TYPOLOGY OF ICE AGE SPOTTED HYENA *CROCUTA CROCUTA SPELAEA* (GOLDFUSS, 1823) COPROLITE AGGREGATE PELLETS FROM THE EUROPEAN LATE PLEISTOCENE AND THEIR SIGNIFICANCE AT DENS AND SCAVENGING SITES

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Abstract—Late Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) phosphatic coprolites from Central Europe are reviewed. These coprolites were predominately found in prey depot and commuting den hyena caves or at open air dens. In two cases pellets were found next to mammoth and straight-tusk elephant skeletons. Coprolites are identical in their shapes to those of modern African spotted hyenas (*Crocuta crocuta crocuta* (Erxleben, 1777). Feces consist of aggregates of pellets, built of several single droplets which are classified into seven different shapes and depend on their position within the aggregate. In most cases, coprolites contain small bone fragments of bone (compact or spongy). These bone remains cannot be attributed to the consumed prey without DNA testing. Pollen in coprolites do not allow a Pleistocene landscape reconstruction, because these originate from the intestines of the consumed prey and therefore reflect the prey's main food source. Radiocarbon dating of coprolites does not allow the determination of the exact time of extinction of the last hyenas of Europe. Fecal pellets are/were used by extant/extinct spotted hyenas to mark their dens and territories against other clans, lion prides and even wolf packs. A large number of coprolites and phosphatic layers, built of trampled excrements, are found at commuting or prey depot den sites (caves and open air), and are often important for distinguishing human and hyena den bone assemblages in Europe.

INTRODUCTION

Phosphatic carnivore coprolites were often either not collected or trampled and subsequently destroyed by shovel and pick axe excavations during the "cave bear bone hunt" in the caves of Europe during the 19th century (Buckland, 1823). The most famous German cave where phosphatic layers were described was the German Lindenthaler Hyänenhöhle Cave in Gera (Liebe, 1876). The first described fossil coprolites of Late Pleistocene "cave hyenas" (Ice Age spotted hyenas: Diedrich, 2011a) were mentioned as Album graecum from Kirkdale Cave in England (Fig. 1; Buckland, 1823). Kirkdale Cave was the first Late Pleistocene hyena den described from the European Ice Age. This cave also preserves many hyena *Crocuta crocuta spelaea* specimens of cubs, old animals (Reynolds, 1902) and hyena prey remains (Buckland, 1823).

After their first description in 1823 (Buckland, 1823), little attention was paid to late Pleistocene hyena coprolites until recently when a few specimens were described from several European caves (Musil, 1962; Horwitz and Goldberg, 1989; Fernandéz-Rodrìguez et al., 1995; Fosse et al., 1998; Tournepiche and Couture, 1999; Tournepiche and Ferrier, unpubl., 2004; Diedrich and Žák, 2006; Figs. 1-2). Late Pleistocene hyena coprolites were also documented at the open air, mammoth site of Siegsdorf (Ziegler, 1994), the elephant graveyard at Neumark-Nord Lake 1 (Diedrich, 2010), from the open air hyena cub raising and commuting den of Bad Wildungen (Diedrich, 2006) and from the Dutch North-Sea coast at Rotterdam (Reumer et al., 2010; Fig. 1).

Diedrich (in press a) proposed a preliminary classification of coprolite types from historically collected material from Sloup Cave in the Czech Republic (Figs. 1-2, Table 1). This classification of pellet morphological types is refined in this paper by including additional material from Central Europe.

Modern excavations in the French La Chauverie Cave (Tournepiche and Ferrier, unpubl., 2004; Fig. 1), the German Westeregeln open air site/Neanderthal camp site (Diedrich, unpubl., 2012b; Fig. 1) revealed coprolites between massive bone layers and Neanderthal artifact horizons (Fig. 3). Their presence/absence is important to understand not only hyena/human bone assemblage origins (e.g., Pickering, 2002; Kuhn et al., 2008), but also hyena den types in more detail. Dens of the extant African Spotted Hyena *Crocuta crocuta crocuta* (Erxleben, 1777) can be differentiated into two main types, a cub raising/natal den, and a communal/commuting den (cf. Cooper, 1993; Frank, 1986; Pokines and Peterhans, 2007), but European Late Pleistocene hyena dens seem to differ by the presence of prey depots in caves (a third type of den for food storage) as a result of cold climates in the Late Pleistocene in cave-rich Europe (Diedrich, unpubl., 2012a-b).

MATERIAL AND METHODS

In total nine aggregate pieces, 81 single pellets and several fragments from four Late Pleistocene cave and three open air sites were studied (Table 1). The coprolite material is housed in the following collections: AMB, Anthropos Museum Brno, Czech Republic; LDA, Landesamt für Archäologie, Saxony-Anhalt, Germany; NHMP, Natural History Museum of Prague, Czech Republic; NHMV, Natural History Museum of Vienna, Austria; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; NHMV, Natural History Museum Vienna, Austria; SBW, Stadtmuseum Bad Wildungen, Germany; and BA, Burgmuseum Attendorn, Germany.

RESULTS

Aggregates and Pellet Morphological Types

Recent and Late Pleistocene spotted hyena feces/coprolites consist of aggregates, which are built of single elements (pellets). These aggregates are up to 6 cm wide and 8 cm long (Fig. 5). The different shaped pellets are mostly deposited in a row (Fig. 4), but sometimes also form large irregular compositions of two to three pellets (Fig. 5). The pellets have an internal granular-like structure and are porous due to shrinking during dehydration.

