Late Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) skeletons from the Czech Republic (central Europe); their pathological cranial features and injuries resulting from intraspecific fights, conflicts with hyenas, and attacks on cave bears

CAJUS G. DIEDRICH

The world's first mounted "skeletons" of the Late Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) from the Sloup Cave hyena and cave bear den in the Moravian Karst (Czech Republic, central Europe) are compilations that have used bones from several different individuals. These skeletons are described and compared with the most complete known skeleton in Europe from a single individual, a lioness skeleton from the hyena den site at the Srbsko Chlum-Komín Cave in the Bohemian Karst (Czech Republic). Pathological features such as rib fractures and brain-case damage in these specimens, and also in other skulls from the Zoolithen Cave (Germany) that were used for comparison, are indicative of intraspecific fights, fights with Ice Age spotted hyenas, and possibly also of fights with cave bears. In contrast, other skulls from the Perick and Zoolithen caves in Germany and the Urșilor Cave in Romania exhibit post mortem damage in the form of bites and fractures probably caused either by hyena scavenging or by lion cannibalism. In the Srbsko Chlum-Komín Cave a young and brain-damaged lioness appears to have died (or possibly been killed by hyenas) within the hyena prey-storage den. In the cave bear dominated bone-rich Sloup and Zoolithen caves of central Europe it appears that lions may have actively hunted cave bears, mainly during their hibernation. Bears may have occasionally injured or even killed predating lions, but in contrast to hyenas, the bears were herbivorous and so did not feed on the lion carcasses. The articulated lion skeletons found in cave bear dens deep within caves scattered across Europe (such as those from the Sloup, Zoolithen and Urșilor caves) can therefore now be explained as being the result of lions being killed during predation on cave bears, either by the cave bears defending themselves or as a result of interspecific fights. • Key words: *Panthera leo spelaea* (Goldfuss, 1810), steppe lion skeletons, Late Pleistocene, Czech Republic, taphonomy and pathology, palaeobiology.

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Cajus G. Diedrich, PaleoLogic Research Institute, Nansenstrasse 8, D-33790, Halle/Westphalia, Germany; cdiedri@gmx.net

The Late Pleistocene Eurasian steppe lion species, a close relative to an extinct subspecies of the modern African lion (from DNA – see Burger *et al.* 2004), was first described and illustrated from the Zoolithen Cave site in Bavaria, southern Germany, and classified as the "cave lion" *Felis spelaea* Goldfuss (1810). The large male holotype skull, with its pathological bite mark features, has recently been relocated and reclassified as the "steppe lion" (popular name by Diedrich 2008) *Panthera leo spelaea* (Goldfuss, 1810) (DNA by Burger *et al*. 2004). The steppe lion population from this cave is the largest known in Europe; it has recently been reviewed and discussed in a broad taphonomic and palaeobiological context relating to predation on cave bears and conflicts with hyenas (Diedrich 2010d, 2011a).

Following this discovery 200 years ago other important Pleistocene lion finds have become famous such as the oldest mounted "cave lion skeletons" described herein from the Sloup Cave (Fig. 1A, B) in the Moravian Karst (Czech Republic, central Europe), a hyena and cave bear den site (Diedrich 2009c, 2011b). The first of the two "skeletons" of Sloup Cave (*cf.* Wankel 1858; "skeleton 2" – Brno, herein; Fig. 1B) is exhibited in the Anthropos Museum, Brno. Wankel (1888) later referred to a second skeleton

("skeleton 1" – Vienna, herein; Fig. 1A) and also illustrated an additional skull from the same cave. The two mounted "skeletons" of the cave lion *Felis spelaea* were compiled from material found in the Cut-Stone Gallery of the Sloup Cave (*cf*. Wankel 1858, 1868, 1888; Fig. 2). This material is critically analysed herein, together with new discoveries from the 1997 Sloup Cave excavations (*cf*. Seitl 1998) that comprise another large male skull and some postcranial bones (Diedrich 2011). Wankel (1892) carried out further excavations at the Sloup Cave and reported two more "lion skeletons", one with a pathological condition on the lower jaw, and the other described as being also "quite complete", but whether these still exist and if so, where they are stored, remains unclear.

Lion remains have also been reported from the Moravian Karst in other publications, particularly from the Sloup and Výpustek caves but also from other caves, and are listed by Musil (1956). A preliminary overview of the Bohemian and Moravian Karst lion localities is presented herein (Fig. 2). The analysis of lion bone material from these sites is incomplete and warrants further investigations.

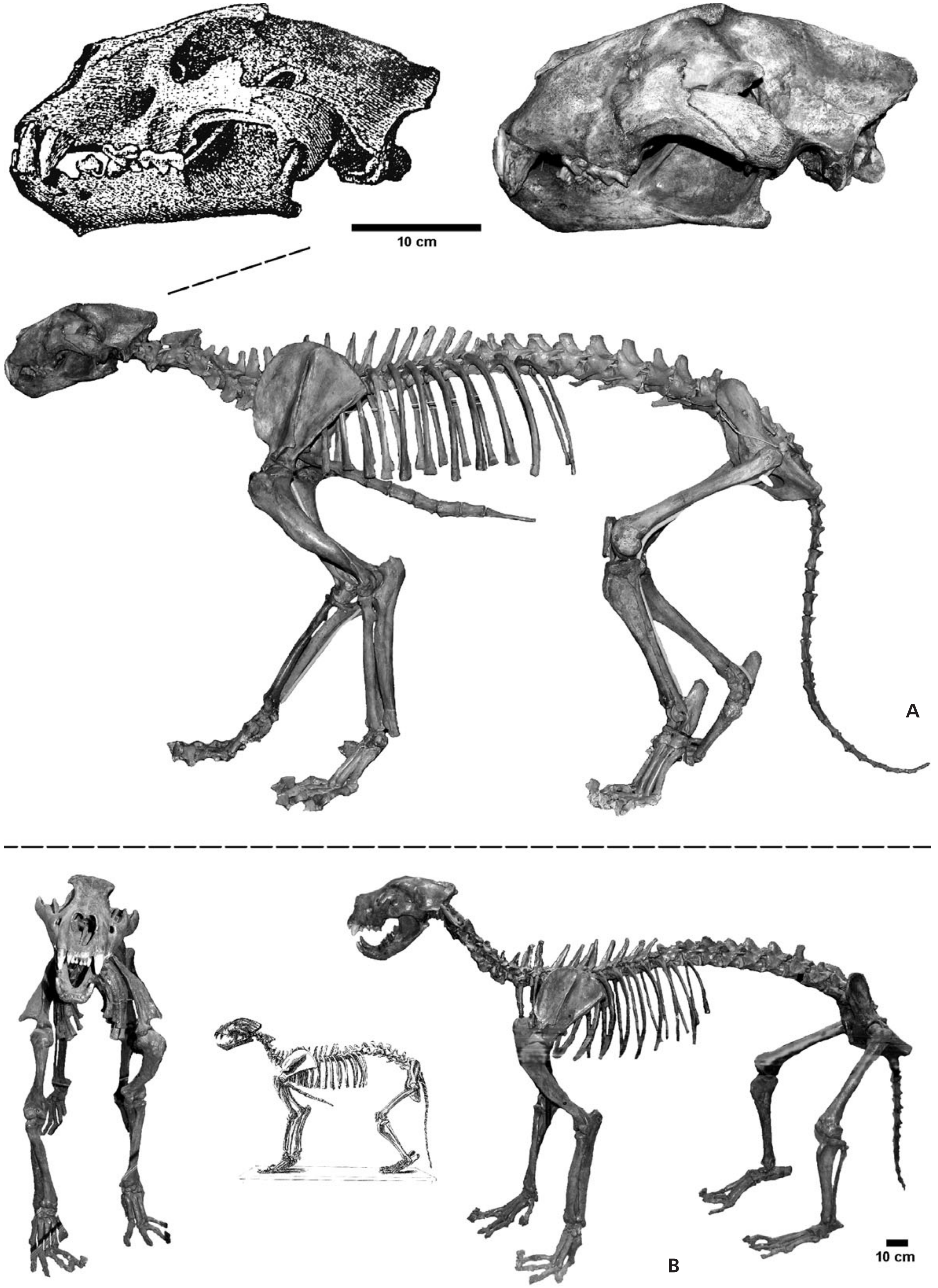
Lion remains have been reported from the Turská Maštal Cave (Kafka 1903) and the Chlupáčova sluj Cave on the Kobyla Hill near Koněprusy (Zázvorka 1954), in the Bohemian Karst in the Czech Republic consisting of just single bones and one single cub skeleton remain have been published, from which these sites have recently been interpreted to be both hyena prey depots and hyena dens (Diedrich & Žák 2006). The material requires further study, however, as it includes a lion cub skeleton from the Chlupáčova sluj Cave. The most complete known lion skeleton in Europe from a single individual (from the Srbsko Chlum-Komín Cave in the Bohemian Karst) had been previously illustrated (Diedrich & Žák 2006) but was relocated and studied in detail about 35 years later herein. This site yielded approximately 1,500 bone remains from horses, apparently accumulated by a hyena clan that had developed a specialization in hunting horses in response to the scarcity of mammoths in the mountainous regions (restricted to the Berounka River valley) of the Bohemian Karst (Diedrich 2010a).

Lion remains from Late Pleistocene open air sites have been reported from localities around Prague (Vltava River terrace; Diedrich 2007a) and Beroun (Berounka River terrace; Kafka 1903, Diedrich 2007a; Fig. 3) in the Czech Republic. This material, which includes a skull, teeth, and isolated skeletal bones, has recently been re-described together with material from several other open air localities in the north-western Czech Republic, including Trmice (Diedrich 2007a).

Skeletons of the Late Pleistocene steppe lion *Panthera leo spelaea* have also been reported from a few other sites in Europe. The oldest known skeleton is from the cave bear den in the Azé Cave (France), and has been dated into the Saalian of the late Middle Pleistocene (Argant 1988). The skeleton of a senile lioness with pathological features, which was found in an elephant graveyard at the German Neumark-Nord-Lake 1 site, was from the Eemian interglacial of the early Late Pleistocene (Diedrich 2010b, c). The number of recorded skeletons then increases during the cold period of the Weichsel/Würm glaciation (Late Pleistocene). A largely intact skeleton of a large, strong male lion was found in the Arrikrutz Cave in Spain (Altuna 1981), another was described from Salzburg in Austria (Tichy 1985), and a third male skeleton was found in an open air site at Siegsdorf in Germany (Gross 1992). The recent discoveries of lion skeletons deep within the Romanian Urșilor Cave (Diedrich *et al.* 2009) are the most spectacular because they represent the first clear evidence that steppe lions hunted cave bears deep within their caves (Diedrich 2011f). Skeletal remains from the Zoolithen Cave have also been reviewed recently but complete skeletons could not be compiled (Diedrich 2010d).

The main objective of this contribution is to critically re-examine the historical Sloup Cave lion skeleton compilations, together with the bones of the only known lioness skeleton from the Czech Republic (from the Srbsko Chlum-Komín Cave), which is illustrated in a bone catalogue (Figs 6–9) for osteological comparisons. A second objective, including this historical (largely unstudied) bone material, was to examine the bite damage and other pathological features on the lion material from the Czech Republic, with respect to interspecific and intraspecific antagonism and resulting skull damage. These important steppe lion cave finds are compared, mainly with respect to their taphonomy and pathological features, to steppe lion material from other caves (Diedrich 2009a, b, 20110d, 2011e) and open air sites, both in Germany and in the Czech Republic (Diedrich 2007a, 2010b, 2011d; Diedrich & Rathgeber 2011).

