection without a collection number), which cannot now be traced in the NMP collection. All the other material he mentioned from different locations is now listed in detail along with important associated information (Tab. 1). All of the pieces, including the earliest inventoried Pleistocene bone in the NMP collection, are also drawn here for the first time with the exception of the cave material, which forms a large body of material and will require a future inventory project.

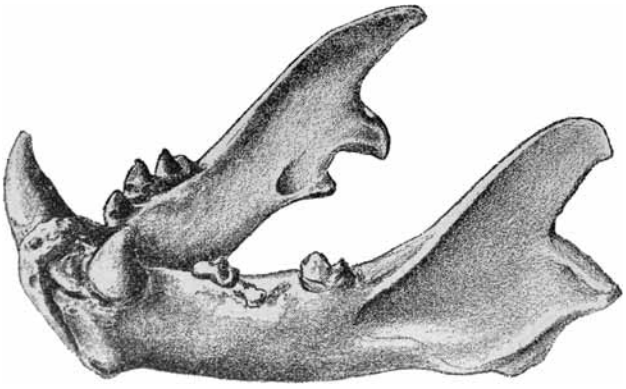


Figure 3. Lower jaw of the "*Felis spelaea*" remain of Praha-Podbaba (as figured by Kafka 1903) with complete canines, which are not preserved that complete today. Also the rami are not original, which can not be seen in this idealized presentation (*cf.* Fig. 8A).

Order Carnivora Bowdich, 1821
Family Felidae Fischer, 1817
Subfamily Pantherinae Pocock, 1917

Genus *Panthera* Oken, 1816

***Panthera leo spelaea* (Goldfuss, 1810)**

Generally the bones from all the open air loess sites in Central Bohemia have been degraded by roots which were dissolving the calcium phosphate. These root ichnofossils can be traced reasonably well on the irregular bone surface and provide indirect evidence for the dense grass vegetation which existed on the loess. Unfortunately, this overprinting has destroyed the chewing or bite marks, which would have provided interesting evidence of the activity of hyenas or other carnivore scavengers. At the site in the Beroun area in which the lion skull was found, the bones are more covered by caliche and have no decalcification structures on the bone surface. Here the caliche covers possible bite mark depressions.

Cranium. – Skull finds are rare, especially at open air sites, where, in most cases, only fragments are found. Only one complete skull with one left lower jaw from the Beroun surroundings can be shown here (Figs 5, 6), and this is exhibited in the MBKB (it can originate from the locality Hýskov gravel/sand pit; now there is a graveyard). The skull contains only the canines without their cusp tips which must have broken off relatively recently. On both sides, the complete, but partially worn P^{3-4} are completely preserved. Some parts are missing in the right jugals and the nasals and other regions.

Osteometric data cannot be recorded from many of the skulls due to their extensive deformation (Figs 4, 5). Some measurements for sex identification can be presented. The total Beroun area skull length of about 30.2 cm is relatively short and suggests a female skull, similar to the female skeleton from Srbsko Chlum-Komín that is 30.5 cm in length or the female skull from the German Perick Caves which measures only 30.2 cm in length (Diedrich 2007b). Male skulls from Siegsdorf, Arrikrutz or Azé are mostly much bigger and their lengths lie in the range, 38 to 42 cm (*cf.* Gross 1992).

The width of the frontals (ectorbital-ectorbital) for the Beroun area skull is 8.8 cm. By way of comparison, the male skull from Siegsdorf measures 10.7 cm. The teeth of the Beroun area skull are, in contrast, slightly larger than in the skull from Srbsko Chlum-Komín. Canines from the skull are 2.5 cm in length at the base of the enamel. In the Srbsko Chlum-Komín skull they are much shorter at 2.1 cm. Furthermore, the P^3 (2.6 cm) and the P^4 (3.7 cm) are wider than in the Srbsko Chlum-Komín skull (Canine 2.1 cm, P^4 3.4 cm) but much narrower than in the previously mentioned male skulls (*cf.* Gross 1992). The mandible height behind the M_1 is more similar to the skulls from the Beroun area (4.9 cm) and Srbsko (4.8 cm). The male skull from Siegsdorf measures 5.5 cm (*cf.* Gross 1992). Finally, the total length of the mandible (21.8 cm) is larger than in the female skull from Srbsko (21.4 cm). The width of the lower jaw teeth are: P_3 2.7 cm and P_4 3.0 cm. These are larger than the mandibles of the Srbsko female individual, but again much smaller than the previously-mentioned male skulls (*cf.* Gross 1992).

The skull proportions of the skull from the Beroun area fit into the range of the smaller (28–32 cm long) adult female *P. leo spelaea* skulls (*cf.* Gross 1992, Diedrich 2007b, c) than to the 36–42 cm long male skulls of Arrikrutz (Altuna 1981), Azé (Argant 1988) or Siegsdorf (Gross 1992). The skull and lower jaw from the Beroun area must be from a single female individual judging by their proportions and the similarity of tooth wear (enamel abrasion) of the upper jaw M^1 and the lower jaw P_4.

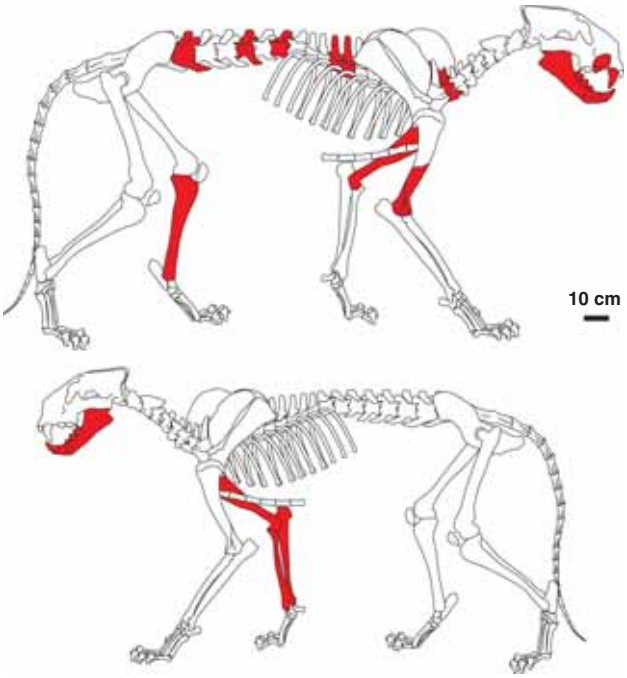


Figure 4. The Ice Age lion skeleton material from Praha-Podbaba let distinguish possibly only two individual remains, an adult male and adult female. Most bones are from the larger male individual. The top skull was destroyed, possibly by the cracking activities of the hyenas. It seems that the lion carcass must have been at the site in partly articulation. From the female lion only the right forelimb longbones are represented, which might have been removed from a carcass which was scavenged by hyenas more far away. Possibly partly articulated carcass remains from more then two animals are represented.

