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UPPER PLEISTOCENE *GULO GULO* (LINNÉ, 1758) REMAINS FROM THE SRBSKO CHLUM-KOMIN HYENA DEN CAVE IN THE BOHEMIAN KARST, CZECH REPUBLIC, WITH COMPARISONS TO CONTEMPORARY WOLVERINES

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Abstract: Wolverine bone material is described from the famous Upper Pleistocene cave Srbsko Chlum-Komin in the Bohemian Karst, Czech Republic, along with an overview of recently known Czech sites. The *Gulo gulo* Linné material was found in one of the largest Ice Age spotted-hyena dens in Europe. As a result of non-systematic excavations, the taphonomy is partly unclear. Lower-jaw remains indicate a minimum of three wolverines. Two of the mandibles are cracked, which is most likely the result of carnivore scavenging. The absence of juvenile *G. gulo* suggests possible importation of the wolverines by hyenas *Crocuta crocuta spelaea* Goldfuss.

Introduction

The vertical caves of the Chlum quarry near Srbsko in Central Bohemia, Czech Republic (Fig. 1) provide sediments and bone rich caves ranging from Middle to Upper Pleistocene (Diedrich and Žák, 2006). The most important Upper Pleistocene site in the Bohemian Karst, and arguably in Europe, is the vertical cave Srbsko Chlum-Komin (Fig. 1). During the Upper Pleistocene, the Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) is believed to have imported large quantities of prey remains into the Komin Cave, including complete carcasses. This site provides the largest deposit of hyena-den bone material in Europe. A general overview of the fauna was given by Diedrich and Žák, (2006).

Geological and Taphonomical Setting

The Chlum-Komin Cave was originally discovered and poorly excavated between 1958 and 1972, primarily by a local speleoclub, and unfortunately, without documentation. Mammal deposition was first thought to be of trapped animals, animals that dropped into the cave, or bones that washed in (Beneš, 1970). Diedrich and Žák (2006) concluded that a clan of the Late Pleistocene spotted hyena *C. crocuta spelaea* used this cave over generations as their den, as evidenced by the abundant presence of hyena bones or partial skeletons, their coprolite material, and chewed and cracked prey bones. The Komin Cave is more or less sloping and in some parts vertical; the entrance was destroyed by the quarry activities. The Komin is connected to a larger, horizontal cave system. Diedrich and Žák (2006) argued that this chimney did not function as a trap and was clearly accessible to hyenas. The Komin contained 3,569 macromammal bones, most notably 350 remains of hyena bones constituting five partial hyena skeletons, including three juveniles, one adult male, and one adult female. Evidence of crushed hyena long bones indicate hyena cub raising and cannibalism as well (Diedrich and Žák, 2006). Prey remains consisted of Przewalski horse (*Equus ferus przewalskii*, including one embryo skeleton), (Diedrich and Zák, 2006), woolly rhinoceros (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*), reindeer (*Rangifer tarandus*), chamoix (*Rupricapra rupricapra*), ibex (*Capra ibex*), wolf (*Canis lupus*), and the herein detailed wolverine material (*Gulo gulo*) (Fig. 2). Finally, the presence of a two- to three-year-old lioness (*Panthera leo spelaea*) with a skull injury, as well as a lion cub about one year of age (Diedrich, 2009a), may indicate either antagonistic conflicts between hyenas and lions in the cave itself or the importation of these individuals as hyena prey.

Chewing and cracking of bones by hyenas is particularly evident on specimens of woolly rhinoceros and steppe bison, as is evidence of hyena cannibalism (Diedrich and Žák, 2006; Diedrich, 2007). This site was also believed to have been used by common foxes (*Vulpes vulpes*). Tens of thousands of micromammal bones have been identified from fox scat and snowy owl (*Nyctea scandiaca*) pellets in the Komin Cave.

Systematic Palaeontology

Sixteen wolverine bones collected from this cave are housed at the National Museum Prague and Museum of the Bohemian Karst Beroun.