Figure 1. Two first complete European (composite) skeletons of the Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810), whose bones were mainly found in the Cut-Stone Gallery of the Sloup Cave, in the Moravian Karst of the Czech Republic (composite phalanges also from Výpustek Cave). • A – skeleton 1 (*cf.* also Figs 2, 3), which was donated in 1885 by the Prince of Liechtenstein to the Natural History Museum in Vienna, Austria (NHMV No. 1885/0014/4302), in lateral view. • B – skeleton 2 (*cf.* also Figs 2, 3) in the Anthropos Museum Brno, Czech Republic (AMB without No.), which has several flaws (the pes are transposed, the atlas is transposed, there are no sternal bones), in lateral and cranial views (historical drawings from Wankel 1888).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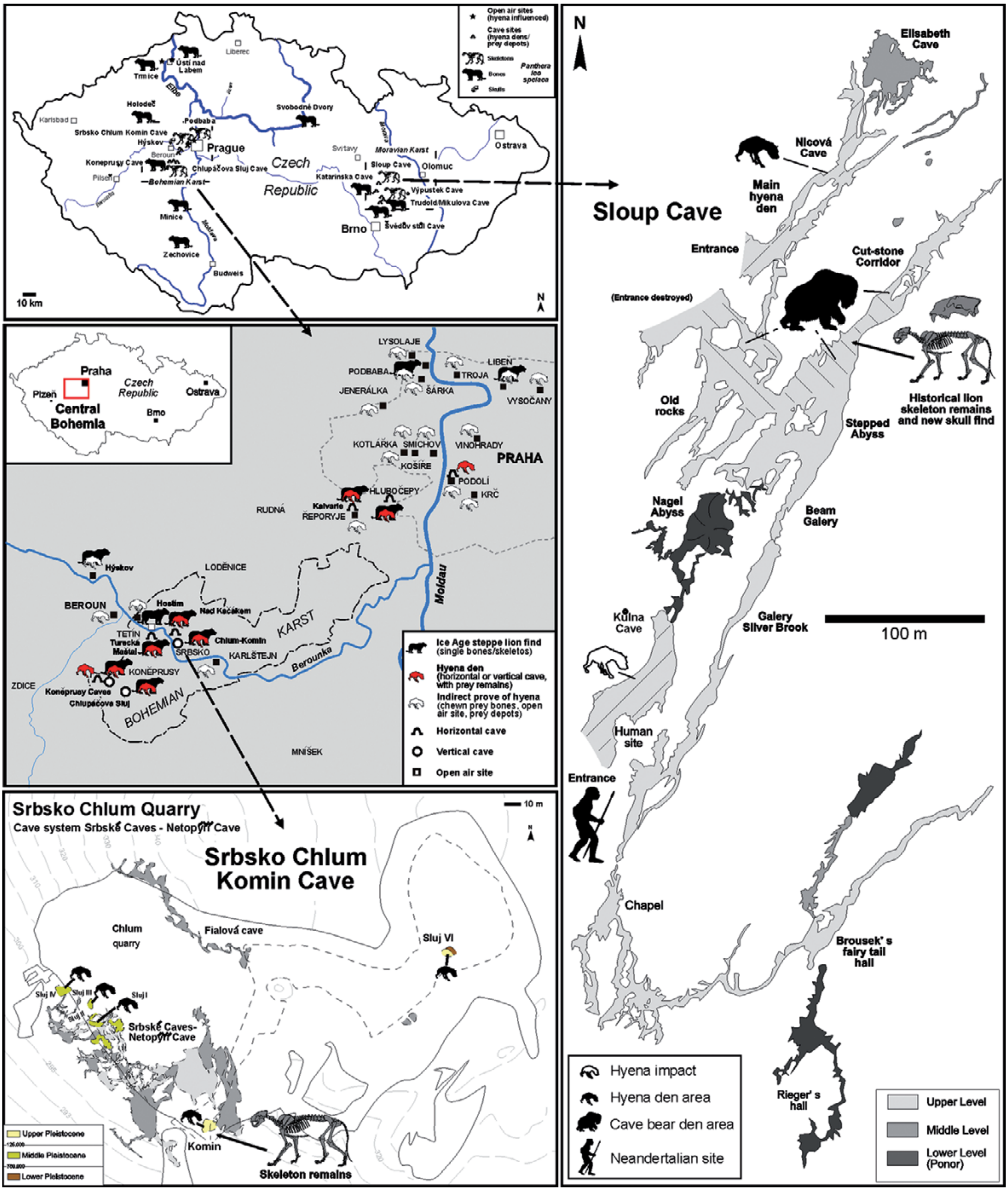


Figure 2. Late Pleistocene steppe lion open air and cave localities and hyena den sites in the Czech Republic, with details from Central Bohemia, Czech Republic (compiled from Diedrich & Žák 2006; Diedrich 2007c, 2011, and the Sloup Cave map after Zajíček 2007).

Material, history and methods

This paper examines three lion "skeletons" from the Sloup (Moravian Karst) and Srbsko Chlum-Komín (Bohemian Karst) caves, together with isolated material from various cave and open air sites in the Czech Republic. Dimensions and bite damage on skulls are compared to steppe lion, hyena (hyena prey), and cave bear material from other

European sites such as the Perick and Zoolithen caves in German and the Urșilor Cave in Romanian. Historically collected steppe lion material from the Sloup Cave is housed in the Natural History Museum, Vienna (NHMV) comprising a single skeleton ("skeleton 1" – Vienna, herein) and some isolated bones. The Sloup Cave megafauna of the Wankel collections was received by the Natural History Museum of Vienna in 1885, forming one of its first palaeontological collections, but had been excavated in 1881–1882 for J. Wankel by V. Sedlák (an employee of the Czech Professor K. Absolon). This material seems to have been used mainly for the skeleton reconstruction donated to the museum in 1885 by the Prince of Liechtenstein. A third lion skull was from the excavations by Seitl in 1998, which was again found in the Cut-Stone Gallery where the other lion bones had been found historically. This material is stored in the Anthropos Museum, Brno (AMB), as is the second "skeleton" from the Sloup Cave ("skeleton 2" – Brno, herein). The Sloup Cave ("Slouper-Höhle" in German) and the Výpustek Cave ("Kiritein Höhle" in German) were explored by the author prior to the 13th International Cave Bear Symposium in 2007 to identify the areas excavated historically by Wankel and Sedlak, and the more recent excavations by Seitl.

The unsystematic pickaxe-and-shovel digs of the Speleoclub Praha in 1968–1969 caused extensive damage to a lion skeleton from the Srbsko Chlum-Komín Cave ("skeleton 3" herein), now housed in the Natural History Museum, Prague (NMP). The skeleton was finally completed in 2005 with the inclusion of many bone fragments found 36 years after the "cave cleaning", including one rib fragment, three scapula fragments from both right and left scapulas, and one upper jaw M^1 tooth. It is now one of very few almost complete European Late Pleistocene steppe lion skeletons from a single individual and includes 149 bones (Table 1). This skeletal material was separated from that from a second, smaller skeleton of a one year old cub, which is represented by only 1/3 of its bones and exhibits typically non-fused joints. The Srbsko Chlum-Komín Cave has yielded more then 3,500 bones, including about 350 hyena remains, as well as their coprolites, and a large quantity of hyena prey (dominated by horse remains – including a foetal skeleton). Cave bear bones have not been recorded in this Srbsko Chlum-Komín hyena den cave.

The dimensions of lion skulls from recently discovered cave and open air sites in the Czech Republic, as well as those from other skeletal and skull remains in Europe (including the long bones dimensions), have been compared for a sex identification purposes. Bones from distal extremities are not useful for this purpose as they have not yet been studied in sufficient quantities, similar as metapodials.

Finally, pathological features and bite marks were observed on the historical material from the Zoolithen Cave in Germany, stored in the Natural History Museum of the Humboldt University, Berlin (MB) and at the University of Erlangen (UE), as well as in material from the Sloup Cave. The pathological features and bite marks indicate interspecific and intraspecific aggression, thus providing important clues for understanding the palaeoecology of steppe lions and their relationships to hyenas and cave bears during the Late Pleistocene of Eurasia.

Systematic palaeontology

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

Genus *Panthera* Oken, 1816

***Panthera leo spelaea* (Goldfuss, 1810)**
Figures 1, 4–10, 12

Skeleton 1, Sloup Cave (Vienna)

The Vienna skeleton is a composite skeleton made up of bones from different animals. It includes bones from male and female animals as well as several casts of bones (Fig. 3A). Some phalanges from the Výpustek Cave (marked "Vý" or "Výpustek"; *cf.* Fig. 4J, O) have also been included in the pedal skeleton. Most of the large bones and the skull of this skeleton seem to be from males, possibly derived from an articulated male skeleton found in the Cut-Stone Gallery of the Sloup Cave in historic times, while many of the remaining bones are either casts or from females.

Skull. – The skull is original and fairly complete, with a total length of 390 mm (*cf.* Figs 1A, 4D, E), but it is missing several teeth such as both P^2, M^1, and the left I^3. Only the root of the right I^2 is preserved, the tip having been flaked during the animal's lifetime. The P^3 length is 28 mm and the P^4 length is 41 mm. The teeth are hardly worn and the skull sutures are fused in the brain-case but not in the nasals, proving this to have been an adult individual 3–8 years old. A bite mark is present on the saggital crest (Fig. 4E). The lower jaws are possibly from the same skull; the left mandible has a total length of 256 mm and the left P_4 tooth has a length of 31 mm.

Vertebral column and pelvis. – The first two cervical vertebrae (atlas, axes) are original; the C3-6, and T1-2 are casts. The T3 up to the L4 (lumbar vertebrae, *cf.* Fig. 4L) are originals, such as the L7, but all other vertebrae are moulds. Eight of the caudal vertebrae are original bones (Fig. 4M), of which the first seven are articulated in anatomic correct row

Table 1. Bones of the adult female *Panthera leo spelaea* skeleton from the hyena den Srbsko Chlum-Komín cave site (Czech Republic, Bohemian Karst).

No.	Coll.-No.	Bone type	Commentary	Left	Right	Collection
1	R 4406	Cranium	Incomplete, without both P2 and M1			NMP
2	R 4407/4408	Lower jaws	Incomplete, without I1	x	x	NMP
3	R 4415	Scapula	Incomplete		x	NMP
4	Ra 4233	Scapula	Incomplete	x		NMP
5	R 4417	Humerus	Complete		x	NMP
6	R 4522	Humerus	Complete	x		NMP
7	R 4418	Ulna	Complete		x	NMP
8	R 4419	Ulna	Complete	x		NMP
9	R 4420	Radius	Nearly complete		x	NMP
10	R 4421	Radius	Complete	x		NMP
11	R 4605	Scapholunatum	Complete		x	NMP
12	R 4606	Scapholunatum	Complete	x		NMP
13	R 4621	Pisiform	Nearly complete		x	NMP
14	R 4934	Pisiform	Nearly complete	x		NMP
15	R 4219	Scaphoulnar	Complete	x		NMP
16	R 5150	Metacarpus	V, complete	x		NMP
17	R 5149	Metacarpus	IV, complete	x		NMP
18	R 5031	Metacarpus	I, complete	x		NMP
19	R 5148	Metacarpus	III, complete		x	NMP
20	R 4535	Metacarpus	IV, complete		x	NMP
21	R 4536	Metacarpus	V, complete		x	NMP
22	R 4628	Phalanx	I, manus, digit V		x	NMP
23	R 5029	Phalanx	I, manus, digit V	x		NMP
24	R 4932	Phalanx	I, manus, digit IV		x	NMP
25	R 4544	Phalanx	I, manus, digit III		x	NMP
26	R 4920	Phalanx	I, manus, digit III	x		NMP
27	R 4626	Phalanx	I, manus, digit I	x		NMP
28	R 4935	Phalanx	II, manus, digit V		x	NMP
29	R 4930	Phalanx	II, manus, digit IV		x	NMP
30	R 4545	Phalanx	II, manus, digit III		x	NMP
31	R 4927	Phalanx	II, manus, digit III	x		NMP
32	R 4928	Phalanx	II, manus, digit II	x		NMP
33	R 4626	Phalanx	II, manus, digit I	x		NMP
34	R 4933	Phalanx	III, manus, ?digit IV		x	NMP
35	R 4625	Phalanx	III, manus, ?digit III		x	NMP
36	R 5153	Phalanx	III, manus, ?digit IV	x		NMP
37	R 4926	Phalanx	III, manus, ?digit V		x	NMP
38	R 4523/4224/4565	Pelvic	Nearly complete, with sacrum			NMP
39	R 4525	Femur	Nearly complete		x	NMP
40	R 4526	Femur	Nearly complete	x		NMP
41	R 4602	Patella	Complete		x	NMP
42	R 4533	Patella	Complete	x		NMP
43	R 4528	Tibia	Nearly complete		x	NMP
44	R 4527	Tibia	Complete	x		NMP
45	R 4607	Fibula	Without proximal joint		x	NMP
46	R 4532	Fibula	Half with distal joint	x		NMP
47	R 4530	Calcaneus	Complete	x		NMP
48	R 4914	Astragal	Complete		x	NMP
49	R 4531	Astragal	Complete	x		NMP
50	R 4937	Cuboid	Complete	x		NMP

