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Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) clans as prezewalski horse hunters and woolly rhinoceros scavengers at the open air commuting den and contemporary Neanderthal camp site Westeregeln (central Germany)

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A B S T R A C T

Late Pleistocene Ice Age *Crocuta crocuta spelaea* (Goldfuss, 1823) hyenas from the open-air gypsum karst site Westeregeln (Saxony-Anhalt, central Germany) is dated into the early to middle Late Pleistocene. Hyena clans apparently used the karst for food storage and as "commuting den", where typical high amounts (15% of the NISP) of hyena remains appear, also faecal pellets in concentrations for den marking purposes. Additionally small carnivores *Meles, Vulpes* and *Mustela* appear to have used some cavities as dens. Several hundreds of lowland "mammoth steppe fauna" bones (NISP = 572) must have been accumulated primarily by hyenas, and not by Neanderthals at the contemporary hyena/human camp site. Abundant caballoid horse remains of "*E. germanicus* Nehring, (1884)" are revised by the holotype and original material to the small *E. c. przewalskii* horse. Woolly rhinoceros *Coelodonta antiquitatis* remains are also abundant, and were left in several cases with typical hyena scavenging damages. *Rangifer tarandus* (11%) is mainly represented by numerous fragments of shed female antlers that were apparently gathered by humans, and antler bases from male animals that were collected and chewed in few cases (only large male antlers) by hyenas. The large quantities of small reindeer antlers must have been the result of collection by humans; their stratigraphic context is unclear but such large quantities most probably resulted from schamanic activities. The hyena site overlaps with a Middle Palaeolithic Neanderthal camp, as well as possibly with a later human Magdalénian site.

1. Introduction

Bone collections assembled by the last spotted hyenas in Europe, late Ice Age *Crocuta crocuta spealea* (Goldfuss, 1823), provide information on the macrofauna and palaeobiology of that time, as well as on the types of dens used by these hyenas (Buckland, 1823; Fosse et al., 1998; Diedrich, 2005a, 2006a, 2007, 2008b, 2010d, 2011b, 2011e, 2011f, 2012a–c; Diedrich and Žák, 2006). These den-type identifications are particularly important for distinguishing bones accumulated by carnivores from those accumulated by humans in general (e.g. Pickering, 2002; Kuhn et al., 2008), and especially from those left at Middle Palaeolithic sites. Few contemporary used hyena and Neanderthal sites have been described from the open air and cave sites of England and northern Germany, or in the mammoth steppe environment and adjacent cave-rich regions of north-central Europe, in England and northern Germany (Aldhouse-Green et al., 1995; Diedrich, 2010a, 2011d).

Although hyena cave den sites predominate in the fossil record, open air sites may have been much more common throughout the mammoth steppe palaeoenvironments of Europe than previously thought, with the associated bone accumulations often having been misinterpreted as being of fluvial origin, or representing Neanderthal "refuse from food preparation" (e.g. Virchow, 1878; Heinrich, 1987). The largest, and probably the best, example of such a revised interpretation is the open air hyena den river terrace site at Bottrop, in northern Germany, where hyenas left hundreds of similarly damaged bones from their giant game prey, mainly from woolly rhinoceros and woolly mammoth (Diedrich, 2012a).

The historically collected bone material from the Westeregeln gypsum karst site in northern Germany in the Magdeburger-Börde lowlands (Fig. 1A), which is reviewed in this paper, was first mentioned by Giebel (1850a,b, 1851), and is today housed at the Martin Luther-University, Halle-Saale. Giebel referred to hyenas and their bone accumulations at Westeregeln, and described selected woolly rhinoceros remains (Giebel, 1850a,b). Additionally bones that were collected by quarry workers and subsequently purchased by Virchow (1878) are today housed in the Landesmuseum in Braunschweig. A collection was also made by Nehring

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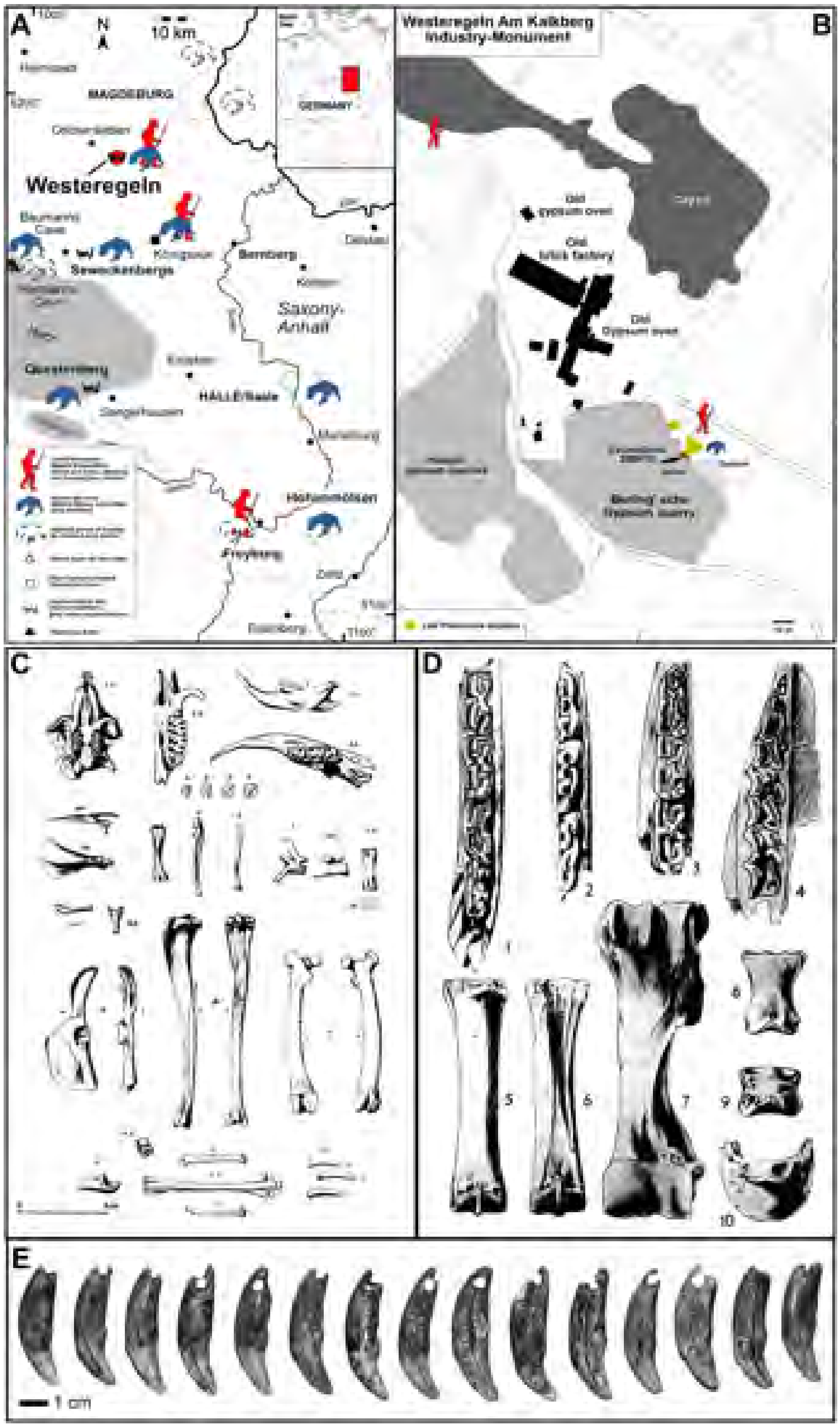

Fig. 1. A. Geographic position of the Late Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) and overlapping Neanderthal gypsum karst sites at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany). B. Hyena den sites from Diedrich (in press-a); Palaeolithic sites from Weber (2004). C. Earliest historical faunal illustrations and non-figured archaeological remains from Westeregeln, central Germany (Nehring, 1876, 1884) "*Alactaga jaculus* Schrebe" (= *A. saliens*) skeletal remains from Westergelen. D. "*Equus germanicus* Nehring" (= *E. caballus przewalskii*) originals from Westergelen (see also Fig. 10). E. Dog canine collar from Neolithic/Bronze Age from the "dark soils" (= layer 1, see Fig. 3) of the Nehring collection (MB without no.).

(1875, 1876) – housed today in the Humboldt-Universität Museum, Berlin – who mainly studied the faunal assemblage and carried out his own excavations for micromammals (Nehring, 1878a,b) but also studied horse remains, both from Westeregeln and from elsewhere (Nehring, 1884, Fig. 1A–B). He also identified a "glacial steppe mammoth fauna" bone assemblage from Westeregeln and other north German localities (Nehring, 1890), but no bone damage by humans or carnivores was mentioned. Badger material from Westeregeln was the theme of Winterfeld (1885). The brain structure of a hyena skull was analysed by Klinghardt (1931). Micromammals were further studied from a more recent doline fill excavation next to the Berling gypsum quarry (Fig. 1A–B) by Heinrich (2003), who dated the bone-bearing layers as mainly "early Late Pleistocene". Following the rediscovery of most of the historically collected bone material in 2005, the locality was classified as a "hyena den" site. Only 398 bones were known at that time, mainly from the historical collections of Nehring (Diedrich, 2007), but this number is increased herein now to 572 bones (see section on Material and Methods).

The discovery of three hand axes on the surface at different locations in the Zechstein gypsum and Buntsandstein clay area within the Westeregeln site since 1950 led to the declaration of an "archaeological monument site" at Westeregeln (Weber, 2004). New excavations in 2009/2010 in the doline fill on the edge of the Berling gypsum quarry, have yielded new information on the stratigraphy, sedimentology, and faunal content, as well as resulting in the discovery of many new stone artefacts (Diedrich et al., 2010, Fig. 1A–B). New additions to the micro- and megafauna from the 8 m thick doline sediments included bird, snake, and frog remains as well as many flint flakes and a few stone tools (Diedrich et al., 2010). Hyena faecal areas were also found in these deposits, overlapping with areas containing bones that appear to have been damaged by Neanderthals, all within a stratigraphic and palaeoenvironmental context (Fig. 2, Diedrich et al., 2010). The Westeregeln site, which was adjacent to terraces of the proto-Bode River and hence subject to the influence of periodical river floods (mainly layer 5, Fig. 2), is an important site in Europe with respect to archaeozoology, and Palaeolithic Neanderthal archaeology, and to questions regarding the origins of bone accumulations at open air sites in mammoth steppe lowlands. The new excavations in 2009/2010, including the Neanderthal stone artefacts and "refuse from food preparation", are described in another paper, while this paper provides a review of the megafauna in the previously collected material, together with some remains from the new excavations.