Modern and Late Pleistocene pellets are classified here into seven shapes (Figs. 4, 6). The parts of the aggregate consist, in anterior to posterior order, of:

A. Conical: Anterior pellets, conical in lateral view, but round in cross-section. These only have one side with an attachment surface for

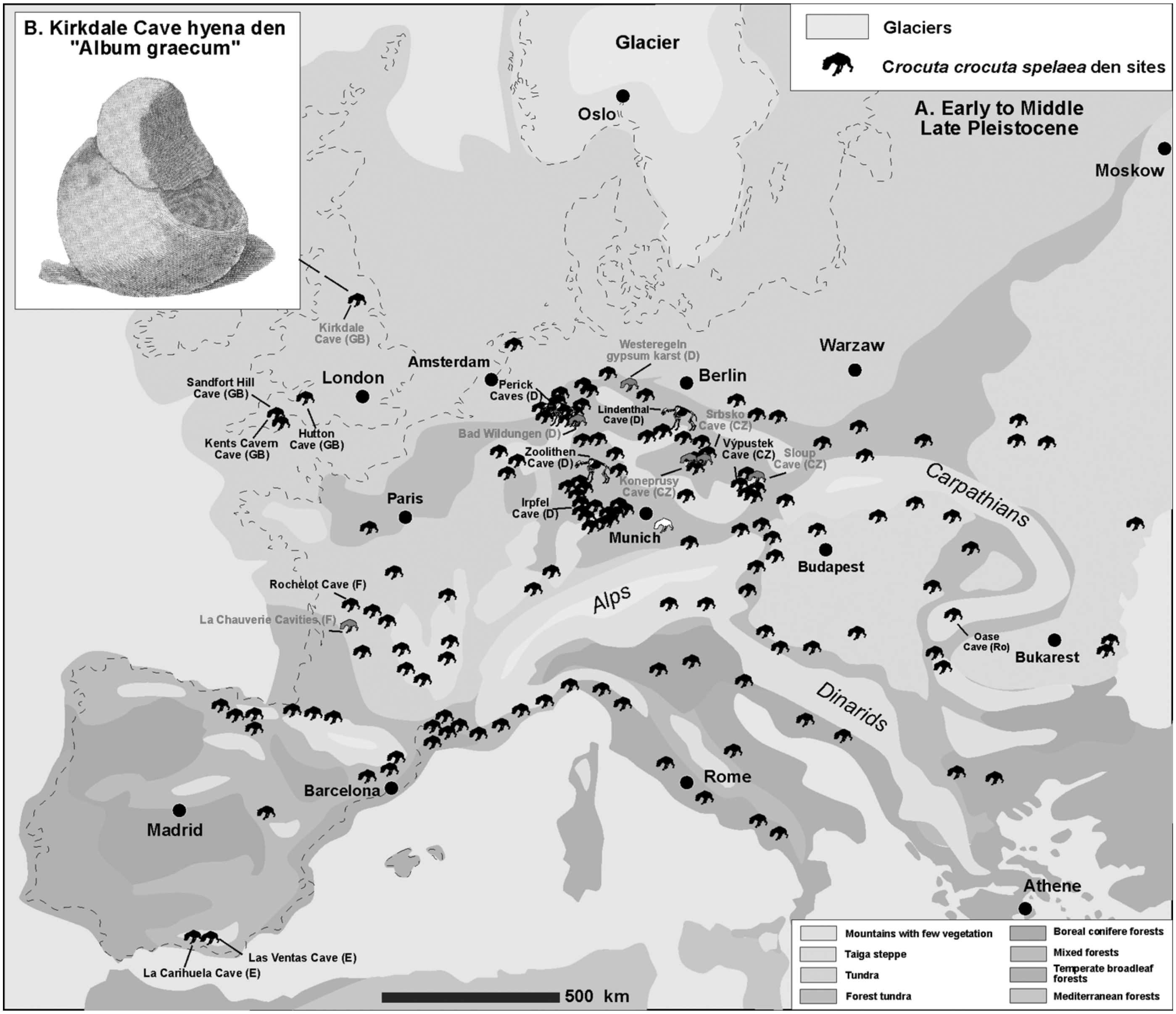

FIGURE 1. Central European hyena den cave and open air site localities in Spain, France, Germany, and Czech Republic of Central Europe (sites from Fosse et al., 1998; Tournepiche and Couture, 1999; Tournepiche and Ferrier, unpubl., 2004; Diedrich, 2011d). **B**, First Album graecum illustrated from the Kirkdale Cave hyena den, England (from Buckland, 1823).

the next pellet, which is commonly disc-shaped.

B. Disc: Laterally these pellets are flattened or triangular shaped with attachment surfaces for other pellets at both sides. Sometimes disk pellet types are attached to others of the same kind.

C. Oval: This middle pellet type usually has two attachment surfaces (sometimes absent or very small). Their size is highly variable, but length and height are of similar size. These are followed by the next type (D).

D. Long-oval: These belong to the second part of the aggregate.

E. Round: These types are usually found at the end of rows of type D pellets. They can also be of polygonal shape, sometimes without attachment surfaces.

F. Irregular: These pellets types have variable shapes and are mainly found at the end of an elongated aggregate, often forming complexes of two to four single pellets.

G. Drop: This pellet type is drop or double drop shaped and they are generally the most posterior pellets of an aggregate and relatively small.

DISCUSSION

Coprolite Taphonomy

Fossil and modern phosphatic hyena feces/coprolites are quite robust due to early diagenesis and cementation of the bone phosphate that starts in the intestines. Dried and hardened single pellets can survive short distance water transport, as for example at the Late Pleistocene Sloup Cave (Diedrich, in press a; Fig. 1), the open air site of Westeregeln (Diedrich et al., 2011) and the marine reworked coprolites found at the North Sea coast (Reumer et al., 2010). Experiments on modern feces support this pattern (Larkin et al., 2000). Porous phosphatic feces of Spotted Hyenas can to a certain degree even withstand trampling at den sites. Trampled feces with small pellet fragments, such as for example found in the sediments at the Srbsko Chlum Komin Cave (Diedrich, 2007; Fig. 1), can result in white phosphatic beds as described for the German Lindenthaler Hyänenhöhle Cave (Liebe, 1876; Fig. 1). At some Late Pleistocene Spotted Hyena den caves coprolites seem to have been