Three additional skulls from three more locations outside Central Bohemia in Czech Republic consist mainly of maxillary material with dentition (Fig. 7A–C). A fragment including premaxillary bone, maxillary bone and parts of the temporal bones along with the I^3, C to P^{3-4}, is the most complete fragment from the open air site Minice near Kralupy (Fig. 7A). The slender canines and distances between the canine and P^4 are quite small and similar to the female skull from Srbsko Chlum-Komín or that from the Beroun area. Also, the right maxillary/temporal fragment from Zechovice near Volyně (Fig. 7B) appears to match the size of a female cranium, especially because of its very slender canine. A right maxillary fragment from Praha-Podbaba (Fig. 7C) could be from a larger male skull, as indicated by the width of the P^3, which is about 2–3 mm larger than the ones from the female skulls described before. The isolated cranial teeth (I^3, C, P^4) from the loess site at Praha-Libeň, Báně (Fig. 7D–F) are, in terms of their preservation, similar to the lower jaw remains (Fig. 8D–F) and may have belonged to a complete skull that was damaged during excavation, or later. Fresh fractures of the teeth and the mandible indicate this. From the mandible, the right part with the large P_{3-4} and the left M_1 may belong to one lower jaw from an adult male animal.

The most complete lower jaw was found in Praha-Podbaba and has already been drawn in idealized form by Kafka (1903), see Fig. 3. This jaw (Fig 8A) lacked both rami and these were artificially recreated. All incisors are missing and both canines are damaged with only the roots being preserved. On the right mandible (Fig. 8Ab) all teeth are more-or-less complete, although the crown tips are broken off. Some of the skull fragments mentioned by Kafka (1903) from Praha-Podbaba are obviously not from a lion skull and are of non-carnivore origin.

The sexual dimorphism of the modern African extant lions and Ice Age extinct lions *Panthera leo* subsp. lions, is well studied and known from cranial and postcranial material (*e.g.*, Schütt 1969, Turner 1984, Gross 1992). This phenomenon can be easily observed from the lower jaws in Fig. 7. The adult male lions have much larger mandibles (Fig. 8I, from Svobodné Dvory) than the adult females (Fig. 8B, from Praha-Podbaba). The largely complete lower jaw from Praha-Podbaba (Fig. 8A) fits into the size range of male lions. The male lion skull from the Siegsdorf skeleton has comparably large lower jaws (*cf.* Gross 1992).

The left mandible from Trmice (Fig. 8H) must be from another male individual, as indicated by the large symphyses and the canine size. Isolated canines from both Holedeč near Žatec (Fig. 8G) and Praha-Podbaba (Fig. 8C), which are believed to be from lower jaws, are again compatible with the larger size of adult male lions. Finally the lower jaw remains (mandible fragment and M_1) from Praha-Libeň, Báně (Fig. 8D–E) have large teeth comparable to the previously-mentioned male lion material.

Vertebral column. – Five vertebrae (Fig. 9A, C–G) are certainly present from the Praha-Podbaba site and all of them are missing most of their processi. The only cervical vertebra (missing its neural arch; Fig. 9A) was deposited in the NMP collection with a label indicating that there have been originally two vertebra contained under one label, one of them labelled "?Praha-Košíře 1880", and the second "coll. Musei 1888". It is impossible to say, which of them the today-preserved specimen is, and at which locality it was found. Most probably it is the "coll. Musei 1888" one, which can originate from the Praha-Podbaba Meilbek loess pit.

All vertebrae were compared directly to the largely complete female lion skeleton from the Srbsko Chlum-Komín location. Two thoracic vertebrae (No. 10, 11) could be identified in terms of their position, mostly from the medium angled (45°) Processus spinosus. The lumbar vertebrae Nos 1, 2 or 3, and 5 seem to be present. All vertebrae from Praha-Podbaba are generally larger in size (2–3 mm in the width of the centrum) than those from the female lion skeleton from Srbsko Chlum-Komín. They are more similar in their larger proportions to the vertebrae from the male lion skeleton from Siegsdorf, with which they were also

directly compared. It is suggested therefore, that all the vertebrae belong to a male, and probably to one vertebral column from a disarticulated individual carcass. The fact that each is represented only once also suggests that they originated from a single skeleton. The posterior parts from the last thoracic to lumbar vertebrae appear, originally, to have been articulated or in close proximity.

One isolated thoracic vertebra (Fig. 9B) was found with a humerus, femur and metacarpus, at the Hostim gravel pit site and was labelled by J. Petrbok in 1959 (Tab. 1). The material may belong to a single female individual as indicated by its small bone proportions. These are very similar in size to the female skeleton bones from Srbsko Chlum-Komín.

Appendicular skeleton. – Forelimb bones predominate the bone material (nine bones) rather than hindlimb bones (only two bones). Certainly the number of bones is insufficient for statistical analysis or definitive interpretation. However, forelimbs can be removed from carcasses by carnivores much more easily than hindlimbs, which are more strong articulated to the pelvis. The preponderance of forelimbs could be the result of some taphonomic selection, for example hyena activity. The sexual dimorphism is easily visible on most of the long bones (Fig. 10).

An incomplete scapula from Praha-Podbaba (Fig. 10A) was compared directly to the largely complete scapulae from the Srbsko Chlum-Komín female skeleton and the male from Siegsdorf. The proportions, especially those of the larger glenoid indicate that it originated from a male (Fig. 4). The male humeri are generally bigger and the width of the distal joint is larger, and this is also well described for *P. leo spelaea* (Gross 1992). The humeri from Praha-Podbaba (Fig. 10B, G) include a right and a left one, and their proportions (9.6 cm width) suggest that they came from the skeleton of an individual male (Fig. 3). Their proportions are closer to those of a male. The male lion skeleton from Siegsdorf has no comparable humeri but the distal joint of skeletons from Arrikrutz or Azé measure between 10.3 and 10.9 cm in width. From Praha-Podbaba, a third humerus (Fig. 10D) is much smaller (distal joint width 8.3 cm) and it must have come from a female individual. Similar small humeri from Hostim (Fig. 10F), are close in terms of their proportions, to the distal joint width of the Srbsko Chlum-Komín female skeleton (8.4 cm). Sex identification of the ulnae and radius from Praha-Podbaba is more difficult, although, again, material from females is smaller. Therefore the ulna (Fig. 10D) and the radius (Fig. 10C), which are too incomplete for comparative measurements, were compared directly to the female Srbsko Chlum-Komín skeleton limb bones, which are very similar in terms of their small proportions. The osteometry and direct comparison allow a right forelimb, consisting of a humerus, ulna and radius, to be reconstructed. This may have belonged to a single female individual at the Praha-Podbaba site (Fig. 3). The ulna fragment from Ústí nad Labem (Fig. 10H) is, in contrast, very large suggesting that it came from a male lion.

The single incomplete metacarpus from Hostim (Fig. 10I) is of similar size to the equivalent bone from the Srbsko Chlum-Komín female skeleton.

Hindlimbs are represented by the femur from Hostim (Fig. 10A). Exact measurements cannot be given, due to missing joint parts. Direct comparison to the left femur from the Srbsko Chlum-Komín female skeleton reveals identical proportions, suggesting that this bone also belonged to a female (*cf.* length femur Srbsko female = 35.9 cm, Siegsdorf male = 41.0 cm). In contrast, the only tibia bone found at Praha-Podbaba (Fig. 11B) is much longer than the one from the Srbsko Chlum-Komín female skeleton (31.2 cm), and its length of 36.4 cm is similar to the long bones from Siegsdorf (35.5 cm) and other sites (*cf.* Gross 1992). It belonged to a male (Fig. 4).

Finally, only one phalanx I from Holedeč near Žatec (Fig. 11C) was found in the collection, and this was incorrectly identified as a cave bear phalanx.

