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An Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the Late Pleistocene hyena den of the Sloup Cave in the Moravian Karst, Czech Republic

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A Late Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) population from the cave bear den Sloup Cave, Moravia (Czech Republic) consists of mainly adult/senior and few cub/juvenile remains and coprolites, and 139 prey bones. Hyenas used the Nicová Cave branch that is connected to the entrance area mainly as a communal den site. Prey bone damage is most visible on the imported woolly rhinoceros remains. The partly excavated prey bone accumulation consists of a single woolly mammoth *Mammuthus primigenius* (Blumenbach 1799) tooth (2%), mainly *Coelodonta antiquitatis* (Blumenbach 1807) remains (16%), 4% *Bos primigenius* (Bojanus 1827) and 1% each of *Megaloceros giganteus* (Blumenbach 1799) and *Rangifer tarandus* (Linnaeus 1758). The other carnivores such as *Panthera leo spelaea* (Goldfuss 1810), *Gulo gulo* (Linnaeus 1758) and *Canis lupus* (Linnaeus 1758) subsp. are less represented (1–3%). Wolverines might have been imported also as prey remains, whereas wolves also possibly used this cave on a short-term basis, whereas steppe lions seem to have preyed upon cave bears deeper in the cave periodically, where even skeletons of *P. leo spelaea* were found in the Elisabeth Cave part.

Keywords: *Crocuta crocuta spelaea* (Goldfuss 1823); population; coprolites; Upper Pleistocene hyena den; paleobiology and cannibalism; Sloup Cave (Czech Republic)

Introduction

The Sloup Cave at 465 m.a.s.l in the Moravian Karst of the Czech Republic (Figure 1A) became, besides the German Zoolithen Cave (Esper 1774; Buckland 1823) and the Austrian Drachen Cave near Mixnitz (Abel and Kyrle 1931) in historical times, one of Europe's most famous caves. It was a den and one of the largest cave bear populations where carcasses accumulated including many skeleton bones with pathologies (Wankel 1868).

Wankel figured the first 'complete cave hyena skull' from the Sloup Cave part called Nicová Cave branch (Figure 1B and C). The skull with its possibly original articulated lower jaw is still preserved (Figure 1D and E). The excavation places in the Sloup Cave of the large bone collection of Wankel, which was excavated in the cave historically at different places by different persons including Sedlak, are marked in one of the first cave maps (cf. Wankel 1868). Those maps and the cave and research history were published in a revision by Musil (2002). The major amount of bones from the Sloup Cave consist of several thousands of cave bear bones and teeth, with a population given at that time of 998 individual minimum individual number (MNI) remains (Wankel 1888). In addition, there are only 139 non-cave bear bones and 23 hyena coprolites. The Wankel collection from the Sloup Cave and Výpustek Cave was donated by the Anthropologische Gesellschaft and bookmarked in the Vienna Museum's catalogue in 1885. Most of this historical collection that was collected between 1868 and 1885 is recently under a new inventory process. The redescription of this material began with the wolverine *Gulo gulo* (Diedrich 2009a) and steppe lion remains (Diedrich 2011b) of which later new finds were made within a new excavation in one central part of the Sloup Cave (U Řezaného kamene = cut-stone branch, Seitl 1998; Figure 2). The new excavations in 1998 also delivered new hyena material with a lower jaw and skull fragment, which were found in the middle cave area.

The 'cave hyena den' research and interpretation of 'hyena-accumulated bone assemblages' versus 'flooding accumulation' started with the revolutionary works of Buckland at the Kent's Cavern in England and the Zoolithen Cave in Germany (Buckland 1823), where the high bone amounts were partly explained by hyena activities, revising Espers (1794) 'biblical flooding' scenarios. Those 'hyena den bone accumulation' discussions continued with works on open air gypsum karst sites in Germany by Giebel (1850) and Nehring (1880). More recent work was published for a Czech Cave in Moravia by Musil (1962), Fosse et al. (1998) and Tournepiche and Couture (1999) for hyena den caves in France, open air and cave den sites in northern Germany (Diedrich 2006b,

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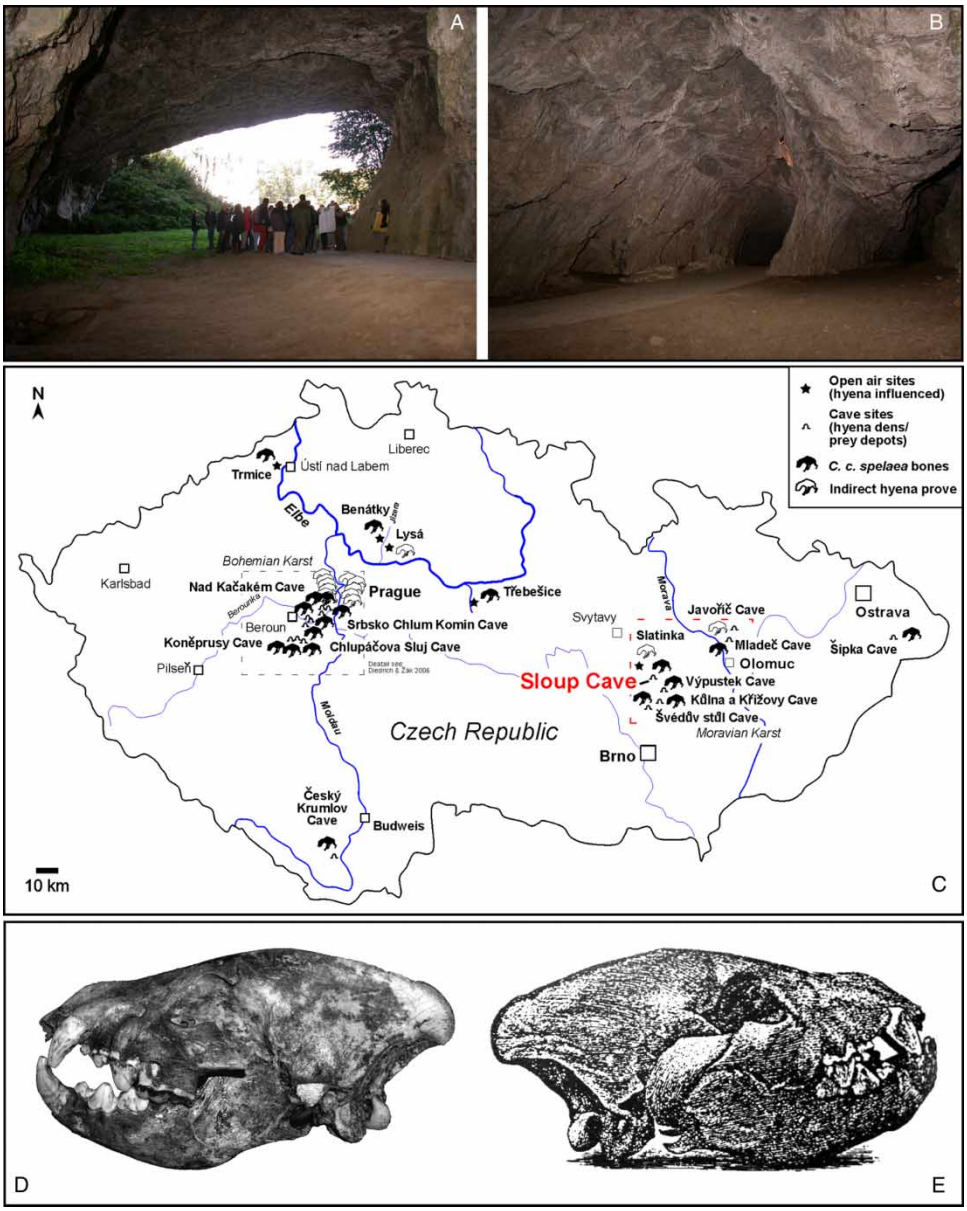

Figure 1. A and B. Nicová Cave branch hyena den of the Sloup Cave with the entrance and branching part (photos from Czech Cave administration). C. Topographical positions of the Upper Pleistocene spotted hyena *C. crocuta spelaea* (Goldfuss) sites in Czech Republic (after Musil 1956, 1962, Diedrich 2011a). The Sloup Cave is situated in the Moravian Karst (frame see: hyena den localities in Central Bohemia around Prague in: Diedrich and Žák (2006)). D. Original skull in lateral left view (NHMV no. 2008z0087/0000), see also Figure 3. E. Historical figuration of the 'hyena skull from the Nicová Cave branch' of the Sloup Cave in lateral right view (from Wankel (1888)).

2007b, 2008b, 2010b) or cave and open air den sites in the Bohemian Karst of the Czech Republic (Diedrich and Žák 2006) or several cave sites in Germany (Diedrich 2005a, 2008b, 2009c, 2011d, 2011h, 2011j). There, the most interesting site is the Teufelskammer Cave in the Neanderthal Valley, because there the question arose, if there was also a competition between Neanderthals and carnivores about the cave entrances and cave use (Diedrich 2011a), such as further recently discussed at the Middle Paleolithic Balve Cave where bones were accumulated not mainly by humans, instead by hyenas (Diedrich 2011e, 2011n).

From the Moravian Karst (Czech Republic), a few sites were described in detail to be hyena dens such as the Švédův stůl Cave (Musil 1962). An overview analysis for hyena dens in this region is a future project. A revision of the hyena dens of the Bohemian Karst was already published with an overview of all cave and open air sites

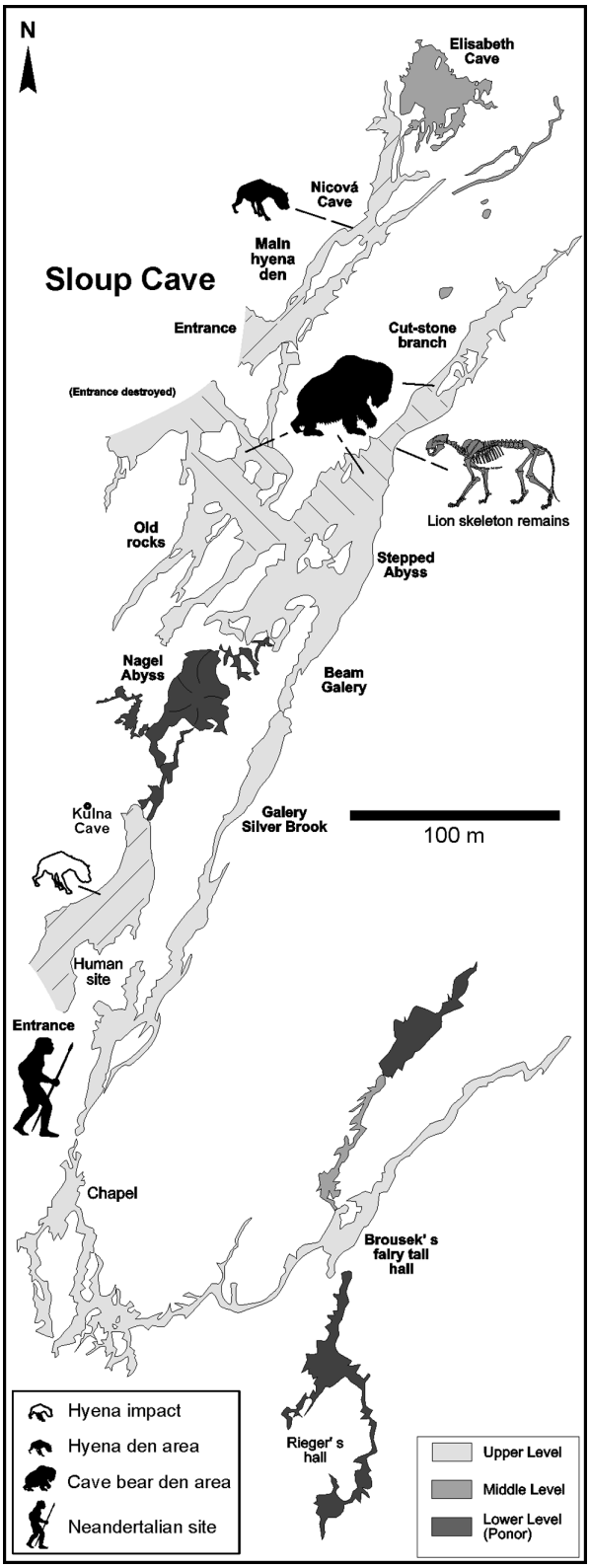

Figure 2. Sloup Cave map with main hyena and cave bear den areas (redrawn cave map after Zajíček 2007; Archaeological site Kůlna Cave after Musil 1988; hyena/cave bear den areas and lion skeleton form Diedrich 2009a, 2011b).

around Prague and typical hyena den indicators (Diedrich and Žák 2006), whereas recently, a large number of identified hyena dens have been found in the Czech Republic mainly in caves, but also at open air sites (see Figure 2). The den type identification is important to understand hyenas not to be real or permanent 'cave inhabitants' and the lack of open air sites as results of overlooking such. The best example of a giant bone accumulation along mammoth steppe environment river streams is the Bottrop hyena den site in northern Germany (Diedrich 2011m). At the moment, there is a discrepancy between Late Pleistocene hyena den cave sites and Modern open air hyena den sites in Africa – but obviously in Europe this is the result of non-interpretations of hyena bone sites outside of caves. Important here is not only the identification of the dens but also as demonstrated here are the faunal hyena prey assemblages, which cannot be used 100% as 'climatic' or 'prey fauna' indicators simply, as a result of prey specialisations of hyenas being dependent upon season, prey abundance and topography and related prey presence or absence (Diedrich 2010b). In the Bohemian Karst, woolly mammoth is nearly absent in mountainous regions (about 200–800 m in elevation), whereas a horse hunting specialisation was reported for the Srbsko Chlum Komin Cave (Diedrich 2010b), such as that known at a French Rochelot Cave (Tournepiche and Couture 1999). Other hyena dens such as the Fuchsluken Cave in Central Germany show a specialisation on hunting steppe bison and urs (Diedrich 2009b). Even so, hyena-accumulated bone assemblages can be used for the reconstruction of the surrounding paleoenvironment, and partly for climatic analyses, especially for megafauna interactions of predators and their prey.