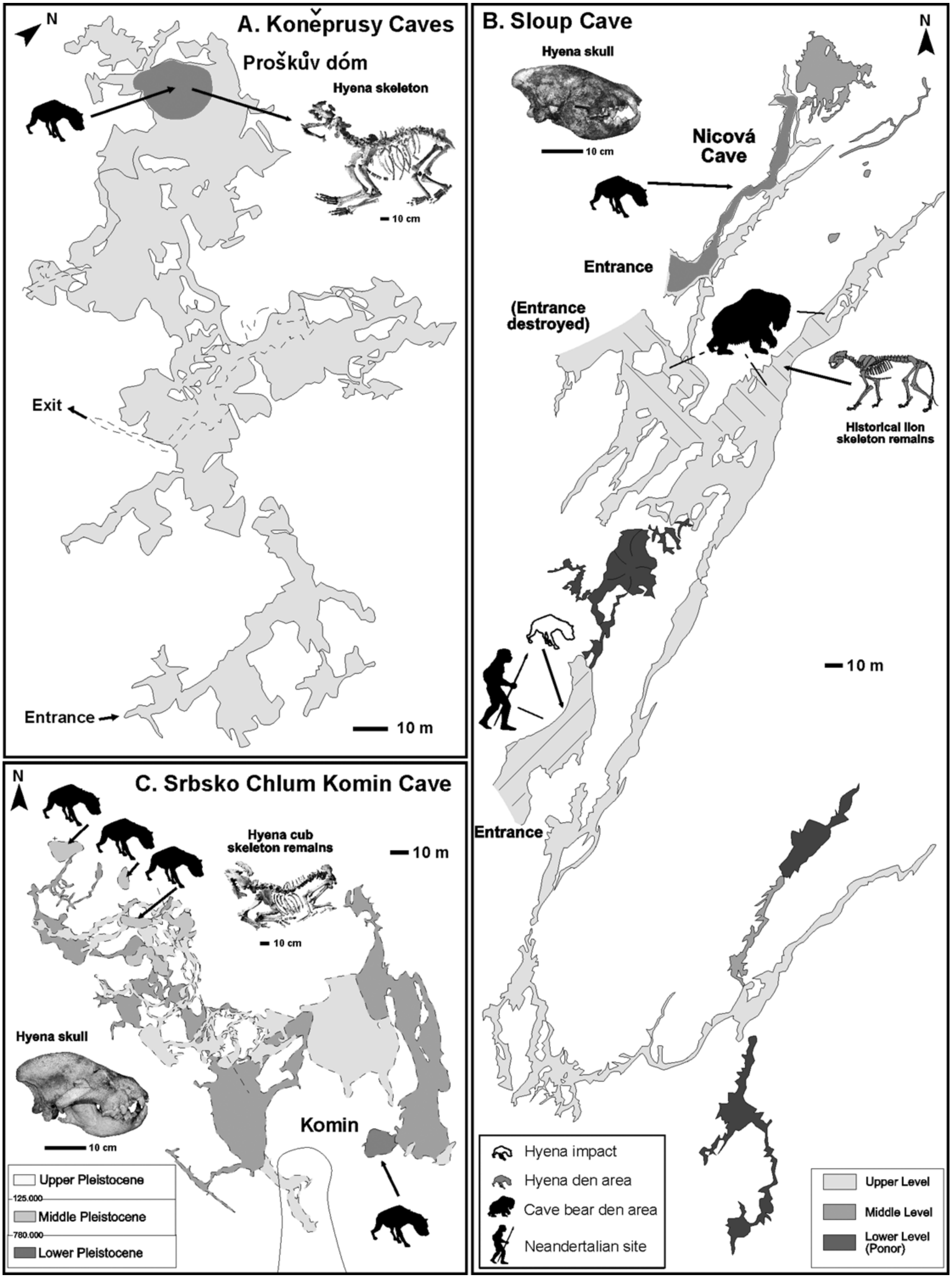

FIGURE 2. Hyena den and coprolite accumulations (in red) in larger cave systems of the Czech Republic (maps from Diedrich and Žák, 2006; Diedrich, in press a).

TABLE 1. Sites with Ice Age Spotted Hyena coprolites in Central Europe.

Locality	Pellet amounts	Den type	Bones	Publication
Caves				
Koněprusy Caves (CZ)	1 aggregate, 23 single pellets, 11 fragments	Late Pleistocene hyena den, and Middle Pleistocene cave bear den	122 hyena bones, including one individual skeleton, 711 prey bones,	Diedrich, C., Žák, K., 2006, Diedrich, 2011e
Pfefferburg Cave (D)	5 single pellets	Hyena, wolf and cave bear den	36 hyena bones, 66 prey bones	Unpublished
Sloup Cave (CZ)	23 single pellets	Hyena, and cave bear den	86 hyena bones, 139 prey bones	Diedrich, 2011a
Srbsko-Chlum-Komín Cave (CZ)	1 aggregate, 2 single pellets, 5 fragments, and many small fragments from sediment sieving	Hyena den	311 hyena bones, including 5 incomplete skeleton remains, 3.596 prey bones,	Diedrich, C., Žák, K., 2006, Diedrich, 2012a
Open air sites				
Bad Wildungen (D)	3 aggregate , 13 single pellets	Hyena den	11 hyena bones, 260 prey bones	Diedrich, 2006
Neumark-Nord Lake 1 (D)	4 aggregate, 4 single pellet fragments	Elephant graveyard, hyena scavenging site	6 hyena bones, approximately 24 forest elephant skeletons, and many other mammal skeletons, Neandertal camps around the lake	Diedrich, 2010
Westeregeln (D)	4 complete, 15 incomplete single pellets	Hyena den, and Neanderthal camp site	84 hyena bones, 572 prey bones	Diedrich, 2012b

destroyed by flooding and redepositied in bonebed layers, such as recently has been demonstrated for the hyena, wolf and cave bear den at Zoolithen Cave in Bavaria (Diedrich, 2011a; Fig. 1).