Family *Mustelidae* Swainson, 1835
Genus *Gulo* Pallas, 1780
Gulo gulo (Linné, 1758)

Four mandibles of at least three individual adult-to-senile wolverines are represented (Figs. 3, 4.1–4.4). Two of

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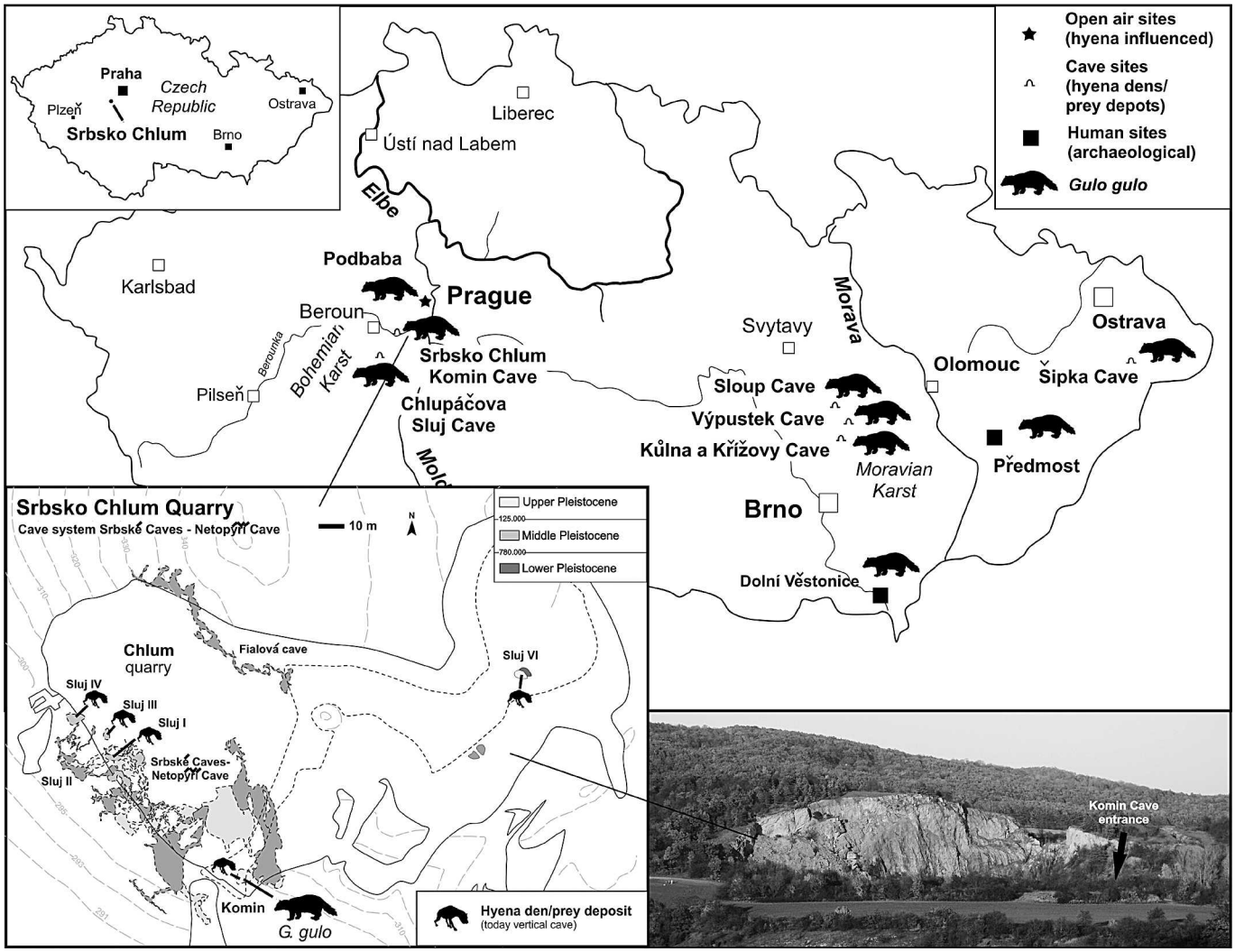