In Central Europe, there are still few hyena den caves that have been well studied in detail, especially with new excavations and exact bone mappings, such as the Rochelot Cave of France, where even Neanderthal remains were found within the hyena prey bone accumulation (Tournepiche and Couture 1999). Most of the hyena den cave sites being restudied (e.g. Teufelskammer Cave, Perick Caves and Zoolithen Caves) lack information and material, as a result of the historical exploration time.

Within the Czech Republic, the only excavated hyena den is Švédův stůl Cave (Musil 1962), which has not yet been compared with modern hyena den types. In the context of 'European Ice Age spotted hyena' research, one of the oldest large bone collections from the Sloup Cave has generated new interest with its hyena and prey bone material, especially for paleoecological studies with hyena den types, bone taphonomy, population structures, cave bear and lion antagonism, megafauna impact and paleoenvironmental and paleoclimatic studies. Herein,

the interactions of hyenas, prey and antagonists, and the den type and cave function are discussed as a contribution to the 'European Ice Age spotted hyena project', which focuses on the paleoecology of those most important Ice Age carnivores.

Material and methods

The 139 non-cave bear bones and 23 hyena coprolites and cave bear bones studied here are housed in different European museum collections. The main Sloup Cave collection was collected and excavated without mapping documentation, but with stratigraphical course context historically (1868–1885) and is mainly housed as one of the first European 'natural cabinet' collections in the Natural History Museum Vienna (NHMW). The bone material in the collection of the NHMW, which is a selection of large and better preserved bones (lacks in hyena dens to expected abundant bone fragments), has the old stamp-like labels attached to the bones; typical of all the Sloup Cave bones is from Wankel and was inventoried for the first time completely within this study by the company Paleologic (Tables 1–7). The Sloup Cave and Výpustek Cave megafauna of the Wankel collection was received in 1885 as one of the first paleontological collections of the NHMW, but was also excavated in 1881–1882 by Sedlak who sold this collection, whereas both sites were partly mixed and mislabelled later (e.g. two locality names on one bone or label) with incorrect locality names. This problem could be solved in most cases, because of the different bone preservations (colour, rounded bone corners, etc.) at both cave sites. Also, the first figured hyena skull from the Sloup Cave (Figure 1D and E) is by its preservation possibly from the Výpustek Cave. This largest known Sloup Cave bone collection was donated by the Anthropologische Gesellschaft, whereas a composed lion skeleton, even including again Výpustek Cave material was a gift to the Vienna Museum by the Prince of Liechtenstein (Diedrich 2009b, 2011b, 2011d). A few hyena jaws are deposited in the Staatliches Museum für Naturkunde Stuttgart (SMNS). Newly excavated material in 1998 by Seitl is housed in the Anthropos Museum Brno (AMB). The cave was finally explored during the 13th International Cave Bear Symposium in 2007 to identify the historical excavation areas of Sedlak and the new ones of Seitl and to understand the cave morphology and different uses by hyenas, cave bears and lions. The metric scheme of teeth and bone measurements was followed as in Gross (1992). Only four tooth wear stages were used to distinguish the main individual ages: (1) Milk dentition = cubs to early juveniles, (2) Non-used permanent teeth = juveniles to early adult, (3) Halfly rubbed permanent teeth = adult and (4) More than 2/3 rubbed teeth or only roots = high adult to senior.

Geology and stratigraphy

The Sloup Cave north of the Moravian Karst (Czech Republic) is situated in the Devonian limestones of the Sloupské Valley at the foot of the eastern valley slope (Zajíček 2007). The cave system comprises upper and lower subhorizontal cave levels interconnected by several chasms up to 70 m deep (Figure 2), whereas the length of the cave system exceeds 6 km (Kadlec et al. 2001). The modern stream, known as the Sloupský Creek, disappears in the western part of the upper level, and passes through unexplored vertical paths and re-appears at the lower level, then flows to the Amatérská Cave (Kadlec et al. 2001). Cave sediments of different ages ranging between Pliocene and Holocene are preserved in the cave system, which allow the reconstruction of the cave genesis and refilling of its different branches (Kadlec et al. 2001; Sroubek et al. 2001) such as that at the cut-stone branch (cf. Figure 2). There, a sequence is present with alternating beds of sand- and silt-dominated sediments and clayey silt containing abundant bones of the Late Pleistocene fauna (mainly cave bears, Wankel 1868) and limestone and greywacke clasts. The bones were polished in several cases by water transport. The sediments in different cave branches seem to originate or were influenced by periodical floods (Kadlec et al. 2001). During the Upper Pleistocene flooding episodes, silt- and sand-sized material with frequent limestone clasts and abundant vertebrate bones was transported from the surface or higher located cavities through karst chimneys into corridors of the upper cave level (Kadlec et al. 2001), which explains the mixing of sub-autochthonous cave faunal remains and sediments from outside of the cave. The bones were transported only in the cave itself at many places (e.g. cut-stone branch, Wankel 1868; Seitl 1998). These detrital sediments were often overlain by a flowstone layer up to 20 cm thick (Kadlec et al. 2001). The Late Pleistocene section at the hyena den Nicová Cave branch is still open (Figure 1B and C) and shows a slightly different profile of about 1.2 m in thickness (Wankel 1868), whereas the lower layers are again fluvial-influenced bone-rich sediments (from which the herein-described material seems to have been collected), but there, the uppermost layers consist of limestone talus pebbles. The hyena den area Nicová Cave branch also delivered many well-preserved large coprolites from the 'bone layer' (Wankel 1868). These pellets could not have been transported far, nor could have been washed into the cave branch from outside of the cave. These pellets indicate faecal aggregate disarticulation into single pellets only due to quick floods (or trampling) in the cave branch itself with a few metres transport only.

Table 1. *C. crocuta spelaea* (Goldfuss 1823) remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type/ coprolites	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
1	2008z0087/0000	Cranium	Nearly complete, without left jugal, no Incisive teeth, right P4, Length 315 mm, Frontal width 89 mm, Condylus width 57 mm, Maxillary width 120 mm, P3 width 26 mm, P4 width 41 mm			Adult	Female		Wankel 1885	Natural History Museum Vienna
2	2008z0087/0001	Cranium	Brain case, Pathology on saggital crest			High adult			1879	Natural History Museum Vienna
3	2008z0087/0002	Cranium	Incomplete, without jugals, no right P^1, Length estimated 315 mm, Frontal width 95 mm, Condylus width 56 mm, Maxillary width 118 mm, P^3 width 25 mm, P^4 width 42 mm			Adult	Female	×	Wankel 1885	Natural History Museum Vienna
4	2008z0087/0003	Cranium	Maxillary, With $P^{2 \text{ to } 3}$, P^3 width 25 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna
5	2008z0087/0004	Cranium	Maxillary, with $P^{3 \text{ to } 4}$ P^4 width 47 mm, P^3 width 26 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna
6	OK 29750	Cranium	Fragment			Adult			Seitl 1998	Anthropos Museum Brno
7	OK 21800	Mandible	Half, with	×		Adult			Seitl 1998	Anthropos Museum Brno
8	2008z0087/0005	Mandible	Without ramus, no Incisives, M^1 width 30 mm, with plaster refilled		×	Adult	Male		Wankel 1885	Natural History Museum Vienna
9	2008z0087/0006	Mandible	Without all I_1, C to M_2, M_1 32 mm, Height 51 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna
10	2008z0087/0007	Mandible	Incomplete, With P_2 to 4, M_1 M1 width 34 mm, Height 50 mm		×	High adult	Female		Wankel 1885	Natural History Museum Vienna
11	2008z0087/0008	Mandible	Incomplete, With $P_{2 \text{ to } 4}$, M1 M1 width 32 mm, Height 51 mm		×	High adult	Female		Wankel 1885	Natural History Museum Vienna
12	2008z0087/0009	Mandible	Incomplete, without ramus, all Incisive, M1 width 32 mm	×		Senile	Female	×	Wankel 1885	Natural History Museum Vienna
13	2008z0087/0010	Mandible	Incomplete, without ramus, with $P_{2 \text{ to } 4}$		×	Senile			Wankel 1885	Natural History Museum Vienna

Table 1 – *continued*

No.	Inv. no.	Bone type/ coprolites	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
14	2008z0087/0011	Mandible	Incomplete, Milk dentition, breaking through of the M_1, M_1 width 31 mm		×	Early juvenile	Male		Wankel 1885	Natural History Museum Vienna
15	2008z0087/0012	Mandible	Incomplete, without ramus, no I_1 M_1 width 33 mm	×		High adult	Female	×	Wankel 1885	Natural History Museum Vienna
16	2008z0087/0013	Mandible	Incomplete, without ramus, no C and I, M_1 width 30 mm, Height 42 mm		×	Adult	Male	×	Wankel 1885	Natural History Museum Vienna
17	2008z0087/0014	Mandible	Incomplete, without ramus, no C and I, M_1 width 3.0 cm		×	High adult	Male	×	Wankel 1885	Natural History Museum Vienna
18	2008z0087/0015	Mandible	Incomplete, with $P_{3\ to\ 4}$		×	Adult		×	Wankel 1885	Natural History Museum Vienna
19	Without no.	Mandible	Incomplete, with			Adult		×	–	Staatliche Naturhistorische Sammlung Stuttgart
20	Without no	Mandible				Adult			–	Staatliche Naturhistorische Sammlung Stuttgart
21	2008z0087/0016	Tooth	C	×		Adult			Wankel 1885	Natural History Museum Vienna
22	2008z0087/0017	Tooth	C			Adult			Wankel 1885	Natural History Museum Vienna
23	2008z0087/0018	Tooth	C			Adult			Wankel 1885	Natural History Museum Vienna
24	2008z0087/00019	Tooth	C			Adult			Wankel 1885	Natural History Museum Vienna
25	2008z0087/0020	Tooth	C			Adult			Wankel 1885	Natural History Museum Vienna
26	2008z0087/0021	Tooth	C			High adult			Wankel 1885	Natural History Museum Vienna
27	2008z0087/0022	Tooth	C			High adult			Wankel 1885	Natural History Museum Vienna
28	2008z0087/0023	Tooth	C			Senile			Wankel 1885	Natural History Museum Vienna
29	2008z0087/0024	Tooth	C			Senile			Wankel 1885	Natural History Museum Vienna
30	2008z0087/0025	Tooth	Upper jaw P^2			Adult			Wankel 1885	Natural History Museum Vienna
31	2008z0087/0026	Tooth	Upper jaw P^3 Width 25 mm		×	High adult	Male		Wankel 1885	Natural History Museum Vienna
32	2008z0087/0027	Tooth	Upper jaw P^3 Width 27 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna
33	2008z0087/0028	Tooth	Upper jaw P^3, half	×		Adult			Wankel 1885	Natural History Museum Vienna