Table 1. continued

No.	Coll.-No.	Bone type	Commentary	Left	Right	Collection
51	R 4635	Navicular	Complete	x		NMP
52	Ra 4232	Tarsal II	Half	x		NMP
53	R 4539	Metatarsus	V, complete		x	NMP
54	R 4538	Metatarsus	IV, complete		x	NMP
55	Ra 4231	Metatarsus	III, proximal joint, fragment		x	NMP
56	R 4537	Metatarsus	II, complete		x	NMP
57	R 4543	Metatarsus	V, complete	x		NMP
58	R 4542	Metatarsus	IV, complete	x		NMP
59	R 4541	Metatarsus	III, complete	x		NMP
60	R 4540	Metatarsus	II, complete	x		NMP
61	R 5038	Phalanx	I, pes, digit V		x	NMP
62	R 4919	Phalanx	I, pes, digit IV	x		NMP
63	R 4632	Phalanx	I, pes, digit III		x	NMP
64	R 4627	Phalanx	I, pes, digit II		x	NMP
65	R 4922	Phalanx	I, pes, ?digit	x		NMP
66	R 5030	Phalanx	II, pes, digit II	x		NMP
67	R 4942	Phalanx	II, pes, ?digit		x	NMP
68	R 4929	Phalanx	II, pes, digit IV		x	NMP
69	R 4633	Phalanx	II, pes, digit III		x	NMP
70	R 5154	Phalanx	II, pes, ?digit IV		x	NMP
71	R 4624	Phalanx	III, pes, ?digit II	x		NMP
72	R 4923	Phalanx	III, pes, ?digit III	x		NMP
73	R 5151	Phalanx	III, pes, ?digit IV	x		NMP
74	R 4924	Phalanx	III, pes, ?digit V	x		NMP
75	R 5152	Phalanx	III, pes, ?digit III		x	NMP
76	R 4630	Phalanx	III, pes, ?digit V		x	NMP
77	R 4409	Cervical vertebra	Atlas, incomplete			NMP
78	R 4410	Cervical vertebra	Axis, incomplete			NMP
79	R 5032	Cervical vertebra	No. 3, incomplete			NMP
80	R 4414	Cervical vertebra	No. 4, incomplete			NMP
81	R 4411	Cervical vertebra	No. 5, incomplete			NMP
82	R 4412	Cervical vertebra	No. 6, incomplete			NMP
83	R 4413	Cervical vertebra	No. 7, incomplete			NMP
84	R 4548	Thoracic vertebra	No. 1, complete			NMP
85	R 4549	Thoracic vertebra	No. 2, incomplete			NMP
86	R 4551	Thoracic vertebra	No. 3, incomplete			NMP
87	Ra 4214	Thoracic vertebra	No. ?, Proc. spinosus			NMP
88	R 4550	Thoracic vertebra	No. ?, incomplete			NMP
89	R 4552	Thoracic vertebra	No. ?, incomplete			NMP
90	R 4553	Thoracic vertebra	No. 9, incomplete			NMP
91	R 4555	Thoracic vertebra	No. 10, incomplete			NMP
92	R 4554	Thoracic vertebra	No. 11, complete			NMP
93	R 4556	Thoracic vertebra	No. 12, incomplete			NMP
94	R 4557	Thoracic vertebra	No. 13, complete			NMP
95	R 4558	Thoracic vertebra	No. 14, incomplete			NMP
96	R 4559	Lumbar vertebra	No. 1, complete			NMP
97	Ra 4229	Lumbar vertebra	No.2, two fragments			NMP
98	R 4561	Lumbar vertebra	No. 3, incomplete			NMP
99	Ra 4230a	Lumbar vertebra	?No. 4, fragment			NMP
100	Ra 4230b	Lumbar vertebra	?No. 4, fragment			NMP

Table 1. continued

No.	Coll.-No.	Bone type	Commentary	Left	Right	Collection
101	Ra 4230c	Lumbar vertebra	?No. 5, 2 fragments			NMP
102	R 4563	Lumbar vertebra	No. 6, incomplete			NMP
103	R 4564	Lumbar vertebra	No. 7, incomplete			NMP
104	R 4566	Caudal vertebra	No. ?, upper, incomplete			NMP
105	R 4567	Caudal vertebra	No. ?, upper, complete			NMP
106	R4568	Caudal vertebra	No. ?, upper, incomplete			NMP
107	R 4569	Caudal vertebra	No. ?, upper, complete			NMP
108	R 4570	Caudal vertebra	No. ?, middle, complete			NMP
109	R 4571	Caudal vertebra	No. ?, middle, complete			NMP
110	R 4597	Caudal vertebra	No. ?, middle, incomplete			NMP
111	R 4572	Caudal vertebra	No. ?, middle, complete			NMP
112	R 4573	Caudal vertebra	No. ?, lower, complete			NMP
113	R 4574	Caudal vertebra	No. ?, lower, complete			NMP
114	R 5377	Caudal vertebra	No. ?, lower, complete			NMP
115	R 5378	Caudal vertebra	No. ?, lower, complete			NMP
116	R 5380	Caudal vertebra	No. ?, lower, complete			NMP
117	Ra 4280	Caudal vertebra	Last two fused			NMP
118	Ra 4224	Costa	No. 1		x	NMP
119	Ra 4225	Costa	No. 2, complete		x	NMP
120	Ra 4226	Costa	No. 3, complete		x	NMP
121	Ra 4227	Costa	No. 4		x	NMP
122	Ra 4228	Costa	No. 5		x	NMP
123	Ra 4248	Costa	No. 6, complete		x	NMP
124	Ra 4230	Costa	No. 7, complete		x	NMP
125	Ra 4232	Costa	No. 8, complete		x	NMP
126	Ra 4233	Costa	No. 9		x	NMP
127	Ra 4234	Costa	No. 10, complete		x	NMP
128	Ra 4235	Costa	No. 11, nearly complete		x	NMP
129	Ra 4236	Costa	No. 12, complete		x	NMP
130	Ra 4237	Costa	No. 13, complete		x	NMP
131	Ra 4238	Costa	No. 1	x		NMP
132	Ra 4239	Costa	No. 2	x		NMP
133	Ra 4240	Costa	No. 3	x		NMP
134	Ra 4241	Costa	No. 4	x		NMP
135	Ra 4242	Costa	No. 5	x		NMP
136	Ra 4243	Costa	No. 6	x		NMP
137	Ra 4244	Costa	No. 7	x		NMP
138	Ra 4245	Costa	No. 8	x		NMP
139	Ra 4246	Costa	No. 9	x		NMP
140	Ra 4247	Costa	No. 10	x		NMP
141	Ra 4249	Costa	No. 11	x		NMP
142	Ra 4250	Costa	No. 12	x		NMP
143	Ra 4251	Costa	No. 13	x		NMP
144	Ra 4252	Sternal bone	No. 1			NMP
145	Ra 4253	Sternal bone	No. ?2			NMP
146	Ra 4220	Sesamoid	Complete			NMP
147	Ra 4221	Sesamoid	Complete			NMP
148	Ra 4222	Sesamoid	Complete			NMP
149	Ra 4223	Sesamoid	Complete			NMP

(possibly from one individual). The positions of one central and one distal caudal vertebrae are uncertain. The coxa is 363 mm long and has an acetabulum diameter of 50 mm; the sacrum of the pelvis is a mould. The right ribs include one from a cub (most probably from a cave bear) with a non-fused head (the 13th rib). All of the other preserved ribs, *i.e*. the 5th, 7th, 9th (with pathological feature, Fig. 4K) 10th, 11th and 12th, have fused rib heads. The left ribs have partly been preserved (Nos. 1, 2, 4, 6, 8, and 11); others are casts, as are all sternal bones.

Appendicular skeleton. – The right scapula is complete (length 312 mm, glenoid width 68 mm, Fig. 4F) but the left scapula is a cast. Both large humeri are similarly proportioned and preserved (length 380 mm, distal width 100 mm, Fig. 4G, H). Neither ulna is original and only the large right radius is complete (with male proportions: length 340 mm, distal width 75 mm, Fig. 4I). All five right metacarpi are originals (Fig. 4J), while the left metacarpi have a cast of the Mc I. The different proportions and lack of symmetry between left and right metacarpals suggest a mixed derivation from both male and female specimens which, in some cases, may have even derived from different caves (*i.e*. the Sloup and Výpustek caves; *cf*. Fig. 4J). All original carpalia in the right manus are missing and only represented by casts while in the left manus the scapholunatae, and probably also the metacarpal bones, are originals. In both forelimb manus skeletons some of the phalanges I–III are casts. The hind limbs have two large symmetrical femora (length 425 mm, distal width 90 mm) and one large right tibia (length 364 mm, distal width 68 mm, Fig. 4N). Both original calcanei are symmetrical and large (128 mm in length). Once again, the metatarsals and phalanges do not originate from a single individual or a single cave site. Whereas most bones are originals, the Mt I is a cast (Fig. 4O).

Skeleton 2, Sloup Cave (Brno)

The skull of this skeleton is a compilation, with at least one mandible derived from a different source; the front legs are less then 50% made up of original bones, and those in the hind legs originate from both males and females. It is unclear which parts might have belonged to the original skeleton because it is such a complete mixture, including material from different skeletons (including both males and females) from the Cut-Stone Gallery of the Sloup Cave, and there are even more casts than in skeleton 1 (Vienna).

Skull. – The original skull (Fig. 4A) has a total length of 357 mm and is missing some of the original teeth. On the right and left it lacks the small M^1, whereas the left side canine tooth is a much too short cast. The frontal width is 98 mm; the left P^4 length is 36 mm. The lower jaw appears to be a composite from more than one original. The right mandible, with its complete dentition, is consistent with a young adult animal skull in which the anterior parts are non-fused, but the brain-case bones are fused. The left mandible is from an older, senile individual, with an M_1 that is highly worn, as are also the $P_{3–4}$ teeth.

Vertebral column and pelvis. – The atlas has been mounted the wrong way round; the axis vertebra is an original. All

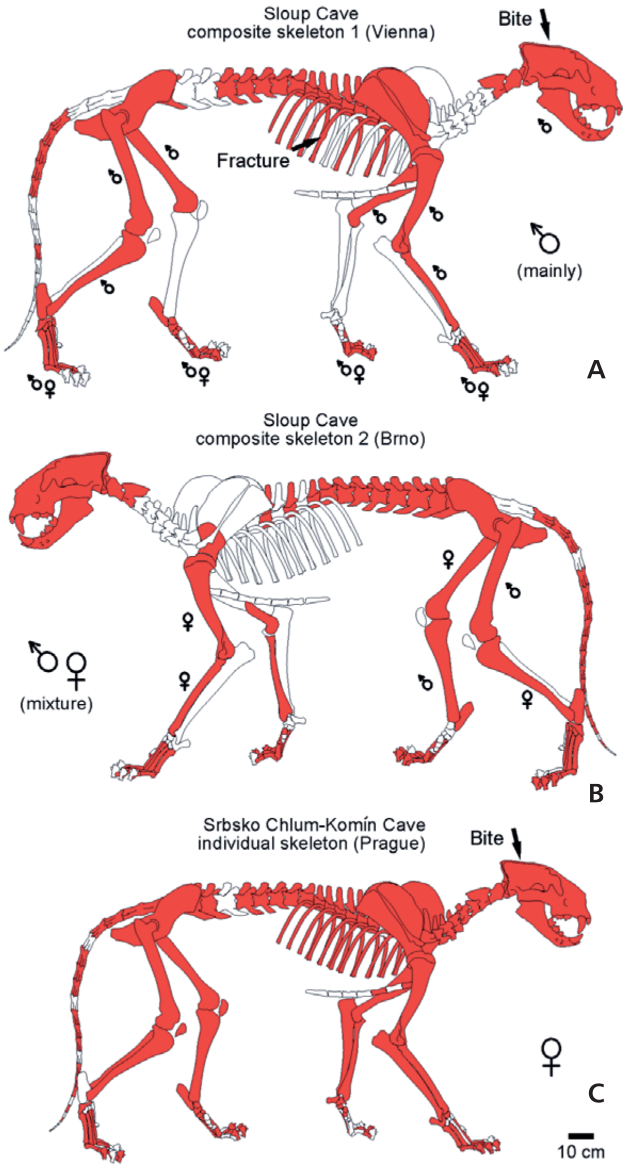


Figure 3. Composite and "real" skeletons of the Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) from Czech Republic cave sites. • A – composite skeleton 1 with bones from the Sloup Cave, in the Natural History Museum, Vienna (NHMV No. 1885/0014/4302, *cf.* Fig. 1A). • B – composite skeleton 2 with bones from the Sloup Cave, on display in the Anthropos Museum, Brno (AMB without No.). • C – single skeleton from the Srbsko Chlum-Komín Cave, in the Natural History Museum, Prague (NMP No. R 4406) (red = original bones, white = casts).