2. Materials and methods

Within the bone material (572 megafauna remains) of the British Natural History Museum in London, the Museum für Naturkunde in Berlin, and the Museum für Vor- und Frühgeschichte in Egeln, the oldest find is labelled with the year 1843 which means that most of the historical material was collected between 1843 and 1944, with a little more material added in 1974. Since then, new material has been recovered from the excavations in 2009/2010.

The material in the earliest large collection was purchased or excavated by Giebel between 1844 and 1848 and is shared between the Museum für Naturkunde at Humboldt University, Berlin (MB: coll. Giebel from the year 1844), and the Institute for Geosciences of the Martin Luther-University, Halle-Wittenberg (MLU.IFG: 178 specimens, coll. Giebel from the year 1848) which houses the majority of the Westeregeln bone material. A second large collection was bought and collected by Nehring (labelled 1878, including Neolithic/Bronze Age dog remains and dog canine collar from the soil layers Fig. 1E) and Werder (labelled 1935), and is mostly housed in the MB, with a few holotypes in the Bundesanstallt für Rohstoffe und Geowissenschaften in Hannover (BGR). The exact history of the material in the Museum für Vor- und Frühgeschichte in Egeln (ME) is uncertain but it appears to be related to the activities of Nehring. The history of the collection in the Naturkundemuseum, Magdeburg (NM), some of which (one hyena skull, one woolly rhinoceros mandible, and one wolf mandible) was moved in 1945 to the British Natural History Museum in London (BMNH), is also uncertain. A small quantity of additional bone material, and some hyena coprolites from faecal places, were excavated during the 2009/2010 at the large doline at the edge of the gypsum quarry Berling (Fig. 1B), and are stored in the Landesmuseum Archäologie, Saxony-Anhalt (LMSA), where a hand-axe was discovered in the 1980s on a stockpile in the quarry below the excavated doline. Within this study most of the material has been cleaned and prepared and with comprehensive inventory made (Tables S1–S15).

The bones were all checked for cut or bite marks. Single bite mark types are less important than bone damage analyses which are best observed on woolly rhinoceros bones (Diedrich, 2012a), and horse remains (Diedrich, 2010b). Of significance is the presence or absence of bones or particular body parts (mainly skulls, legs, or axial skeleton remains), and the damage-stage of especially large bones or long bones.

The historical bone collection was compared to a bone assemblage recently excavated from the doline, but this is problematic because of the much larger quantity of historical megafauna (NISP = 572) that may have been selectively collected, relative to the few remains from the small recent excavations (NISP = 39). The absence of bone fragments in the historical material and their predominance in the recently excavated material appears to reflect the rejection of bone fragments by quarry workers, who possibly collected only large, complete bones in order to sell them. Nevertheless, by combining both collections quite a good picture can be obtained of the palaeoenvironment, the biology of extinct hyenas, and the prey faunas of both hyenas and humans from remains that they left behind.

3. Geology and stratigraphy

A detailed study of the stratigraphy and palaeoenvironment of the fill material from the doline on the edge of the Berling gypsum quarry (Fig. 1A–B) is included in a separate publication and only a generalized section is included herein in order to assist in interpreting the origin of the bones recovered historically from large doline depressions in the Westeregeln gypsum karst. Bones from megafauna and micromammals were found within an 8 m deep doline depression during the recent excavations of 2009–2010 (in Layers 3–5), together with Middle Palaeolithic artefacts including hand axes and bifacially backed knife, which age these layers into the glacial period of the early to middle Upper Pleistocene, before the Last Glacial Maximun (Fig. 2A). These deposits were overlain by a periglacial soil, and a loess deposit was subsequently formed between about 14,000 and 12,000 years BP on the Magdeburger-Börde lowlands (Diedrich and Weber, in press). The recently excavated bones, as well as the historical material, are partly encrusted with caliche and are well fossilized. The surrounding sediments have impregnated the bones with a dark brown colour, except for those that were in close contact with the gypsum, which are grey–brown. All of the historical and recently excavated bones exhibit a similar stage of preservation, which suggests that they may all have derived from similar stratigraphic layers and be of similar ages. Decalcification has made all of the bones fragile, and also the coprolites (except for those that were partly encrusted by caliche and hence better preserved). Many of the historically collected bones showed modern danage, due either

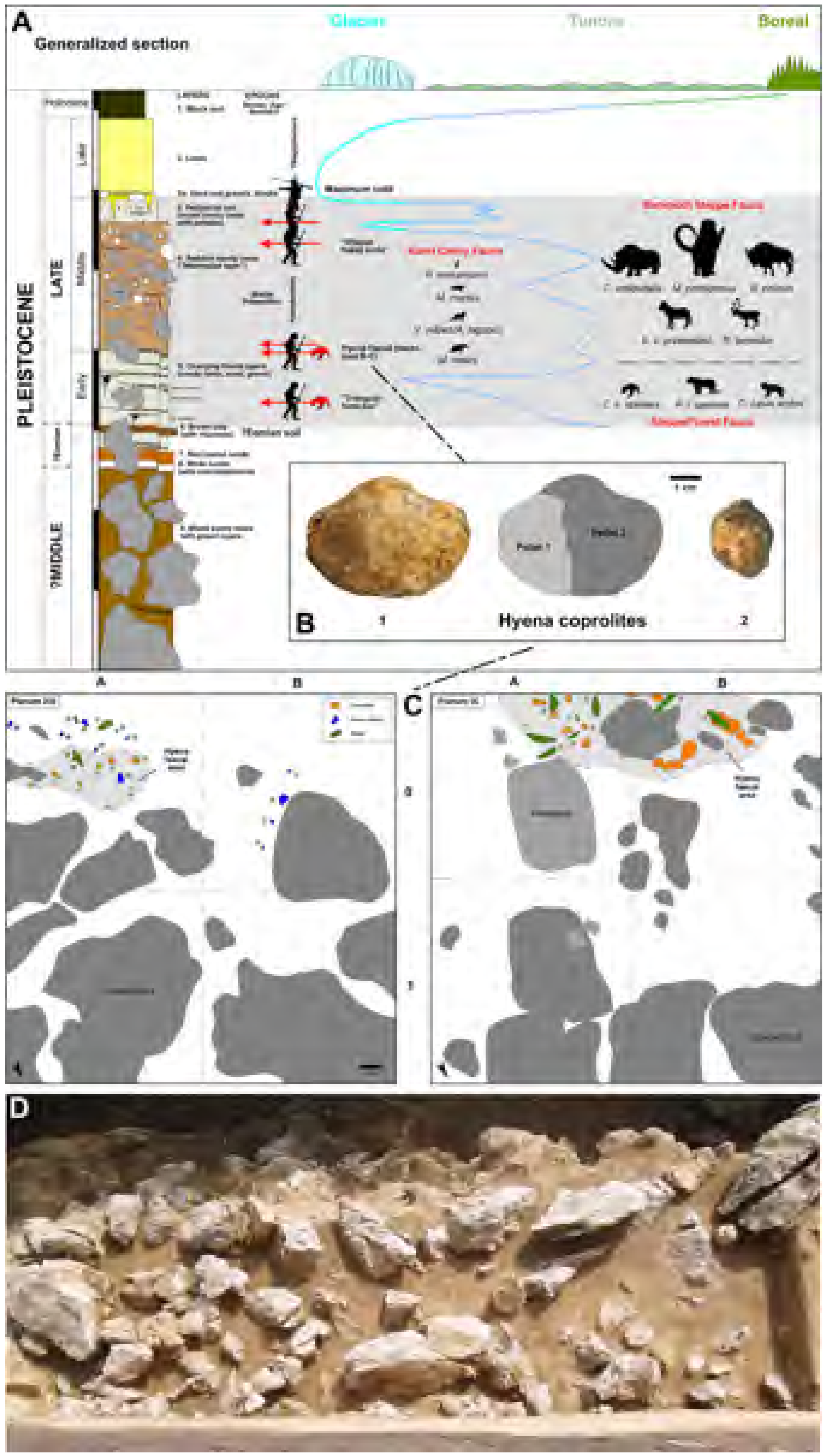

Fig. 2. A. Generalized stratigraphy from the Late Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) and overlapping Neanderthal gypsum karst sites at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany). B. Coprolites from two different levels. C. Hyena faecal areas in the early Late Pleistocene Layer 5, next to Neanderthal artefacts and bones that have been crushed by Neanderthals (mainly rib fragments from woolly rhinoceros). D. Excavated gypsum block layer in upper part of Layer 4 of the doline fill, from which a bifacial flaked knife and other stone artefacts and bone remains were excavated systematically (surface plan view from above). The section on the edge of the Berling gypsum quarry (see Fig. 1) reaches to a depth of 8 m (upper part of the photo).

to quarrying activities or in the movement of collections during the world wars, and are often incomplete, including most of the hyena skulls. In a few cases the bone surfaces are covered by a decalcification network resulting from grass rhizomes, whose roots penetrated much the loess in the upper layers (Layer 3; Fig. 2). Such caliche-encrusted and decalcified bone surfaces could, in many cases, conceal impact or bite marks.

4. Paleontology

4.1. The hyena remains

4.1.1. *Crocuta crocuta spelaea* (Figs. 7–9)

The eight skulls or fragments consist mainly of brain-cases or isolated maxillaries. Most of these have recent fractures. Only one of the skulls is complete or with dentition. Some of the maxillary fragments have teeth and may belong to some of the brain-cases, but it was not possible to match them together. One skull is from a cub (Fig. 4(1)), but all others are from adult to senile individuals (Table S1). There are relatively few postcranial remains (Table S1).

4.1.2. Cranial remains

The first skull with its non-fused sutures and round brain-case (Fig. 4(1a–d)) is the most complete cub skull known from this species in Europe. At this age the animal would originally have had a full milk dentition, from which the maxillaries and premaxillaries are now missing. The second skull is the most complete of all skulls (Fig. 3(2)) and belongs to an adult aged individual and possibly matches a right mandible of a similar wear stage. This has similar tooth wear stage as the skull dentition and belongs to an adult aged individual. The brain-case sutures are fused, not are the anterior sutures, also indicating an adult age. The sagittal crest is "slightly convex". Measurements for the condyles and teeth are given in Table S1, but the total length of the skull remains unclear due to recent occipital damage. Only the M^1 teeth and the right I^3 are missing. The right jugal arch is also missing. The posterior part of the brain-case has been preserved from a third skull (Fig. 3(3)), which is from an adult to senile animal and has a highly convex sagittal crest. Fused sutures and the well developed sagittal crest indicate the animal to have had a mature adult to senile age. A fourth skull is again represented by another brain-case from an adult to senile hyena (Fig. 3(4)), this time with only a slightly convex sagittal crest. A fifth skull (Fig. 4(1)) is represented by another adult to senile brain-case, this time with a flattened sagittal crest, similar to that of the brain-case from the sixth skull (Fig. 4(2)). A seventh skull (Fig. 4(3)) is represented by another brain-case from an adult animal, but this time with a highly convex sagittal crest. The eighth skull is only represented by the posterior part of a brain-case, which does not extend to the frontals. This brain-case had previously been cut in into two halves for brain-case studies (Fig. 4(4)). All sutures are strongly fused and the sagittal crest is well developed and flattened. The ninth, tenth, and eleventh skulls are again represented only by the posterior parts of the brain-cases of adult animals (Fig. 4(5–7)). The fragmented maxillaries (Fig. 4(8–12)), together with the illustrated teeth (Fig. 4(13–18)), were from adult to senile individuals. A few mandibles and isolated lower jaw teeth are present, mostly from adult to senile individuals (Fig. 3(5–13)), but the only nearly complete lower jaw is from the second skull (the right lower jaw) (Fig. 3(2d)).