Figure 1. Positions of wolverine *G. gulo* (Linné, 1758) sites in Czech Republic focusing on the Bohemian Karst and adjacent areas around Prague, Czech Republic. Srbsko quarry caves have provided thousands of bones from the Middle to Upper Pleistocene.

them are nearly complete, lacking only incisor teeth. The other two (Figs. 4.3 and 4.4) were cracked by carnivores, with the ramus missing. One mandible is from an adult animal (Fig. 4.2), two are from old-age adult wolverines (Figs. 4.1 and 4.3), and the fourth represents an older individual, as evidenced by severely worn teeth (Fig. 4.4). A single canine tooth without half of the used cusp (Fig. 4.5) is, again, from an older animal. Additionally, two incisor teeth (not figured, Table 1) are from adult-to-senile animals.

The postcranial material is from adult-to-senile individuals and consists of a right complete radius (Fig. 4.6) and a right complete ulna (Fig. 4.7). Two metacarpi, one recently damaged (Fig. 4.12) and one complete left Mc IV (Fig. 4.13), are from the manus skeleton. The hind limb bones include a distally incomplete left femur (Fig. 4.8) that was damaged during the excavations. Also the right and left tibia bones (Figs. 4.9 and 4.10) are similar in length (14.6 cm), indicating they may have come from the same individual. A right astragal is complete (Fig. 4.11). Finally, from the pedal skeleton, the right Metatarsus IV (Fig. 4.14) was found in the sediment dump in front of the cave during a sieving program in 2005. A fractured femur and metacarpus appeared freshly broken.

Discussion

Processing of samples from the Srbsko-Komin hyena den showed that about 60% of the sediment was hyena coprolite material. Some of the excrements were pellet aggregates, while others were single large pellets of up to 8 cm. These single large pellets were drop-shaped, round or oval and flat on the attachment sides, the shape of the entire pellet depends on the moisture and amount of phosphate obtained by swallowing bone fragments. Bone fragments generally adhere to bone compacta and spongi-

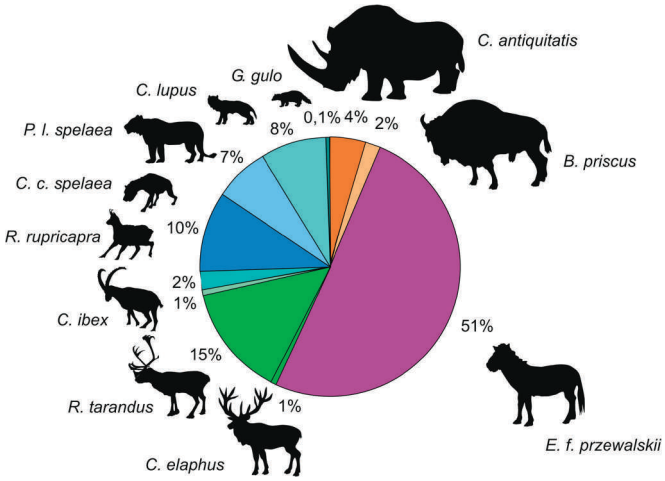

Figure 2. Percentages of hyena *Crocuta crocuta spelaea* (Goldfuss) prey remains in the Srbsko Chlum-Komín vertical cave (n = 3,569 bones) (after Diedrich and Žák, 2006).

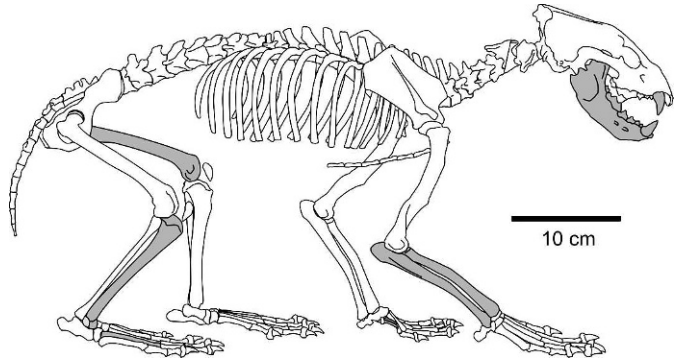

Figure 3. Anatomical locations of bones of three adult-to-senile *Gulo gulo* (Linné, 1758) individuals from the Upper Pleistocene Srbsko Chlum-Komin Cave, Bohemian Karst, Czech Republic. See Figure 4 and Table 1 for details on the bones.