Typology of Feces Morphology

Previously there was no classification of the shape of Recent and Late Pleistocene Spotted Hyena pellets and they were often simply classified as of hyena origin without study of the complete den assemblage (e.g. Carriòn et al., 2001). In order to distinguish rare wolf pellets from hyena excrements at Late Pleistocene sites, a first terminology and description of seven different pellet shape types within aggregates is presented for fossilized pellets from Late Pleistocene Spotted Hyena coprolites. This material was visually compared to images of similar-shaped feces of Recent Spotted Hyena feces from Diedrich and Žák (2006) and Diedrich (2010d).

Hyena coprolites are present or were collected in Czech caves in the Moravian mountain region (e.g., Sloup Cave, Šipka Cave, Sveduv Stul Cave) and in hyena den caves of the Bohemian Mountains (cf. Diedrich and Žák, 2006).

Coprolite pellet shapes of Late Pleistocene Spotted Hyenas are the same as found in Recent members of the species that produce fecal aggregates consisting of differently shaped pellet forms that are attached to each other (Diedrich and Žák, 2006; Diedrich, 2010d, Fig. 4). Of all the potential shape and size possibilities, the single pellets of the Late Pleistocene described herein are most similar to pellet aggregates from dry feces of African Spotted Hyenas (cf. Diedrich, 2010d, Fig. 4). Pellet sizes are variable depending on their position (Fig. 4), the pellet producer's age, water content and the percentage of digested bone material. Softer coprolites are documented, due to caliche encrustation in loess sediment, from Bad Wildungen, where coprolites are often strongly flattened (Diedrich, 2006). A larger amount of consumed bones stabilized the phosphatic feces, and resulted in a good three dimensional preservation of shapes. To confirm this pattern, a German Shepherd dog was fed different diets. Soft material (meat, flesh and little bone) had more water content, which resulted in less clear shaped pellets that easily fell apart. A diet rich in bone, on the other hand produced harder, well-shaped pellets.

The Record of Prey in Coprolites

Spotted Hyena pellets from the Recent and Pleistocene nearly always contain bone fragments, which are partly visible on the pellet surfaces or on incomplete and broken specimens. In most cases they are compact bone fragments (Fig. 7) and surfaces can exhibit a sponge-like structure. At some sites the thin-walled bone spongiosa pieces were well preserved in pellets (Fig. 7), and could for example be attributed to the main scavenged prey, the Woolly Rhinoceros (*Coelodonta antiquitatis*), whose bones are completely filled with spongiosa at Bad Wildungen, which was a site utilized for food storage and cub raising (Diedrich, 2006). The lack of dissolution of the thin-walled bone spongiosa pieces is likely to be the result of the large amount of consumed bone material. The preservation of bone fragments in feces is also described for the Recent African Spotted Hyena feces (Horwitz and Goldberg, 1989; Larkin et al., 2000). There has yet to be any DNA analyses of such bone fragments from Pleistocene or Recent pellets.

Radiocarbon Dating of Hyena Coprolites

Radiocarbon dating of fossil coprolites is difficult because of their porous structure, into which younger carbon can penetrate. A good example is the radiocarbon dating of the Late Pleistocene hyena coprolites at the Westeregeln site in Germany (Diedrich and Weber, unpubl., 2012), which estimated a coprolite age of 14,101 ± 70 BP (latest Late Pleistocene) with two sigma range of BC 15246 – 14426 with a probability 95.4 % (sample KIA 40326). However, the site stratigraphy at Westeregeln site and its Palaeolithic specimens dated the coprolites to the Early to Middle Late Pleistocene (Diedrich, in press d). These coprolites were partly covered by caliche and fossilized by calcium carbonate that penetrated into the spongious excrement pores. This calcium carbonate must originate from the overlying periglacial loess sediments and therefore the C14 dating probably represents the date of calcification (fossilization), and not the true age of the coprolites. For this reason the dating of the youngest coprolite records of Europe in Spain, which were collected for pollen analyses without any stratigraphic or faunal context (Carriòn et al., 2001) are probably erroneous. The accelerator mass spectrometry (AMS) radiocarbon dating of two coprolite samples gave ages of 10,759 BP (BC 10,871-10,636) and 12,780 (BC 12,949-12,618) (Carriòn et al., 2001). However, recent analysis shows that hyenas became extinct during the High Glacial. No bone dating has demonstrated later dates and coprolites therefore seem to be of little use for dating the last Spotted Hyenas of Europe, because of their carbonate contaminations.

Pollen from Hyena Coprolites

The pollen content of Recent Spotted Hyena feces was first studied in Africa by Scott (1987). Pollen were extracted from Las Vantanas Cave and La Carihuela Cave in southern Spain from Late Pleistocene fossil hyena coprolites (Fig. 1). These pollen were supposed to reflect the landscape vegetation (Carriòn et al., 2001) but this did not take into account that extant Spotted Hyenas always consume the intestines of hunted or scavenged herbivorous prey (e.g. Kruuk, 1972; Diedrich, unpubl., 2012a). Therefore these pollen probably reflects the plant diet of the prey animals that were consumed by hyenas. The pollen cannot simply be interpreted as having been ingested during drinking as proposed by Carriòn et al. (2001). Pollen from the stomach and intestines of the prey are selective for each species of each megafaunal herbivore. A floral reconstruction based on the pollen from coprolitres may be in error if the prey fauna at the hyena den site is not evaluated. At the Czech Srbsko Chlum Komín Cave, for example, the horse hunting specialization of hyenas (Diedrich, unpubl., 2012a) should presumably result in the coprolite pellets representing the pollen from horse intestines, and not pollen of the exact landscape flora reconstruction, a hypothesis that is still to be tested. However, pollen from the intestines of prey species can be used at least to qualitatively reconstruct parts of the local vegetation.