34	2008z0087/0032	Tooth	Upper jaw P^4	×		Adult			Wankel 1885	Natural History Museum Vienna	
35	2008z0087/0033	Tooth	Upper jaw P^4, Width 41 mm		×	Adult			Wankel 1885	Natural History Museum Vienna	
36	2008z0087/0029	Tooth	Upper jaw P^4, fragment	×					Wankel 1885	Natural History Museum Vienna	
37	2008z0087/0030	Tooth	Lower jaw P_3		×	High adult			Wankel 1885	Natural History Museum Vienna	
38	2008z0087/0031	Tooth	Lower jaw P_3		×	Senile			Wankel 1885	Natural History Museum Vienna	
39	2008z0087/0034	Tooth	Lower jaw P_4, width 24 mm	×		Adult			Wankel 1885	Natural History Museum Vienna	
40	2008z0087/0035	Tooth	Lower jaw M_1, width 33 mm		×	Adult	Female		Wankel 1885	Natural History Museum Vienna	
41	2008z0087/0036	Tooth	Lower jaw M_1, width 33 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna	
42	2008z0087/0037	Tooth	Lower jaw M_1, width 31 mm	×		Early adult	Male		Wankel 1885	Natural History Museum Vienna	
43	2008z0087/0038	Tooth	Lower jaw M_1, width 32 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna	
44	2008z0087/0039	Tooth	Lower jaw M_1, width 34 mm	×		Adult	Female		Wankel 1885	Natural History Museum Vienna	
45	2008z0087/0040	Tooth	Lower jaw M_1, width 30 mm		×	Adult	Male		Wankel 1885	Natural History Museum Vienna	
46	2008z0087/0041	Humerus	Complete, Length 261 mm, Distal width 61 mm		×	Adult to senile	Female		Wankel 1885	Natural History Museum Vienna	
47	2008z0087/0042	Humerus	Complete, Length 255 mm, Distal width 60 mm	×		Adult to senile	Female		Wankel 1885	Natural History Museum Vienna	
48	2008z0087/0043	Humerus	Nearly complete, Length 234 mm, Distal width 54 mm		×	Adult to senile	Male		Wankel 1885	Natural History Museum Vienna	
49	2008z0087/0044	Radius	Complete Length 243 mm Distal width 48 mm	×		Adult to senile	Female		Wankel 1885	Natural History Museum Vienna	
50	2008z0087/0045	Radius	Complete Length 238 mm Distal width 46 mm	×		Adult to senile	Female		Wankel 1885	Natural History Museum Vienna	
51	2008z0087/0046	Radius	Complete Length 236 mm Distal width 48 mm		×	Adult to senile	Female		1881, Wankel 1885	Natural History Museum Vienna	
52	2008z0087/0047	Radius	Without distal joint	×		Adult to senile	Female	chewed	Wankel 1885	Natural History Museum Vienna	
53	2008z0087/0048	Metacarpus	Mc IV, complete, Length 96 mm		×	Adult to senile			Wankel 1885	Natural History Museum Vienna	
54	2008z0087/00049	Metacarpus	Mc III, complete, Length 87 mm	×		Adult to senile			Wankel 1885	Natural History Museum Vienna	

Table 1 – *continued*

No.	Inv. no.	Bone type/ coprolites	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
55	2008z0087/0050	Metacarpus	Mc II, complete, Length 78 mm		×	Adult to senile			Wankel 1885	Natural History Museum Vienna
56	2008z0087/0051	Cervical vertebra	Atlas			Adult to senile			Wankel 1885	Natural History Museum Vienna
57	2008z0087/0052	Cervical vertebra	Atlas, incomplete			Adult to senile			Wankel 1885	Natural History Museum Vienna
58	2008z0087/0053	Thoracic vertebra	T2, complete			Adult to senile			Wankel 1885	Natural History Museum Vienna
59	2008z0087/0054	Sacrum	Incomplete			Adult to high adult			Wankel 1885	Natural History Museum Vienna
60	2008z0087/0055	Femur	Nearly complete, Length 2.1 mm, Distal width 5.7 cm	×		Adult to senile	Female		Wankel 1885	Natural History Museum Vienna
61	2008z0087/0056	Femur	Nearly complete, Length 281 mm, Distal width 57 mm		×	Adult to senile	Female		Wankel 1885	Natural History Museum Vienna
62	2008z0087/0057	Tibia	Nearly complete, Length 218 mm, Distal width 42 mm		×	Adult to senile			Wankel 1885	Natural History Museum Vienna
63	2008z0087/0058	Tibia	Complete, Length 202 mm, Distal width 40 mm		×	Adult to senile	Male		1881, Wankel 1885	Natural History Museum Vienna
64	2008z0087/0059	Coprolite	Double pellet						1887, Wankel 1885	Natural History Museum Vienna
65	2008z0087/0060	Coprolite	Middle disc pellet						1887, Wankel 1885	Natural History Museum Vienna
66	2008z0087/0061	Coprolite	Middle disc pellet						1887, Wankel 1885	Natural History Museum Vienna
67	2008z0087/0062	Coprolite	Middle disc pellet						Wankel 1885	Natural History Museum Vienna
68	2008z0087/0063	Coprolite	Drop-shaped end pellet						Wankel 1885	Natural History Museum Vienna
69	2008z0087/0064	Coprolite	Oval middle pellet						Wankel 1885	Natural History Museum Vienna
70	2008z0087/0065	Coprolite	Drop-shaped end pellet						Wankel 1885	Natural History Museum Vienna
71	2008z0087/0066	Coprolite	Drop-shaped end pellet						Wankel 1885	Natural History Museum Vienna
72	2008z0087/0067	Coprolite	Oval end pellet, bone fragment visible						1878, Wankel 1885	Natural History Museum Vienna
73	2008z0087/0068	Coprolite	Middle part of pellet aggregate						Wankel 1885	Natural History Museum Vienna
74	2008z0087/00069	Coprolite	Middle part of pellet aggregate, bone fragment visible						1878, Wankel 1885	Natural History Museum Vienna

75	2008z0087/0070	Coprolite	Drop-shaped end pellet, pebble visible	Wankel 1885	Natural History Museum Vienna
76	2008z0087/0071	Coprolite	Middle disc pellet	Wankel 1885	Natural History Museum Vienna
77	2008z0087/00072	Coprolite	Middle part of pellet aggregate	Wankel 1885	Natural History Museum Vienna
78	2008z0087/0073	Coprolite	End part of pellet aggregate	Wankel 1885	Natural History Museum Vienna
79	2008z0087/0074	Coprolite	Double pellet	Wankel 1885	Natural History Museum Vienna
80	2008z0087/0075	Coprolite	Double pellet	Wankel 1885	Natural History Museum Vienna
81	2008z0087/0076	Coprolite	Single small pellet from aggregate, bone fragment visible	Wankel 1885	Natural History Museum Vienna
82	2008z0087/0077	Coprolite	Single small pellet from aggregate	Wankel 1885	Natural History Museum Vienna
83	2008z0087/0078	Coprolite	Single small pellet from aggregate, bone fragment visible	Wankel 1885	Natural History Museum Vienna
84	2008z0087/0079	Coprolite	Small double drop shaped pellet	Wankel 1885	Natural History Museum Vienna
85	2008z0087/00480	Coprolite	Small oval pellet	Wankel 1885	Natural History Museum Vienna
86	2008z0087/0081	Coprolite	Small oval pellet	Wankel 1885	Natural History Museum Vienna

Table 2. *M. primigenius* remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
1	2008z0087/0082	Tooth	M_3, incomplete	×		Adult			Sedlak 1897	Natural History Museum Vienna

Table 3. *C. antiquitatis* remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
1	2008z0092/0001	Maxillary	Fragment, with P^4, M^1			Senile			Sedlak 1897	Natural History Museum Vienna
2	2008z0092/0002	Tooth	Dm3	×		Calf			Wankel 1885	Natural History Museum Vienna
3	2008z0092/0003	Tooth	Dm3		×	Calf			Wankel 1885	Natural History Museum Vienna
4	2008z0092/0004	Tooth	Upper jaw P^4	×		Adolescent			Wankel 1885	Natural History Museum Vienna
5	2008z0092/0005	Tooth	Upper jaw M^1	×		Adult			Wankel 1885	Natural History Museum Vienna
6	2008z0092/0006	Tooth	Upper jaw M^1		×	Adult			Wankel 1885	Natural History Museum Vienna
7	2008z0092/0007	Tooth	Upper jaw P^4	×		Senile			Wankel 1885	Natural History Museum Vienna
8	2008z0092/0008	Tooth	Lower jaw PM3		×	Adult			Wankel 1885	Natural History Museum Vienna
9	2008z0092/0009	Tooth	Lower jaw M1		×	Adult			Wankel 1885	Natural History Museum Vienna
10	2008z0092/0010	Ulna/Radius	Incomplete		×	Adult		×	Wankel 1885	Natural History Museum Vienna
11	2008z0092/0011	Radius	Incomplete	×		Adult		×	Wankel 1885	Natural History Museum Vienna
12	2008z0092/0012	Ulna	Incomplete	×		Adult		×	Wankel 1885	Natural History Museum Vienna
13	2008z0092/0013	Atlas	Incomplete			Adult		×	Wankel 1885	Natural History Museum Vienna
14	2008z0092/0014	Cervical vertebra	Middle, incomplete			Adult		×	Wankel 1885	Natural History Museum Vienna
15	2008z0092/0015	Cervical vertebra	Middle, incomplete			Adult		×	Wankel 1885	Natural History Museum Vienna
16	2008z0092/0016	Pelvis	Acetabulum		×	Adult		×	Wankel 1885	Natural History Museum Vienna
17	2008z0092/0017	Pelvis	Acetabulum	×		Adult		×	Wankel 1885	Natural History Museum Vienna
18	2008z0092/0018	Tibia	Incomplete		×	Adult		×	Wankel 1885	Natural History Museum Vienna
19	2008z0092/0019	Tibia	Incomplete		×	Adult		×	Wankel 1885	Natural History Museum Vienna

Paleontology

The Sloup Cave bones of the Wankel collection were determined with the Late Pleistocene megafauna: *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bos primigenius*, *Equus caballus* cf. *przewalski*, *Megaloceros giganteus* and *Rangifer tarandus*, mainly *Ursus* '*spelaeus*' (subspecies unclear), *Crocuta crocuta spelaea*, *Panthera leo spelaea* (cf. Diedrich 2011d, 2011k), *G. gulo* (cf. Diedrich 2009a) and *Canis lupus* ssp. Only 5% of the megafauna can be related to non-cave bears.

Bone preservation and taphonomy

The bones from the Sloup Cave have mostly a typical preservation (reddish colour), whereas bones are often polished and rounded on corners, which indicate water transport or fluent waters at least. Some bones from the Sloup Cave seem to have been obviously mixed, especially the Sedlak 1881–1882 collection, which was bought and not collected by Wankel himself. The bone preservation of material from the Výpustek Cave is much different from the one of the Sloup Cave. Bones are more

Table 4. *B. primigenius* remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
1	2008z0091/0005	Metacarpus	Half	×		Adult		cracked	Wankel 1885	Natural History Museum Vienna
2	2008z0091/0006	Metacarpus	Complete		×	Adult			Wankel 1885	Natural History Museum Vienna
3	2008z0091/0004	Cervical vertebra	C2			Adult		×	Wankel 1885	Natural History Museum Vienna
4	2008z0091/0002	Cervical vertebra,	C3			Adult		×	Wankel 1885	Natural History Museum Vienna
5	2008z0091/0003	Cervical vertebra	C4			Adult		×	Wankel 1885	Natural History Museum Vienna
6	2008z0091/0001	Vertebra lumbalis	Incomplete			Adult		×	Sedlak 1897	Natural History Museum Vienna
7	2008z0091/0007	Phalanx I	Complete			Adult			Wankel 1885	Natural History Museum Vienna

Table 5. *M. giganteus* remains from the Sloup Cave hyena den in the Moravian Karst mountains (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Original	Old collection	Collection
1	2008z0093/0001	Antler	Fragment			Adult			×	Sedlak 1897	Natural History Museum Vienna
2	2008z0093/0002	Antler	Base, dropped antler	×		Adult		×	×	Sedlak 1897	Natural History Museum Vienna
3	2008z0093/0003	Mandible	Fragment, with P_4, M_{1-3}	×		Adult		×	×	Wankel 1885	Natural History Museum Vienna

Table 6. *R. tarandus* remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Old collection	Collection
1	2008z0094/0001	Antler	Base, dropped antler			Adult		×	Sedlak 1897	Natural History Museum Vienna
2	2008z0094/0002	Antler	Base, dropped antler	×		Adult		×	Wankel 1885	Natural History Museum Vienna

Table 7. *C. lupus* subsp. remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic).

No.	Inv. no.	Bone type	Commentary	Left	Right	Individual Age	Sex	Bite marks	Old collection	Collection
1	2008z0090/0001	Mandible	Fragment, with P_{3-4}, M_1	×		Adult			Wankel 1885	Natural History Museum Vienna
2	2008z0090/0002	Humerus	Complete		×	Adult			Wankel 1885	Natural History Museum Vienna
3	2008z0090/0003	Metatarsus	III	×		Adult			Wankel 1885	Natural History Museum Vienna

yellowish, and greyish mineral impregnated, and are not rounded to which preservation type the first hyena skulls fit well (Figures 1 and 3), whereas all other bones described here have the typical Sloup Cave bone preservation.

Systematics

Family *Hyaenidae Gray 1821*

Genus *Crocuta* Kaup 1828

Species *Crocuta crocuta* Erxleben *1777*

Crocuta crocuta spelaea (Goldfuss 1823)

Figures 4–8, Table 1.