The postcranial bones are from all body parts. The remains of forelimbs and hind limbs and a few vertebrae are 99% from adult to senile animals (Table S1), but there are at least some early adult hyena remains present (humerus: Fig. 5(2); tibia: Fig. 5(7); vertebra: Fig. 5(37)). The foreleg remains consist of humeri, ulnae, carpalia, and metacarpi bones (Fig. 5(1–5, 9–10, 12–16), Table S1). Some of the postcranial bones such as the two ulnae illustrated in Fig. 5(4 and 5)) exhibit chew marks from large carnivores and the proximal and distal parts have been chewed off, most probably as a result of cannibalism. Males and females can mostly be separated on the basis of their long bones, e.g., the tibiae (Fig. 5(7–8)), which are a little longer and slightly more massive in female hyenas than in males. The femur illustrated in Fig. 5(6) is long (286 mm) and the distal width (58 mm) matches that of other female hyena femora. The metapodials are also varied in their sizes (Fig. 5(12–19)), but no detailed analysis has yet been published for European specimens. The metacarpus in Fig. 5(18) has a lateral bone growth, which indicates a pathology and suggests a senile animal. It is not clear whether the phalanges I–II (Fig. 5(24–29)) are from forelegs or hind legs. Eight sesamoid bones, which are quite small, are included in the collections (Fig. 5(20–23)). Ten vertebrae (cf. Table S1, Fig. 5), some of which are illustrated herein (Fig. 5(30–39)), are all from adult to senile animals. The axis and C5 are the only neck vertebrae. Most of the six thoracic vertebrae are incomplete; the processi transversi and spinosi are mostly damaged or missing. Only one caudal vertebra is preserved which, from its large size, appears to be from the upper part of the tail.

4.2. Micromammals, anures, reptiles, and birds

Good qualitative listings and descriptions of the micromammals were provided by Nehring (1890), and updated by Heinrich (2003). The specimens are from a "cold period fauna", which has been mainly dated into the early Late Pleistocene Heinrich (2003) and includes the medium-sized rodents *Marmota bobac*, *Spermophilus refuscens*, *Alactaga saliens*, and *Lagomys pusillus*, and smaller rodents and mice *Arvicula amphibius*, *Arvicola gregalis*, *Arvicula ratticeps*, *Arvicula arvalis, Plecotus auritus, Lemus lemmus, Microtus torquatus* and *Sorex vulgaris*. A small proportion of the fauna listed herein is from the sinkhole sediments excavated in 2009–2010, i.e. *S. refuscens* (skull and lower jaw), *A. saliens*, *A. amphibius*, *L. lemmus*, *M. torquatus* and *A. gregaris*. Some of these are illustrated herein from Nehring collection (Fig. 6A), and skeletal remains of *A. saliens* were also described by Nehring (1876, see Fig. 1A) in the context of mammoth steppe fauna. Some of the material illustrated herein is from Nehring collection (Fig. 6A(4–5)), whereas a new humerus find from the excavated doline will be published in future. *S. refuscens* has also been found in the doline material. A few postcranial bones from *M. bobac* are from early adult to adult individuals and exhibit chewing damage that might have been caused by small carnivores (Fig. 6A(6–11)). The main species of mice remains are illustrated herein from the historical Nehring coll. with skull remains of *A. amphibius* (Fig. 6A(1)), *A.gregalis* (Fig. 6A(2)), and *M. torquatus* (Fig. 6A(3)). No quantitative or taphonomic analyses have been completed (nor were they in Heinrich, 2003) due to the small quantity of material recovered from the recent doline excavations. However, from the descriptions by Nehring (1876), the micromammal-rich areas seem to have been in fox den accumulations (as their prey) or in their own burrows (e.g., for *Spermophilus* and mice) as a result of natural mortality. The situation in the doline is, however, a little different. Snakes and frogs seem to have mainly accumulated as result of hibernating in the karstic area, whereas micromammals are rare and may have washed into the doline during floods. A coprolite/pellet, possibly from a fox or an owl, contains many micromammal remains.

Bats (*Vespertilio murinus, Myotis daubentonii,* and *Myotis dasycneme*) from Westeregeln were mentioned by Nehring (1890) but have yet to be identified in the doline fill material. However, their presence is indicative of moist environments in the surrounding areas, and of the cavities that they would have required for hibernation.

Only a few bird remains were recognized by Nehring (1890) but frog remains (*Bufo* sp. and *Rana* sp.) and snake remains (*Columber* sp. and *Natrix* sp.) are quite common in the doline fill. Neither the

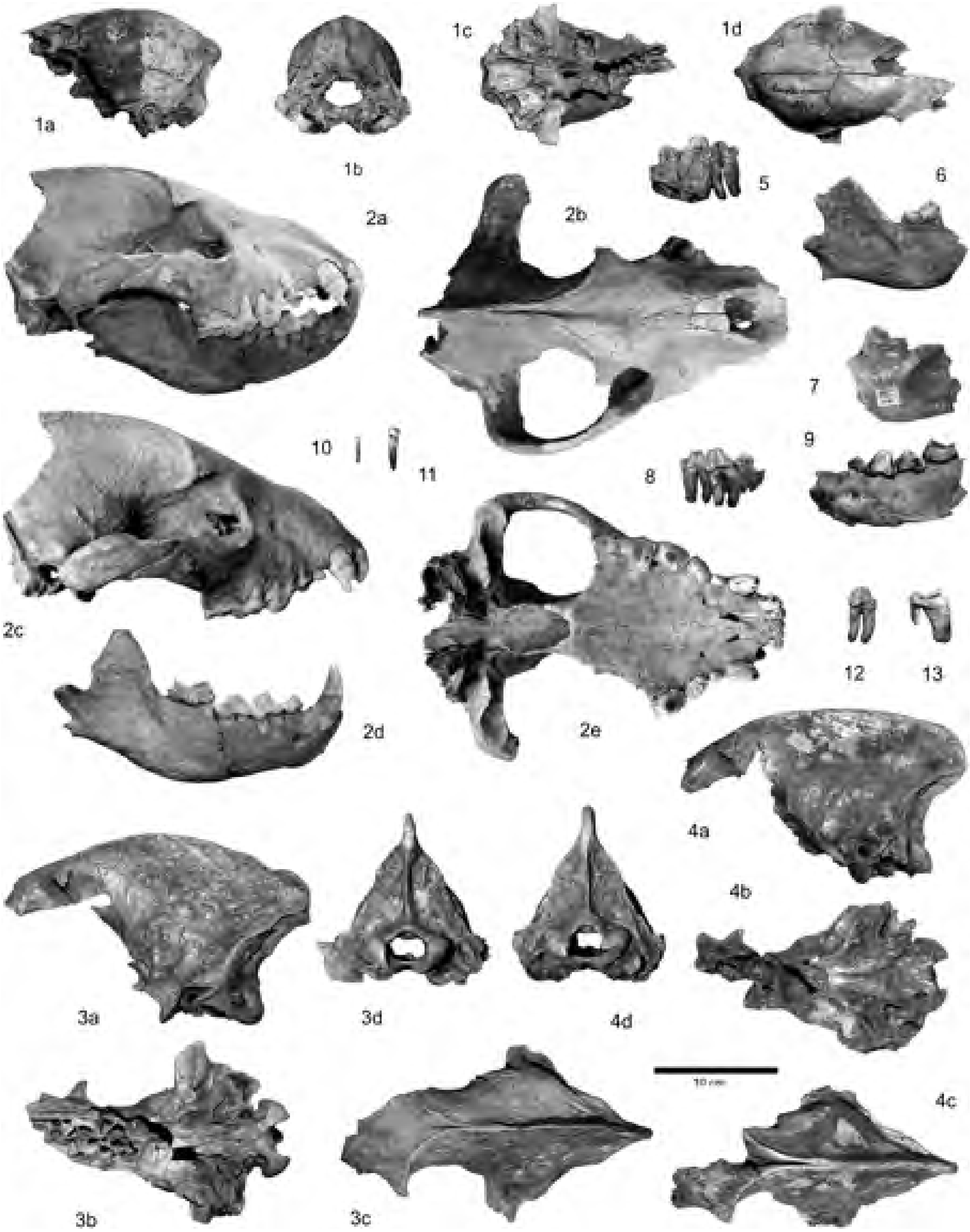

Fig. 3. Skull remains of Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823), from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

small nor the large fragmentary pieces in the new material from the doline fill have yet been studied in their species attribution.