Coprolites and the Analysis of the Origin of Bone Assemblages

Recently, coprolites have been important in the Late Pleistocene for the identification and differentiation of human and non-human bone

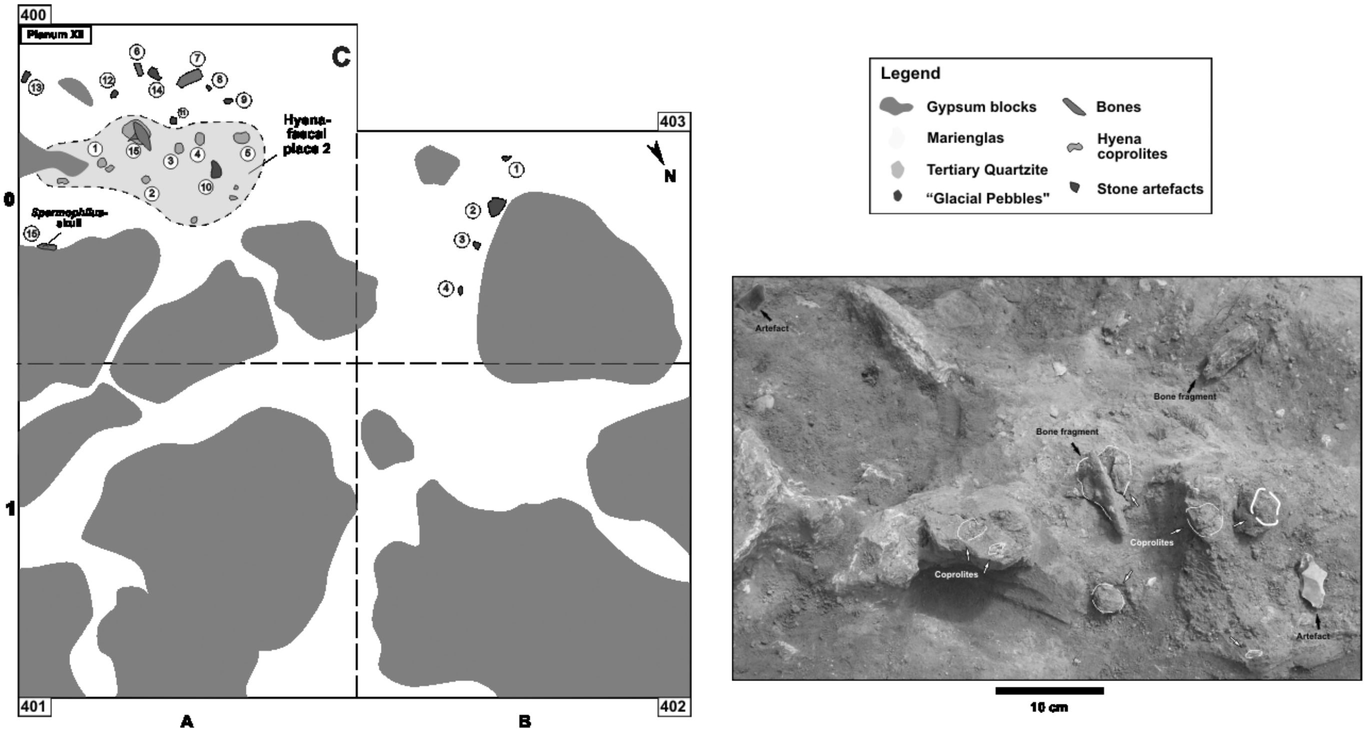

FIGURE 3. Hyena den marking area at the German Westeregeln open air site (from Diedrich, unpubl., 2012b).