Discussion

In some cases, such as for the skull from MBKB and one cervical vertebra from the NMP collection, the location of origin could not be discerned from labels, and a variety of methods were therefore used to estimate the original location as discussed in the following.

The skull with lower jaw from the "Beroun area" deposited in MBKB is an important find and the only remaining non-cave skull. Open air bone-bearing localities around Beroun opened during the period of this find are briefly discussed below, to show its possible original location. The "Beroun area" skull may have been found in a locality containing both sand and gravel, and loess.

Karlštejn sand pit bone material does not have caliche encrustations, does not have dark-brown impregnation and is much less fossilized than the discussed skull. Sediment did not stick to bone material from Karlštejn in the NMP. The Beroun-Ovčín sand pit was situated at the same elevation as the Hostim sand pit and is still accessible for the study. It is located south of Beroun, close to the Hospital. A *Capra ibex* scull from this site has been seen by the author in the NMP collection, that has no caliche encrustations. It was figured by Petrbok (1955). Beroun pit (near Eternitka) has yielded some bones from *C. antiquitatis* (Blumenbach) which were compared to those in the MBKB collection. They are few in number and no caliche was attached to them. Again, this site does not appear to have been the original location of the lion skull. Hýskov (today a grave yard), is by the opinion of the author the most probable original

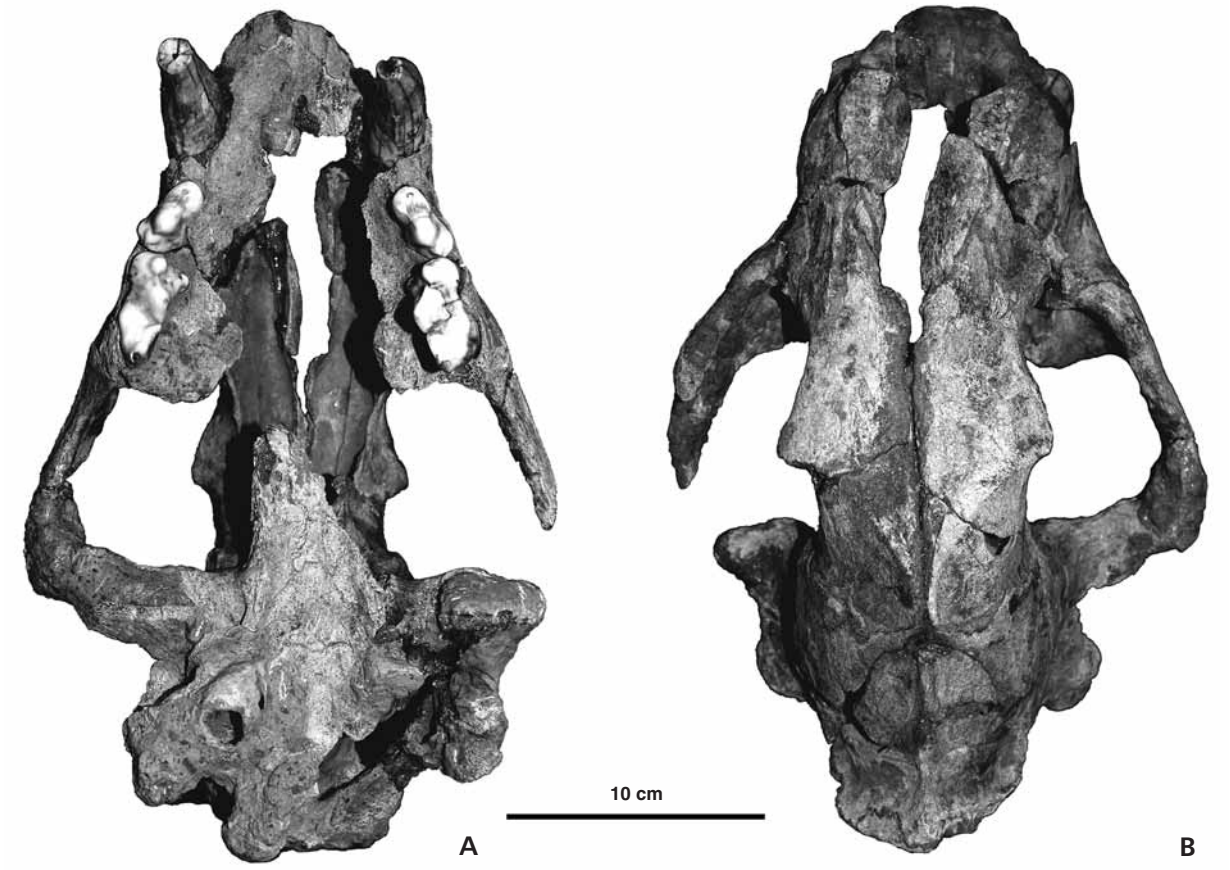


Figure 5. Skull of *Panthera leo spelaea* (Goldfuss, 1810) from an open air site in Central Bohemia. Skull of a female individual from Beroun area (MBKB No. 363a). • A – dorsal. • B – ventral.

location. Hýskov had two sand and gravel pits. Only the small pit at lower elevation (which is today a graveyard) has yielded bone material and this was found mainly around 1900. The existing evidence for the mammoth, *M. primigenius* (Blumenbach), and other bone finds of *Equus ferus* Boddaert and *R. tarandus* (Linnaeus), was: "Agenda protocols of the Association Museum and public library in Beroun from 1894–1913." A lion skull was not mentioned. In these "Agenda protocols" it is mentioned, that in 1901, J. Suchomel gave the Museum in Beroun three mammoth bones (one jaw and two molars), which are still there. The caliche attached to the lion material, a typical loess product, contains many cemented, 2–3 mm large, well-rounded and weathered small pebbles, probably composed of a shale. Very little quartz sand grains and pebbles were present. Other macromammal bones of mammoth (molar teeth, tusks) or reindeer (antler) from the Beroun-Hýskov sand pit have exactly the same caliche concretions attached to them as the lion bones; in some cases sand and pebbles are attached. The bones seem to have been deposited partly in loess and partly in river gravels. The material of the bones is not rounded and a fluvial transport can be more-or-less ruled out. Hýskov is therefore the most probable original location for the lion skull and jaw drawn here, labelled as coming from "Beroun surrounding". This conclusion is supported by the similar bone fossilization and dark brown iron and manganese mineral impregnation of all the bones which can be definitively linked to that pit. The Hýskov sand pit (grave yard) has, in its northern corner, loess on the gravels, and is in direct contact with Upper Proterozoic shale. It has yielded the main macrofaunal remains from the "Beroun surrounding". The presence of the remains of what appears to have been a mammoth carcass and a few other faunal remains (*Coelodonta antiquitatis*, *Bison priscus*, dropped antler from *Rangifer tarandus*, *Equus* sp.) would fit the taphonomy of hyena prey depots and mammoth carcass scavenging sites (Diedrich 2005b). This macrofauna is more typical of the early to middle Upper Pleistocene and the loess sites in the region, but could also have been found in the older Saalian loess deposits. The age of the macrofauna from Hýskov can not be given precisely yet, but it cannot be older than the late Middle Pleistocene. Its topographic position on the Saalian river terrace suggests that it was probably from the early Upper Pleistocene Age, or late Saalian Age. The loess on this terrace was possibly deposited in the Upper Pleistocene. On the other hand it con-