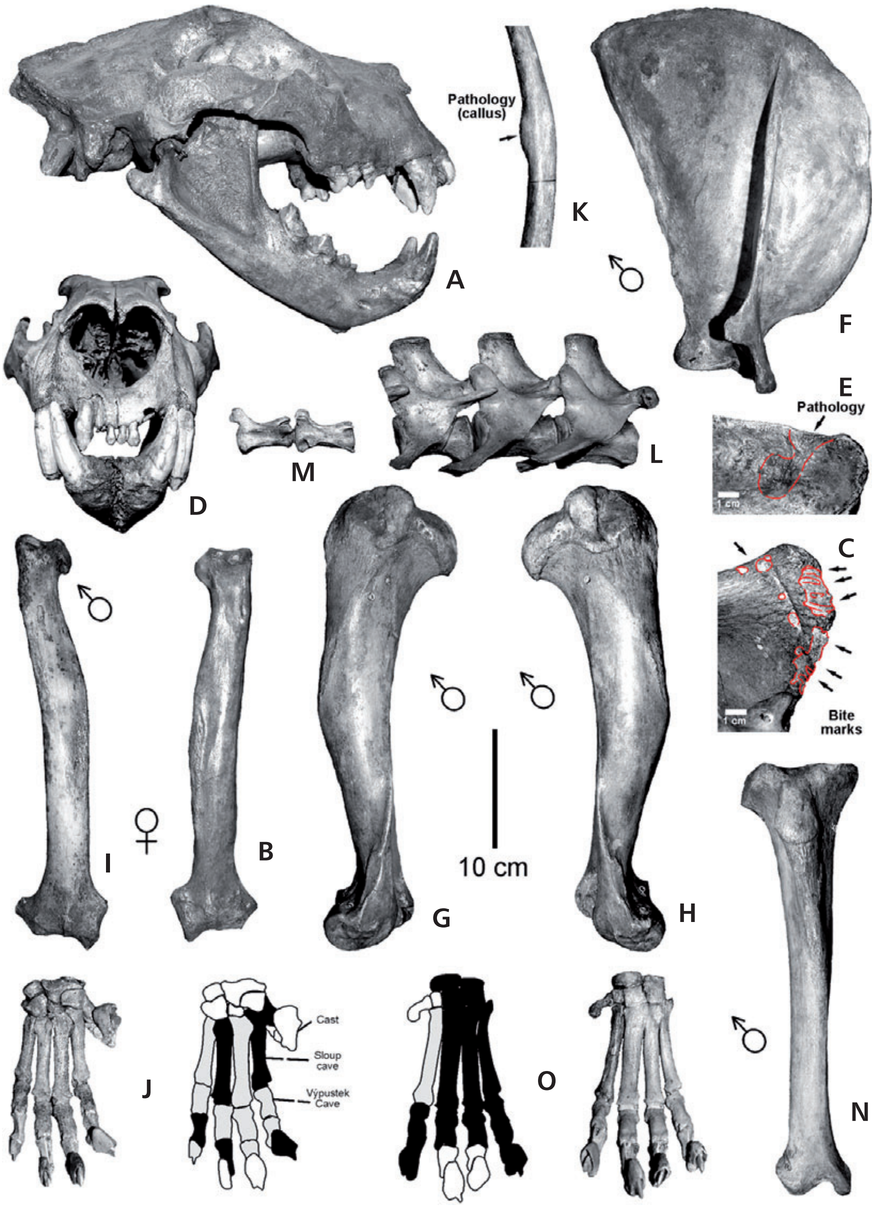


Figure 4. Selected bones from skeletons 1 and 2 of the Late Pleistocene lion *Panthera leo spelaea* (Goldfuss, 1810), from the Cut-Stone Gallery of the Sloup Cave, Moravian Karst (Czech Republic). • A – skeleton 2 (Brno) skull (*cf.* Fig. 1A), lateral. • B – skeleton 2 (Brno) left radius, lateral. • C – skeleton 2 (Brno) pelvis with large carnivore bite marks (*cf.* Fig. 3). • D – skeleton 1 (Vienna) skull, frontal. • E – skeleton 1 (Vienna) skull, detail of the pathology on the left side of the brain-case (*cf.* also Fig. 12B), lateral left. • F – skeleton 1 (Vienna) right scapula, lateral. • G – skeleton 1 (Vienna) left humerus, lateral. • H – skeleton 1 (Vienna) right humerus, lateral. • I – skeleton 1 (Vienna) right radius, lateral. • J – skeleton 1 (Vienna) right composite manus skeleton, cranial. • K – skeleton 1 (Vienna) middle rib with pathology, lateral. • L – skeleton 1 (Vienna) middle lumbar vertebrae, lateral. • M – skeleton 1 (Vienna) middle caudal vertebrae, lateral. • N – skeleton 1 (Vienna) right tibia, cranial. • O – skeleton 1 (Vienna) composite left pes skeleton, cranial.

the cervical vertebrae are casts. The 3–7, 9, 11, 13 and 14 (last) thoracic vertebrae are originals, as is the entire lumbar vertebral column L1-7 which may thus have derived from a single individual. Sixteen of the caudal vertebrae are originals but the distal vertebrae are casts. None of the ribs are original; all of the sternal bones are missing.

Appendicular skeleton. – The left scapula is not original but a fragment (including the glenoid) is preserved from the right scapula. The left humerus is complete and 362 mm long, while only the distal half of the right humerus is preserved (distal width 92 mm). The left radius is missing the anterior joint but the right radius is complete (length 324 mm, Fig. 4B). Both ulnae are casts, as are most of the carpals. The left manus has the original pisiform, and possibly one other original carpal bone. The metapodials in the manus skeletons are composites that appear to all be from the right hand side, with the Mc II–V having been derived from a single individual. All phalanges I–II are originals, as are three phalanges III – the fourth is a cast. The right manus again has original Mc II–V metapodials, as are all phalanges I–II, but only the middle two phalanges III are bones, the outer phalanges are casts. The hind limbs are in both cases made up of original femora and tibiae bones but they are not symmetrical and do not have the same proportions, suggesting that they do not come from a single individual. The left femur is longer (440 mm) than the right femur (380 mm). In contrast, the right tibia is only 345 mm long, the left one is 362 mm, proving these to be composites made up of both male and female hind limb bones. The

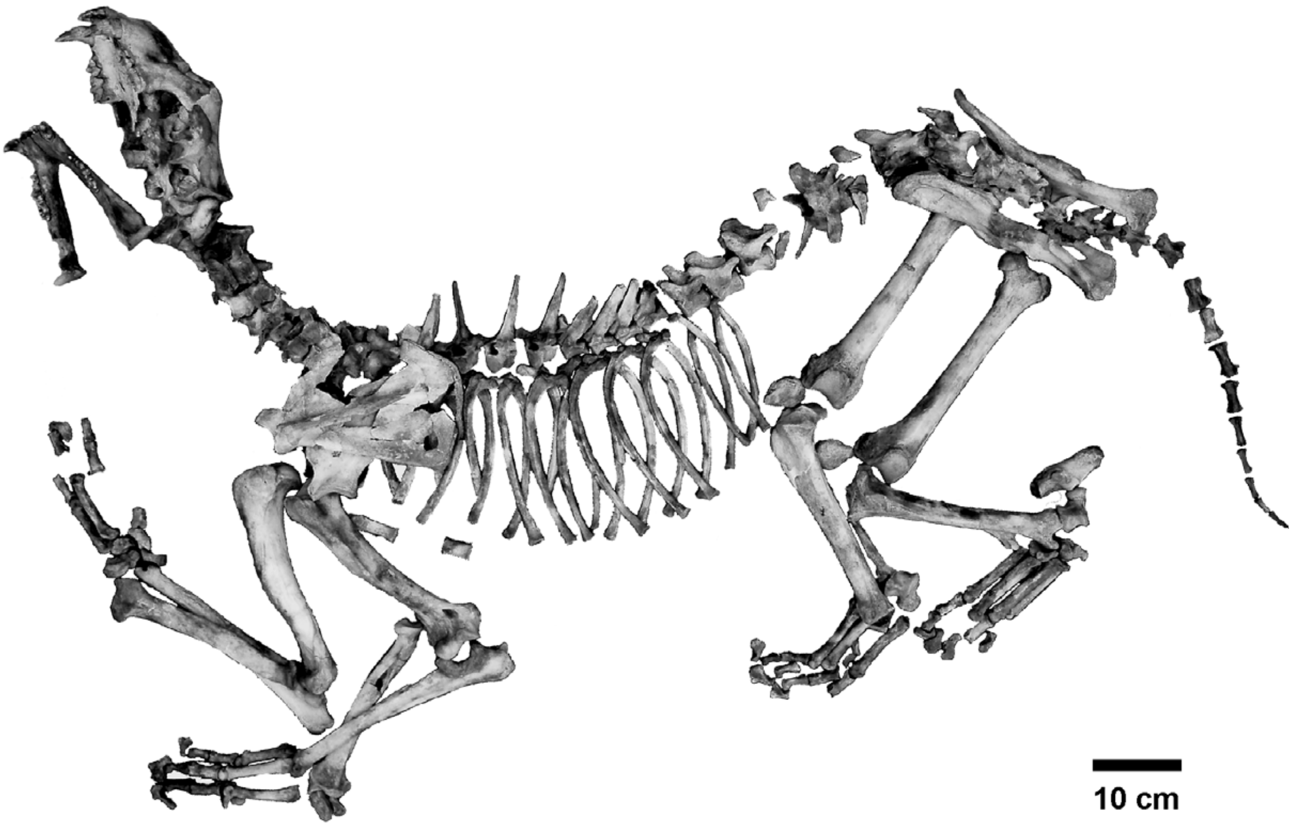


Figure 5. The articulated and almost complete skeleton 3 of the steppe lion *Panthera leo spelaea* (Goldfuss, 1810) from the Srbsko Chlum-Komín Cave (NMP No. R 4406). The pathologically damaged brain-case was in the process of healing (after Diedrich & Žák 2006).

feet are incorrectly mounted. The right calcaneus has proximal bite marks and is incomplete, while the left calcaneus is complete. The left pes skeleton has all tarsalia, the Mt II–V, phalanges I–II, and three phalanges III; the inner phalanx III is a cast. The missing digit I has not even been reproduced on either foot. The right pes skeleton consists of all tarsalia, the Mt II–V, 3 phalanx I and all phalanx II; within the phalanx III one digit II is a cast. All the phalanges of the pedal skeletons seem to be composites and often phalanx II is in the wrong position, as are some of the other phalanges.

Skeleton 3, Srbsko Chlum-Komín Cave (Prague)

This skeleton has 149 bones that belong to the original skeleton of a young adult lioness (Fig. 5, Table 1), whereas the phalange III and some phalange II may, in some cases, have derived from a second skeleton of a juvenile animal. The distal extremity bones (starting from the metapodials) are therefore not illustrated herein. All other non-pedal bones have larger dimensions and belong to the original skeleton illustrated herein of a young adult lioness. No scavenging marks are present on the bones. Many modern fractures are present and some pieces of bone are missing, all of which are the result of careless excavation. Evidence that the bone material is from a single individual is provided by the symmetry of the skeleton, the consistent proportions, and the lack of any repetition in the bones. The origin of the small pedal bones (phalanges) is more problematic and these may have come from a second, juvenile skeleton.

Skull. – In many of the views illustrated herein the cranium with lower jaw (Fig. 6) can be seen to be extensively damaged. Both upper jaw P^2 are missing, as is the left M^1. The incisors, both canines, and the $P^{3–4}$ are in their alveoli. The nasal bones and front of the skull have been damaged. The lower jaw (Fig. 6F, G) has been badly damaged but both mandibles fit together exactly in their symphyses. The right mandible includes the $I_{2–3}$, C, and $P_{3–4}$; the left mandible has no incisors in its alveoli. Both mandibles are incomplete in the vicinity of the ramus. One more isolated fragment belongs to this jaw. The important mandible measurements for sex identification are listed in Table 2 for the more complete right mandible. The teeth in both upper and lower jaws are similarly unworn and unpolished.

Vertebral column and pelvis. – Many of the 39 vertebrae preserved (Fig. 7; Table 1) are almost complete, but also