Material: The hyena material from the Sloup Cave consists in a total of three skulls and skull remains, 14 mandibles, 20 postcranial bones and 26 teeth plus 23 coprolites.

Cranium: The first skull (Figures 1D,E and 3A) is composed of mandibles of different individuals and is quite large with a total length of 315 mm and with a condyle width of 57 mm.

The left jugal arch has modern damage and is missing. The dentition is incomplete with a right C, P^{3-4} and left C, P^{1-4}. The lower jaw is composed of two different preserved mandibles, but both have similar proportions and tooth wear stages and might belong with the right mandible to the skull (possibly both). The right mandible is only missing the $I_{1 \text{ and } 3}$, whereas the left mandible has modern fractures and is missing part of the ramus. This damage would likely correlate to the modern damage to the left jugal arch if both were found in anatomic connection. Tooth wear and suture fusion allow an estimation of an adult individual age. The skull seems to have been found in the Nicová Cave branch (after descriptions of Wankel (1868)), but the bone preservation fits more to the material that was found in the Výpustek Cave.

The second skull (Figure 4A) is also more or less complete with fresh damage on the posterior sagittal and parietal. They were likely chewed by carnivores (see repeating cranial damages on modern and fossil hyena skulls in Diedrich (2011h)) as indicated mainly by triangular bite impact marks (see bite mark types of hyenas in Diedrich (2009d)). The total length was estimated after completing the skull to be around 315 mm, with a condyle width of 56 mm. The dentition is only missing the small M^1 teeth. The tooth wear stage is typical for an adult animal with medium rubbed enamel.

The third skull consists only of the braincase and seems to have modern damage. There appears an unusual and strong pathologic deformation to the middle sagittal crest (Figure 5A). The skull shows preservation typical for Sloup Cave bones, and was thus likely excavated in the Nicová Cave branch. Whereas here both localities are labelled on the skull in different historical times ('Výpustek Cave and Sloup Cave'), the real origin is confusing, but is attributed here to the Sloup Cave using bone preservation comparisons.

From the fourth skull only the anterior part is preserved. This skull, damaged in several pieces, shows the tooth wear stage of an adult animal (Figure 4B). This material was excavated in the Nagel Abyss first level area during the Seitl excavations in 1998.

Fourteen mandibles are from the animals of different ages (Figure 5C–G). These specimens were excavated from the Nicová Cave branch, and one, from the Nagel Abyss first level area (Figure 5H). The mandibles have incomplete anterior halves that bear carnivore tooth impact marks of irregular and triangular shapes and are mainly preserved with cannibalistic cracked incomplete anterior halves (Figure 6A–F), which similarly figured at many open air and cave hyena den sites of central Europe (Diedrich 2006b, 2011a, 2011e, 2011h, 2011j, 2011m) and are explained and discussed also for the cracked and damaged Late Pleistocene lion skulls (Diedrich 2011f). One lower jaw is from a young cub and has two milk teeth in place, whereas the M_1 has just broken through with the P_4 erupting (Figure 5C). The second juvenile individual jaw fragment displays and has already erupted permanent dentition (Figure 5D). All other jaws are from prime adult to senile adult animals, and one might be from a senile hyena (Figure 6A). Important measurements for the cranial material are listed for the sex identification analyses (Table 1). About 26 single teeth (Figures 4C–E and 5I–K) are all, except one, of adult to senile hyenas. Single milk teeth are absent possibly as a result of non-sieving of the sediments in historical excavation times.

Postcranial bones: The forelimb bones from the Nicová Cave branch consist of three humeri (Figure 7A–C) and four radii (Figure 7D–G); one radius of a juvenile animal was distally chewed (Figure 7G); and finally three metacarpal bones (Figure 7H–J). A few vertebrae are present and include the first cervical vertebra (atlas), and a thoracic vertebra (Figure 7K–L). Only one incomplete sacrum was found from the pelvic area (Figure 7M). The hindlimbs are represented by a right and left femur and two right tibiae (Figure 7N–Q), all of adult to senior individuals, but the latter ones are most probably of different sexes.

Coprolites: The 23 coprolites (Figure 8, Table 1) from the Nicová Cave branch are quite important, firstly for the hyena den identification and secondly as a result of the few preserved and uncollected hyena coprolites in the Moravian Karst. A classification of the pellet shape types is presented with a new terminology compared to modern spotted hyena faeces figured in Diedrich and Žák (2006) and Diedrich (2010d). The pellets from the Sloup Cave have four main shapes resulting mainly from the pellet position in the excrement aggregate: (1) the distal ones are 'conical' forms (Figure 8G–J), (2) the middle ones are 'oval shaped' (Figure 8A–F), whereas also (3) 'disc-like' forms occur (Figure 8L–N) such as (4) 'double drop-shaped' ones (Figure 8K). Their sizes are variable depending on the position, and pellet producer individual age. Here, the pellets are large – about 5 cm in length/4 cm height for the oval-shaped forms. Disk-like ones are also up to 4 cm in height, but always much shorter in width (2–3 cm). The drop-shaped forms are in-between the former mentioned sizes. Finally, some irregular excrements are smaller in their proportions (about 2 × 2 cm).

Prey fauna remains

A single medium-sized incomplete lower jaw molar is possibly from an early adult woolly mammoth (*M. primigenius*) and presents the only proboscidean remain (Figure 10A, Table 2).

The woolly rhinoceros (*C. antiquitatis*) is represented from the Nicová Cave branch by a maxillary fragment with two teeth of a senior animal (Figure 9G), and five upper jaw and two lower jaw teeth are preserved of adult to

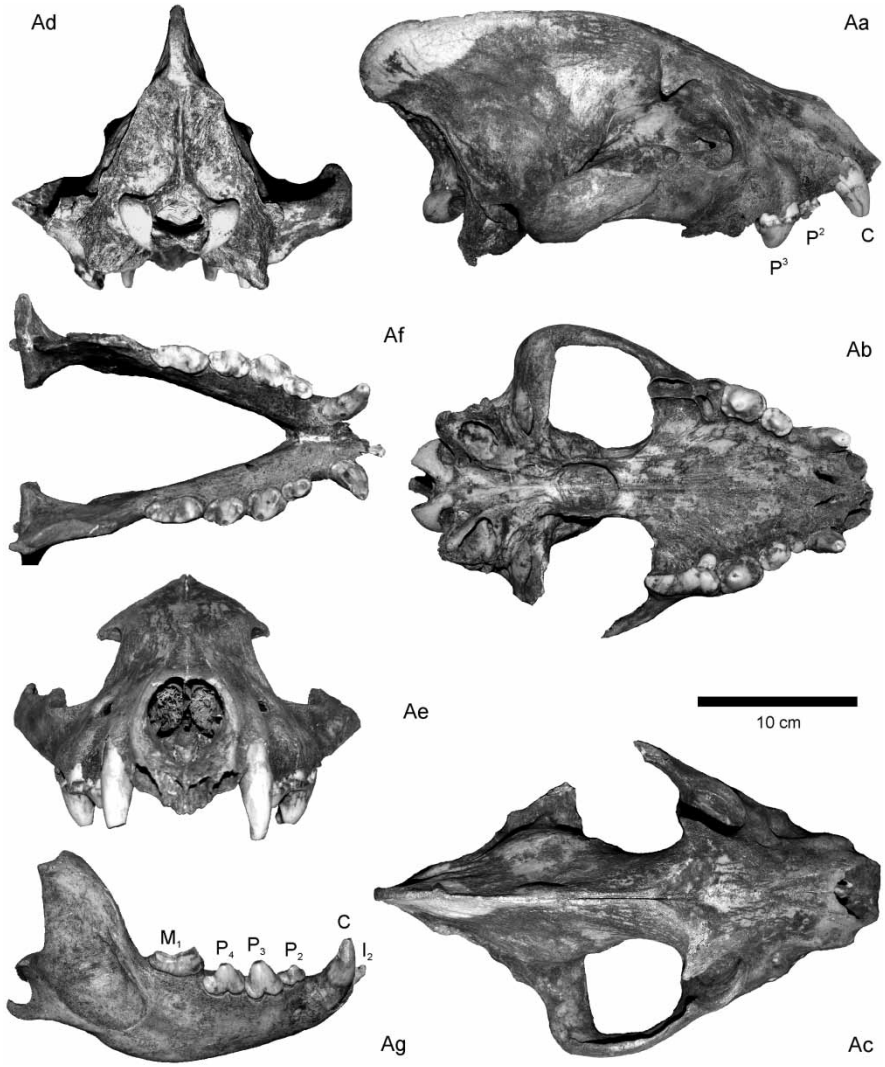

Figure 3. Skull and mandible of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Skull of a female with lower jaw (NHMW no. 2008z0087/0000), a. lateral, b. ventral, c. dorsal, d. occipital, e. frontal, f. lower jaw dorsal, g. right mandible lateral view.

senior animals such as all other bones (Figure 9A–F and H–I, Table 3). Two milk molars (Figure 9 A and B) are the only evidence for imported rhinoceros calves. All long bones such as the ulna, radius and tibia and the pelvic remains and vertebrae have bite marks and are missing their joints or margins as a result of carnivore activities (Figure 9J–R). An articulated ulna/radius (Figure 9J) and two cervical vertebrae (Figure 9N) establish the import of articulated carcass remains.

The urs (*B. primigenius*) material consists of the first three articulated cervical vertebrae, two metapodials and one phalanx (Figure 10B–E, Table 4). The vertebrae have somewhat strong scavenging marks and are overlapping, indicating their original articulation during their importation into the Nicová Cave branch. One massive metacarpus is untouched, another one is cracked and proximally chewed (Figure 10D).

The giant deer (*M. giganteus*) is represented only by antler fragments only from the Nicová Cave branch. One of those was a dropped antler that has chewing and cracking marks (Figure 10I, Table 5). It must have been collected and imported by hyenas, such as deer antlers mentioned below.

Four reindeer (*R. tarandus*) antler fragments are found in the Nicová Cave branch, and are dropped antlers that must have been also collected by hyenas. These were strongly chewed by hyenas which only left damaged basal parts with scratch and bites covering the surface (Figure 10G–H, Table 6).

The steppe lion (*P. leo spelaea*) remains must have been found mainly in the cut-stone branch area of the Sloup Cave including skeleton remains, which are described and analysed separately. In the Nicová Cave branch, possibly an atlas and metapodial bone were

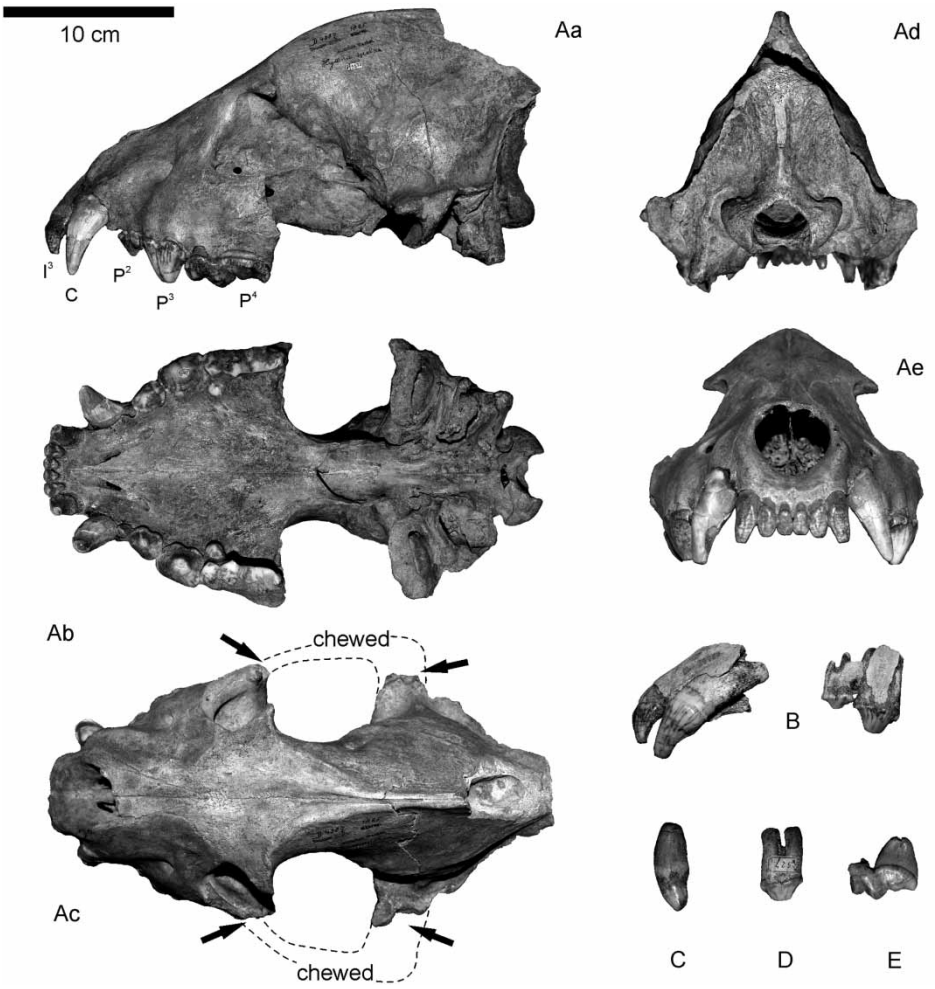

Figure 4. Skull remains of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Skull of an adult female with cannibalistically damaged jugal arches (NHMW no. 2008z0087/0002), a. lateral, b. ventral, c. dorsal, d. occipital, e. frontal. B. Premaxilla/maxilla of one fragmented skull (AMB no. OK 29750), lateral. C. Canine (NHMW no. 2008z0087/0024), lateral. D. Right P^3 (NHMW no. 2008z0087/0026), lateral. E. Right P^4 (NHMW no. 2008z0087/00032), lateral.

excavated (Diedrich 2011d). The main lion material originates from lion carcasses, which are the result of lion/cave bear conflicts during cave bear predation deeper in the Sloup Cave rather than from hyena prey (Diedrich 2011k).