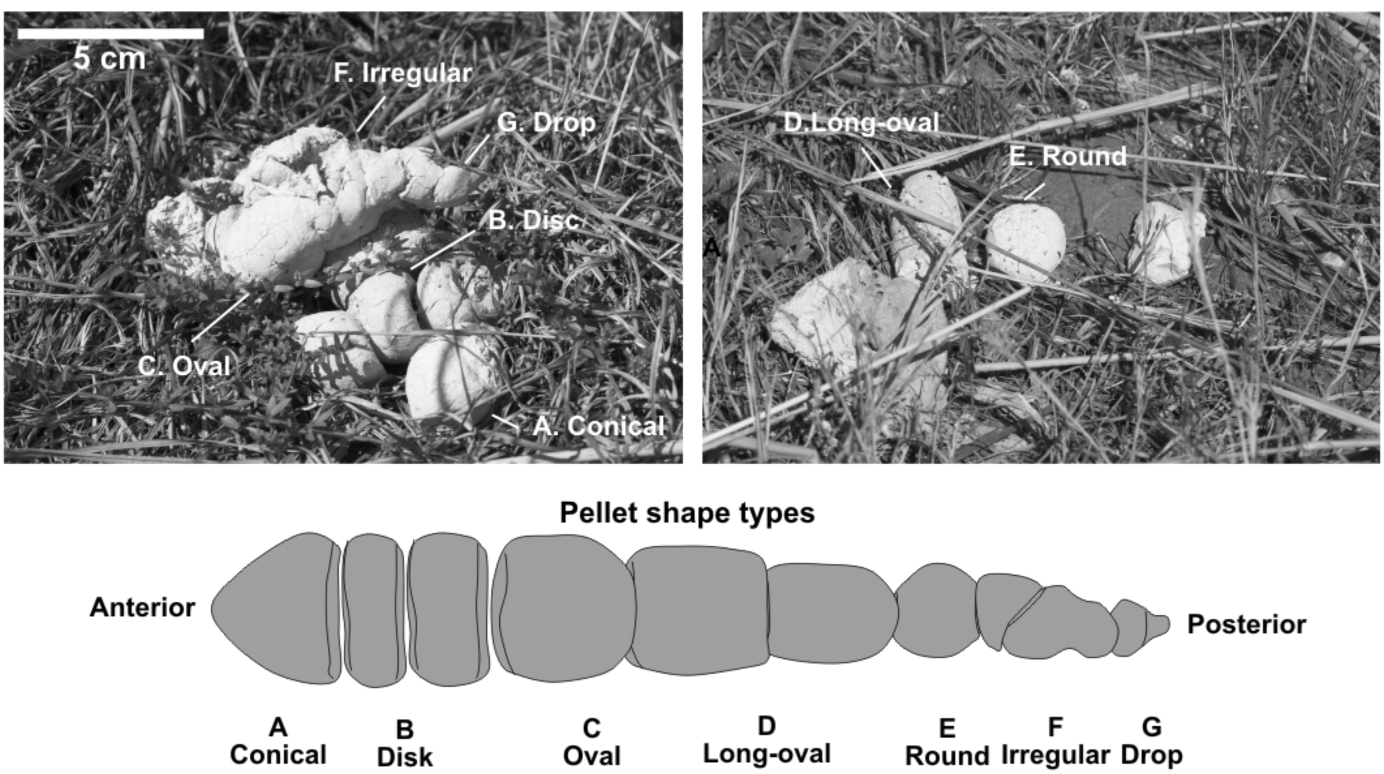

FIGURE 4. Modern extant spotted hyena *Crocuta crocuta crocuta* (Elxleben, 1777) feces aggregates with different shapes from Africa (photos used with permission from: www.predatorconservation. com/spotted%20hyena.htm), and pellet morphology terminology.

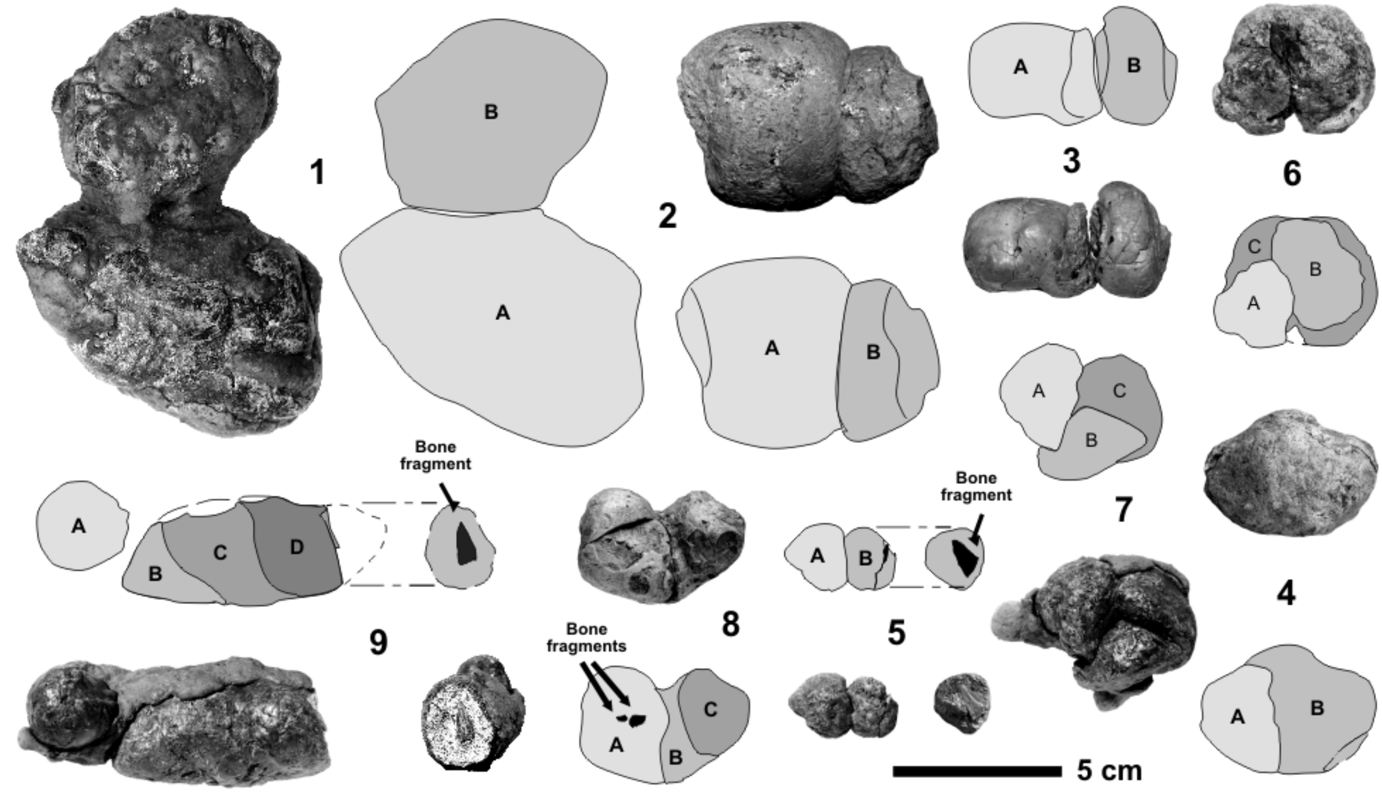

FIGURE 5. European Late Pleistocene fossil spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite aggregates with different shapes from hyena open air and cave dens. **1**, Two large pellets Bad Wildungen (SBW no. Bi-52/221); **2**, Two middle pellets Neumark-Nord Lake 1 (LDA no. 2007:47705-1); **3**, Two first and second pellets "Neumark-Nord Lake 1" (LDA no. 88:19-1 und 2); **4**, Two pellets from Westeregeln open air (LDA no. WE2933); **5**, Two first and second pellets Bad Wildungen (SBW no. Bi-52/219); **6**, Three pellets from Koneprusy Caves (NHMP no. Ra4068); **7**, Three pellets from Bad Wildungen (SBW no. Bi-52/214); **8**, Three pellets from Srbsko Chlum-Komín Cave (NHMP no. Ra 4281); **9**, Four pellets from Bad Wildungen (SBW no. Bi-52/210).

assemblages (Pickering, 2002; Stiner, 2004; Pokines and Peterhans, 2007; Lansing et al., 2007, Kuhn et al., 2008). The most recent work on the hyena/Neanderthal Westeregeln site demonstrated the importance of coprolite analysis in classifying the site as a hyena den through interpretation of the prey of the hyenas and the kitchen refuse produced by the humans (Diedrich, unpubl., 2012b). A similar discovery was made at the open air cavity site of Rochelot Cave in France where a large amount of pellets and the presence of only a few Middle Palaeolithic Neanderthal artifacts supported the interpretation of the assemblages as being of predominately hyena origin (Tournepiche and Ferrier, unpubl., 2004). This highlights that the presence of a few human artifacts in a bone assemblage does not allow a simple attribution to human hunting or kitchen refuse

Hyena Den Marking by Feces

The use of feces for territorial and den marking is well known in Recent African Spotted Hyenas (Kruuk, 1972; Bearder and Randall, 1978; Hill, 1980; Frank, 1986; Cooper, 1993; Hofer, 1998) and is also known from European Pleistocene hyena dens (Fosse et al., 1998; Diedrich and Žák, 2006; Diedrich, 2006b, 2007, 2010c).