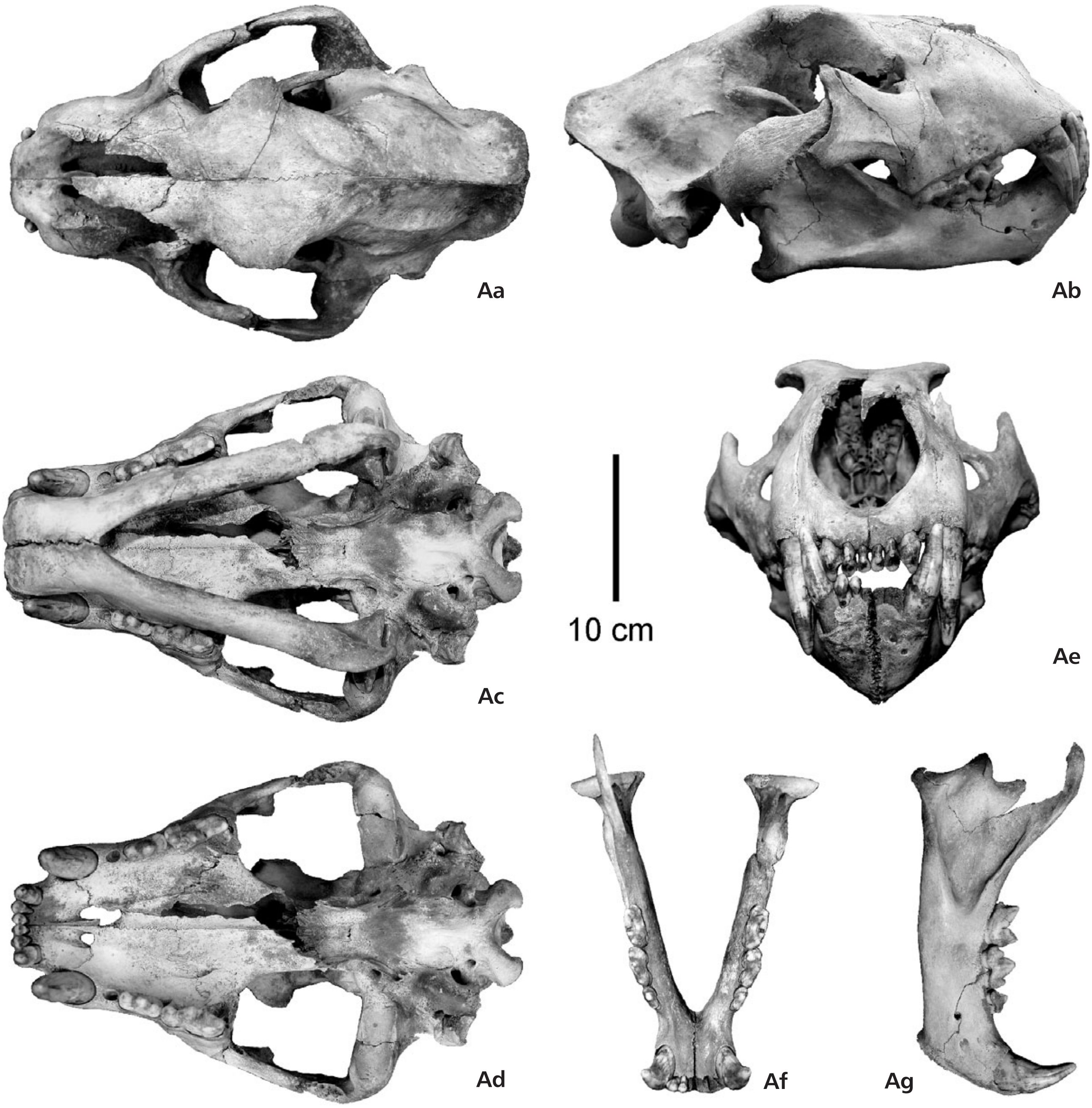
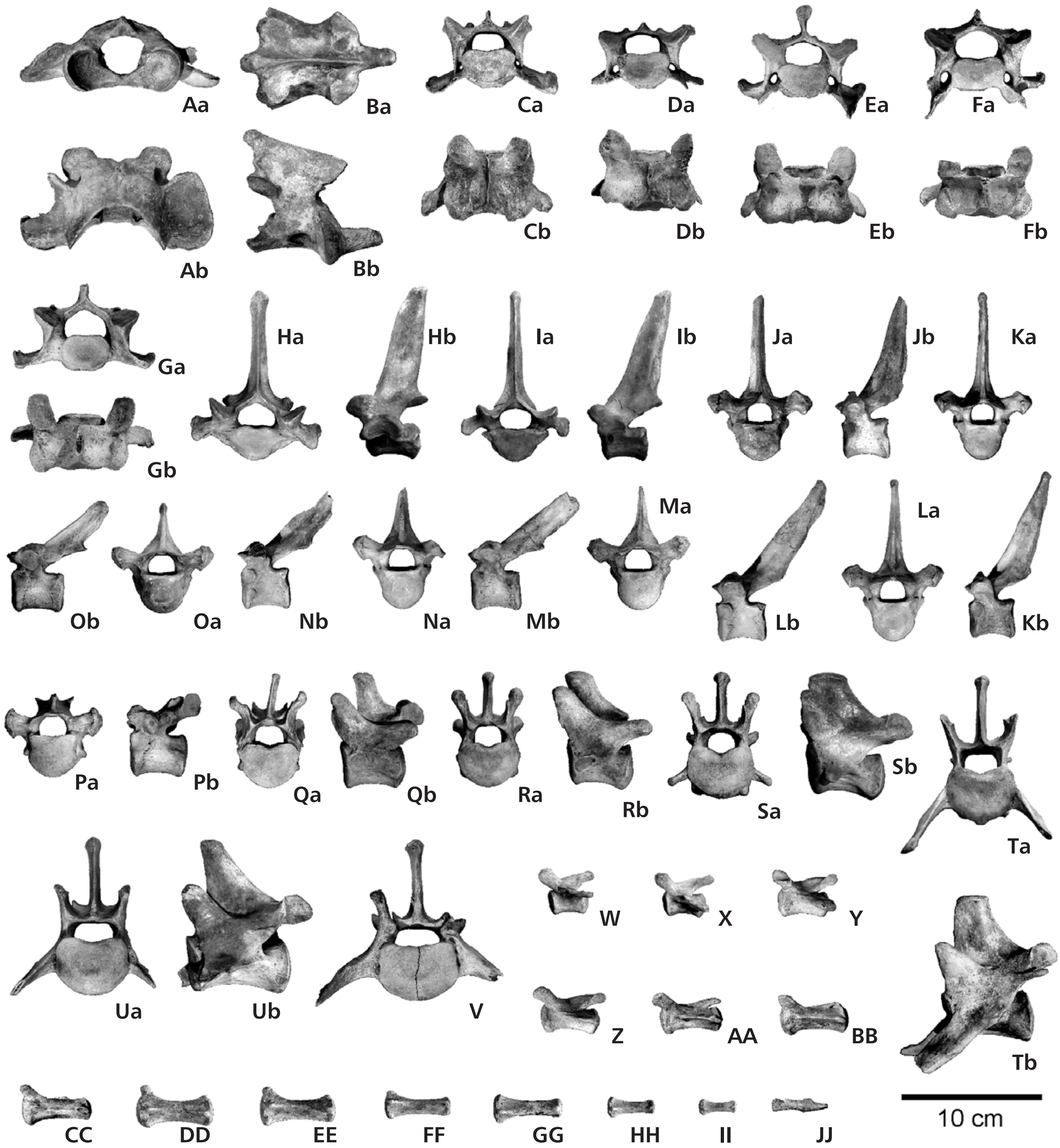


Figure 6. Cranium of the young adult lioness *Panthera leo spelaea* (Goldfuss, 1810) skeleton (skeleton 3) from the Srbsko Chlum-Komín Cave of the Bohemian Karst (Czech Republic). • A – skull with mandible dorsal, B – skull with mandible lateral right, C – skull with mandible ventral, D – skull ventral, E – skull frontal, F – mandible dorsal, G – mandible lateral right (NMP No. R 4406).

Figure 7. Vertebral column of the young adult lioness *Panthera leo spelaea* (Goldfuss, 1810) skeleton (skeleton 3) from the Srbsko Chlum-Komín Cave of the Bohemian Karst (Czech Republic). • A – first cervical vertebra, atlas (NMP No. R 4409), a – cranial, b – dorsal. • B – second cervical vertebra, axes (NMP No. R 4410), a – dorsal, b – lateral. • C – third cervical vertebra (NMP No. R 5032), a – cranial, b – dorsal. • D – fourth cervical vertebra (NMP No. R 4414), a – cranial, b – dorsal. • E – fifth cervical vertebra (NMP No. R 4411), a – cranial, b – dorsal. • F – sixth cervical vertebra (NMP No. R 4412), a – cranial, b – dorsal. • G – seventh cervical vertebra (NMP No. R 4413), a – cranial, b – lateral. • H – first thoracic vertebra (NMP No. R 4548), a – cranial, b – lateral. • I – second thoracic vertebra (NMP No. R 4549), a – cranial, b – lateral. • J – third thoracic vertebra (NMP No. R 4551), a – cranial, b – lateral.



• K – 6–7 thoracic vertebra (NMP No. R 4550), a – cranial, b – lateral. • L – 7–8 thoracic vertebra (NMP No. R 4552), a – cranial, b – lateral. • M – ninth thoracic vertebra (NMP No. R 4553), a – cranial, b – lateral. • N – tenth thoracic vertebra (NMP No. R 4555), a – cranial, b – lateral. • O – eleventh thoracic vertebra (NMP No. R 4554), a – cranial, b – lateral. • P – twelfth thoracic vertebra (NMP No. R 4556), a – cranial, b – lateral. • Q – thirteenth thoracic vertebra (NMP No. R 4557), a – cranial, b – lateral. • R – fourteenth and last thoracic vertebra (NMP No. R 4558), a – cranial, b – lateral. • S – first lumbar vertebra (NMP No. R 4559), a – cranial, b – lateral. • T – third lumbar vertebra (NMP No. R 4561), a – cranial, b – lateral. • U – sixth lumbar vertebra (NMP No. R 4563), a – cranial, b – lateral. • V – seventh and last lumbar vertebra (NMP No. R 4564), a – cranial, b – lateral. • W – upper caudal vertebra (NMP No. R 4566), lateral. • X – upper caudal vertebra (NMP No. R 4567), lateral. • Y – upper caudal vertebra (NMP No. R 4568), lateral. • Z – upper caudal vertebra (NMP No. R 4569), lateral. • AA – upper caudal vertebra (NMP No. R 4570), lateral. • BB – middle caudal vertebra (NMP No. R 4571), lateral. • CC – middle caudal vertebra (NMP No. R 4597), lateral. • DD – middle caudal vertebra (NMP No. R 4572), lateral. • EE – middle caudal vertebra (NMP No. R 4573), lateral. • FF – lower caudal vertebra (NMP No. R 4574), lateral. • HH – lower caudal vertebra (NMP No. R 5378), lateral. • II – lower caudal vertebra (NMP No. R 5380), lateral. • JJ – last two fused lower caudal vertebrae (NMP No. Ra 4218), lateral.

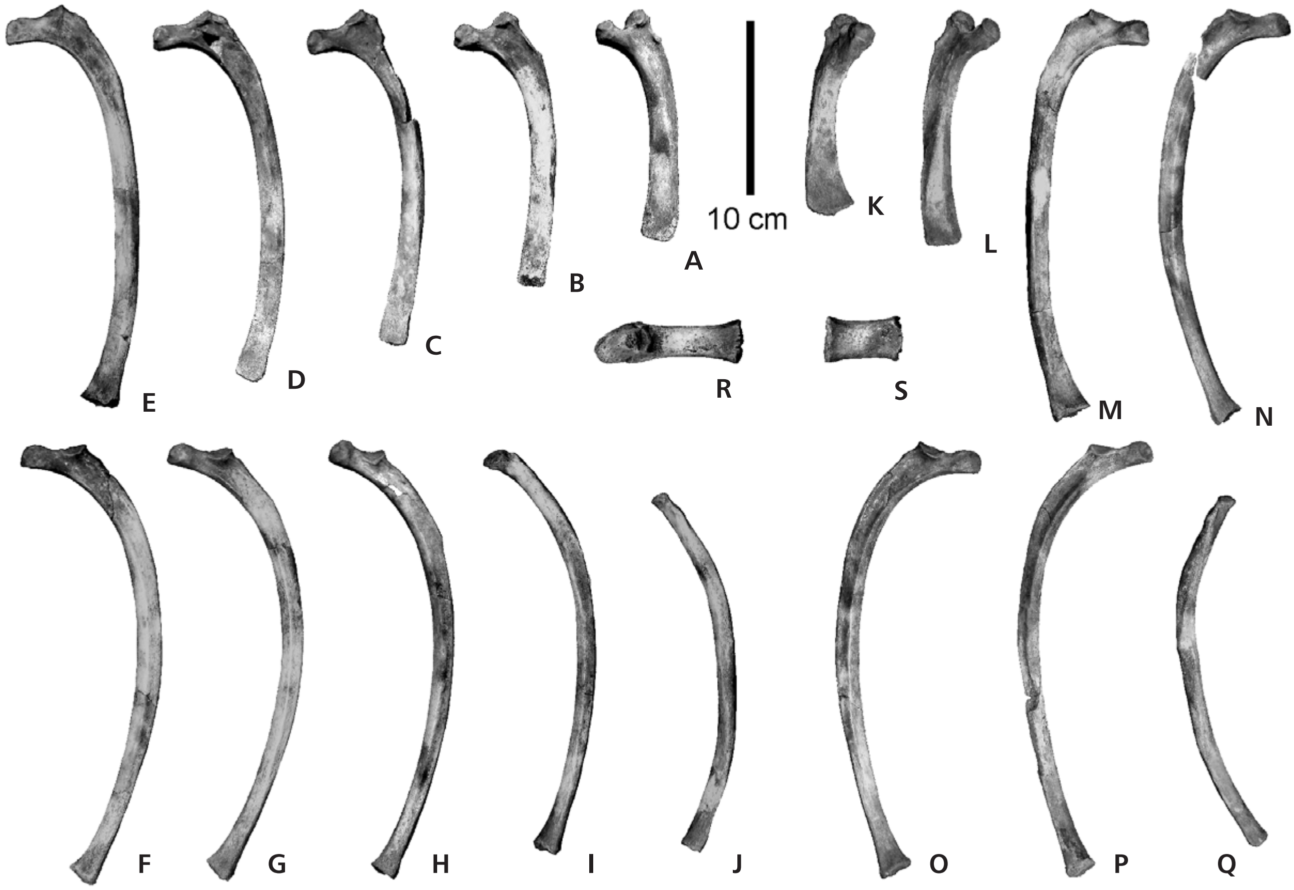


Figure 8. Thoracic costae and sternal bones of the young adult lioness *Panthera leo spelaea* (Goldfuss, 1810) skeleton (skeleton 3) from the Srbsko Chlum-Komín Cave of the Bohemian Karst (Czech Republic). • A – second right costa (NMP No. Ra 4225). • B – third right costa (NMP No. Ra 4226). • C – fourth right costa (NMP No. Ra 4227). • D – fifth right costa (NMP No. Ra 4228). • E – sixth right costa (NMP No. Ra 4248). • F – ninth right costa (NMP No. Ra 4233). • G – tenth right costa (NMP No. Ra 4234). • H – eleventh right costa (NMP No. Ra 4235). • I – twelfth right costa (NMP No. Ra 4236). • J – thirteenth and last right costa (NMP No. Ra 4237). • K – first left costa (NMP No. R 4238). • L – second left costa (NMP No. Ra 4239). • M – sixth left costa (NMP No. Ra 4243). • N – seventh left costa (NMP No. Ra 4244). • O – ninth left costa (NMP No. Ra 4246). • P – tenth left costa (NMP No. Ra 4247). • Q – thirteenth and last left costa (NMP No. Ra 4251). • R –first sternal bone (NMP No. Ra 4252). • S – middle sternal bone (NMP No. Ra 4253). All in inner lateral view.