C. lupus ssp. remains consist of a lower jaw fragment, one complete humerus and a left Mt III, all from adult to senior animal (Table 7).

The cave bears subspecies (*U. spelaeus* ssp. and possibly *U. ingressus*, with unclear modern DNA subspecies determination) are numerous (non-catalogued and estimated about 1.500 bones in the NHMW), whereas the material has not yet been restudied. Much pathology on different bones can be observed. Also, some bones seem to have hyena or lion bite damage, which have also not yet been studied in detail. Therefore, the prey fauna of the Sloup Cave hyenas must be further described and extended with the 'cave bear predation theme' in future, which is obviously present there due to several chewed, cracked and incomplete cave bear bones.

Discussion

Hyena population

The Late Pleistocene 'cave hyena' was figured by 'some teeth of cave animals' from the Zoolithen Cave in southern Germany by Esper (1774), but the species was established as '*Hyena spelaea*' on a skull from the Zoolithen Cave (Bavaria, South-Germany) by Goldfuss (1823) which was recently re-described with its cranial and postcranial paratypes from a new identified hyena cub raising den (Diedrich 2008a, 2011b). The first monograph of Late Pleistocene hyena remains from England (Reynolds 1902) described a material from the 'Wooky Hole Cave', which was recently revised (Diedrich 2011c) to have originated from the Sandfort Hill Cave, but these are not clearly attributed to the proposed 'two individual' skeletons

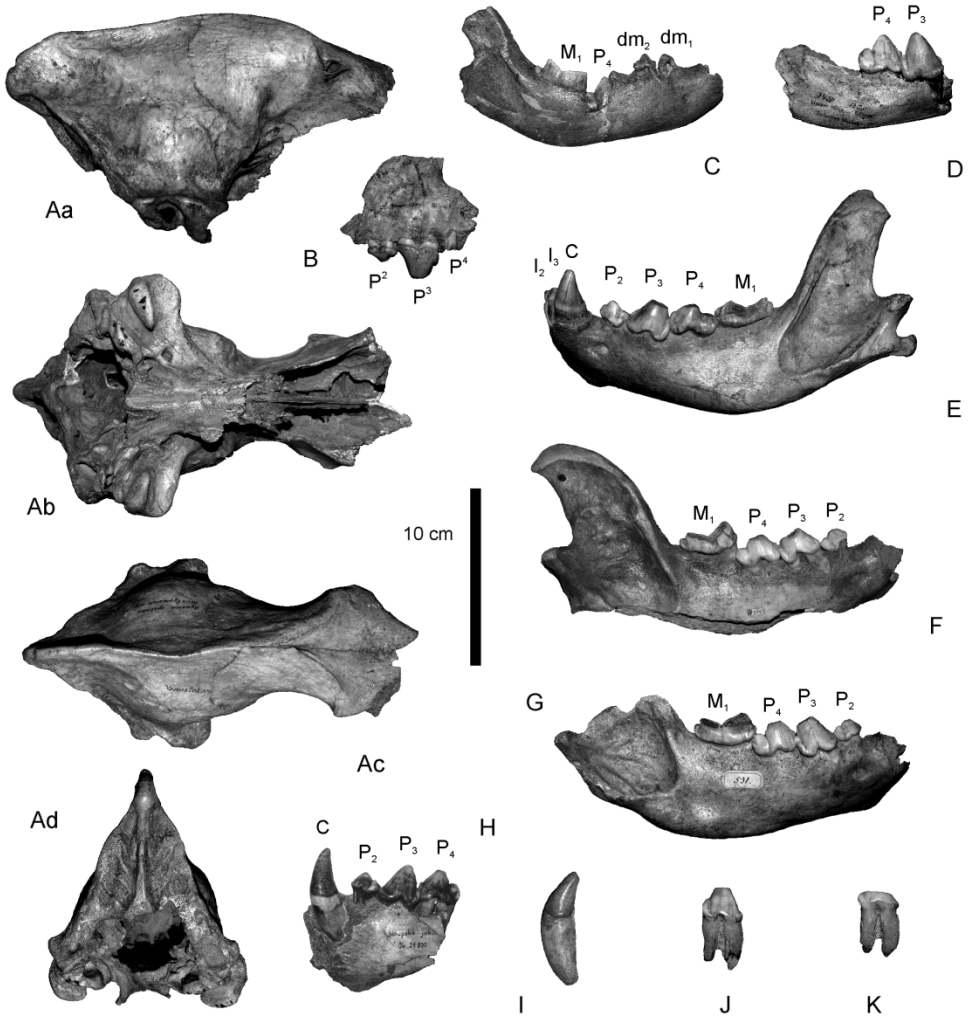

Figure 5. Skull remains of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Skull of an adult animal with sagittal crest deformation pathology (NHMW no. 2008z0087/0001), a. lateral, b. ventral, c. dorsal, d. occipital. B. Left maxillary of an adult animal (NHMW no. 2008z0087/0003), lateral. C. Right mandible of a young cub with milk dentition in tooth eruption (NHMW no. 2008z0087/00011), lateral. D. Right mandible of a juvenile animal (NHMW No. 2008z0087/00015), lateral. E. Left mandible of an adult individual (NHMW no. 2008z0087/0006), lateral. F. Right mandible of an adult individual (NHMW no. 2008z0087/0008), lateral. G. Right mandible of an adult individual (NHMW no. 2008z0087/0007), lateral. H. Left half mandible of an adult animal (AMB no. OK 21800), lateral. I. Canine of an adult animal (NHMW No. 2008z0087/0020), lateral. J. Left P_3 of an adult animal (NHMW no. 2008z0087/0030), lateral. K. Left P_3 of an older adult animal (NHMW no. 2008z0087/0031), lateral.

(cf. Reynolds 1902) because the hyena material from both the cave sites consists of many individual remains. The only known European individual skeletons are from the Koněprusy Cave (Bohemian Karst) and the Výpustek Cave hyena dens (Moravian Karst) in the Czech Republic (Diedrich 2011g). 'Cave hyenas' were figured first in the Czech Republic by Kafka (1903) from open air sites, which were recently re-described from the localities Trmice and Ustí nad Labem (Diedrich 2011h; Figure 2).

Whereas a strong 'size variability' is known in the Late Pleistocene (warm and cold periods) hyenas (e.g. Baryshnikov 1999), sexual dimorphism is well known for the Late Pleistocene (Diedrich 2011g, 2011h, 2011i, 2011j) and modern spotted hyenas in which the females are larger (cf. James and Hofer 1999). The smaller Late Pleistocene spotted hyena male skulls (around 280 mm) and larger female ones (about 320 mm in length; Figure 11A), as well as skull shape variability for the Late Pleistocene hyenas, were recently figured and discussed on more than 30 European hyena skulls, including the Sloup Cave skulls (Diedrich 2008c, 2011h). The large nearly complete first skull is from the Sloup Cave and plots into the larger female-sized ones with an estimated length of 315 mm such as the second skull (Figure 11A). The postcranial hyena consists of long bones from Sloup Cave plot within the male and female morphospaces when

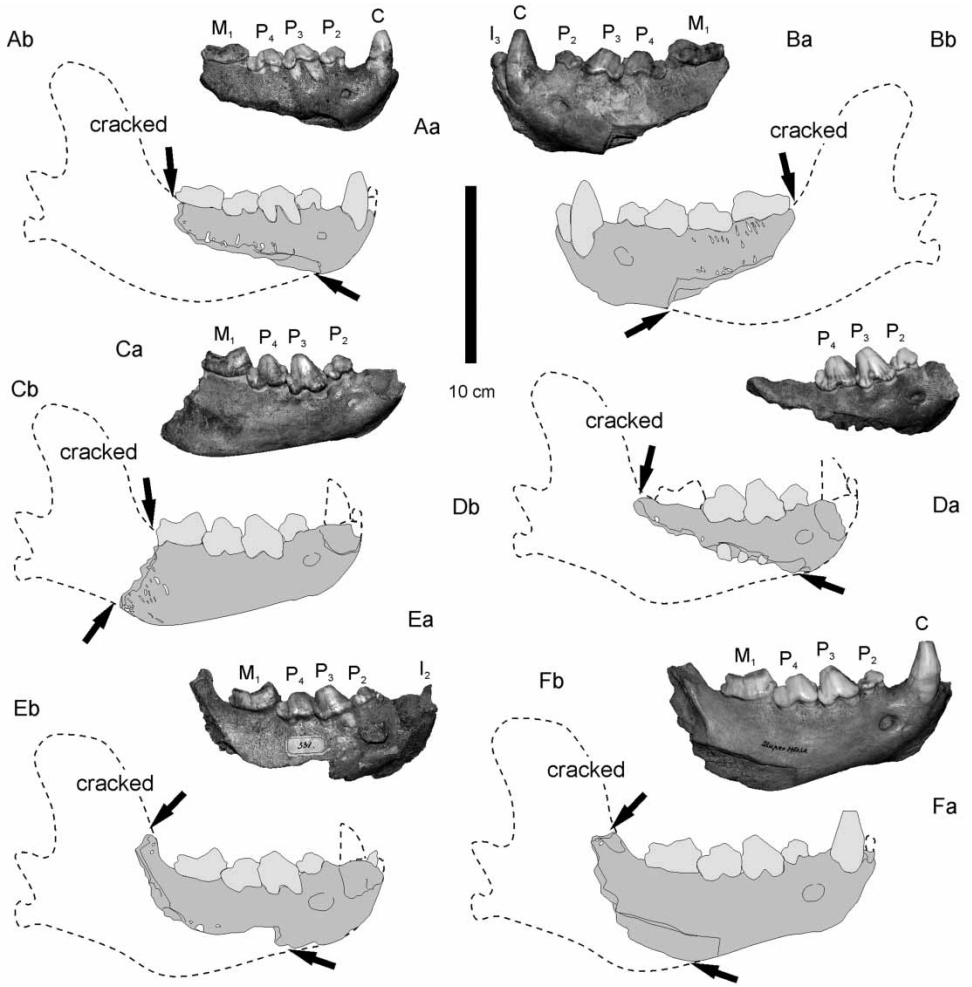

Figure 6. Cannibalistically cracked mandibles of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Right cracked mandible (NHMW no. 2008z0087/0009), lateral. B. Left cracked mandible (NHMW no. 2008z0087/0012), lateral. C. Right cracked mandible (NHMW no. 2008z0087/0013), lateral. D. Right cracked mandible (SNSD no. Sloup-1), lateral. E. Right cracked mandible (NHMW no. 2008z0087/0014), lateral. F. Right cracked mandible (SNSD no. Sloup-2), lateral.

compared with the different Late Pleistocene hyena populations of Central Europe (Figure 11B–E).

Using population analysis statistics (Figure 12C), only 2 males and 13 female bones are represented in the Sloup Cave material. Using cranial material and teeth, the ratio is 21 females/9 males. Female remains seem to be of 66.6%, whereas only 33.3% represent males. Only two bones (3%) are from cubs and five (8%) are from young individuals. Seventy-three bones (89%) belong to adult to senior hyenas. Compared to other hyena dens and their populations (cf. also Diedrich 2007a, 2011h), The Sloup Cave is more closely related to typical hyena communal den and prey depot den types such as Koněprusy Cave (Figure 12Cd), where all hyena remains including one skeleton (Diedrich 2011g) are from adult to senior ones. At such caves, where prey was hidden against lions and other predators in more difficult to reach small caves, no cubs were raised. In contrast to such caves, Nad Kačakem Cave has about 56% cubs and also a larger amount of young and adolescent hyena remains (Figure 12Ca) indicating cub-raising den sites similar to what is found in the Zoolithen Cave cub-raising den (Diedrich 2011j). Such larger cub remain amounts are also known for modern spotted hyena cub-raising dens (East et al. 1989). The Srbsko Chlum Komin Cave population structure (Figure 12Cb) is somewhat between Nad Kačakem Cave and Sloup Cave, and therefore must have been used as a cub-raising, commuting and prey storage den site during different periods. Sloup Cave must have been mainly a commuting site for grownup hyenas, which stored their prey remains in the Nicová Cave branch and used it rarely as a cub-raising den.