osa fragments, which are then rounded by stomach acids (Diedrich, 2006; Diedrich and Žák, 2006). Such pellets were often trampled, building a phosphatic yellow-to-white layer in the cave sediments. The fecal pellet markings (Bearder and Randall, 1978; Fosse et al., 1998; Diedrich and Žák, 2006) and the megafauna assemblage, with its preservation, along with the large quantity of hyena remains, confirm the site as a well-frequented and long-term hyena-den cave site (Diedrich and Žák, 2006).

We compared the wolverine bone material to modern wolverines of Canada (Collection of Archeozoology, University Alberta, Canada), a well-preserved skeleton from the Salzofenhöhle in the Tote Gebirge (Pacher and Döppes, 1997), Pleistocene material from the catalogue of the Middle European sites (Döppes, 2001), and material from the German Perick Caves (Diedrich and Döppes, 2004). The small complete mandibles (lengths 10.7 to 10.9 cm) indicate females (Döppes, 2001), as do the tibiae and the radius. The ulna was consistent with the length of larger males. The other material is not useful for sex identification. All material appears to be from adult animals; juveniles are absent. Predation or scavenging on wolverines is evident primarily in the mandible remains, which were cracked out of the skulls by hyenas or other carnivores (e.g., Diedrich, 2006). A few wolverine skull fragments were also discovered, although postcranial bones are generally intact and show no evidence of chewing.

The presence of wolverine in the Komin is most likely due to predation or scavenging. Wolverines, as scavenging carnivores themselves, may have been drawn to carrion in the cave, such as reindeers (Fig. 5), which also have been found in the Srbsko Komin Cave, leaving them vulnerable to larger predators such as hyenas, or they may have been preyed upon and transported to the cave. While the ecology of Pleistocene wolverines is unclear, contemporary wolverines are not known to use caves for anything other than periodic resting or foraging sites (Magoun and Copeland, 1998). Wolverines produce their young during winter, and reproductive den sites are most commonly reported as occurring within the snow layer or associated with woody debris or boulder structures beneath the snow layer (Magoun and Copeland, 1998). Overhanging cliffs and shallow caves are occasionally used as secondary dens and rendezvous sites (Magoun and Copeland, 1998), but use of caves that are protected enough to preserve the remains of either wolverines or their prey has not been reported for modern wolverines. Additionally, reproductive den sites of contemporary wolverines are often characterized by the presence of latrine sites wherein large numbers of scats are present. Had caves been used as reproductive dens by Pleistocene wolverines, one might expect the presence of such latrines. The lack of wolverine corprolites in the Komin also precludes the possibility that wolverines fell into vertical passageways, as has been reported by White et al. (1984) and Parmalee (1967), which can not be concluded for the Srbsko-Cave at all. Predation