include fragments of the processes. Some vertebrae still have parts missing as a result of damage that occurred during excavation. The cervical column (Fig. 7A–G) is complete, with all seven vertebrae present, but most of these show recent damage on their processes. The thoracic vertebral column (Fig. 7H–R) is incomplete, as only 12 vertebrae are present; there should be 13 in the Felidae. One vertebra from the middle thoracic region is missing and another is only represented by the dorsal spine. The lumbar vertebral column (Fig. 7S–V), which in the felids consists of seven vertebrae, is missing three large vertebra centra, of which most of the processes seems to be present. Even the half lumbar vertebra 7 is present. Fifteen caudal vertebrae (Fig. 7W–JJ) are present from the tail, including the last two fused vertebrae from the tip. Since a complete tail in the Felidae has about 22 vertebrae, some are clearly missing.

The thorax includes one of the best preserved and most complete rib cages known (Fig. 8A–Q). Some ribs are missing the rib heads, but their distal ends have at least been preserved. *P. l. spelaea* has 13 ribs on each side correlating to the 13 thoracic vertebrae. All 26 ribs are represented in this lioness skeleton, and are more or less complete. The right rib

Figure 9. Appendicular skeleton of the young adult lioness *Panthera leo spelaea* (Goldfuss, 1810) skeleton from the Srbsko Chlum-Komín Cave of the Bohemian Karst (Czech Republic). • A – right scapula (NMP No. R 4415), lateral. • B – left scapula (NMP No. Ra 4233), lateral. • C – right humerus (NMP No. R 4417), cranial. • D – left humerus (NMP No. R 4522), cranial. • E – right ulna (NMP No. R 4418), cranial. • F – left ulna (NMP No. R 4419), cranial. • G – right radius (NMP No. R 4420), cranial. • H – left radius (NMP No. R 4421), cranial. • I – right pisiform (NMP No. R 4621), dorsal. • J – left pisiform (NMP No. R 4934), cranial. • K – left scapholunatum (NMP No. R 4606), cranial. • L – pelvis, a – dorsal, b – lateral left. • M – right femur

(NMP No. R 4525), cranial. • N – left femur (NMP No. R 4526), cranial. • O – incomplete right fibula (NMP No. R 4607), lateral. • P – incomplete left fibula (NMP No. R 4532), lateral. • Q – right patella (NMP No. R 4602), cranial. • R – left patella (NMP No. R 4533), cranial. • S – right tibia (NMP No. R 4528), cranial. • T – left tibia (NMP No. R 4527), cranial. • U – left calcaneus (NMP No. R 4530), cranial. • V – right astragal (NMP No. R 4914), dorsal. • W – left astragal (NMP No. R 4531), dorsal. • X – left tarsal II (NMP No. Ra 4232), cranial.

Table 2. Important measurements of the *Panthera leo spelaea* skeleton from Srbsko Chlum-Komín of the Bohemian Karst (Czech Republic) for the sex identification (in cm). The measurements show low proportions and indicate well a female individual (all in mm).

1	R 4406	Cranium	Total length: 305	165	Width P4: 34	Width C: 21
2	R 4407	Lower jaw	Total length: 214	Height behind M1: 48	Width M1: 28	Width C: 21
3	R 4522	Humerus (left)	Total length: 319	Smallest width middle of shaft: 29	Proximal width: 75	Distal width: 84
4	R 4419	Ulna (left)	Total length: 342	Width under proximal joint: 48	Proximal width: 60	Distal width: 34
5	R 4421	Radius (left)	Total length: 288	Smallest width middle of the shaft: 29	Proximal width: 39	Distal width: 62
6	R 4523	Pelvic	Total length: 312	Width "canal": 92	Acetabular width: 132	Sacrum length: 102 Acetabulum length: 42 Length foramen obturatum: 77
7	R 4525	Femur	Total length: 359	Smallest width middle of the shaft: 34	Proximal width: 88	Distal width: 81
8	R 4528	Tibia	Total length: 312	Smallest width middle of the shaft: 29	Proximal width: 84	Distal width: 59

cage has the following complete ribs: Nos. 2, 5, 6, and 9–13. Of the other ribs, Nos. 1, 3, and 4 have small parts missing, No. 7 has no distal part, and No. 8 has no proximal rib head. In the left rib cage the ribs 1–2, 6, 9 and 13 are complete; all others have some distal parts (Nos. 3–5) or the proximal part (No. 12) missing or, in a few cases, minor damage in the central part of the rib shaft (Nos. 8, 10). The first sternal bone is present as well as one other which could be either the second or third sternal bone (Fig. 8R, S).

The pelvis is almost complete (Fig. 9L) but is still missing a large portion of the posterior part. All bone sutures, except the ones between the pelvic bones and sacrum, are fused, indicating a young adult age.

Appendicular skeleton. – The forelimbs (Fig. 9A–K) are almost fully preserved. Only the distal elements are problematic, *i.e*. the last phalanges (II–III). The left scapula is almost complete while the right scapula is less complete (Fig. 9A, B). The right humerus has a small fragment missing, while the left one is complete (Fig. 9C, D). The right ulna (Fig. 9E) is complete, as is also the left one (Fig. 9F). Both radii have similar proportions: the left one (Fig. 9H) has a large fragment missing but the right one is complete (Fig. 9G). Both complete pisiform bones are present (Fig. 9I, J). The right scapholunatum is present (Fig. 8K). Half of the metacarpals are missing. All pedal bones have been sorted from the nearly complete manus and pes metapodial sets of the juvenile animal, which are again smaller and contain all Mc II–V of the right and left manus. Only the right Mc III–V and the left Mc I, IV–V seem to be present from the adult female skeleton. At least one phalanx I was separated from the juvenile material. Only three phalanges from the right manus and three from the left manus can probably be attributed to the lioness skeleton. The origin of phalanx II was much more difficult to distinguish and it is even difficult to determine a right or left position. The exact positions of the phalanx II, and also the phalanx III, have therefore not yet been identified. They may even belong to the pedal skeletons, or have derived from the cub skeleton.

Both hind limb bones (Fig. 9M–X) are almost complete. Both femora, the patellae and the tibiae are only partly complete (Fig. 9S, T). Only half of the fibulae are present. The left calcaneus (Fig. 9U) is present but the right one is absent. Both astragals (Fig. 9V, W) are preserved and are larger then those from the juvenile animal. Two left tarsals (cuboid, navicular) are complete, whereas only half of the tarsal II is present (Fig. 9X). The left pes includes all large metatarsi II–V. From this left pes two more first phalanges (digit IV, and digit?), one second phalanx (digit II), and possibly all third phalanges are present. There is again a problem in the attribution of an exact position to this part of the skeleton. The phalanges III can be distinguished between the right and the left side as a result of their different angles to the phalanx bases. The exact position of the digits is also uncertain, due at least in part to their being incomplete. Some small phalanx III, which have been attributed to the outer digits, may actually came from to the middle digits of the smaller juvenile animal. The right pedal skeleton has only three complete large metatarsi (V, IV, and II) and half of the proximal metatarsus II. The first phalanx is present from the digits II, III and V. Phalanx II may be represented on digits II–IV, but this is uncertain. Finally, the position of the phalanges III in relation to digits II and V remains unclear.

Discussion

Sexual dimorphism and individual ages

The sex of the lions from the Czech Republic can be interpreted through comparisons with other fossils of female and male lions (*cf.* Turner 1984, Gross 1992, Diedrich 2009b). Females are much smaller then males, as defined differently for cold and warm periods, using osteometrics for the cranium and postcranial bones (Fig. 11) within cold and warm periods, but not between those times. The lioness skeleton from the Eemian site at Neumark-Nord Lake 1

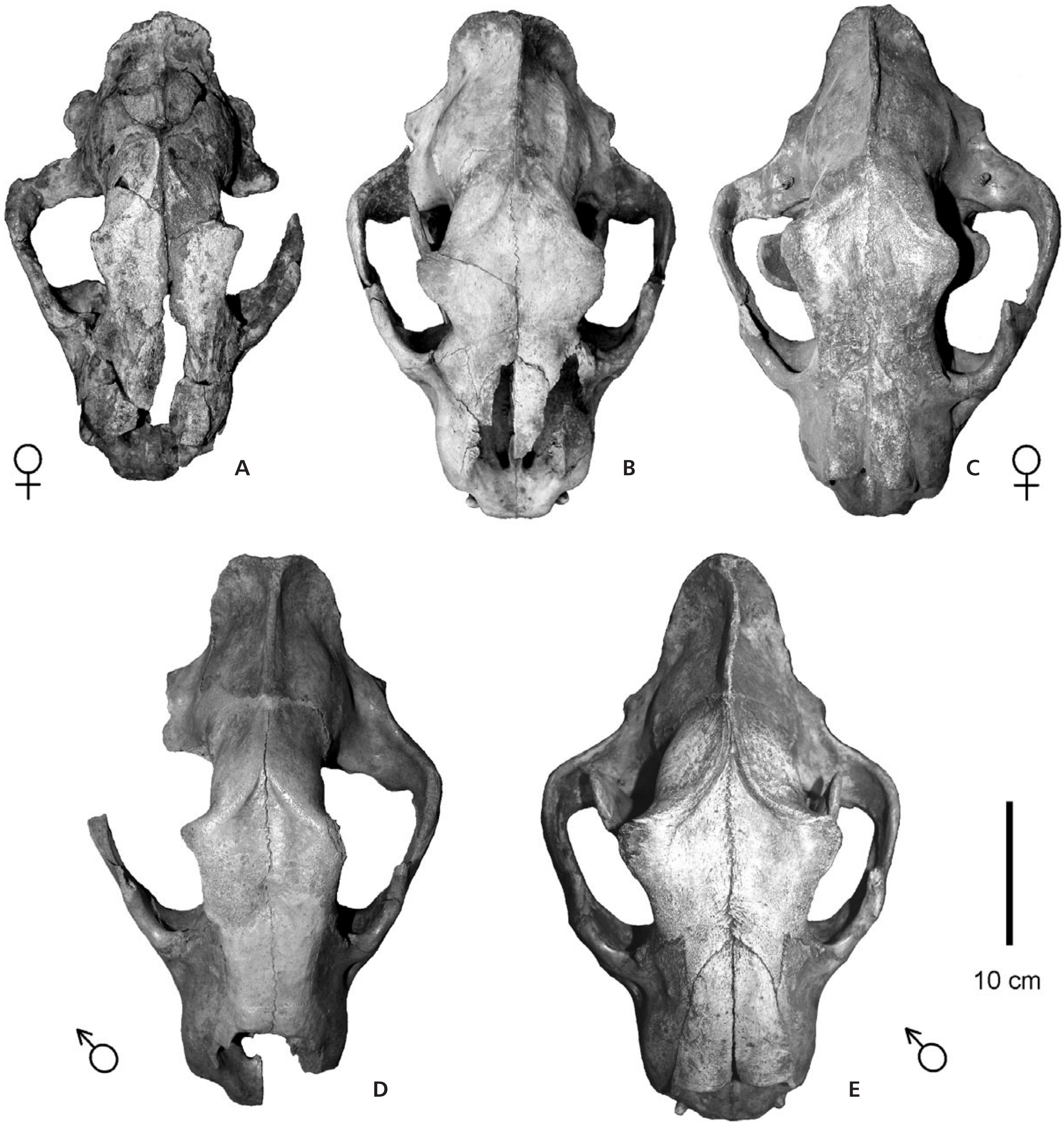


Figure 10. All recently discovered Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) crania from the Czech Republic. • A – skull from the open air loess Berounka River terrace Hýskov site near Beroun (MBKB No. 363a). • B – skull with lower jaw from skeleton 3, the young adult lioness skeleton from the Srbsko Chlum-Komín Cave (NHMP No. R 4406). • C – skull with lower jaw from the Cut-Stone Gallery of the Sloup Cave composite skeleton 2 (AMB without No.). • D – skull from the Cut-Stone Gallery of the Sloup Cave (AMB No. OK 130570). • E – skull with lower jaw from the Cut-Stone Gallery of the Sloup Cave composite skeleton 1 (NHMV No. 1885/0014/4302). All in dorsal view.