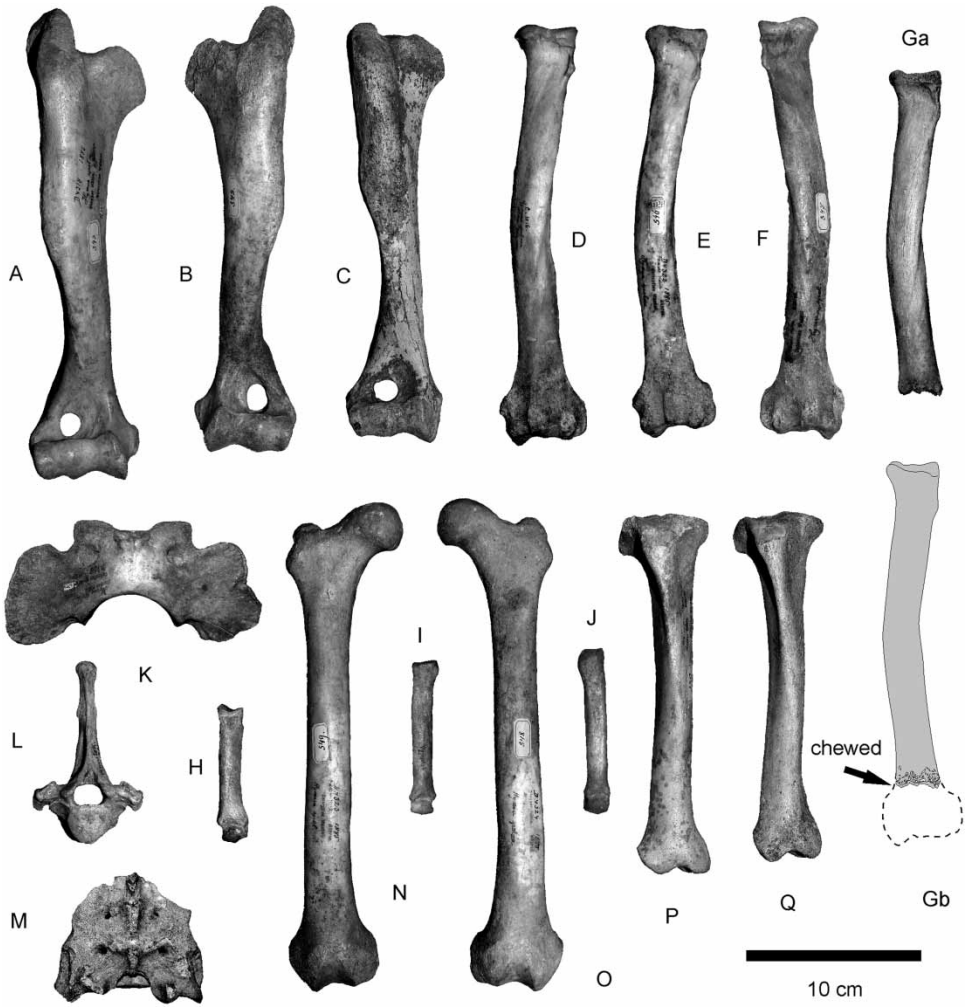

Figure 7. Limb and vertebral column bones of adult to senior animals (except Figure 7G) individuals of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Right humerus of a female (NHMW no. 2008z0087/00041), cranial. B. Left humerus of a male (NHMW no. 2008z0087/00042), cranial. C. Right humerus of a male (NHMW no. 2008z0087/00043), cranial. D. Left radius of a female (NHMW no. 2008z0087/00044), lateral. E. Left radius of a female (NHMW no. 2008z0087/00045), lateral. F. Right radius of a female (NHMW no. 2008z0087/00046), lateral. G. Left radius of a young individual distally chewed (NHMW no. 2008z0087/00047), lateral. H. Right Mc II (NHMW no. 2008z0087/00050), dorsal. I. Left Mc III (NHMW no. 2008z0087/00049), dorsal. J. Right Mc IV (NHMW no. 2008z0087/00048), dorsal. K. Atlas (NHMW no. 2008z0087/00051), dorsal. L. Second thoracic vertebra (NHMW no. 2008z0087/00053), cranial. M. Sacrum (NHMW no. 2008z0087/00054), dorsal. N. Right femur of a female (NHMW no. 2008z0087/00056), cranial. O. Left femur of a female (NHMW no. 2008z0087/00055), cranial. P. Right tibia of a female (NHMW no. 2008z0087/00057), cranial. Q. Right tibia of a male (NHMW no. 2008z0087/00058), cranial.

Hyena cannibalism

Within the population of the Sloup Cave, hyena cannibalism is well documented especially on the cranial material (Figures 4A, 6 and 7G). Typically, and for other hyena den sites which reported damaged skulls with missing jugal arches and cracked lower jaws (Diedrich 2005a, 2006b, 2007b, 2011h, 2011i, 2011j), Sloup Cave material also displays cannibalistic skull damage. Compared also to a modern African hyena den cave of the Ngorongoro Crater in Kenya (material in the BMNHL) where a spotted hyena skull was collected, the jugal arches were supposed to have been cracked cannibalistically while feeding on the tongue and jaw muscles (Diedrich 2011h). Additional proof of hyena cannibalism can be found on one radius (Figure 7G) in which only the upper part was left. Similar incomplete radii are figured from the Perick Caves hyena den (Diedrich 2005a), Koněprusy Caves and Srbsko Chlum Komin Cave (Diedrich and Žák 2006).

Hyena prey remains

The small amount of prey bones (number of identified specimens) (NISP = 139) does not allow for very precise prey statistics (Figure 12A), but does show a trend typical

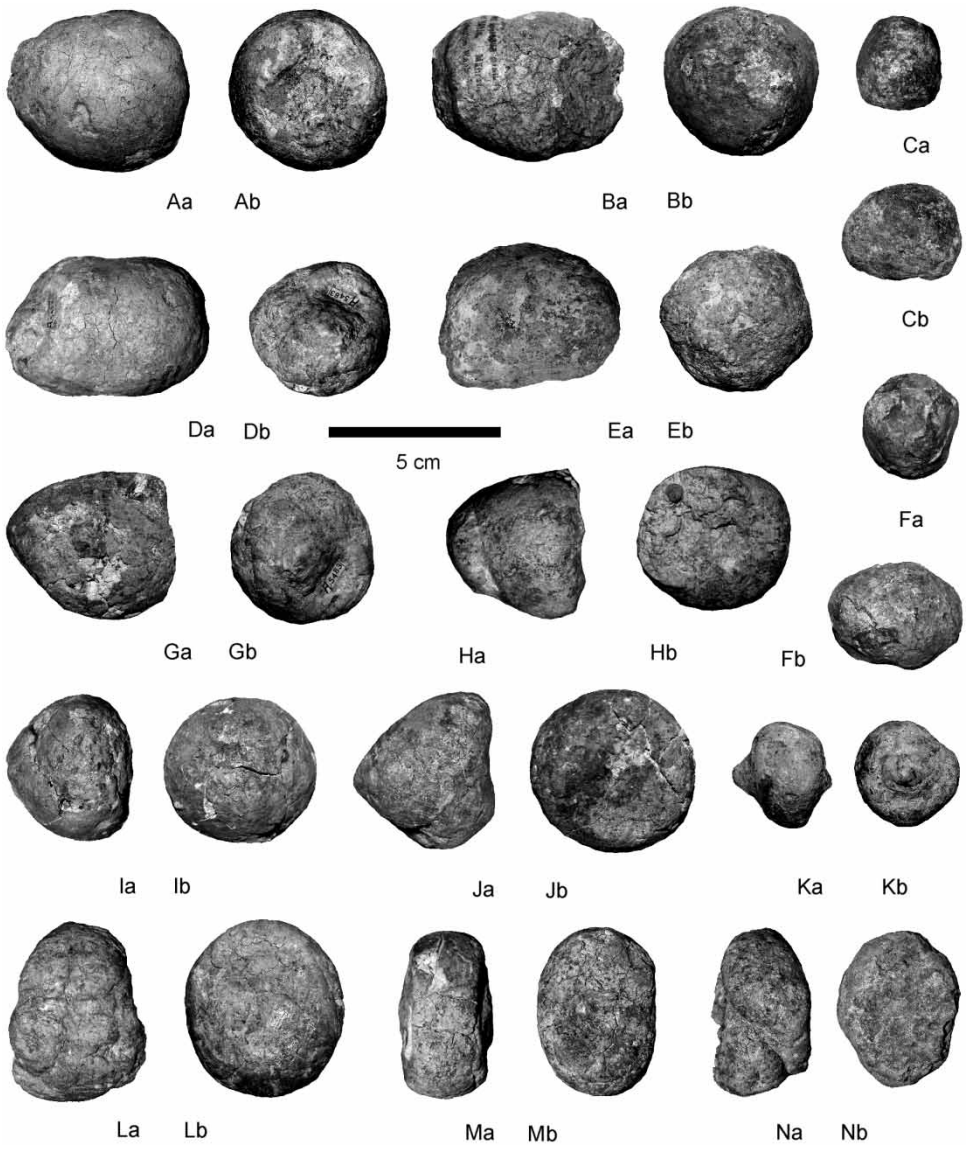

Figure 8. Coprolite pellets of *C. crocuta spelaea* (Goldfuss 1823) from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). a. lateral, b. frontal. A. Oval terminal-pellet (NHMW no. 2008z0087/00067). B. Oval middle pellet (NHMW no. 2008z0087/00064). C. Oval pellet (NHMW no. 2008z0087/00080). D. Oval pellet (2008z0087/00059). E. Oval pellet (NHMW no. 2008z0087/00060). F. Small oval pellet (NHMW no. 2008z0087/00081). G. Drop-shaped terminal-pellet (NHMW no. 2008z0087/00065). H. Drop-shaped terminal-pellet (NHMW no. 2008z0087/00070). I. Drop-shaped terminal-pellet (NHMW no. 2008z0087/00063). J. Drop-shaped terminal-pellet (2008z0087/00066). K. Double drop-shaped pellet (NHMW no. 2008z0087/00079). L. Middle disc pellet (NHMW no. 2008z0087/00060). M. Middle disc-pellet (NHMW no. 2008z0087/00060). N. Middle disc-pellet (NHMW no. 2008z0087/00062).

of many hyena den sites of Central Europe, that is, large amounts of woolly rhinoceros bones and teeth remains, which are always damaged in a similar manner at all studied hyena dens over Central Europe (cf. Diedrich 2006a, 2008b, 2011a, 2011e, 2011g, 2011j; Diedrich and Žák 2006; cf. Figure 9J–R). Therefore, the 'bone damage analyses' representing bones in similar damage/destruction stages are much more efficient instead of using only 'carnivore bite mark analysis'. The latter does not allow in most cases the determination to a single or main carnivore predator. Bone damage stages produced mainly or only by Late Pleistocene hyenas are demonstrated successfully on cave bear (Diedrich 2011j, 2011l), steppe lion (Diedrich 2011b, 2011f), elephant (Diedrich 2010c) and especially several times on woolly rhinoceros (Diedrich 2006a, 2008b, 2011a, 2011e, 2011m) bones.