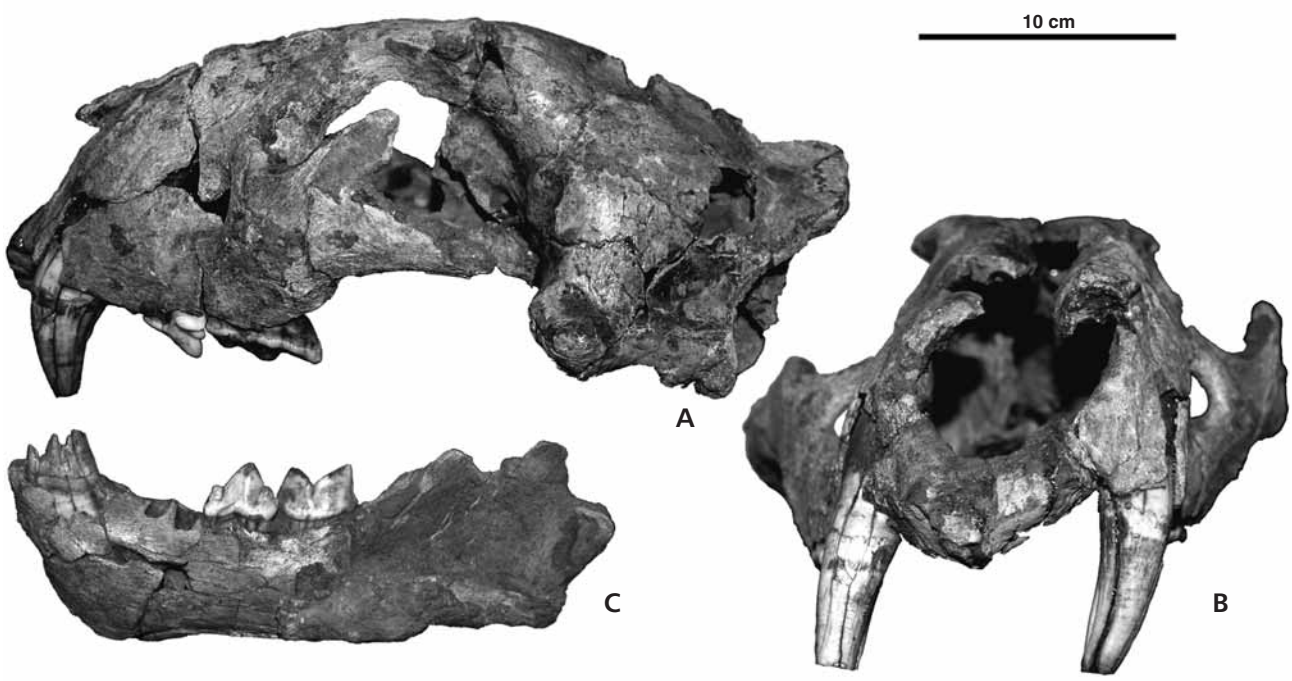


Figure 6. Skull of *Panthera leo spelaea* (Goldfuss, 1810) from an open air site in Central Bohemia. Skull of a female individual from Beroun area (MBKB No. 363a). • A – lateral left. • B – frontal. • C – mandible (P363b) possibly of the same individual (see also Fig. 5).

tains a cold period mammoth steppe fauna, which fits well with the first glaciation maximum in the early Upper Pleistocene, which would be similar to the other findings around Praha, at the many loess pits. The loess here was also deposited onto the old river terraces in the Weichselian.

The only one described here cervical vertebra had in the NMP collection a label indicating that there have been originally two vertebra contained under one label, one of them labelled "?Praha-Košíře 1880", and the second "coll. Musei 1888". From the descriptions of Kafka (1903) the Košíře location was the Bulovka loess pit. There are several reasons why the Praha-Košíře location does not relate to the described vertebra. Firstly, it was the only example of lion remains at this loess location that has yielded hundreds of non-carnivore macromammal bones from the above-mentioned glacial fauna. Secondly, and more importantly, these non-carnivore bones have no sediment residues on them, similar to those on the vertebra. The sediment with gravel breccias is comparable to all the other sites mentioned here and is similar to the material from Praha-Podbaba Meilbek brick pit that was found to contain such a sediment type. Kafka (1903) mentioned the position at which the Praha-Podbaba Meilbek lion remains were found as being on the boundary of the lower gravel and the loess layers. Accordingly there are some small extraclasts embedded in the sediment, which are lacking at finds from other loess pits around Praha. At Praha-Podbaba Meilbek, many vertebrae are present from the thoracic and lumbar region of what appears to have been a single lion. Cervical vertebrae were not present. The final piece of evidence comes from the publications of Woldřich (1897) and Kafka (1903) neither of which mention lion remains in their faunal lists from Košíře wherease all the other bones described here can be found in the lists of other sites. Interestingly, all the Praha-Podbaba Meilbek finds have the year 1888 on their labels including the vertebra (labelled 1880/1888). Therefore it appears that the lion vertebra came from the Praha-Podbaba Meilbek brick pit.

The few descriptions of lion remains from Central Bohemia, from the rich cave at Bohemian Karst and the Turská Maštal cave near Tetín (Woldřich 1893, Kafka 1903), the Kobyla-Chlupáčova Sluj vertical cave (Petrbok 1954, Zázvorka 1954) or the cave at Srbsko Chlum-Komín mentioned by Beneš (1970) have recently been interpreted as being hyena prey depots and den caves (Diedrich & Žák 2006, see Fig. 1). Former excavations extensively damaged and broke material from Kobyla-Chlupáčova Sluj, which therefore has not been studied until now. This site contained previously undescribed skeleton remains from a juvenile lion individual, bones of which were misidentified in some cases (*e.g.*, one femur) as reindeer bones.

In a contrast to the cave localities, the bone material from historical open air sites was mainly listed with only a few drawings being made and was dated, in some cases, by some section drawings and the micromammal work of Woldřich (1888, 1897), or Kafka (1893, 1903).

With the study and first description of the newly completed female lion skeleton from the Upper Pleistocene

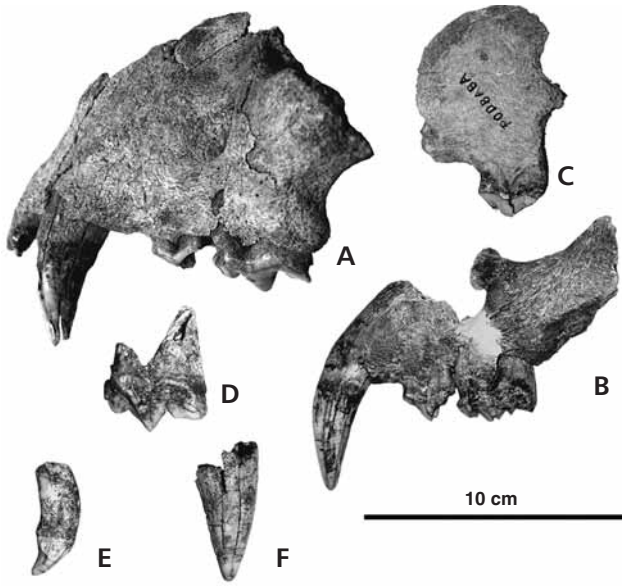


Figure 7. Skull remains of *Panthera leo spelaea* (Goldfuss, 1810) from open air loess sites in Central Bohemia and other sites in the Czech Republic. • A – left premaxillary/maxillary/temporal of a female individual from Minice near Kralupy (NMP No. R 3), lateral left. • B – left maxillary/temporal of a female individual from Zechovice near Volyně (NMP No. R 2425), lateral left. • C – right maxillary fragment with P^3 from Praha-Podbaba (NMP No. R 5), lateral right. • D – right maxillary P^4 of an adult animal from Praha-Libeň, Báně (NMP No. R 6156), lingual. • E – left premaxillary I^3 of an adult animal from Praha-Libeň, Báně (NMP No. R 1288), lateral. • F – upper jaw canine fragment from Praha-Libeň, Báně (NMP No. R 1292), lingual.