(*cf*. Diedrich 2010b, c) and a solitary skull from an Italian cave (Bona 2006) were not included in the statistics because steppe lions seem to have been smaller during warm periods (including the present) than in cold periods (*cf*. Gross 1992), although this is not yet well documented in the fossil record because of the scarcity of Eemian lion material in Europe.

Skeletons 1 and 2 and skull remains from the Sloup Cave. – Both skulls of skeletons 1 and 2 from the Sloup Cave fall within the range of those from small to medium-sized males (Fig. 11A). The third Late Pleistocene skull from the Sloup Cave, which is the largest of the isolated Czech skulls (Fig. 10D, total length 378 mm, condylus width 72 mm), is intermediate in size between skulls 1 and 2. Male skulls from Siegsdorf and Azé are even larger (with lengths between 380 and 420 mm, *cf.* Gross 1992; Fig. 11), as is the skull of the large male skeleton from Arrikrutz (407 mm, *cf.* Altuna 1981). The long bones of both the Sloup Cave skeletons are dissimilar in length (except the humeri in skeleton 1) but are less mixed in skeleton 1 (Vienna), which consists mainly of male bones (*cf.* Fig. 11B–F). Skeleton 2 (Brno) is a mixture of male and female remains (Fig. 3B) with significant variations in long bone dimensions (*cf.* Fig. 11B–F).

Skeleton 3 (Srbsko Chlum-Komín Cave). – The total skull length of this specimen is about 302 mm which is the same as that of the adult female skull from the Perick Caves in Germany (Fig. 12G; Diedrich 2007b). However, skeleton 3 appears to be from a young animal whose skull proportions are similar to the immature lioness skull from the Urşilor Cave (*cf.* Fig. 12A, D). A more useful indicator for sex identification is the small upper jaw P^4 (Perick Caves: 39 mm; Srbsko Chlum-Komín: 34 mm; Siegsdorf: 40 mm; Arrikrutz: 43 mm). Finally, the lower jaws are smaller than those from Siegsdorf and Arrikrutz. The mandible height behind the M_1 for the Srbsko Chlum-Komín specimen is only 48 mm, whereas for Siegsdorf it is 55 mm and for Arrikrutz 60 mm, which which suggests that it is in the female size range. Measurements from skull 3 are clearly inconclusive with regard to the age or sex of this specimen.

Similar variations in dimensions are apparent between the long bones from the Srbsko Chlum-Komín lioness and those from the male lion skeletons of Siegsdorf and Arrikrutz (see Fig. 11). The Srbsko Chlum-Komín specimen is a large female (or young male), while the lion from Siegsdorf is a medium sized male and the lion from Arrikrutz is a very large male.

The lioness from the Srbsko Chlum-Komín Cave is the only immature lion material from that cave and 99% of the steppe lion material from the Sloup Cave can be attributed to adult animals. A similar situation occurs in almost all of the European cave bear dens in which lion remains have been found, supporting the claim that these caves were not used as "cave lion dens" (*cf.* Perick Caves, Bilstein Caves: Diedrich 2009a, b, Urşilor Cave: Diedrich *et al.* 2009).

Lion skull – in-vita damages – lions, hyenas and cave bears as possible bite mark producers

Three skulls, from the Srbsko Chlum-Komín, Sloup and Zoolithen caves, exhibit damage that occurred while the animal was still alive (Fig. 12A–C). All show damage to the brain-case and saggital crest that was in the process of healing. The observed callus formation and deformation structures were probably a reaction to bite damage. One long tooth scratch mark is clearly visible on the Zoolithen Cave holotype skull (Fig. 12C). The brain-case of the Srbsko Chlum-Komín lion exhibits a trauma on the left side (Fig. 12B) affecting the parietal bone and leaving an elongated depression with a parallel crest. This feature runs parallel to the crista saggitalis over the centre of the parietal bone. This damage also caused a marked deformation of the left side of the brain-case and resulted in complete fusion of the suture between the left parietal and the frontal bones. The parietal fracture or scratch may have affected the entire left side of the brain including motor function, auditory, and sensory areas. The skull from skeleton 1 (Vienna) also seems to have bite damage that caused minor deformation on the parietal. This was almost completely healed by the time of death. Frontal damage to a cave bear skull from the Zoolithen Cave is also partly healed (Fig. 13C). Other brain-case pathologies on a *P. l. spelaea* cranium from the open air site at Haltern, north-western Germany, that occurred while the animal was still alive, have been described and illustrated previously (Diedrich 2004). This skull shows a large bone growth 1cm in diameter on the parietal, close to the saggital crest, which has not yet been explained. Damage and pathologies reported in modern African *P. leo* (such as partial cerebella hernia – Tuch & Pohlenz 1973), have not been observed in Late Pleistocene steppe lion skulls, and appear different to the bite damage and pathologies on Pleistocene cranial material discussed herein. Other types of depressions in parietals, occurring in the Late Pleistocene sabre tooth cat *Smilodon fatalis* (*e.g.*, deep pits believed to be neoplasms), have been interpreted to be the result of mechanical strain (Duckler 1997). They are not comparable to the parietal damage presented on the three steppe lion skulls of Fig. 12A–C, which are believed to have had traumatic causes and to most probably result from bite damage caused by canine teeth during fights.

Intraspecific fights between present-day female lions or between male and female lions are quite common and occasionally result in the death of one of the combatants (*cf.* Palomares & Caro 1999, Packer & Pusey 2001). Fights in which lions are critically injured or killed may occur during an attempted takeover of the clan by a male lion or when females vigorously defend their cubs (Estes 1999, Packer & Pusey 2001). Fighting lions often bite each other in the face and head (Schaller 1972, Packer & Pusey 2001). Such scenarios could explain the parietal injury and brain damage in the Pleistocene early adult female lion skeleton (Fig. 5) from Srbsko Chlum-Komín and the skulls from the Sloup and Zoolithen caves (Fig. 12A–C), and would also explain the brain-case damage of other Late Pleistocene steppe lions.

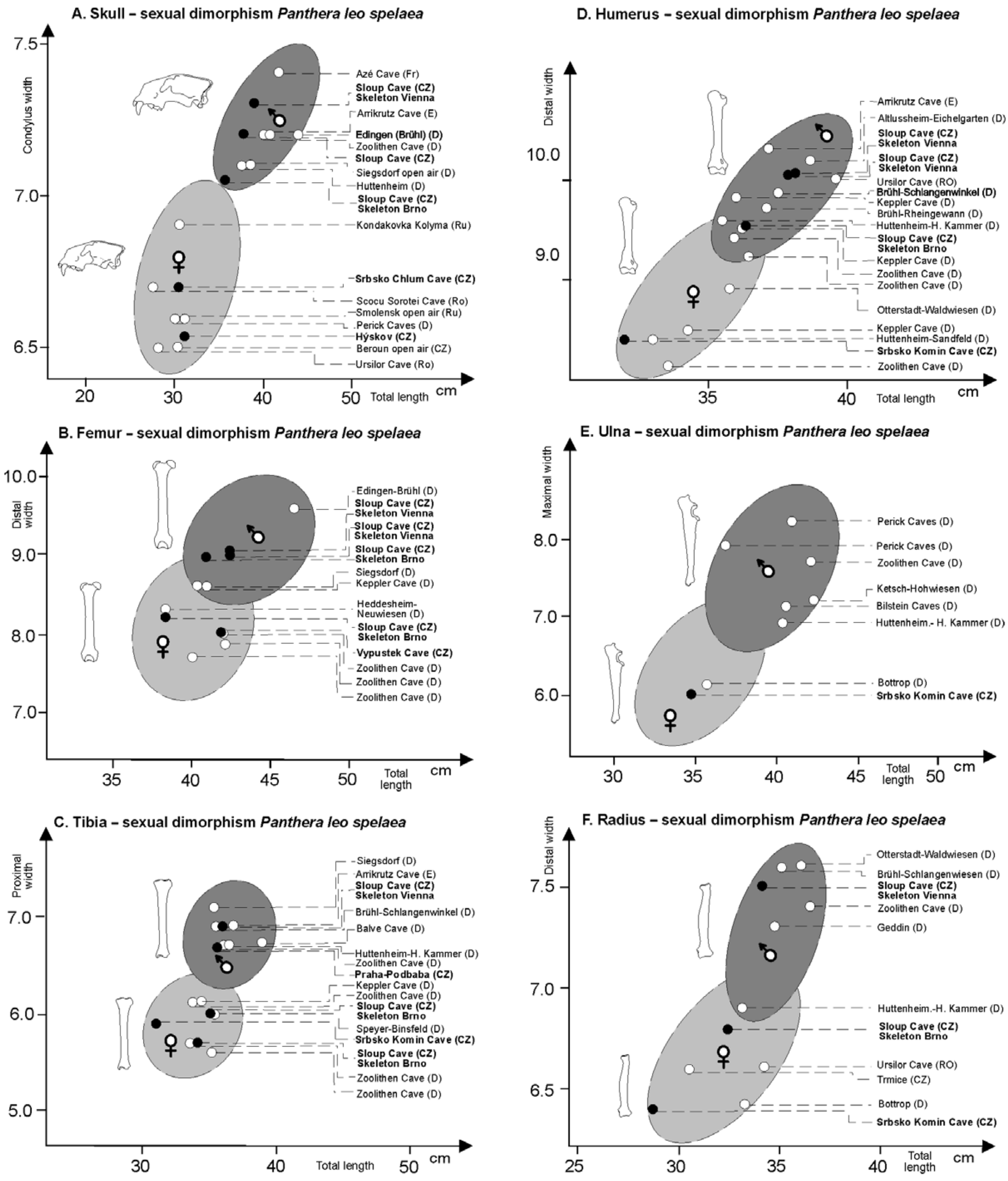


Figure 11. Late Pleistocene Weichselian/Wuermian steppe lion *Panthera leo spelaea* (Goldfuss, 1810) sexual dimorphism: comparisons of skull and long bone dimensions for Czech Republic material with those from other European sites (composed after Altuna 1981; Argant 1988; Diedrich 2009b, 2011a; Diedrich & Rathgeber 2011).

Lions are also known to fight for other reasons, including disputes while feeding on a carcass, territorial disputes between prides, and fights between groups of males, which can all result in similar bite wounds (Schaller 1972, Estes 1999, Packer & Pusey 2001).

Interspecific fights also occur between present-day

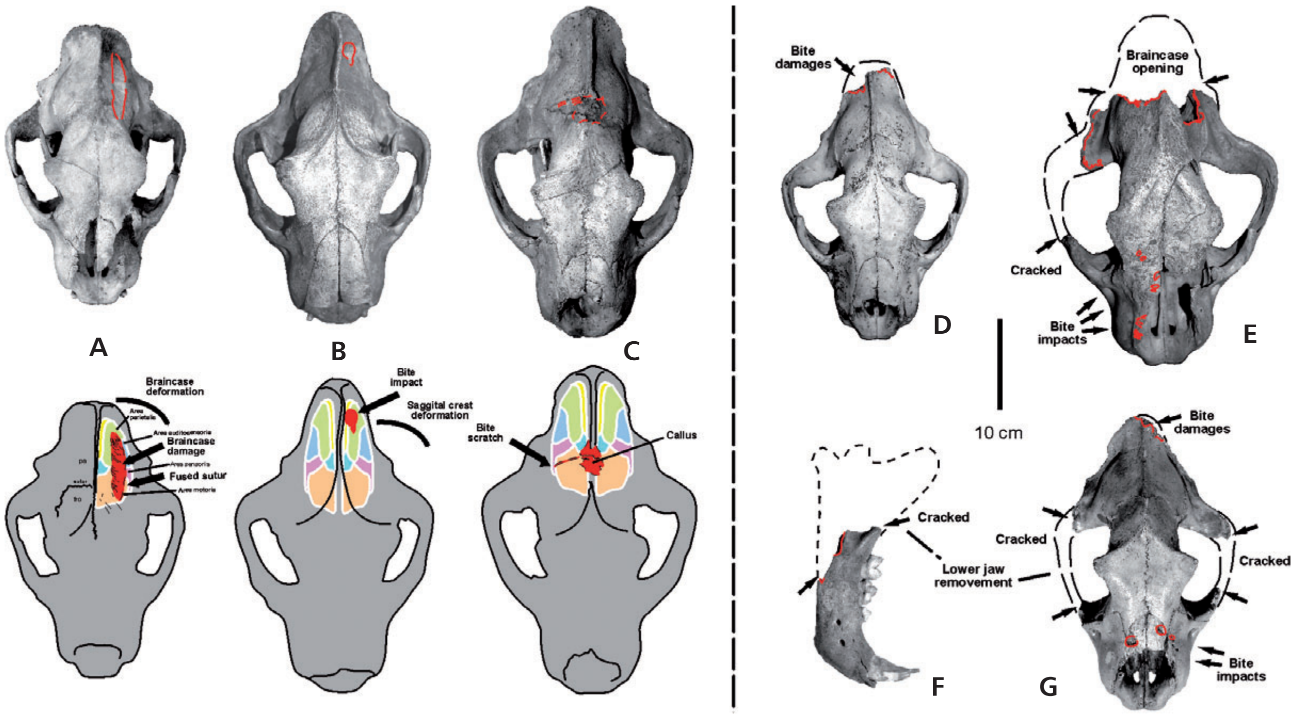


Figure 12. Pre mortem pathologies and post mortem skull damage of the steppe lion *Panthera leo spelaea* (Goldfuss, 1810). • A – skeleton 3 skull from the Srbsko Chlum-Komín Cave with bite damage on the brain-case, in the process of healing. • B – skeleton 1 skull from the Sloup Cave with bite damage in the process of healing and skull deformation. • C – holotype skull from the Zoolithen Cave with bite and scratch damage on the saggital crest of the brain-case. • D – scavenged skull from the Urșilor Cave skeleton with bite damage on the occipital. • E – skull from the Zoolithen Cave with brain-case opening and fractured jugal. • F – lower jaw from the Perick Caves, fractured to remove it from the skull. • G – skull from the Perick Caves with jugal arches fractured for lower jaw removal.