The newest studies and bone damage stages are demonstrated on about 1.600 bones of *C. antiquitatis* at the open air hyena den Bottrop (Diedrich 2011m) to which the few *Coelodonta* remains from the Sloup Cave can be

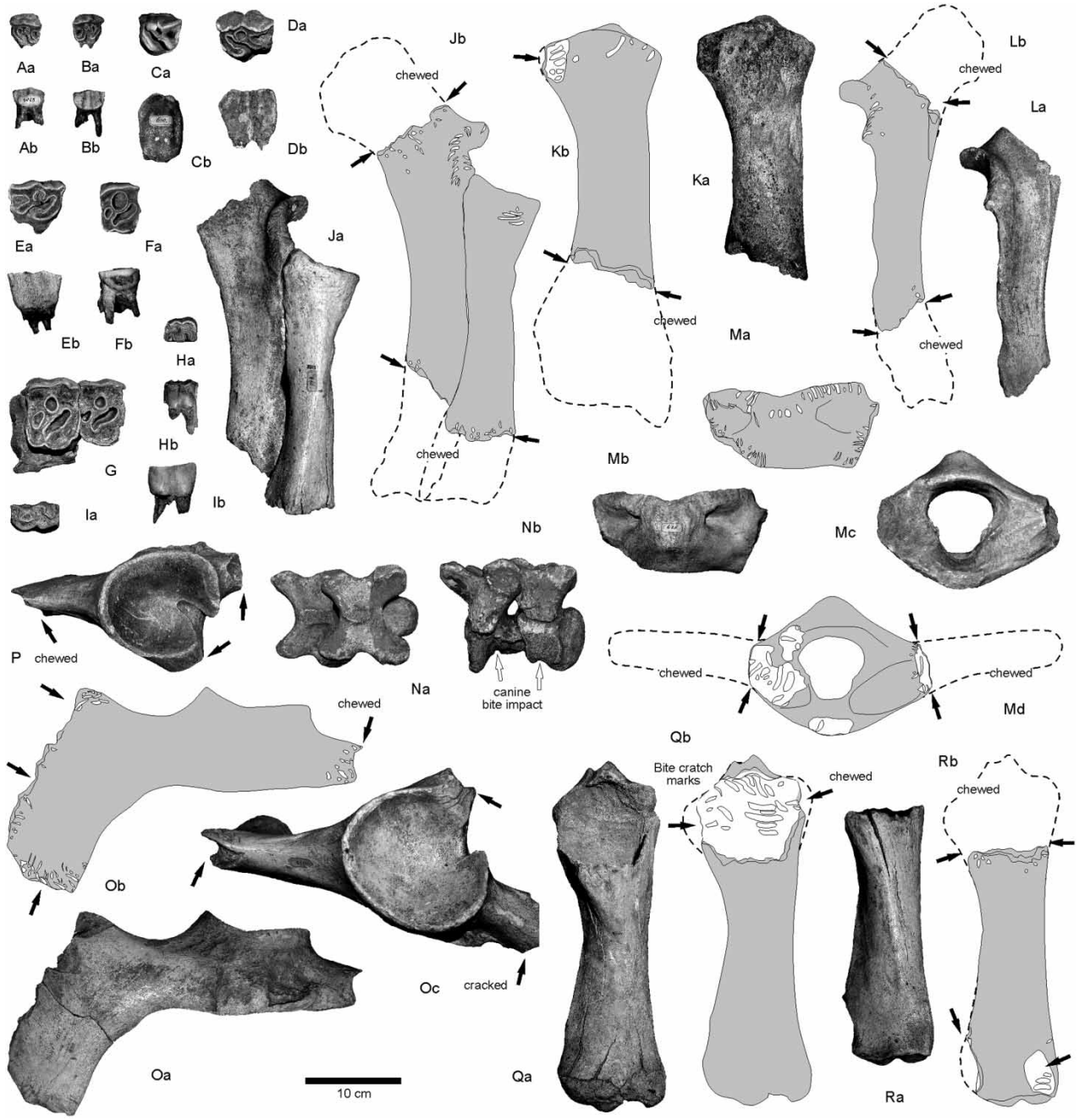

Figure 9. Woolly rhinoceros *C. antiquitatis* (Blumenbach 1799) remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. Left maxillary milk molar dm^3 of a calf (NHMW no. 2008z0092/0002), a. occlusal, b. labial. B. Right maxillary milk molar dm^3 of a calf (NHMW no. 2008z0092/0003), a. occlusal, b. labial. C. Left maxillary P^4 of an adolescent animal (NHMW no. 2008z0092/0004), a. occlusal, b. labial. D. Left maxillary M^1 of an adult animal (NHMW no. 2008z0092/0005), a. occlusal, b. labial. E. Right maxillary M^1 of an adult animal (NHMW no. 2008z0092/0006), a. occlusal, b. labial. F. Left maxillary P^4 of a senile animal (NHMW no. 2008z0092/0007), a. occlusal, b. labial. G. Left maxillary fragment with P^4 and M^1 of a senile animal (NHMW no. 2008z0092/0001), a. occlusal, b. labial. H. Right mandible P_3 of an adult animal (NHMW no. 2008z0092/0008), a. occlusal, b. labial. I. Right mandibular M_1 of an adult animal (NHMW no. 2008z0092/0009), a. occlusal, b. labial. J. Articulated right ulna/radius chewed proximal/distal (NHMW no. 2008z0092/0010), lateral. K. Left radius of an adult animal (NHMW no. 2008z0092/0011), lateral. L. Left ulna proximal and distal chewed of an adult animal (NHMW no. 2008z0092/0012), lateral. M. Atlas chewed of an adult animal (NHMW no. 2008z0092/0013), a. caudal, b. dorsal. N. Middle cervical vertebrae with canine bite impact marks of an adult animal (NHMW no. 2008z0092/0014 to 15), a. dorsal, b. lateral. O. Right cracked and chewed acetabulum of an adult animal (NHMW no. 2008z0092/0016), acetabular. P. Left cracked and chewed acetabulum of an adolescent animal (NHMW no. 2008z0092/0017), acetabular. Q. Right chewed tibia (NHMW no. 2008z0092/0018), cranial. R. Right chewed tibia (NHMW no. 2008z0092/0019), cranial.

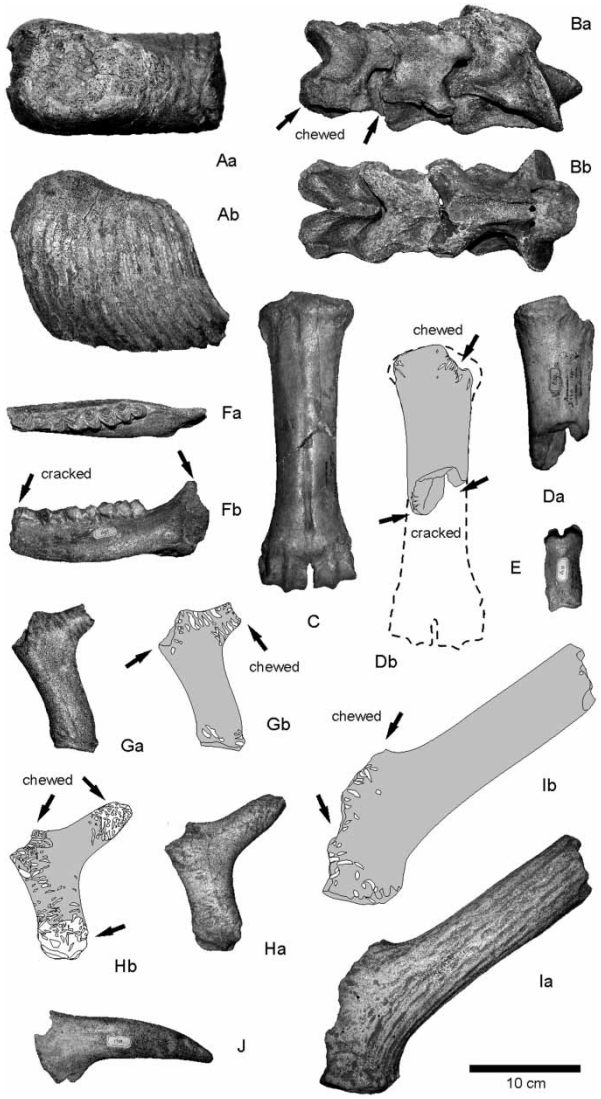

Figure 10. Woolly mammoth, urs, reindeer and giant deer remains from the Sloup Cave hyena den in the Moravian Karst (Czech Republic). A. *M. primigenius* (Blumenbach 1799) left mandible m_3 (NHMW no. 2008z0087/00082), a. occlusal, b. lateral. B. *B. primigenius* (Bojanus 1827) first three articulated cervical vertebrae of one individual with bite impact marks (NHMW no. 2008z0091/0002 to 4), a. lateral, b. dorsal. C. *B. primigenius* (Bojanus 1827) metacarpus (NHMW no. 2008z0091/0006), cranial. D. *B. primigenius* (Bojanus 1827) cracked and chewed metacarpus (NHMW no. 2008z0091/0005), cranial. E. *B. primigenius* (Bojanus 1827) phalanx I (NHMW no. 2008z0091/0007), dorsal. F. *M. giganteus* (Blumenbach 1799) left mandible, cracked (NHMW no. 2008z0093/0003), a. dorsal, b. lateral. G. *R. tarandus* (Linnaeus 1758) antler base, chewed (NHMW no. 2008z0094/0002), lateral. H. *R. tarandus* (Linnaeus 1758) antler base, chewed (NHMW no. 2008z0094/0001), lateral. I. *M. giganteus* (Blumenbach 1799) antler base, chewed (NHMW no. 2008z0093/0002), lateral. J. *M. giganteus* (Blumenbach 1799) antler fragment (NHMW no. 2008z0093/0001), dorsal.

compared regarding their damage stage types. Here, the figured articulated ulna/radius and single ulna and radius (Figure 9J–L), or the acetabulum (Figure 9O–P) and tibiae (Figure 9Q–R) display precisely the same type of damage and incomplete distal ends such as similarly damaged finds from the hyena dens in the Bohemian Karst cave sites, Koněprusy Caves, Srbsko Chlum Komín Cave and open air site Praha-Podbaba (Diedrich and Žák 2006), the Perick Caves (Diedrich 2008b), the Teufelskammer Cave (Diedrich 2011a), the Balve Cave (Diedrich 2011e) or the open air site Bad Wildungen-Biedensteg (Diedrich 2006a) and the open air site Bottrop (Diedrich 2011m). The bone remains of *C. antiquitatis* (Figure 12B) result from carcass destruction and feeding (= systematic slaughtering and decomposition techniques of hyenas, Diedrich 2011m) mainly on adult to senior rhinoceros carcasses outside the caves (Diedrich 2011m), but calf remains from the Sloup Cave and many other hyena den sites (Diedrich and Žák 2006; Diedrich 2006a, 2008b, 2011a, 2011e, 2011m) might be interpreted as 'hunted' prey. Modern hyenas also kill rhinoceros calves in hunting parties (e.g. Kruuk 1972). Two articulated cervical vertebrae and an articulated ulna/radius of the woolly rhinoceros are the best indicators for understanding hyenas as carcass importers, which did not consume and moved primary single bones to dens. This phenomenon is reported from several other hyena den sites of Europe (Diedrich and Žák 2006; Diedrich 2006a, 2008a, 2011a, 2011e, 2011m). The Late Pleistocene hyenas were not at all 'bone collectors', instead they mainly hunt prey actively (e.g. Diedrich 2010b), but rather often stole 'carcasses' from lion prides, such as that documented in Modern African spotted hyenas (e.g. Kruuk 1972). Other evidence for carcass body part importation to denning behaviour is the articulated cervical vertebrae of *B. primigenius*, which explain the taphonomy and bone accumulations in hyena dens such as those the Sloup Cave. The habit of collection of cervid dropped antlers such as of giant deer, red deer, reindeer and others seem to be typical for Ice Age spotted hyenas. This behaviour has been documented at many hyena den sites all over Central Europe (cf. Stiner 2004; Diedrich 2006a, 2007a, 2007b, 2011a, 2011e, 2011g, 2011m). Hyenas typically left only the base from the dropped antlers (Figure 10G–I), whereas nibbling, chewing and gnawing and tooth impact marks can cover those antler fragments all over. Similar to the *Megaloceros* antlers from the Sloup Cave are the nibbled ones that were figured from the Perick Caves or Balve Cave hyena dens (Diedrich 2005b, 2011e). Also, strongly damaged reindeer antler bases are similar to those preserved in other caves figured for the Bohemian Karst (Diedrich and Žák 2006).