Srbsko Chlum-Komín site in the Bohemian Karst (Diedrich & Žák 2006), other material from the Praha region, especially from the Bohemian Karst and the entire Czech Republic was selected from the NMP and the MBKB collections to receive a first overview of the distribution and taphonomy of the Late Pleistocene lions in Central Bohemia. Similar research has been done before in north-western Germany, where comparable taphonomic and landscape conditions are present as in Central Bohemia. In north-western Germany a flatland region (Münsterland Bay), in which thousands of Weichselian mammal bones have been found (Siegfried 1983), but in which only a few lion remains were present (Diedrich 2004, 2007a, b), is close to a mountainous region, the Sauerland. The Devonian limestones found there are penetrated by more than 500 caves (Zygowski 1988, Hammerschmidt *et al*. 1995) including some famous cave bear and hyena den sites (Diedrich 2005a). It is one of the richest Pleistocene faunal areas of central Europe and hyenas were responsible for most of the bone enrichments in caves and mud pits along the rivers (Diedrich 2005a). Similar conditions are present in the Bohemian Karst cave-rich region and the Weichselian river valley of the Vltava and Berounka Rivers, where hyenas played the most important role in producing bone accumulations in caves (Diedrich & Žák 2006).

Most of the bones from the open air loess sites around Praha are from non-carnivores. The near absence of bones of important Upper Pleistocene hyena prey such as *Megaloceros giganteus*, and rare *Mammuthus primigenius*, and the presence of several thousand *Capra ibex* (Linnaeus) and *Rupricapra rupricapra* (Linnaeus) Upper Pleistocene bones from the Weichselian/Würmian loess sites of Central Bohemia, indicate a more alpine faunal influenced by conditions during the Late Pleistocene in this hilly land region. *Coelodonta antiquitatis* (Blumenbach) was the most abundant large animal. Other cervids included the common *Rangifer tarandus* (Linnaeus), and the rarer *Cervus elaphus* Linnaeus. This region was well-frequented by woolly rhinoceroses and horses, *Equus ferus* [partly *przewalskii* (Poljakoff)], and even by Ice Age donkeys, *Equus hemionus* (Pallas). The bison, *Bison priscus* (Bojanus), was not very common, but it was present. The saiga antelope, *Saiga tatarica* Linnaeus, a typical flatland steppe animal, or the musk ox, *Ovibos moschatus* Zimmermann, have not yet been identified in the bone material from the described loess pits. The absence or, at least, the very rare presence of these macromammals fits to the topographical and climatic conditions in Central Bohemia. In contrast, the mountain goat, *Capra ibex* Linnaeus, is well documented by some skulls (*e.g*., Hostim, Praha-Smíchov) and postcranial finds from open air and cave sites. The main enemies of *Panthera leo spelaea* (Goldfuss) were the Ice Age spotted hyenas, *Crocuta crocuta spelaea* (Goldfuss), whereas wolves, *Canis lupus* (Linnaeus), and wolverines, *Gulo gulo* (Linnaeus), were ecologically adapted to caves and were less influenced by the landscape and climatic situation (*cf*. Koenigswald 2002). The large carnivorous cave bear, *Ursus* cf. *spelaeus* (Rosenmüller) (*cf*. Diedrich 2006a), like the lion, is rare among the thousands of non-carnivore bones.

The lion bone material from the NMP and MBKB represents the main *P. leo spelaea* material from Central Bohemia which can be studied. The open air site material, which is less comprehensive (35 bones and teeth), than the bones and teeth (several hundred items) and even three skeleton remains from the Bohemian Karst and Praha cave sites (*cf*. Diedrich & Žák 2006), show interesting correlations to hyena prey depot open air loess sites in Praha (Fig. 1). Similar observations were described recently from the Münster Bay flatland region of north-western Germany, where only a few lion remains were found at open air sites (Diedrich 2004), and these were generally at hyena prey depot and bone accumulation sites (Diedrich 2005a).

The most famous open air hyena den and prey accumulation open air site in the Münster Bay is at Herten-Stuckenbusch, which is in the Upper Pleistocene fluvial deposits of the Lippe River (Heinrich 1983). More similar in its taphonomy to this German region are the lion finds from Hostim near Beroun in the Bohemian Karst. At both