4.3. Other carnivores

Those are represented by few material partly with large carnivore bite marks of the lion *Panthera leo spelaea* (Table S2, Fig. 6B(1–14)). Cranial and postcranial bones from *Canis lupus* subsp. (cf. *spelaeus*) have also been preserved (Table S3, Fig. 6B(15–29)). A single upper I^3 tooth from a mature *Ursus spelaeus* subsp. cave bear is of uncertain subspecies (Fig. 6B(33)). A *Meles meles* badger skull from an adult animal (Fig. 6B(30)) is the only specimen of this species (Table S5). The red fox *Vulpes vulpes* is only represented by individual post-cranial elements (Fig. 6B(31–32), Table S6). A coxa seems, from its small proportions to belong to the smaller polar fox *Alopex lagopus*

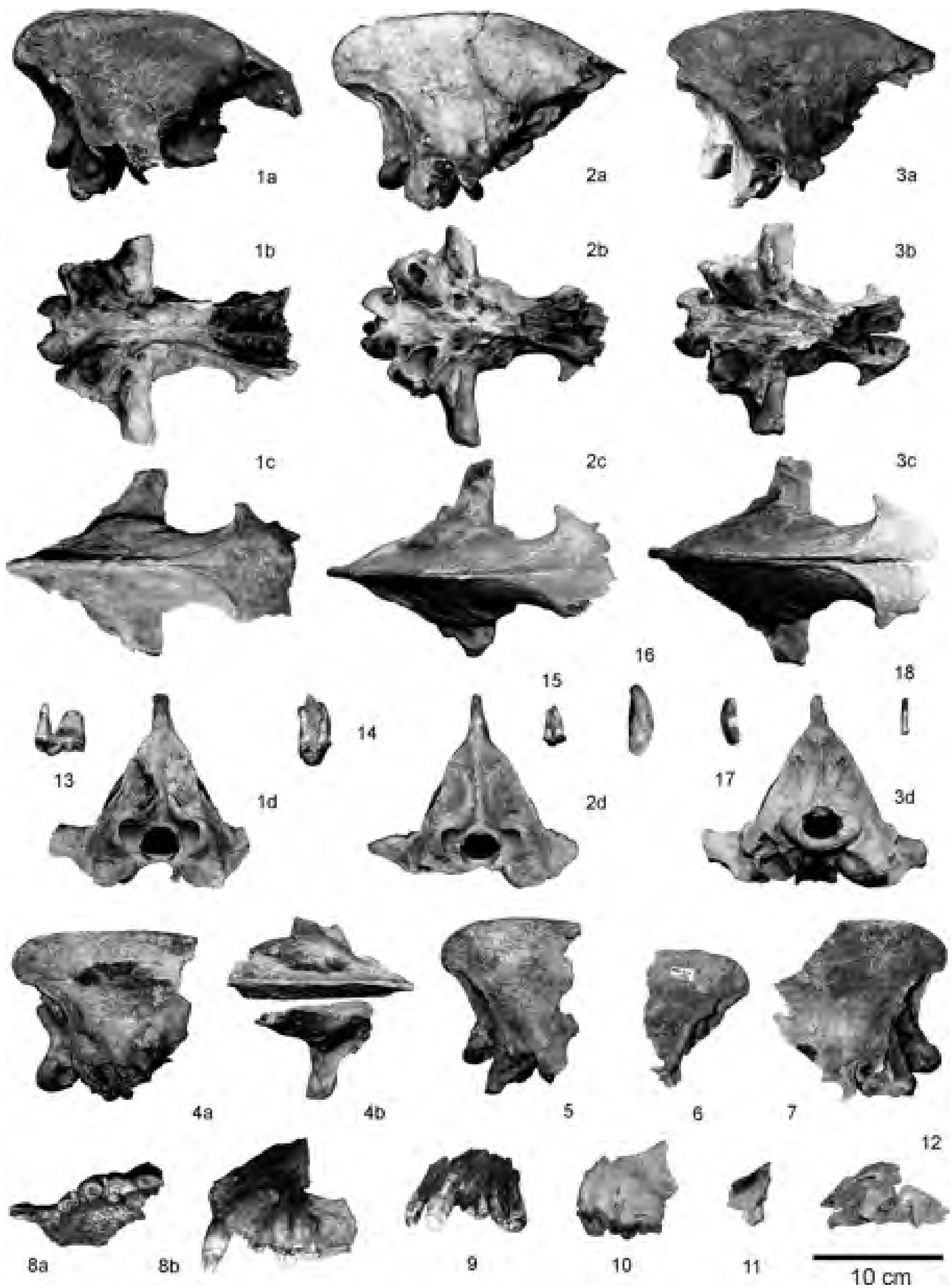

Fig. 4. Skull remains of Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

Fig. 5. Forelimb and hindlimb bones of adult to senile Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) hyenas from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

(Table S7). A single canine from a smaller mustelid weasel is the sole specimen from *Mustela* sp. (Table S8).

4.4. Hyena prey remains

A few *Bison priscus* remains with partly chewed vertebrae (Table S11, Fig. 6C(1–4)), some *Bos primigenius* aurochs remains (Table S12, Fig. 6C(6–7)). *Mammuthus primigenius* remains were reported in Nehring (1878a,b), but have long ago been either lost or destroyed through the sale of bones to a bone mill. A tusk, several teeth and mainly fragmented postcranial bones from these woolly mammoths are included in the material from the Westeregeln locality (Table S9, Fig. 7). Of these remains, 36% are from juveniles and calves, 7% are from early adult animals, and the remaining 57% are from adult to senile woolly mammoths. 55% of the remains are teeth and 45% are bones. Most remains are from woolly rhinoceros *Coelodonta antiquitatis* totalling 196 bones (Table S10, Figs. 8 and 9). Of these, 22% are from neonate animals and calves, 17% are from young adults, and 61% from adult to senile animals. There are 141 teeth and bones listed from the Przewalski horse *Equus caballus przewalskii* (Table S13, Fig. 10), of which 7% are from neonate animals to young foals, 7% from young adults, and 86% from adult to senile horses. *Megaloceros giganteus* is possibly represented by a chewed vertebra (Table S13, Fig. 6C(2)). *Rangifer tarandus* remains and shed antlers are from a taphonomic point of view, which consists of 62 specimens (Table S15, Fig. 11), are of mixed human and carnivore origin (Fig. 13).

5. Discussion

5.1. The megafauna biodiversity

The vertebrate fauna remains have been compiled and revised herein from Nehring (1876, 1884, 1890), Heinrich (2003), and herein new material – see Table 1.

The megafauna of the historical collected material (Table S15) is a "mammoth steppe lowland fauna" sensu Koenigswald (2002), which includes *M, primigenius*, *C. antiquitatis*, *B. priscus*, *E. c. przewalskii*, and *R. tarandus*. Rare herbivorous elements are undifferentiated *B. primigenius* or *M. giganteus*. Large carnivores present are *P. l. spelaea*, *C. c. spelaea*, and *C. lupus* subsp., while the small carnivores are *M. meles*, *V. vulpes*, *A. lagopus*, and *Mustela* sp. Theses small mustelids appear to have made use of small cavities or burrows in the karstic area. The single cave bear remain would not be expected in a lowland landscape (Diedrich, 2011b). The bird, snake, lizard, and frog remains have not yet been thoroughly studied but the genera are common ones found in cold and warm periods.

Absent from the megafauna are the "*Equus hemionus*" and "*Saiga tartarica*" in Giebel (1851), which were also mentioned by Toepfer (1966). The only evidence mentioned of "saiga antelopes" was

Fig. 6. A. Micromammal remains from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany). B. Cranial remains and postcranial bones of adult to senile Upper Pleistocene carnivores from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany). C. *Bison priscus*, *Bos primigenius* and ?*Megaloceros giganteus* bones from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

a lower jaw, which possibly came from the Neolithic to Bronze Age layers and may simply represent a Holocene *Ovis* or *Capra*. This probably applies to younger periods also the dog remains and a dog canine teeth collar (Fig. 1E). The misidentification of "*S. kirchbergensis*" has previously been revised by Schroeder (1930), while the dental material studied herein confirms the absence of this species.

5.2. Small caballoid Przewalski horses from Westeregeln

Toepfer (1966) mentioned "*E. hemionus*" and this reference was also cited by Diedrich (2007), but this can no longer be validated on the basis of the equid material studied herein. Other material may have been present in the Nehring collection but subsequently lost. The Ice Age donkey has not to date been recorded at Westeregeln, but only a "small caballoid horse". Nehring (1884) described this-caballoid horse material from Westeregeln as a new species "*E. germanicus* Nehring (1884)", illustrating selected cranial and postcranial remains (Fig. 1B). Some of the originals (a humerus in his Fig. 7, and a lower jaw in his Fig. 3) have been re-identified (Fig. 10(1) and (33)).

Metric analyses (see data in Table S14) and comparisons of the few complete long bones indicate sexual dimorphism, with the few large males and the females all falling within the range of small Late Pleistocene horses, using the sizes of humeri, radii, metacarpi III, tibiae and metatarsi III known from Przewalski horses (cf. Spöttel, 1926; Forsten, 1987; Volf, 1996; Cramer, 2002). The six complete metacarpi III (Fig. 10(44–50)) all range between 217 and 230 mm in length and between 52 and 55 mm in width. The two metatarsi III (Fig. 10(72–73)) have lengths between 276 and 282 mm and widths of around 53 mm. These data overlap with both "larger small" and "smaller medium" horses (Forsten, 1987), which can be best explained by sexual dimorphism. The humerus used by Nehring (1884) (Fig. 1A) seems to be from a large male and was therefore declared to be "medium-sized". The lengths of the three complete humeri (Fig. 10(33–34)) range between 302 and 322 mm, with a distal width of between 87 and 92 mm. The three complete radii (Fig. 10(36–38)) are 318–346 mm in length and 87–92 mm in distal width. Three complete tibiae are between 350 and 370 mm in length and 72–83 mm in distal width, whereas the metatarsus III bones (Fig. 10(72–73)) are 275–282 mm long, with a distal width of 53–60 mm.

The few complete long bones, when compared to the studies on Przewalski horse bone proportions (Forsten, 1987; Cramer, 2002), also reflect sexual dimorphism. The dimensions of the Westeregeln "caballoid horse population" fall within the upper range of Przewalski horse dimensions (average metacarpus III lengths less than 225 mm, and average metatarsus III lengths less than 270 mm, with average distal widths of 52 mm). On the basis of their measurements, it is proposed that the Westeregeln horses described by Nehring (1884) as *E. germanicus* are in fact the small Przewalski horses *E. c. przewalskii*. A further discussion of comparable "small" horse material from many different hyena den sites in Germany e.g. Perick Caves (Diedrich, 2005d) and the Czech Republic e.g. the Srbsko Chlum-Komín Cave (Diedrich, 2010b) will be a future project and will include hyena den sites, both open air and in caves, that have accumulations of horse remains (Fig. 14).