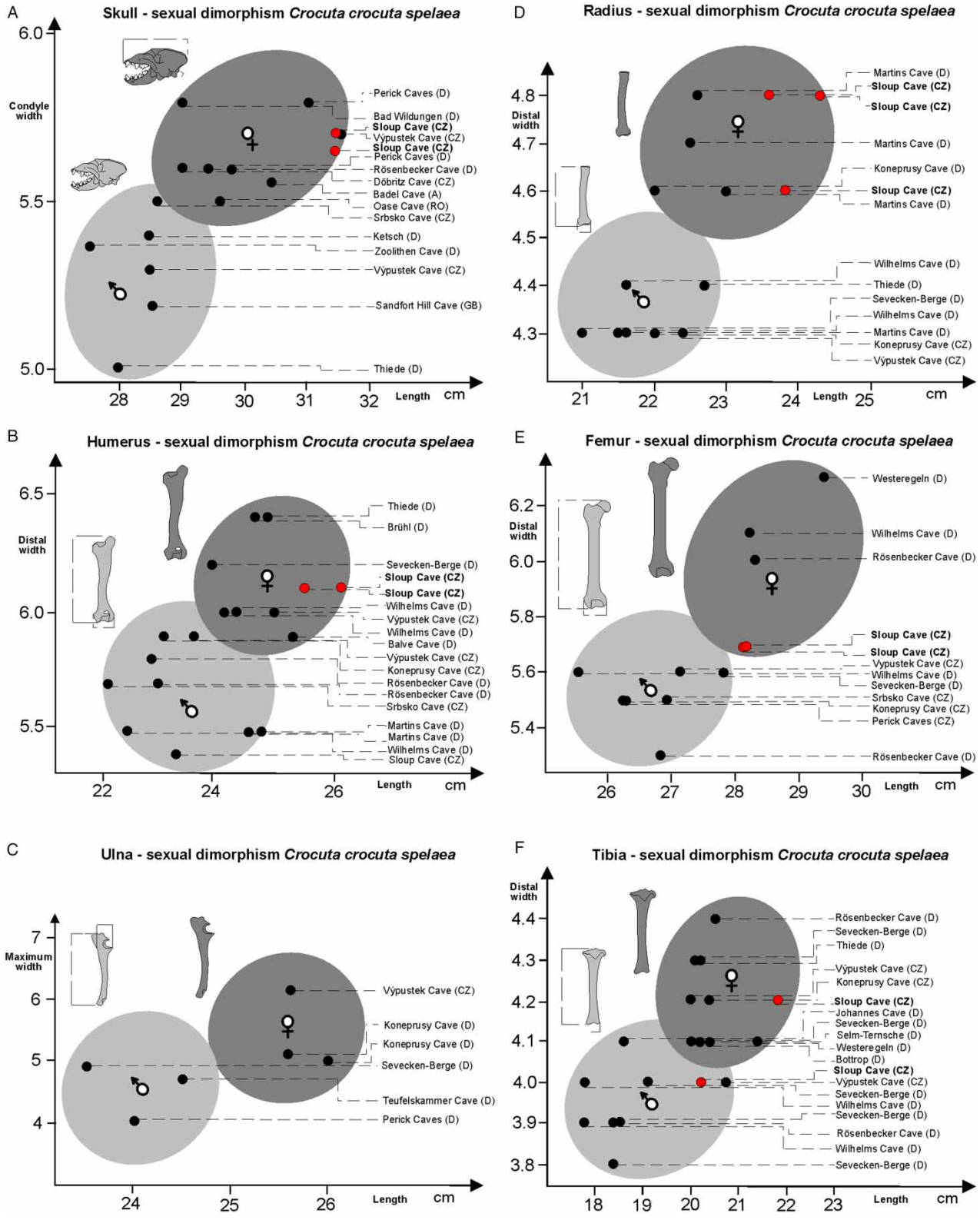

Figure 11. Sexual dimorphism in skulls and long bones of the hyena population from the Sloup Cave hyena den in the Moravian Karst (Czech Republic) in comparison to other European open air and cave sites (composed after data in Diedrich 2011a, 2011c, 2011j).

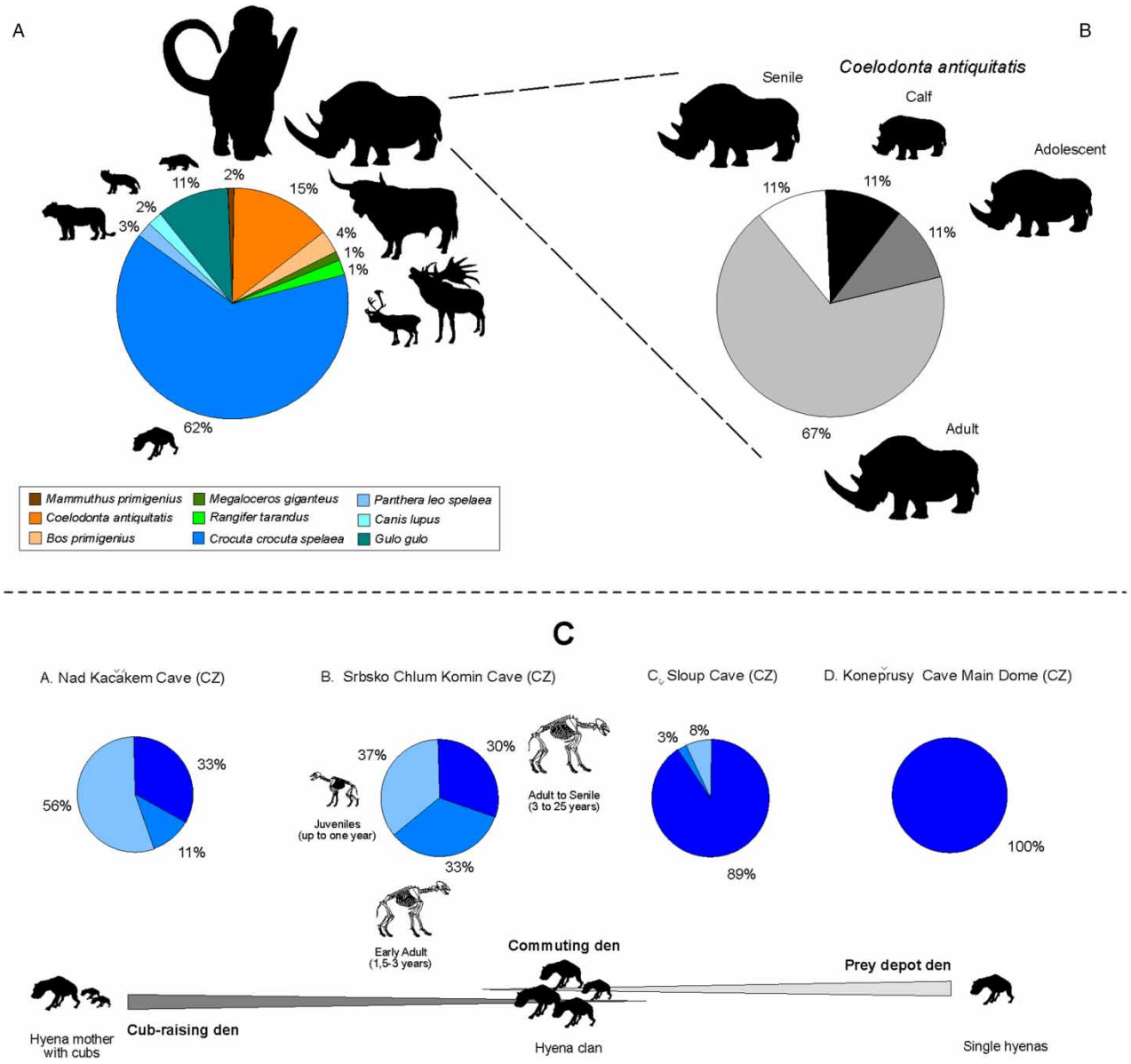

Figure 12. Faunal statistics from the Sloup Cave hyena den in the Moravian Karst (Czech Republic) of the A. hyena prey (NISP = 139) and B. Individual ages (NISP = 19) of woolly rhinoceros prey. C. Individual ages of hyena population (NISP = 38) in comparison to other hyena dens in Czech Republic.

Hyena den areas and den type

C. crocuta spelaea used the Sloup Cave mainly in the Nicová Cave branch and accumulated different body part remains of its prey there most likely to avoid battles with other hyenas and especially lions. Such behaviour is well documented in Africa with modern lions/hyenas (e.g. Kruuk 1972). The hyenas seem to have deported such prey remains often for food storage in caves where a perfect temperature and humidity preserved those remains well for a couple of days. The best examples of 'hyena food storage sites' are the Koněprusy Cave, the Srbsko Chlum Komin Cave and Nad Kacakem Cave (Diedrich and Žák 2006), but also the Teufelskammer Cave (Diedrich 2011a). Even modern spotted hyenas have quite similar den and general ecology behaviours and accumulate bones in and around their dens or at prey storage and bone dump sites in high numbers (cf. Kruuk 1972; Hill 1980; Avery et al. 1984; Frank 1986; Lam 1992; Cooper 1993; Hofer 1998).

Hyena faecal den marking

Typical for hyena dens is the marking by their excrement or coprolites. At their dens, modern hyenas (cf. Bearder and Randall 1978) and the Pleistocene spotted hyenas of Europe (Fosse et al. 1998; Diedrich and Žák 2006;

Diedrich 2006b, 2007a, 2010c) used faecal pellets to mark their territories and dens. The coprolites presented here seem to have been excavated only from the Nicová Cave branch of the Sloup Cave. There are few caves in the Moravian Karst, where hyena coprolites survived or were collected in historic times (e.g. Sloup Cave, Sipka Cave and Sveduv Stůl Cave). This situation is similar to what was found in the Bohemian Karst hyena den caves (cf. Diedrich and Žák 2006). The faecal pellet shape of the Late Pleistocene spotted hyenas is exactly the same as that found in modern spotted hyenas that produce faecal aggregates, which consist of a few differently shaped pellet forms that are attached to each other (Diedrich and Žák 2006; Diedrich 2010d). Of all the potential shape and size possibilities, the single pellets of the Sloup Cave are most similar to pellet aggregates of more dry dung figured from African spotted hyenas (cf. Diedrich 2010d). These also typically contain bone fragments, which are partly visible on the pellet surfaces.

Multiple cave use by carnivores and cave bears

The Sloup Cave bone taphonomy can be reconstructed quite well due to the documentation of excavation areas in historic times (cf. Wankel 1858; Musil 1988, 2002; Seitl 1998; see Figure 2). Only the Nicová Cave branch has delivered a larger amount of hyena remains, their excrements and their prey, which is here interpreted as the 'hyena den area' of the Sloup Cave system (cf. Figure 2). The hyenas must have used the cave 'in similar times' during the Late Pleistocene, whereas the herbivorous cave bears intensively used the deeper cave areas for their hibernation such as the Cutted-stone branch (cf. Figure 2). As recently discussed for all those cave bear dens and overlapping hyena dens, the scavenging of cave bears by hyenas and lions (possibly even killing) has increasingly been documented at similar caves such as the famous Perick Caves or Zoolithen Cave hyena and cave bear dens in Germany or Romania (Diedrich 2010a, 2011a, 2011b, 2011c, 2011d, 2011f, 2011j, 2011k, 2011l). It is unclear by the bone remains if both antagonists lived at the same time in the cave (possibly hyenas in the summer season and cave bears more in the winter season for hibernation) using different cave branches or parts of the Sloup Cave or if they used the caves in different years or seasons. Finally, the role of the largest field predators and hyena and cave bear antagonists (Diedrich 2010a, 2011b, 2011n) has become clearer for the Sloup Cave lion finds, which were found mainly between the cave bear hibernation areas also with the skeleton remains mainly in the cut-stone branch (cf. Figure 2; Diedrich 2011k). As demonstrated for other caves in Europe, lions are shown to have been found in cave bear dens between cave bear skeletons and bones as a result of 'active cave bear hunting', which took place possibly mainly during the cave bear hibernation times in winter (Diedrich 2009d, 2009e, 2010a, 2011l, 2011n). The taphonomic record of the lion remains nearly all found in the cutting-stone branch area of the Sloup Cave is taphonomically similar to that of the Romanian Urşilor Cave, Romania (Diedrich 2011c, 2011l), the Zoolithen Cave, southern Germany (Diedrich 2011b) and the Bilstein Cave or Keppler Cave, northern Germany (Diedrich 2009c, 2011n). Steppe lions must have died in the caves (even quite deeply) in a few cases during battles with cave bears during their predation, whereas in all studied caves, the lion remains and cave bear remains have a ratio of about only 1–2% NISP of lion bones which reflects the rare kill or death of a lion in a cave over tens of thousands of years (Diedrich 2009e, 2011b, 2011n). This finally explains well why in the cut-stone branch of the Sloup Cave about three lion skeleton remains were also found, which were composed of skeletons consisting of Sloup and Vypustek Cave lion bone material (Diedrich 2011k).

Conclusions

The Nicová Cave branch of the Sloup Cave was used as a hyena commuting and prey storage den, and less for raising cubs, and was marked well by faecal pellets. Hyaena prey remains from the Nicová Cave branch of the Sloup Cave are dominated by woolly rhinoceros (*C. antiquitatis*) cranial and postcranial bones. The latter are for hyena den bone assemblages typically damaged and incomplete exposing bite mark scratches in the spongiosa as well as chewed joints. Despite the fact that there is a little prey material for comprehensive statistical analysis it is clear that the woolly rhinoceros was one of the main prey items, whereas mammoth seems to have been rare in the Moravian Karst mountainous region much like hyena den prey bone assemblages in other middle high mountainous regions of Central Europe of the Sauerland Karst and Bohemian Karst. Also, damaged incomplete cave bear bones indicate hyena scavenging at the Sloup Cave, such as cannibalism as evidenced especially on the lower jaws and some skulls, but also postcranial bones of *C. crocuta spelaea*. Hyenas possibly shared the same caves in the same times with cave bears, but hyenas used smaller branches or cave parts as dens or food storage sites not only in the Sloup Cave but also in many caves of Europe, whereas cave bears hibernated mostly as deep as possible in the caves to protect themselves against their largest antagonistic predators, the steppe lions and Ice Age spotted hyenas. Lion skeletal remains were found as a result of deathly conflicts during their cave bear predation. These carcasses and skeletons remained untouched but often trampled and disarticulated in the cave bear hibernation areas similar to what has been documented for several other cave bear den sites of Europe; here in the Sloup Cave in the cut-stone branch.

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