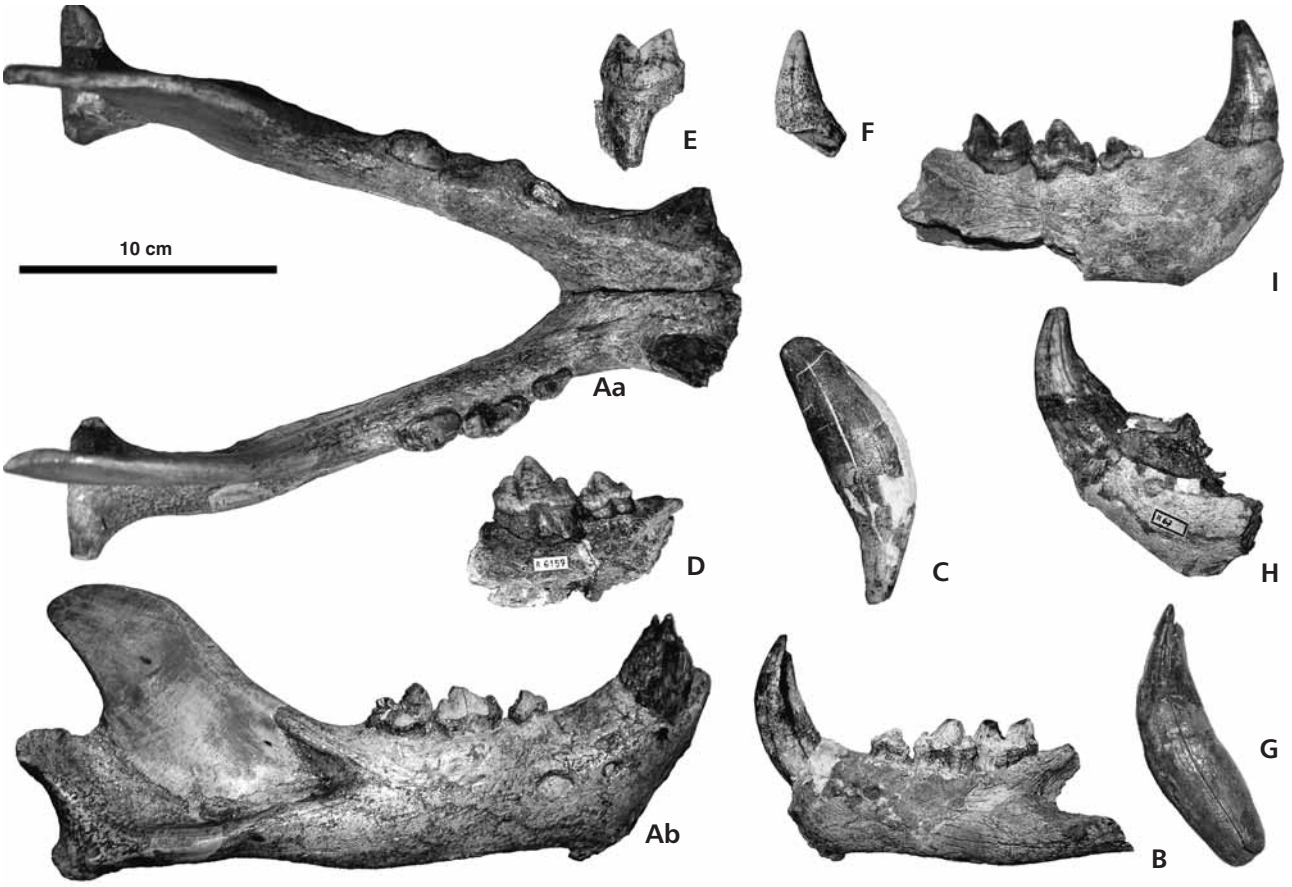


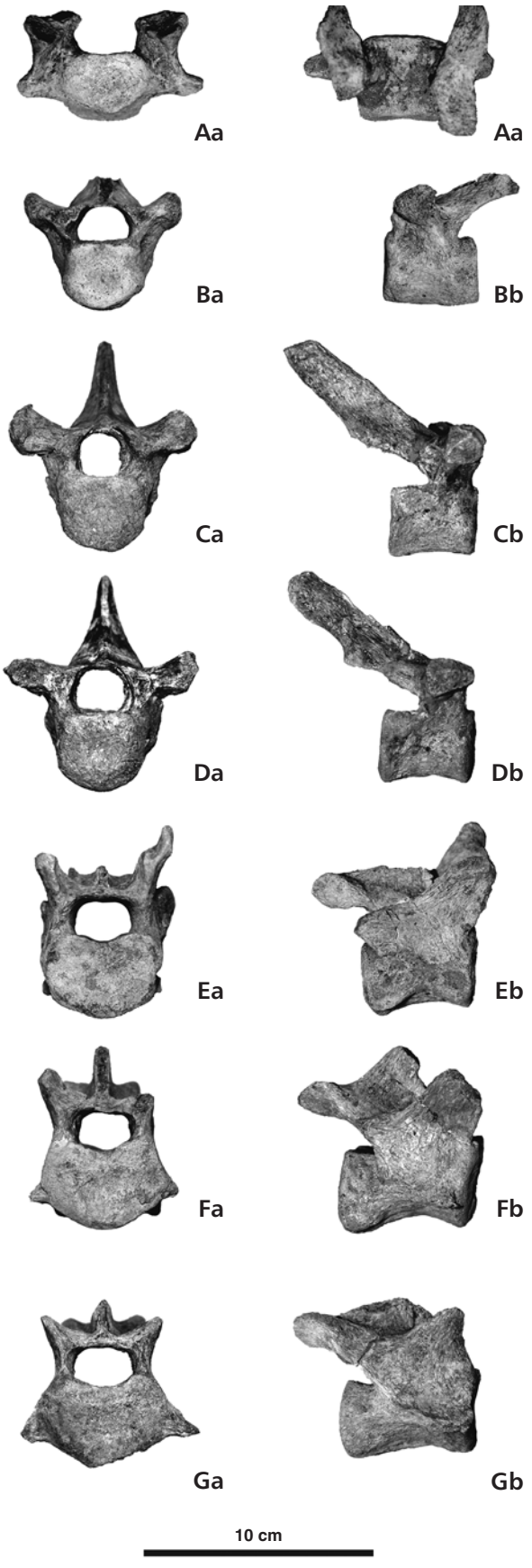
Figure 8. Mandible remains of *Panthera leo spelaea* (Goldfuss, 1810) from open air loess sites in Central Bohemia and other sites in the Czech Republic. • A – lower jaw of an adult male individual from Praha-Podbaba (NMP No. R 2630/2640), a – dorsal, b – right mandible lateral. • B – left mandible of an adult female individual from Praha-Podbaba (NMP No. R 1), lateral. • C – upper jaw canine of an adult male individual from Praha-Podbaba (NMP No. R 65), lingual. • D – right mandible of an adult animal from Praha-Libeň, Báně (NMP No. R 6157), lateral. • E – left mandible M_1 of an adult animal from Praha-Libeň, Báně (NMP No. R 4), labial. • F – lower jaw canine from Praha-Libeň, Báně (NMP No. R 1289), labial. • G – lower jaw canine of an adult male individual from Holedeč near Žatec (NMP No. R 121), labial. • H – left mandible of an adult male individual from Trmice (NMP No. R 67), lateral. • I – right mandible of an adult male individual from Svobodné Dvory (NMP No. R 2), lateral.

locations the bones were found in fluvial sediments. In Herten-Stuckenbusch it seems to have been an inactive branch of the river, which was filled up with clay-rich sediments. These were good storage sites for hyena prey remains. Hundreds of chewed woolly rhinoceros bones were collected there, many of which are stored undescribed in the collection of the Eiszeithalle Bottrop, and in some cases in the Geological-Palaeontological Museum of the University of Münster. Furthermore, at these hyena-influenced bone sites, *C. c. spelaea* and *P. l. spelaea* are only rarely represented with bones or jaws (Heinrich 1983, Diedrich 2004). Hyena prey and bone accumulations at open air sites sometimes even lack carnivore remains.

At the Hostim location close to the Berounka River the sediments in which the bones were found are fluvial sands and gravels. Sand is still to be found preserved in some of the bone cavities and also on other faunal remains from that site. Bones were corroded by flowing water and sand at the Hostim location. The surfaces are polished and the joints are quite heavily eroded (Figs 9B, 10F, I, 11A). In this case the influence of hyenas cannot therefore be seen. The taphonomy here may have been the result of fluvial influence.

The situation around Praha and parts of Beroun is different to north-western Germany and very interesting in terms of its bone accumulations in loess sediments. Loess sites with bone accumulations are not known in the Münster Bay region of north-western Germany. The first hyena prey depot and den site being described is located in loess sediments is Bad Wildungen-Biedensteg, east of the mountainous and cave-rich Sauerland region. This hilly area was well frequented by hyenas and cave bears or lions (Diedrich 2006b).

The bones from the loess pits around Praha are preserved differently to the bones from the fluvial deposits. However, in both situations overprinting or erosion of the bone surface has occurred, and therefore most bite or chewing marks,



which could have provided evidence for carnivore scavenging activity have been lost. Bite marks are still preserved in many cases, however, on the massive bones of the woolly rhinoceros (*C. antiquitatis*) at these sites. At both lion locations at Praha-Podbaba and Praha-Libeň, rhino bones chewed by hyenas were found. The high numbers of bone accumulations of macromammals, the nature of the body parts (dominance of leg bones), and the chewing and cracking marks, suggest that these sites, and others around Praha, were hyena prey depots and possibly also den sites. The latter cannot be defintively proved, due to lack of coprolites, which were generally not collected in the past. As is known for caves in north-western Germany and now for Central Bohemia (Diedrich & Žák 2006) bones from the Upper Pleistocene lions were always found in hyena dens and prey depots. Even in the Bohemian Karst, the coincidence of the presence of both hyenas and lions at the same location explains this taphonomy. Lions must have been brought by hyenas into their dens or prey depots after they had been killed in most cases. A very important example of this, which is discussed in a separate publication, is the lion skeleton from Srbsko Chlum-Komín which provides strong evidence for this new theory of postmortem carcass importation of lions by hyenas.