lions and hyenas, with *C. c. crocuta* being one of the main predators in Africa. There are several animal species that can kill hyenas, but lions are their main killers (*cf.* Joubert & Joubert 2003). In one study 13 out of 24 hyena carcasses found had been killed by lions (Kruuk 1972, Joubert & Joubert 2003) and a similar situation is likely to have existed with the Late Pleistocene lions and Ice Age spotted hyenas. Possible supporting evidence comes from hyena skull from the Zoolithen Cave (Fig. 13A) which exhibits considerable bite damage that had partly healed, although it can not yet be accurately determined from the fossil record whether specific injuries were conspecific or inflicted by another species. Similarly for attacks on the steppe lion skull from the same cave (Fig. 13B). Actualistic comparisons will need to be made in future on present day hyenas and lions to compare the different types of damage inflicted by their bites. Where lions are separated from their pride or are not integrated into a pride, individual African lions do feed on carcasses in order to survive in emergencies (Estes 1999). If the injured young lioness from the Srbsko Chlum-Komín Cave tried to intrude into a hyena den, the chances of it winning a battle with hyenas defending their prey-storage and cub-raising den site would be extremely low. Such a defence of dens and juveniles provides the reason for most of the lion kills by present-day hyenas in Africa (Estes 1999, Packer & Pusey 2001). In contrast, African spotted hyenas are well known to kill lion cubs, juveniles, and weak or sick adult lions (Schaller 1972, Estes 1999). Consumption of the victim appears to be more common when food is scarce or a matter of dispute (Palomares & Caro 1999), which explains the presence of complete Pleistocene lion carcasses in hyena or cave bear den sites.

Interspecific fights between lions and cave bears have no modern equivalent and, possibly as a result, the taphonomy of cave bear den caves in Europe has not been well studied. The theory that steppe lions may have hunted cave bears during the Ice Age was established on the basis of new discoveries at the Urșilor Cave and other sites in Germany and the Czech Republic (*cf.* Diedrich 2009b, 2010e, 2011f). A first study of the cave bear bone taphonomy in the Zoolithen Cave (Diedrich 2011f) has suggested new explanations for partly healed bite marks on the brain-cases (frontals) of cave bears (*cf.* Fig. 13C). Only in the Zoolithen Cave have such impressively damaged skulls of the two large cave inhabitants (hyenas and cave bears) and other cave dwellers (lions) been found, prompting the theory that hyenas scavenged on cave bears and that the cave bears were actually hunted by lions (Diedrich 2010e, 2011f). The cranial damage inflicted on living cave

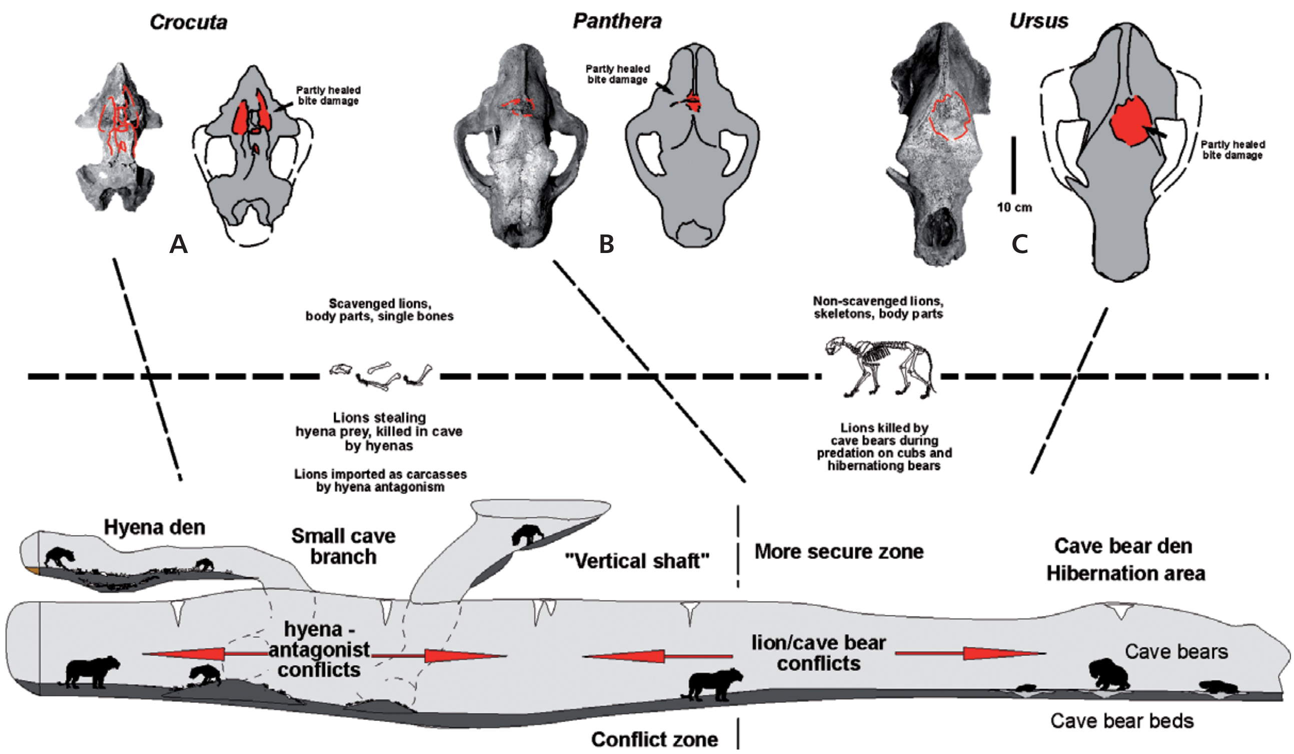


Figure 13. Cave model for the Sloup Cave, Zoolithen Cave, and other large European caves that were used as hyena and cave bear dens. • A–C – three skulls from the Zoolithen Cave all have partly healed bite damage on the brain-case (material in the MB and UE). Such damage could have resulted from different scenarios such as conflicts between hyenas or lions and their cave bear prey, or from interspecies fights, either inside or outside the cave. Lion skeletons from cave bear dens, such as those from the Sloup Cave, are all found deep within the caves whereas incomplete and gnawed lion bones in the hyena den area appear in several cases to have been imported lion remains.

bears could also be possibly attributable to intraspecific aggression. It is further postulated that battles between cave bears and lions may have occurred deep within the cave, in areas that would have been inaccessible to hyenas due to their relatively poor climbing skills (*e.g.* Urșilor Cave, Diedrich 2011f). Cave bears may thus have deliberately sought deep caves in which to hibernate, as protection against lion predation (Diedrich 2009b, 2011f).

Lion skull – post mortem damage and hyena scavenging

Some of the bite damage on lion skulls is obviously post mortem damage, including that seen on the three skulls from the Urșilor, Zoolithen and Perick caves (Fig. 12D–G). The bite marks show no sign of healing and are typically round or oval to triangular, many with associated scratch marks. In some instances portions of the bones have been chewed off. In the Zoolithen Cave skull, the brain-case must have been opened from the occipital side by a large carnivore as a missing jugal arch has also been chewed. Jugal arch damage is also demonstrated on both sides of the skull from the Perick Caves (Fig. 12G). The lower jaw from this skull has also been fractured diagonally behind the last molar tooth in order to facilitate its removal from the skull (Fig. 12F). The predation of Ice Age spotted hyena on lions and importation of their carcases into hyena cave dens may provide an explanation for the general male/female ratios in late Pleistocene bone sites (*cf.* Diedrich 2009a). Modern spotted hyenas do not usually hunt adult male lions, although exceptions to this generality have been reported (Kruuk 1972, Estes 1999). Some carcasses of Ice Age steppe lions may have been left outside the caves (or partly imported to hyena dens), as in Praha-Podbaba river terrace open air site and at the Siegsdorf open air river terrace and lake site in Germany, although the importation of male lion carcasses has now been demonstrated in some European hyena dens (*cf.* Diedrich 2007c, 2009a). There is a correlation between the more damaged lion bones and their occurrence at hyena den sites and prey-bone accumulations. Where there were no hyenas occupying the entrances or side-branches of cave bear den cave systems (*cf.* Fig. 13) the damage to skeletons is reduced, as has recently been shown for the Urșilor Cave (Diedrich 2011f). In the Zoolithen Cave, the large hyena population was also thought to have been responsible for the high proportion and degree of damaged cave bear bones, as has also been described for the Perick Caves and other cave bear den sites in Europe (*cf.* Diedrich 2011f). The bite damage left by hyenas on cave bear bones is similar to that illustrated herein on lion remains. The lion skulls from the Perick Caves (Fig. 12F, G) – as well as remains from the Sloup Cave (*cf*. Diedrich 2011b) – that have possibly been chewed and cracked by hyenas exhibit typical damage to the jugal arches caused during removal of the lower jaw, which also resulted in cracking of the mandibles. While hyenas seem to have been the main scavengers on lion carcasses it remains a possibility that, in stressful situations, lions that perhaps became trapped in a complex cave system with several different levels might have engaged in cannibalism (*e.g*. Urşilor Cave: Diedrich 2011f).

Conclusions

The historical skeleton finds from the Cut-Stone Gallery in the Sloup Cave of the Moravian Karst (Czech Republic) are both composite skeletons. Skeleton 1 (Vienna) includes a higher proportion of original bones, which have come from a single male skeleton. Both of these composite skeletons include about 30% to 50% bone casts and also pedal bones from the Výpustek Cave in the Czech Republic. The lion bones and skeletal remains were found either within hyena dens and prey-bone accumulations, or deeper within cave bear dens. The material from the Sloup Cave indicates derivation from several different steppe lion *Panthera leo spelaea* (Goldfuss, 1810) skeletons, found within the cave bear hibernation areas deep inside the cave, with all of the material being from adult lions or lionesses. This situation is different from the relatively complete original skeleton of a diseased, young adult lioness from the Srbsko Chlum-Komín Cave hyena den site in the Bohemian Karst (Czech Republic), which may have been killed by the hyena clan that occupied the same cave, when it attempted to steal their prey. In overlapping hyena and cave bear dens such as the Sloup Cave and the German Zoolithen Cave, the lion bone taphonomy is more complex. Hyenas appear to have dispersed the lion skeletons and may also have imported parts of some lion carcasses for consumption inside the cave. In so doing, they damaged bones, opened brain-cases in order to feed on the brain, and fractured the lower jaws. Injuries on steppe lion skulls from different caves, that were in the process of healing, provide evidence of either intraspecific conflicts between lions or interspecific fights between lions and either hyenas or cave bears (*e.g*., partly healed cranial bite damage, Zoolithen Cave (Fig. 12). The presence of articulated lion skeletons deep inside cave bear dens can be explained by interspecific fights during predation by lions on cave bears, in which lions were killed by bears. Less then 1% of the bones in cave bear dens are from steppe lions but it appears that, from time to time, a lion intent on predation may have been killed by the cave bears protecting their cubs. Cave bears were not carnivorous and hence would not have fed on any lions that they killed, and hyenas often had no access to the deeper passages in the caves. The presence of steppe lion skeletons such as the three recently discovered between articulated cave bear skeletons and bonebeds on hibernation plateaus deep within the Romanian Urşilor Cave, appear to offer a taphonomic model for the presence of steppe lion carcasses and bones in other large cave bear dens such as the Sloup Cave, the Výpustek Cave, the Zoolithen Cave, the Perick Caves, and many other European sites.

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