5.3. Reindeer antlers – hyena accumulations or human shamanic stores?

The postcranial remains and individual teeth from the historical Westeregeln collection show signs of bone crushing by large carnivores, such as the mandible in Fig. 11B(44). The overrepresentation of distal leg elements, similar to that for horse and woolly rhinoceros remains (see discussion below), would indicate their likely origin to have been as hyena prey (Figs. 12–14), as does the woolly rhino bones illustrated are far from complete i.e. heavily gnawed when compared to remains that have been used by prehistoric humans (see Boyle, 1997). Hyenas also must have collected shed reindeer antlers, but the quantities documented from other hyena den sites are very small (1–5 in maximum each site) and large female antlers

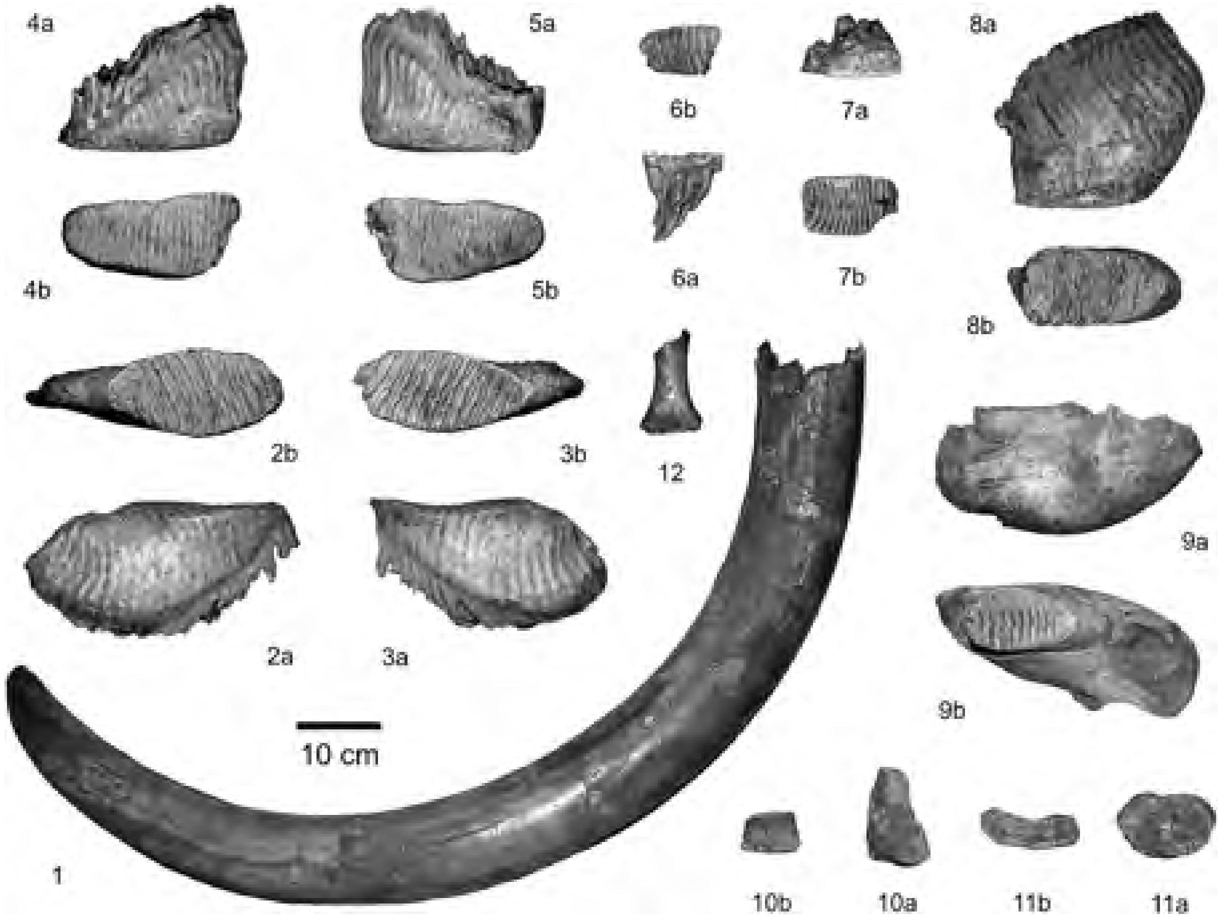

Fig. 7. *Mammuthus primigenius* remains from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

appear to have been collected preferentially. Only the lower parts of these larger antlers remain and these show considerable hyena bite-mark damage (Fig. 11B(31–32)), as is the case for red deer and giant deer shed antler remains imported into other hyena dens across Europe (Stiner, 2004; Diedrich, 2005c, 2010a, 2012b, 2011d, Diedrich and Žák, 2006).

In contrast to these large hyena-damaged antler bases, there have been a large number of small, thin antlers (only about 20–25 mm in diameter at the base) from juvenile and female reindeers found at Westeregeln (Fig. 11B(1–30)). Those that are broken are all shed antlers, but no extensive carnivore damage or human caused cut marks can be observed. This material must therefore be seen in a human context, although they may possibly not have been collected (and separated from male antlers which were for used as harder adult antlers for tools and carving) by Neanderthals but by Modern human populations such as? Magdalenians during the Late Palaeolithic. The historical collected material is lacking exact stratigraphic context but seem have been found between Layers 2 and 3, below the loess, which would date into the Late Palaeolithic period (Fig. 2). Following comparisons with as yet unpublished material consisting of similarly selected small shed antlers from various caves in the Sauerland Karst of northwest Germany, and material documented from the Oeger Cave (northwest Germany, Bleicher, 1993), the preliminary interpretation is that this represents an "antler store" of Magdalenian shamanic origin (Bleicher, 1993). The modern Sami people in Scandinavia are also known to build up antler stores, but at special locations and not in their settlements (Bleicher, 1993), which could explain the absence of any other evidence of Magdalenians such as stone or bone artefacts and tools. The gypsum karst was at that time an exposed hill, and would have provided a strategic outlook from which to hunt the reindeer herds that migrated seasonally during the Late Palaeolithic (Weinstock, 2000).

The few reindeer remains that have been recovered from the new doline excavations consist only of single teeth and fragmented long bones. At least 8% of the NISP are reindeer remains (Fig. 12B), which seem to be mainly the result of prehistoric human hunting and feeding activities based on comparisons with, for example, final Late Palaeolithic Magdalenian or Ahrensburgian bone assemblages in "kitchen refuse" from camp sites (e.g. Bosinski, 1979; Feustel, 1980; Tromnau, 1980; Grönnow, 1987; Baales, 1996; Boyle, 1997) (Fig. 11).

5.4. Hyena versus human prey-bone accumulations, and bone taphonomy

About 25% of the megafauna remains from Westeregeln are from large carnivores (lions, hyenas, or wolves) (Fig. 12A), which would at first appear to exclude the possibility of the bone accumulation being due a human activity, since humans usually hunted non-herbivorous during the Middle Palaeolithic and generally only a few percent of the bones at their camp sites are from carnivores (Aldhouse-Green et al., 1995; Fosse et al., 1998; Pickering, 2002; Lansing et al., 2007; Kuhn et al., 2008). The remains of these large carnivores at Westeregeln are dominated by hyena remains (Fig. 12A), which is typical of most Late Pleistocene hyena den sites (Fosse et al., 1998; Diedrich, 2005a, 2006a, 2007, 2008a, 2010a, 2011b,d,e, 2012b,c). In addition, a large proportion of the

Fig. 8. *Coelodonta antiquitatis* bones from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

prey bones identified herein (see discussion below) fit into the pattern of hyena dens and prey storage situations that have been described for modern spotted hyenas in Africa (cf. Sutcliffe, 1970; Kruuk, 1972; Henschel et al., 1979; Scott and Klein, 1981; Skinner et al., 1986).

The Westeregeln site is, however, without a doubt also a Middle Palaeolithic Neanderthal archaeological site, as indicated by the three hand axes (Weber, 2004), a bifacial flaked knife, and a large quantity of flint flakes and debris and few cores, as well as bones that have been broken open. The different types of bone material in the historical excavations and the more recent doline excavations therefore each need to be critically analysed in the context of possibly having resulted from either human or hyena activities. These possibilities are discussed for the principal prey species of mammoths, woolly rhinoceroses, and horses.

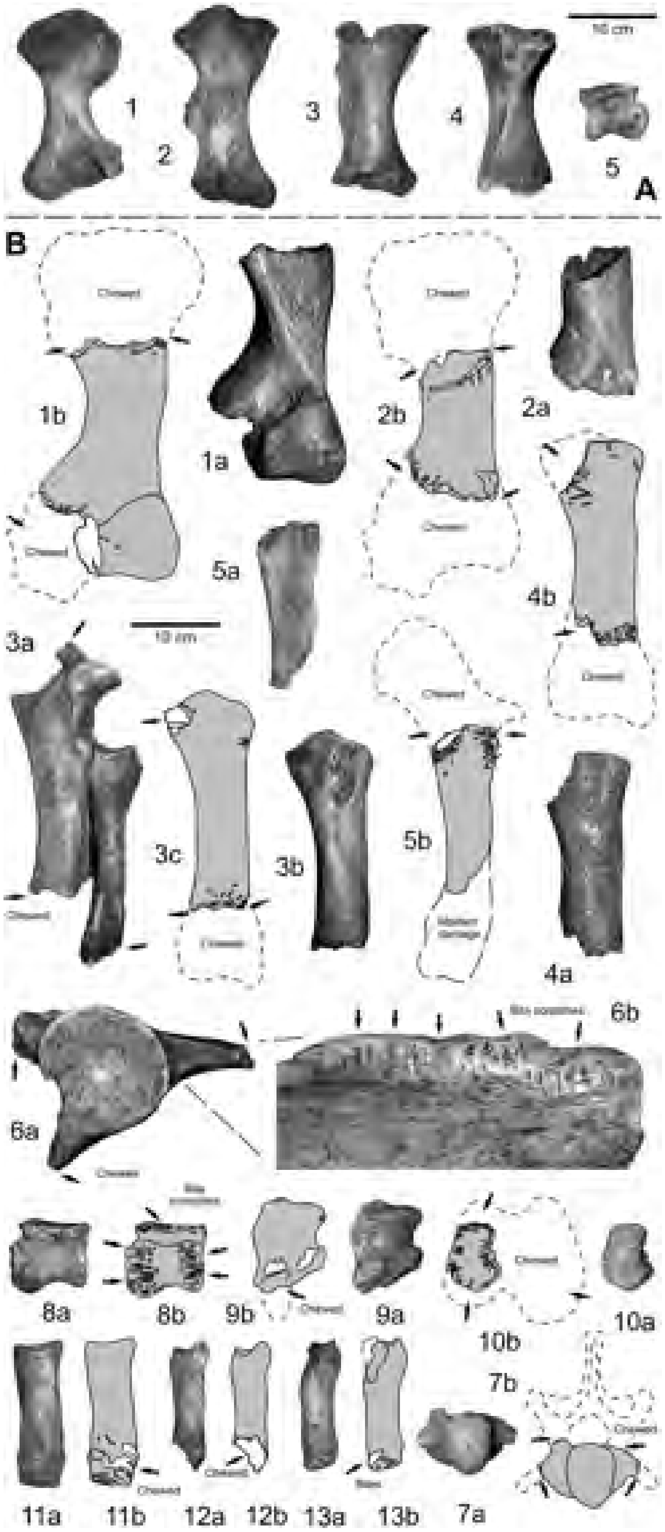

Fig. 9. *Coelodonta antiquitatis* bones from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

5.5. Destroyers of mammoth carcasses – hyenas or humans?

The mammoth remains from Westeregeln are limited to their massive molar and single tusk and several molar teeth and a few leg and pedal elements (Fig. 13). The mammoth remains at the contemporanous hyena and Neanderthal site in the Balve Cave of northern Germany (Diedrich, 2011c,d) are similar to those at Westeregeln in having a large quantity of teeth and in the presence of a single tusk at each location. A small quantity of calf remains has also been documented at both sites. They differ, however, in the number of chewed bones. Several of the mammoth bone fragments from the Balve Cave site exhibit considerable hyena gnaw damage (Diedrich, 2011d), but none of those from Westeregeln show any similar damage. At Balve Cave mammoth long bones seem to have been fragmented by Neanderthal or Aurignacian humans for use as "bone coal", which has also been found at this site (Diedrich, 2011d). Westeregeln also has some small "burned bone fragments" but neither the use of bone coal nor a mammoth origin can yet be proven. Indirect support for the use of mammoth bones as fuel may be provided by the absence of any massive bones. The absence of hyena-damaged material could be simply the result of selective collecting of complete and undamaged bones and teeth by quarry workers. Massive and chewed bones are present at hyena dens sites such as the northern German Perick Caves hyena den (Diedrich, 2005e) and the Balve Cave contemporanous hyena den and Neanderthal site (Diedrich, 2011d), and the removal of body parts from carcasses has been demonstrated at the Eemian Neumark-Nord Lake 1 site, where Neanderthals settled around a shallow lake leaving their traces in the form of smashed prey bones and stone artifacts (Diedrich, 2010c). The mammoth carcass taphonomy at Westeregeln cannot at this stage be resolved, but tusks must have been imported to the Westeregeln camp site by humans, rather than by hyenas.