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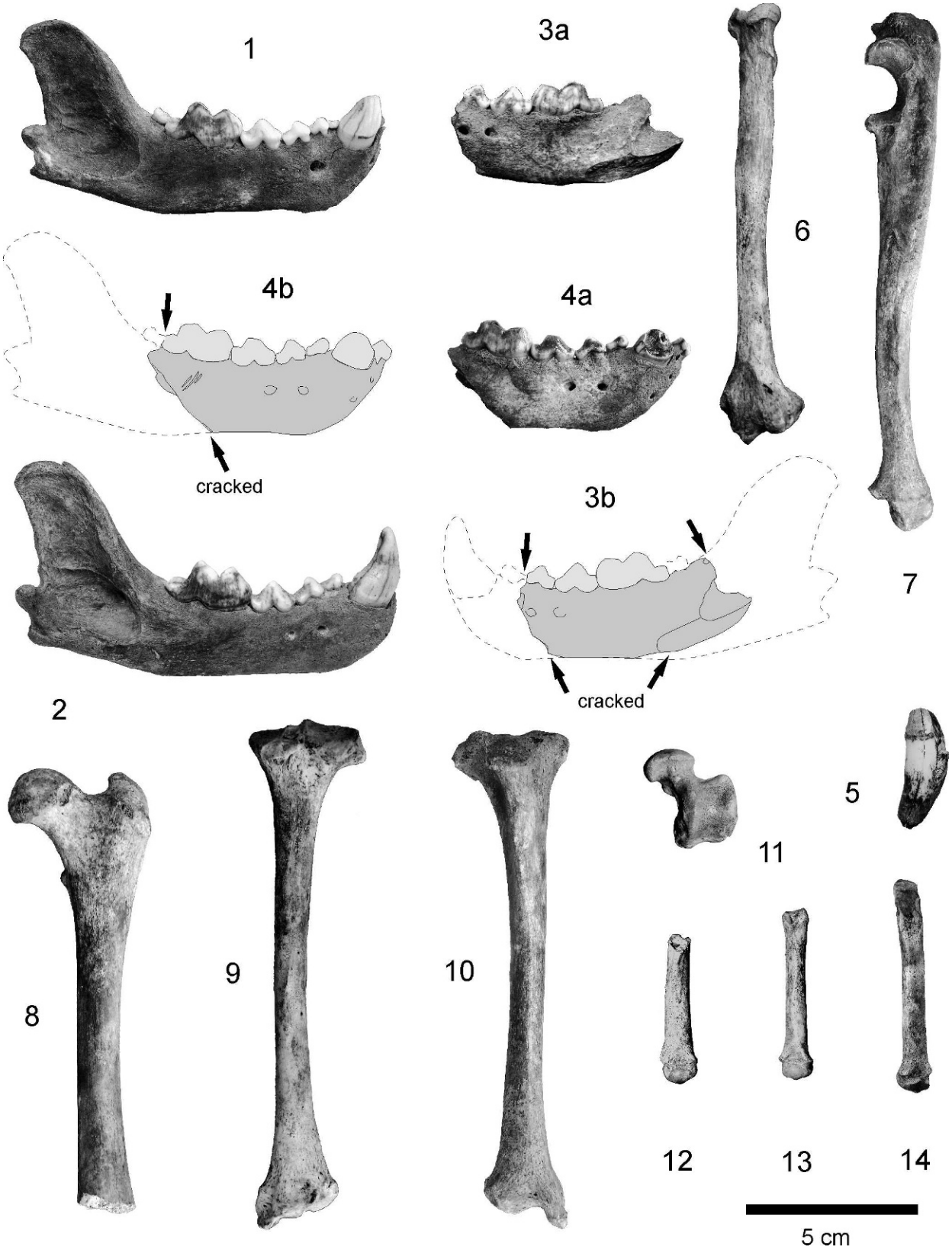
Figure 4. *Gulo gulo* (Linné, 1758) remains from the Upper Pleistocene Srbsko Chlum-Komin Cave, Bohemian Karst, Czech Republic. NMP = National Museum Prague. 1. Right mandible of an adult animal (NMP No. R 4376), lateral. 2. Right mandible of an adult animal (NMP No. R 4377), lateral. 3. Left mandible of an adult animal (NMP No. R 4858), lateral. 4. Right mandible of a senile animal (NMP No. R 4853), lateral. 5. Canine of a senile animal (NMP No. R 4202), lateral. 6. Right radius of an adult-senile animal (NMP No. R 4257), cranial. 7. Right ulna of an adult-senile animal (NMP No. R 4256), lateral. 8. Left femur of an adult-senile animal (NMP No. Ra 3764), cranial. 9. Right tibia of an adult-senile animal (NMP



No. Ra 3765), caudal. 10. Right tibia of an adult-senile animal (NMP No. R 5320), cranial. 11. Right astragal of an adult-senile animal (NMP No. R 4378), dorsal. 12. Metacarpal bone fragment (NMP No. R 4204), cranial. 13. Left metacarpal IV of an adult-senile animal (NMP No. R 4203), cranial. 14. Right metatarsal IV (Museum of the Bohemian Karst Beroun without number), cranial.