Cave researchers have recently recognized that areas with concentrations of feces are important to interpreting the multiple uses of large cave systems by carnivores (hyenas, wolves, lions - only for dwelling) and herbivorous cave bears as was demonstrated in the Sloup Cave, Koněprusy Caves and Zoolithen Cave (cf. Diedrich, 2011a-b; in press a, c; Fig. 2). Hyena den areas in large, complex cave systems can be differentiated from wolf and cave bear den areas by mapping the location and density of coprolites within non-cave bear bone accumulations (e.g., Tournepiche and Ferrier, unpubl., 2004).

Hyena coprolites and aggregate remains were found next to the complete skeleton of a Late Pleistocene Spotted Hyena, which was scattered in the Main Dome area of the prey storage site of Koněprusy Cave (Diedrich and Žák, 2006; Diedrich, in press c) in boreal forest environments of central Europe. Hyenas carried prey remains, including a complete Woolly Rhinoceros skull and leg, carcass pieces of a Steppe Bison and horse specimens into the cave (Diedrich, 2007, in press c). Only this specific part of the cave was marked with feces by the last spotted hyenas of the region, possibly to avoid other hyena and even lion intrusions.

Pellets at Scavenging Sites

Pellets were found at two scavenging sites in Germany. Some coprolites were collected in the center of the Neumark-Nord-Lake 1 site (Eemian interglacial) in central Germany, where 24 straight-tusked elephant (*Palaeoloxodon antiquus*) carcasses were found. The carcasses were partly scavenged and dismembered by Spotted Hyenas (Diedrich, 2010; in press c-d). Other hyena coprolites were collected around a mammoth (*Mammuthus primigenius*) skeleton at Siegsdorf in southern Germany, which was also found in a wetland environment (Ziegler, 2004) and which shows clear signs of scavenging and carcass dismemberment by hyenas (Diedrich, in press d).

CONCLUSIONS

Most records of the den areas of spotted hyena from the European Late Pleistocene that yield coprolites are from caves due to an extensive history of research and favorable preservation environments.