5.6. Hyena populations, cannibalism, and den types

The hyena bone material from Westeregeln comprises mostly skull and cranial remains, which is similar to that reported from modern African and Late Pleistocene European hyena den sites as a result of cannibalism (e.g. Frank, 1994; Diedrich, 2005a). Skulls from Late Pleistocene *C. c. spelaea* (Goldfuss, 1823) are more common herein Westeregeln than in any other European open air or cave den sites (Diedrich, 2011e). The cub skull is comparable to the open-air hyena den site at Bad Wildungen (Diedrich, 2006a). The incomplete and fragmentary adult cranial material from Westeregeln has previously been compared to several other Late Pleistocene hyena crania from across Europe (England, Germany, Czech Republic, Romania: Diedrich, 2011e). The skulls of adult male and female hyenas from Westeregeln all fall within the size range of three shapes (1. flat, 2. slightly convex, 3. or highly convex crest) of *C. c. spelaea* (cf. Diedrich, 2011e).

The hyena remains from the Westeregeln are from cubs (1%), early adults (2%), and adult to senile individuals (97%) (Fig. 14A). The scarcity of cub and juvenile remains excludes the likelihood of an exclusive birth den site (cf. Modern: East at al. 1989, Pleistocene: Diedrich, 2012a), although there may periodically have been such a site within the gypsum hill area. Other open-air hyena den sites are at this stage identified as both, birth and commuting den sites, as have been documented at Bad Wildungen and Bottrop, in Germany (Diedrich, 2006a, 2012a). The cavities around the gypsum hills at Westeregeln were apparently not used by hyenas for raising and protecting their cubs (i.e. as birth den sites) in the manner of modern African hyenas (cf. Cooper, 1993; East et al., 1989; Frank, 1986; Boydston et al., 2006), since very little of the cub material that is normally abundant in birth den sites has been found (Mills and Mills, 1977). The quite large quantities of skulls and material from adult individuals seem to be the result of hyena cannibalism, as has been reported in modern African spotted hyenas which leave mainly cranial remains (Frank, 1994; Lam, 1992). Such cannibalism explains the higher percentage of cranial material at open air sites in the Upper Rhine Valley, at Bad Wildungen and Bottrop (cf. Diedrich, 2006a, 2012a), and finally at Westeregeln, than at cave den sites (cf. Ehrenberg et al., 1938; Musil, 1962; Tournepiche and Couture,

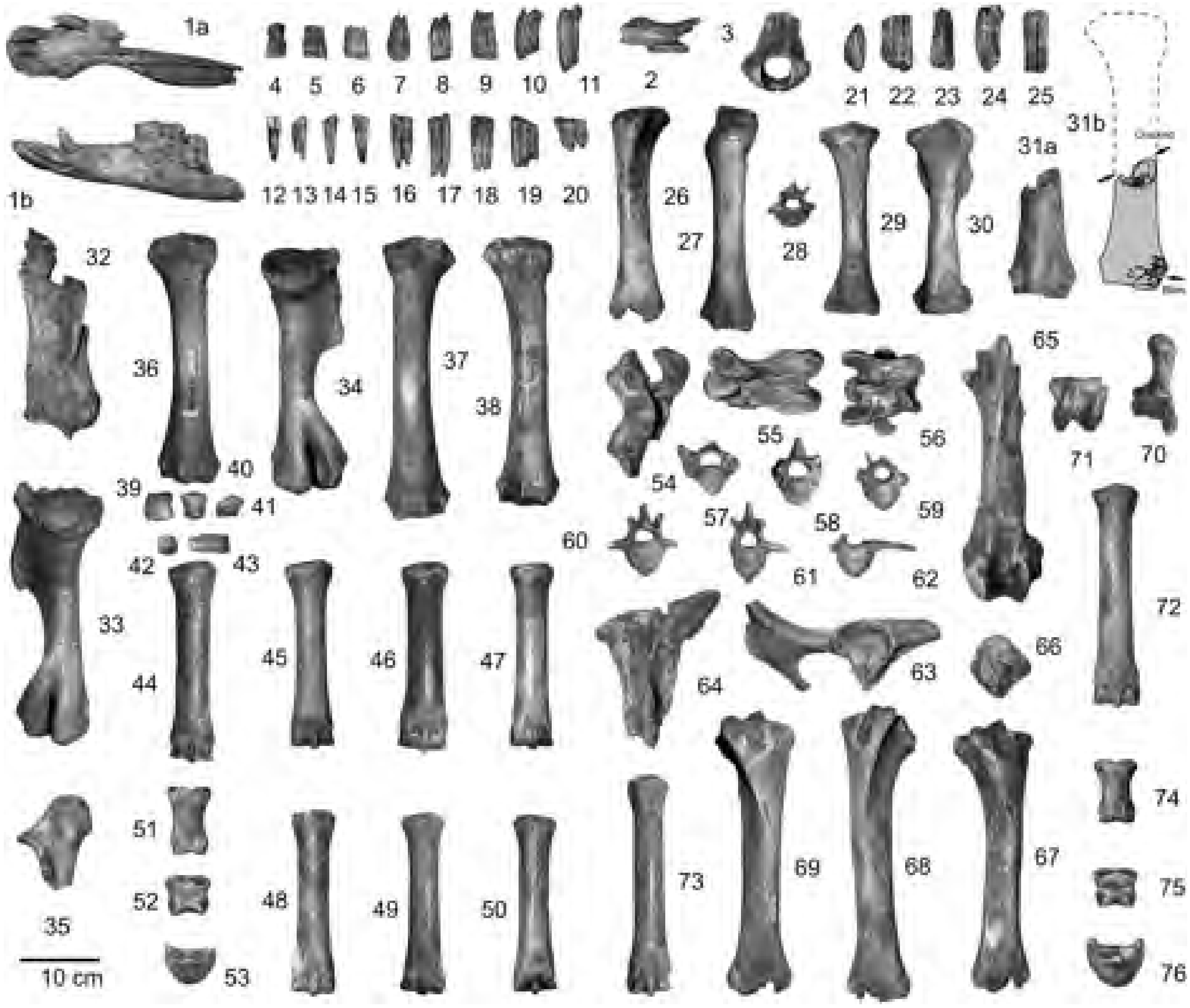

Fig. 10. *Equus caballus przewalskii* cranial, postcranial early juvenile, and other damaged remains from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

1999; Diedrich, 2005a, 2008a, 2010a, 2011b,d,e, 2012b,c). The large quantity of hyena bones, which are sometimes damaged, indicates a well-frequented open air commuting den at Westeregeln. By comparison with the variable quantity of hyena remains found at modern African hyena den sites (Lam, 1992; Pokines et al., 2007; Lansing et al., 2007), the Westeregeln hill area must have been used by many generations of hyenas over thousands of years during early to Middle Late Pleistocene repeatedly, which can be estimated by comparisons with modern African spotted hyena clans that are made up of between 25 and 80 individuals depending on the availability of prey and the size of the den (cf. Hofer and East, 1995), where about only a few bones accumulate per year (cf. Lam, 1992). Such a hyena clan could have easily accumulated the large quantity of prey bones scattered all over the den area, mainly by importing their carcasses for further feeding and final bone crushing for bone marrow feeding or even collagen consumption (Diedrich, 2005b–e). Similar habits have been described for modern African spotted hyenas, which mainly import prey into their dens (e.g., Brain, 1980; Hofer, 1998) in order to protect it from other predators (in this fossil record case, the steppe lions, and other hyenas), and as food for the cubs in the den. They may also have imported individual bones in order to store them, which modern African hyenas occasionally do (cf. Brain, 1980; Skinner et al., 1986), but the bones mainly represent articulated body parts from hunted Ice Age animals, in this case especially from woolly rhinoceros or Przewalski horses. Even lion remains seem to have been imported into the Westeregeln site, as indicated by the bite marks of large carnivores on their bones. Such scavenging and importation of *P. l. spelaea* carcasses by hyenas has also been recognized in the Perick Caves (Diedrich, 2009), the Zoolithen Cave (Diedrich, 2011b), and at various open air sites in Germany (Diedrich, 2011a).

5.7. *Hyenas as hunters of, and scavengers on woolly rhinoceroses*

The large quantities of woolly rhinoceros and horse remains in particular, at the Westeregeln site (Fig. 14B–C), must be explained in terms of taphonomy, predator selection, and bone damage, as has been previously demonstrated for the hyena open air bone accumulation sites at Bottrop (Diedrich, 2012a) and Bad Wildungen (Diedrich, 2006b).