Table 1. *Gulo gulo* (Linné, 1758) bone remains from the Upper Pleistocene Srbsko-Chlum-Komin Cave, Bohemian Karst, Czech Republic.

No.	Coll.-No.	Locality and Collector	Bone Type	Remarks	Left	Right	Individual Age	Photoplate Original	Collection
1	R 4376	Chlum-Komin (Beneš 1968)	Mandible (length 8.7 cm)	Nearly complete, without $I_{1–3}$		x	Senile	x	National Museum Prague
2	R 4377	Chlum-Komin (Beneš 1968)	Mandible (length 8.9 cm)	Nearly complete, without $I_{1–3}$, M_2		x	High Adult	x	National Museum Prague
3	R 4858	Chlum-Komin (Beneš 1971)	Mandible	With $P_{3–4}$, M_1	x		Senile	x	National Museum Prague
4	R 4853	Chlum-Komin (Beneš 1971)	Mandible	Without ramus, and I_1, M_2		x	Senile	x	National Museum Prague
5	R 4202	Chlum-Komin (Beneš 1964)	Canine	Incomplete			Senile	x	National Museum Prague
6	R 5317	Chlum-Komin (Beneš 1968)	I_2	Incomplete	x		Adult/Senile		National Museum Prague
7	R 4855	Chlum-Komin (Beneš 1971)	I_3	Incomplete		x	Adult/Senile		National Museum Prague
8	R 4257	Chlum-Komin (Beneš 1965)	Radius (length 10.3 cm)	Complete		x	Adult/Senile	x	National Museum Prague
9	R 4256	Chlum-Komin (Beneš 1964)	Ulna (length 12.2 cm)	Complete		x	Adult/Senile	x	National Museum Prague
10	R 4204	Chlum-Komin (Beneš 1964)	Metacarpus	Fragment			?	x	National Museum Prague
11	R 4203	Chlum-Komin (Beneš 1964)	Metacarpus	IV	x		Adult/Senile	x	National Museum Prague
12	Ra 3764	Chlum-Komin (Fejfar 1964)	Femur	Without distal joint	x		Adult/Senile	x	National Museum Prague
13	Ra 3765	Chlum-Komin (Fejfar 1964)	Tibia (length 11.6 cm)	Complete		x	Adult/Senile	x	National Museum Prague
14	R 5320	Chlum-Komin (Beneš 1972)	Tibia (length 11.6 cm)	Complete		x	Adult/Senile	x	National Museum Prague
15	R 4378	Chlum-Komin (Beneš 1968)	Astragalus	Complete		x	Adult/Senile	x	National Museum Prague
16	Srbsko-G1	Chlum-Komin (Diedrich 2005)	Metatarsus	IV		x	Adult/Senile	x	Museum Bohemian Karst Beroun

upon wolverines by conspecifics (Persson, 2003; Krebs et al., 2004), mountain lions (*Puma concolor*) (Krebs et al., 2004), and wolves (Burkholder, 1962) indicates the vulnerability of the species to large predators, which likely included the European hyena during the Late Pleistocene. The practice of modern African spotted hyenas (*Crocuta crocuta crocuta*) to kill and scavenge other predators up to lion sizes is evidenced by numerous descriptions of the bones of prey species at modern hyena dens (Sutcliffe, 1970; Kruuk, 1972; Scott and Klein, 1981) and recently proven for Late Pleistocene (*Crocuta crocuta spelaea*) hyena dens (Diedrich, 2009a). The lack of wolverine corprolites and the association of chewed wolverine bones with numerous other macromammal remains in other prey-storage cave sites (Diedrich and Žák, 2006) support our contention that wolverines were most likely killed at or near the cave and transported there to be eaten by hyenas, such as recently proposed for two other Late Pleistocene

Figure 5. Wolverine on reindeer carcass near the Srbsko Chlum-Komin Cave, Bohemian Karst, Czech Republic (illustration courtesy of G. "Rinaldino" Teichmann by permission).

hyena den sites, the Sloup Cave (Czech Republic: Diedrich, 2009b), and the Perick Caves (Germany: Diedrich, 2008).

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