The presence of articulated lion skeletons, or at least articulated bones, at such hyena prey depots (Srbsko Chlum-Komín, Praha-Podbaba) and dens is interesting and unexpected. Recently, spotted hyenas have been found to kill lions sometimes during food or cub protection conflicts, but they do not like to scavenge on carnivores, in the same way that other carnivores do (Kruuk 1972, Bateman 1987). Modern hyenas sometimes kill lions, and lion bone remains can be found in "bone accumulations" of present-day spotted hyena open air den sites in Africa (Scott & Klein 1981). The unwillingness of hyenas to scavenge on lions could explain why, at the open air site Praha-Podbaba, one partial skeleton of an adult male individual was not heavily scavenged. The foreleg of the female individual may have been removed from a carcass and was possibly imported to the hyena den site. The removal of carcass-limbs is fairly typical for present-day spotted hyenas (Kruuk 1972) and also for the Ice Age spotted hyenas (Diedrich & Žák 2006). This is the

Figure 9. Vertebrae of *Panthera leo spelaea* (Goldfuss, 1810) from the open air loess sites in Central Bohemia. a – cranial, b – lateral right. • A – seventh cervical vertebra of an adult male individual from of Praha-Podbaba (NMP No. K207). • B – posterior thoracic vertebra of an adult animal from Hostim (NMP No. R 7360), a – cranial, b – lateral. • C – ninth thoracic vertebra of an adult male individual from of Praha-Podbaba (NMP No. R 1286). • D – tenth thoracic vertebra (NMP No. R 1287). • E – first lumbar vertebra of an adult male individual from of Praha-Podbaba (NMP No. R 1280). • F – second to third lumbar vertebra of an adult male individual from of Praha-Podbaba (NMP No. R 1284). • G – fifth lumbar vertebra of an adult male individual from of Praha-Podbaba (NMP No. R 1283).

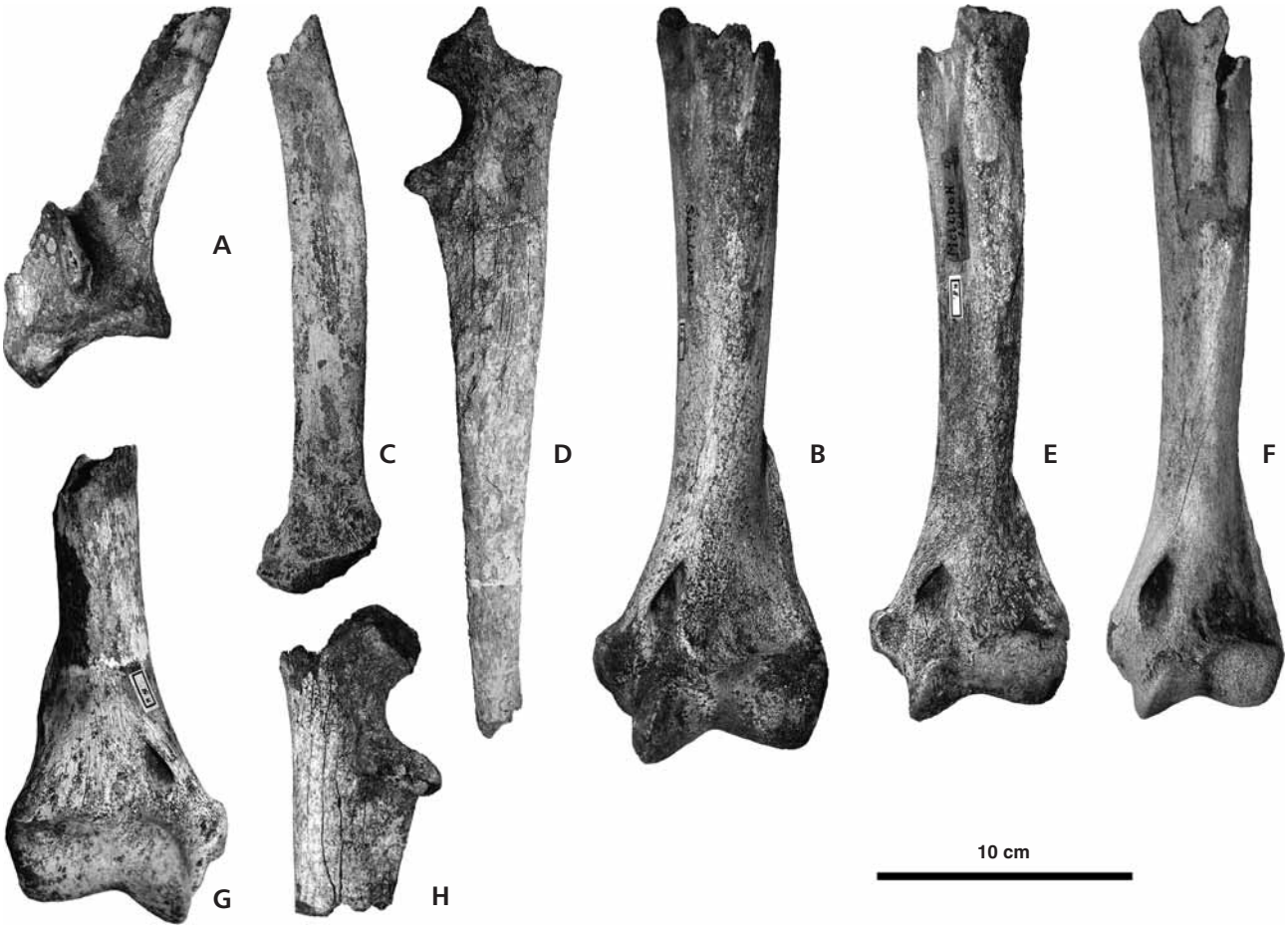


Figure 10. Forelimb bone remains of *Panthera leo spelaea* (Goldfuss, 1810) from open air loess and sand pit sites of Central Bohemia and other sites in the Czech Republic. • A – left scapula from a male individual of Praha-Podbaba (NMP No. R 2310), lateral. • B – right humerus of an adult male individual from Praha-Podbaba (NMP No. R 9), cranial. • C – left radius of an adult female animal from Praha-Podbaba (NMP No. R 1278), lateral. • D – left ulna of an adult ?female individual from Praha-Podbaba (NMP No. R 1279). • E – right humerus of an adult female individual from Praha-Podbaba (NMP No. R 8), lateral. • F – right humerus of an adult female individual from Hostím (NMP No. R 6208), cranial. • G – left humerus of an adult male individual from Praha-Podbaba (NMP No. R 6), cranial. • H – right ulna from Ústí nad Labem (NMP No. Ra 859), lateral.

reason why at many "bone accumulations" which are prey storage sites of the hyenas long bones seem to be over-represented. In particular, horse and bison metapods and phalanges survive well, because they were not further cracked or chewed. Vertebrae and costae are much less well represented at such sites of carcass importation. This provides further evidence that the lions from Praha-Podbaba represented imported articulated carcasses or carcass body parts. A final piece of evidence for this scavenging and hyena activity is the ulna from Podbaba (Fig. 10D) which is clearly chewed by carnivores on its proximal portion.