In general, the large bite marks on rhinoceros bones (as well as others) from Westeregeln, which appear as triangular, oval, and elongated scratch marks and are similar to those observed on rhinoceros bones from various other late Pleistocene hyena den sites (e.g., Diedrich and Žák, 2006; Diedrich, 2006b, 2008b, 2012b) and by comparison to modern damaged bones and bite mark types (e.g. Hill, 1989; Faith, 2007; Pokines and Peterhans, 2007), are

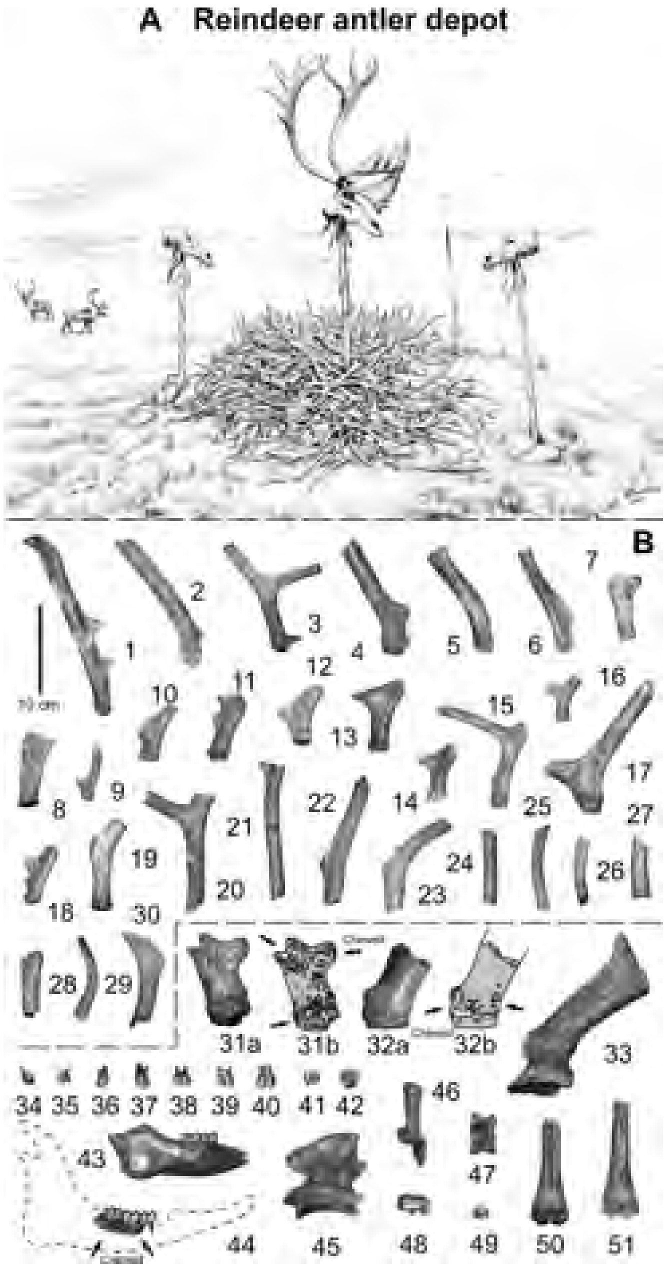

Fig. 11. A. Reindeer antler store made by Magdalenian humans at religious ritual sites such as the Westeregeln gypsum karst hill (Illustration G. "Rinaldino" Teichmann 2011). B. *Rangifer tarandus* antler remains and bones from the gypsum karst site at Westeregeln, near Magdeburg (Saxony-Anhalt, central Germany).

interpreted as caused mainly or only by hyenas. The various types of bite marks and the different teeth from which they originated have been illustrated in detail for the Bottrop open air site (Diedrich, 2012a).

The proportion of the woolly rhinoceros remains in the Westeregeln material that are from calves (22%) is quite high (Fig. 14B), and even higher percentages have been reported from some of the German (Sauerland Karst) and Czech hyena cave dens (Diedrich and Žák, 2006; Diedrich, 2006b, 2008b, 2012b), possibly as a result of hyena clans specifically targeting *C. antiquitatis* calves in their hunts. At open air sites for example at Bottrop about 5% of the NISP of rhinoceros are calf remains, and some calf long bones have been illustrated showing bite marks and damage from chewing (Diedrich, 2012a). Hyena clans may have therefore not only scavenged the

Table 1
Vertebrate megafauna and NISP amounts of the Upper Pleistocene from the gypsum karst hyena den and overlapping Neanderthal site Westeregeln (Saxony-Anhalt, Germany).

Species	NISP	Palaeoenvironment	Climate
Humans			
Homo sapiens neanderthalensis	Only artefacts	Indifferent	Warm/Cold
Carnivora			
Crocuta crocuta spelaea	84, and coprolites	Indifferent	Warm/Cold
Panthera leo spelaea	14	Indifferent	Warm/Cold
Canis lupus subsp.	38	Specialized	Cold
Meles meles	1	Indifferent	Warm/Cold
Vulpes vulpes	4	Indifferent	Warm/Cold
Alopex lagopus	1	Specialized	Cold
Martes sp.	1	Indifferent	Warm/Cold
Mustela sp.	1	Indifferent	Warm/Cold
Ursus spelaeus subsp.	1	Indifferent	Warm/Cold
Herbivora			
Mammuthus primigenius	19	Specialized	Cold
Coelodonta antiquitatis	196	Specialized	Cold
Bison priscus	10	Specialized	Cold
Bos primigenius	2	Indifferent	Warm/Cold
Megaloceros giganteus	1	Indifferent	Warm/Cold
Equus caballus przewalskii	141	Specialized	Cold
Rangifer tarandus	62	Specialized	Cold

carcasses of dead rhinoceros calves, but also specifically targeted young animals when hunting. While such hunting tactics must remain purely speculative, the targeting of smaller and younger prey in migrating big game is well known among present-day hyenas (Kruuk, 1972; Cooper, 2008).

Most of the known Upper Pleistocene open air bone accumulations in the lowlands of northern and central Germany, including Westeregeln, appear to be related mainly or only to hyena activities, especially when woolly rhinoceros bones with damage similar to that mentioned above are used as indicators of hyena den sites, as has been demonstrated for the open air site at Bottrop (Diedrich, 2012a). A few Neanderthal artifacts, such as hand axes, were also collected (Heinrich, 2003). Material from open air sites in the Münsterland Bay and Magdeburger-Börde lowlands demonstrates repetitions of identical destruction stages (cf. Fig. 9) to those seen (in smaller quantities) at Westeregeln. Similarly damaged rhinoceros bones have also been illustrated from a number of open-air sites in Austria, Germany and the Czech Republic (Zapfe, 1939; Thenius, 1961; Wernert, 1968; Diedrich, 2006b; Diedrich and Žák, 2006). Characteristic damage caused by hyeneas is known from many sites (Diedrich, 2012a), also from German caves such as the Lindenthaler Hyena Cave Gera where some were formerly misidentified as "Glockenschaber" human produced "bone tools" (Liebe, 1876), the Perick Caves (Diedrich, 2008a), Teufelskammer Cave (Diedrich, 2010c), and Balve Cave (Diedrich, 2011c), as well as caves in Austria such as the Teufelsluken Cave (Ehrenberg et al., 1938) and several hyena den caves in the Czech Republic (Musil, 1962; Diedrich and Žák, 2006). An analysis of the presence or absence of woolly rhinoceros body parts in the Westeregeln material supports the identification of the bone assemblage as having been accumulated by hyenas in their dens, since leg bones are significantly overrepresented in these open air bone accumulations (Fig. 14B), as has also been described for the Bottrop open air hyena den (Diedrich, 2012a).

A similar predominance of leg bones at hyena bone accumulation sites is well known from both Late Pleistocene hyena den sites (e.g. Arribas and Palmqvist, 1998; Tournepiche and Couture, 1999) and modern African hyena dens (Hill, 1980, 1989; Scott and Klein, 1981; Arribas and Palmquist, 1998; Avery et al., 1984; Pickering, 2002; Pokines and Peterhans, 2007; Lansing et al., 2007). Hyenas

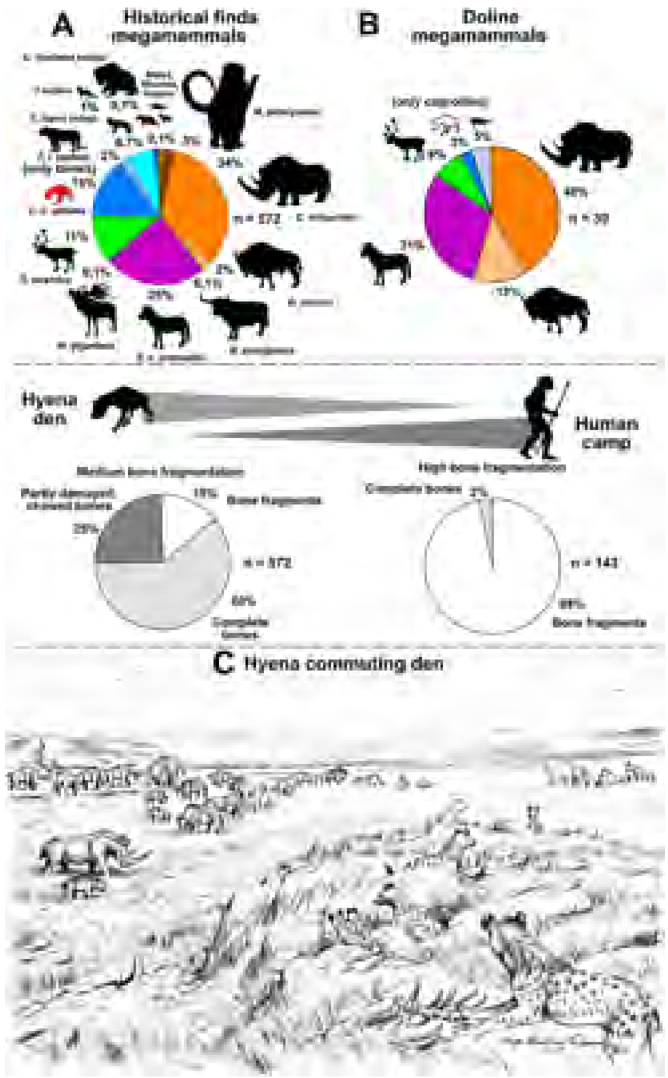

Fig. 12. Comparison of the A. historical megafauna remains (NISP = 572) from the Westeregeln gypsum karst area, with the B. excavated vertebrate fauna from the doline in the Berling gypsum quarry (NISP = 39). C. The Westeregeln gypsum karst hills with the proto-Bode river in the distant background, during the early to middle Late Pleistocene. These were used by Ice Age spotted hyenas *Crocuta crocuta spelaea* (Goldfuss) looking for the typical mammoth steppe megafauna as their prey.