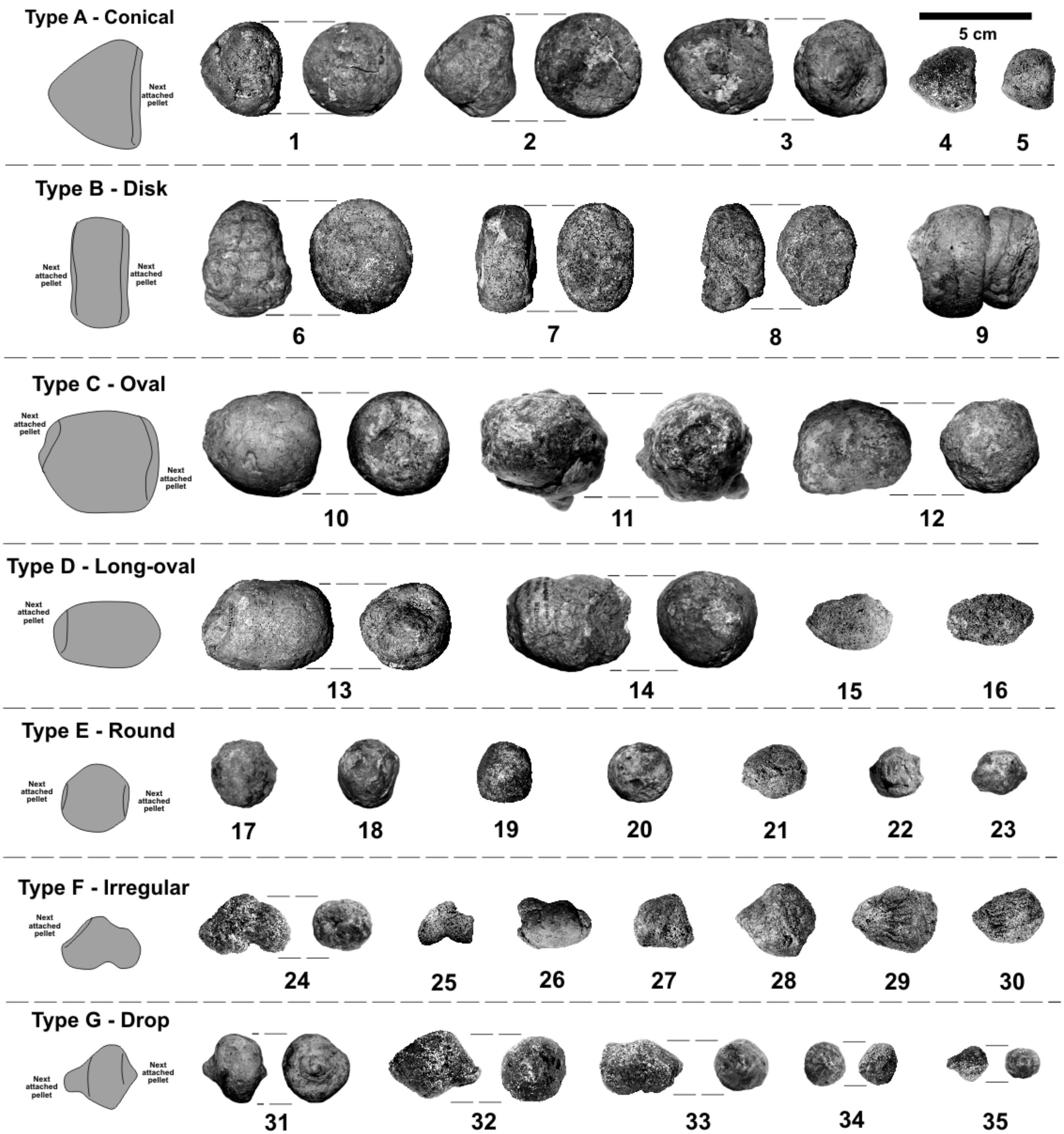

FIGURE 6. European Late Pleistocene fossil spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite pellet types. **1**, Sloup Cave (NHMW no. 2008z0087/00063); **2**, Sloup Cave (NHMV no. 2008z0087/00066); **3**, Sloup Cave (NHMV no. 2008z0087/00065); **4**, Bad Wildungen (SBW no. Bi-52/220); **5**, Koneprusy Caves (NHMP no. Ra 4066); **6**, Sloup Cave (NHMW no. 2008z0087/00060); **7**, Sloup Cave (NHMW no 2008z0087/00060); **8**, Sloup Cave (NHMW no 2008z0087/00062); **9**, Neumark-Nord Lake 1 (LDA no. 2007: 47705-2); **10**, Sloup Cave (NHMW no. 2008z0087/00067); **11**, Bad Wildungen (SBW no. Bi-52/213); **12**, Sloup Cave (NHMW no. 2008z0087/00060); **13**, Sloup Cave (NHMV no. 2008z0087/00059); **14**, Sloup Cave (NHMW no. 2008z0087/00064); **15**, Koněprusy Caves (NHMP no. Ra 4073); **16**, Srbsko Chlum-Komín Cave (NMP no. Ra 4130); **17**, Pfefferburg Cave (BA without no.); **18**, Sloup Cave (NHMW no. 2008z0087/00081); **19**, Sloup Cave (NHMW no. 2008z0087/00080); **20**, Šipka Cave (AMB without no.); **21**, Koneprusy Caves (NHMP no. Ra 4072); **22**, Koněprusy Caves (NHMP no. Ra 4089); **23**, Westeregeln (LDA no. WE2933-478); **24**, Bad Wildungen (SBW no. Bi-52/207); **25**, Neumark-Nord Lake 1 (LDA no. 2007:47689); **26**, Koněprusy Caves (NHMP no. Ra 4070); **27**, Koneprusy Caves (NHMP no. Ra 4067); **28**, Koněprusy Caves (NHMP no. Ra 4071); **29**, Koněprusy Caves (NHMP no. Ra 4069); **30**, Koněprusy Caves (NHMP no. Ra 4076); **31**, Sloup Cave (NHMW no. 2008z0087/00079); **32**, Bad Wildungen (SBW no. Bi-52/209); **33**, Bad Wildungen (SBW no. Bi-52/207); **34**, Bad Wildungen (SBW no. Bi-52/218); **35**, Bad Wildungen (SBW no. Bi-52/211).

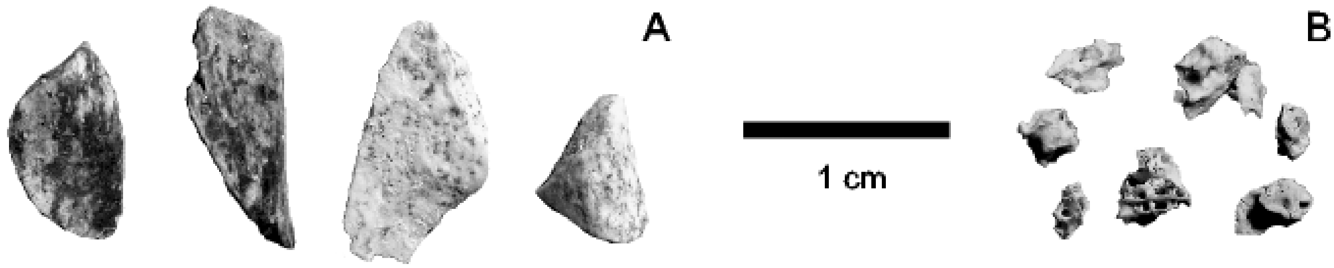

FIGURE 7. Prey bones from hyena pellets of the Bad Wildungen open air hyena den site, Germany. **A**, Rounded small bone compacta; **B**, bone spongiosa fragments (from Diedrich, 2006).

Coprolites of Late Pleistocene Spotted Hyenas are not useful for pollen analyses (botanical landscape reconstruction), nor for radiocarbon dating (hyena extinction in Europe). The aggregates of modern and fossil hyena coprolites contain at least seven different shaped single pellet types, whose form and consistency depend on the consumed meat, bone percentage and water content of the feces. Late Pleistocene *Crocuta crocuta spelaea* marked their commuting den areas in the same way as the extant African *Crocuta crocuta crocuta*. The difference in both subspecies is the presence/absence of prey storage sites, which are abundant in Europe for Late Pleistocene spotted hyenas, but nearly absent at small cave sites in Africa. Prey storage sites marked by pellets are abundant in European caves as a result of the colder climates, possibly because permafrost conditions or hard winter seasons meant that meat would freeze outside caves. Prey depot sites, at which large amounts of prey bone remains are found, were marked by feces against intrusion of other hyena clans and lions, who could steal stored food remains. Information from characteristics of Recent open air hyena dens and excavations at loess and gypsum karst sites indicate the marking of dens, prey depots and territories, in mammoth steppe lowland environments and at also at contemporaneous hyena dens and Neanderthal camp sites. Mapping of hyena den areas, using both, accumulated prey bones and coprolites allows a better understanding of the use of parts of larger cave systems by hyenas and other carnivores such as wolves, and also permits better discrimination of these areas from herbivorous cave bear den areas, that might have been occupied simultaneously.

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