The material from all the other sites is too fragmented for taphonomic interpretation. The incompleteness of the lower jaws at many of the cave and open air sites is very obvious and has already been discussed for the imported lion remains in the Perick Caves of north-western Germany (Diedrich 2007a). Hyenas damage and break the rami and mandible joints when they crack the lower jaws out of the skull. They do this with all carnivores including cave bears, lions and even on skulls of their own species (Diedrich 2005a). The lower jaws of the lions from Praha-Podbaba (Fig. 8B) and Svobodné Dvory (Fig. 8I) show the characteristic fractures as do mandibles from the hyena den Perick Caves.

Certainly the manner of collection, rather than Pleistocene animal behaviour, may have led to some selection on the basis of bone size. Finally some bones, such as the humeri fractures drawn here, do not allow to distinguish whether the proximal joints are missing as a result of hyena chewing or from bone damage occurring during excavations. The humeri of lions do often lack their proximal and sometimes distal joints as a result of hyena scavenging.

Lions were present during the Weichselian in the Vltava River valley and all around the Bohemian Karst as well (Fig. 1). At least 20 lion individuals have been recorded for the Upper Pleistocene based on available finds in Central Bohemia by their bone occurrence in open air

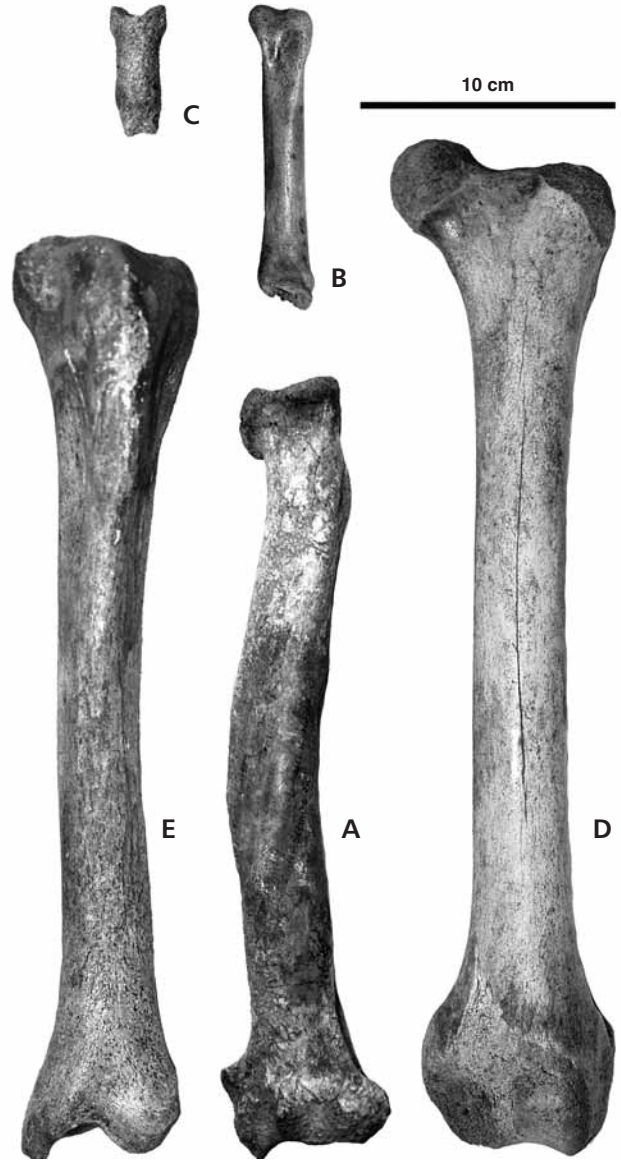


Figure 11. Bone remains of *Panthera leo spelaea* (Goldfuss, 1810) from open air loess and sand pit sites of Central Bohemia and other sites in the Czech Republic. • A – left radius from Trmice of an adult male lion (NB No. MB.Ma.30092), lateral. • B – right metacarpal III from Hostím (NMP No. R 6207), cranial. • C – phalanx I of an adult individual from Holedeč near Žatec (NMP No. R 5505), dorsal. • D – left femur of an adult female animal from Hostím (NMP No. R 7377), cranial. • E – left tibia of an adult male individual from Praha-Podbaba (NMP No. R 1277), cranial.

and cave sites. The detailed mapping of sites in Central Bohemia extends the recent knowledge of their presence in Europe and their range becomes larger with continuing reseach. It is especially important to understand the palaeoecology of the rare open air sites which contain only a few bones (*cf*. Diedrich 2006d).

Panthera leo spelaea must have lived in tribes dominated by a number of females in a similar fashion to modern *Panthera leo* subsp. lions in Africa (Schaller 1972, Estes 1999). To gather more information on population statistics all the cave finds must be considered and this will form the basis of future work. The scarce material consisting of one largely complete skull and 35 other bones from the open air sites cannot yield any representative conclusions on the social patterns of *Panthera leo spelaea*. There are at least seven male lion individuals compared with three females represented by this material and the sexual dimorphism can be easily seen from the cranial and postcranial bones (especially humerus, but also jaws and cranium).

With more material from open air and cave sites, the evidence surrounding lion kills or scavenging by hyenas (Diedrich 2007c) may become clearer. For the moment, it is interesting to note that female lions are found more often in caves (*e.g*., Perick Caves, Diedrich 2007a) whereas males are more common in open air sites (*e.g*., Siegsdorf, Gross 1992). A very similar phenomenon of selection of female lions as prey by hyenas was also found for the cave bears (Diedrich 2006a, b). Similar differences in the taphonomically predicted predation selection by hyenas arise, but the carnivore material from the open air sites is still too scarce compared to the material from caves. Trends are, however, apparent. Hyena predation on other carnivore females outside the cave and the importation of their carcases into their cave dens may be the reason for the differences in male and female "populations" on bone sites generally. Extant hyenas do not hunt adult male lions, so their carcasses may have been left, or found more often outside the caves, such as in Praha-Podbaba. In contrast female lions are sometimes killed by hyenas and their carcasses are imported mainly into cave den sites such as Srbsko Chlum-Komín, in which the complete skeleton of a brain case damaged during its life, and therefore strongly ill lion was found (Beneš 1970), in the most famous Czech and European hyena prey depot and den site (Diedrich & Žák 2006).

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Pleistocene lion skeleton of the open air mammoth site Siegsdorf (Bavaria, South Germany). Some bones from the Heinrichs cave were integrated in the studies by the assistance of the Arbeitsgemeinschaft Höhle und Karst Hemer e. V., especially H.-W. Weber. The museums head of the Staatliche Naturhistorische Sammlungen Dresden, U. Linnemann, allowed the study of the old Sack collection from the Perick Caves. The historically by Nehring 1893 collected bone Material from Türmitz (= Trmice) was rediscovered in the Museum für Naturkunde der Humboldt-Universität zu Berlin with the support of PD O. Hampe and N. Klein. Finally bone material from the hyena open air prey depot site Herten-Stuckenbusch in the collection of the Museum für Ur- und Ortsgeschichte Quadrat Bottrop could be compared with the kind support of M. Walders.

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