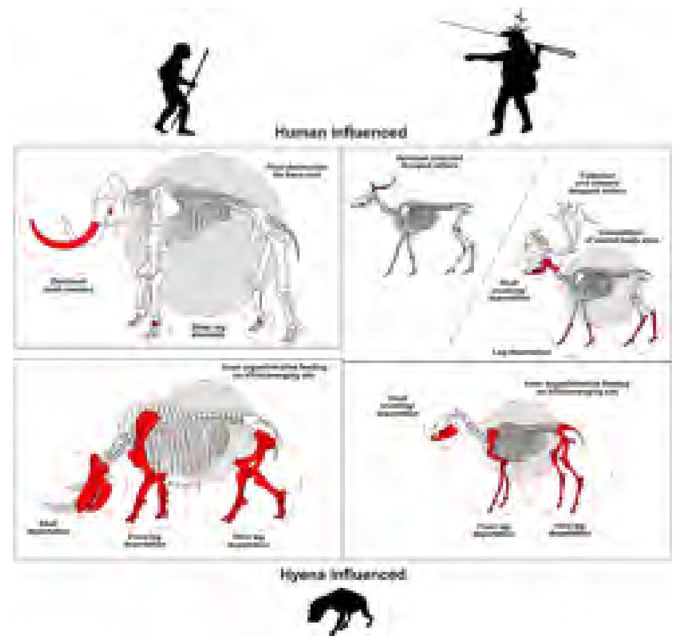

Fig. 13. Body part presence and absence related to the influence of humans and hyenas on the main megafauna prey.

generally remove the legs from megafauna carcasses (cf. for zebras/horses: Pokines and Peterhans, 2007; Diedrich, 2010d), which explains the predominance of fore and hind leg bones at Westeregeln. Other bones typically scavenged by modern hyenas are from the thorax, and include the vertebral column, ribs, and even pelvic remains (Behrensmeyer and Boaz, 1980; Avery et al., 1984; Di Silvestre et al., 2000).

5.8. *Hyenas as specialized horse hunters*

The presence of Przewalski horses in the Late Pleistocene (Weichselian/Würmian) of Europe and Asia is well known (Forsten, 1987; Cramer, 2002; Koenigswald, 2002), and their remains have been recorded from several hyena prey storage areas at cave and "open air loess" den sites in central Europe (Tournepiche and Couture, 1999; Diedrich, 2005c, Diedrich and Žák, 2006; Diedrich, 2010b). Their presence is also indicated by the caballoid horse material from Westeregeln. The tracks of small horses have even been mapped (together with other trackways) in Late Pleistocene river-bank sands along the Emscher River in the "Münsterland Bay" of northern Germany (Diedrich, 2012a). During the Upper Pleistocene the small caballoid horse *E. c. przewalskii* was common in central Europe, especially during the glacial periods (Bosinski, 1992; Cramer, 2002; Koenigswald, 2002; Bignon and Eisenmann, 2006). Przewalski horse remains have been reported from early Upper Pleistocene (middle Palaeolithic) sites and late Upper Pleistocene to even Holocene (early Mesolithic) sites in northern Germany (Bosinski, 1992; Springhorn, 2003). Many artistic representations of *E. c. przewalskii* from the Late Palaeolithic (especially from the Magdalénian) are known from the cave and mobile art of Europe (Capitan et al., 1910; Leroi-Gourhan, 1971; Vialou, 1986; Chauvet et al., 1995).

The Ice Age spotted hyenas imported horse carcasses (Fig. 14C) into their cave and open air dens in order to be able to avoid conflict with lions while feeding, to feed their cubs, and to store prey for periods of food shortage. Similar examples of the import and storage of prey remains has also been documented from the Rochelot Cave hyena den in France (Tournepiche and Couture, 1999), and from the Srbsko Chlum-Komín Cave hyena den in the Czech Republic, which contains the greatest known accumulation of Przewalski horse bones (1500 bones) (Diedrich, 2010b). At many other late Pleistocene hyena den caves in the Czech Republic (Diedrich and Žák, 2006; Diedrich, 2010b) and northern Germany (Diedrich, 2010b, 2011d) all the different body parts of these horses can usually be found, but articulated legs are predominant. These were often imported and then left untouched by hyenas, as seen at the Rochelot Cave (Tournepiche and Couture, 1999) and the Srbsko Chlum-Komín Cave (Diedrich, 2010b) hyena dens, and in the gypsum karst open air hyena den site at Westeregeln (Fig. 10). Modern spotted hyenas engage in a similar type of "horse" hunting (although in Africa the prey are zebras), resulting in a similar overrepresentation of distal leg remains, as well as large quantities of teeth from crushed skulls. In the Ngorongoro Crater, for example, zebras can form up to 70% of hyena prey (Kruuk, 1972) and can be dismembered in 5 min with the hyenas then escaping with the skull, legs and vertebral column, as has been documented photographically (Diedrich, 2010c).

It is clear that hyenas also concentrated on hunting adult horses at Westeregeln, as they did at the Srbsko Chlum-Komín Cave

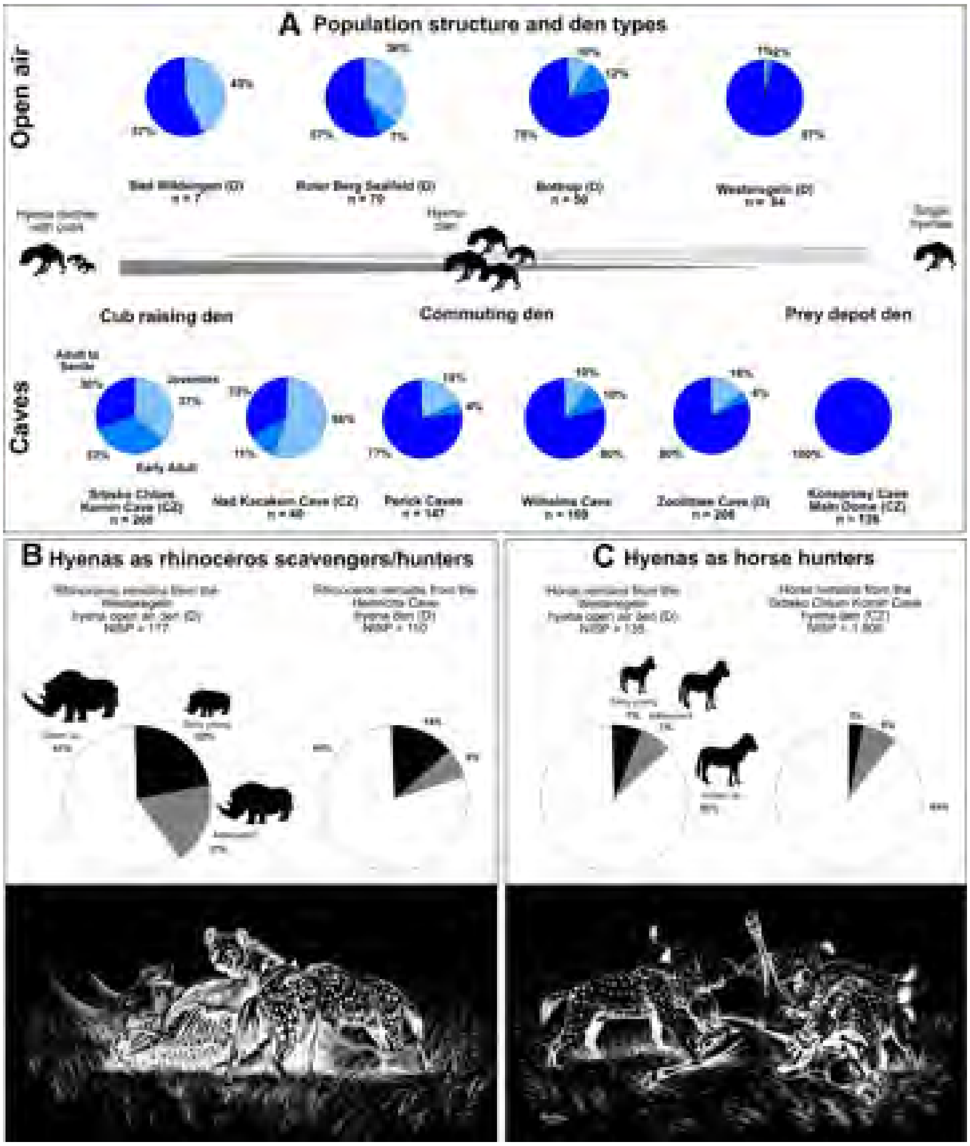

Fig. 14. A. Comparison of population structures (=animal age groups) in European Late Pleistocene cave and open air hyena den sites. B. Specialized woolly rhinoceros (C. antiquitatis) scavengers and C. horse (*E. caballus przewalskii*) hunters in comparison of the prey statistics in comparisons to hyena den caves of central Europe (NISP data sources: Perick- and Sloup Caves, from Diedrich, 2008a, 2010b. Hyena night-action hunting and scavenging by G. "Rinaldino" Teichmann).

(Diedrich, 2010b, Fig. 14C), in a similar manner to the modern African spotted hyenas (*C. c. crocuta*) that hunt adult zebras (Kruuk, 1966, 1970, 1972) but in certain areas or at certain times may switch to hunting more juvenile zebras (Cooper, 2008).

The hyena dens of the Srbsko Chlum-Komín and Koněprusy Caves (Czech Republic) have the highest proportions of horse remains (about 50%) in hyena bone assemblages, whereas most other hyena den sites in Europe have 25–40% horse remains (e.g., Sauerland Karst, northern Germany: Diedrich, 2005a-c, 2010b, Czech Republic: Diedrich and Žák, 2006; Diedrich, 2012c). At Westeregeln, the large quantities of horse remains (25%) could indicate a hyena bone assemblage, but as has been shown for the doline fill (Fig. 12A–B), these quantities may also have been influenced by significant human activities, and only the taphonomy can distinguish between human and hyena bone assemblages at Westeregeln.

Late Pleistocene hyena clans must have hunted horses in a very similar manner to the modern spotted hyenas hunting zebras (Diedrich, 2010b). The large quantities of unchewed horse prey remains, especially distal leg remains, both here and at the Rochelot Cave and Srbsko Chlum-Komín Cave hyena dens (Tournepiche and Couture, 1999; Diedrich, 2010b), is astonishing and can be only explained by good hunting seasons and large horse populations.

5.9. Hyena den marking

Modern African hyena commuting dens are generally marked with phosphatic excrements for territorial purposes against other hyena clans and lion prides (Kruuk, 1972; Bearder and Randall, 1978; Cooper, 1993). Coprolites have been illustrated from various European caves, such as the Czech Srbsko Chlum-Komín Cave (Diedrich and Žák, 2006), the Sloup Cave (Diedrich, 2012b) and the Koněprusy Caves (Diedrich, 2012c). At some German cave sites the white excrement has even built up to form phosphatic layers, as documented at the famous central German Lindenthaler Hyena Cave in Thuringia (Liebe, 1876). Many coprolites from the Bad Wildungen open air hyena den site have been analysed and were found to contain a large number of prey bone fragments, predominantly from rhinoceroses (Diedrich, 2006a). In the central German province of Saxony-Anhalt a few hyena coprolites have recently been illustrated from the Late Pleistocene Neumark-Nord Lake 1 site (Diedrich, 2010d). Preliminary illustrations from the Westeregeln material have also been made (Diedrich, 2011f). At Westeregeln (Fig. 12C) this den marking behaviour is illustrated by two faecal areas in the doline excavation (Layers 4–5; Fig. 2)B, where these occur together with bones that have been smashed by humans and Neanderthal artefacts.

6. Conclusion

By combining various historical bone collections from an hyena commuting den and human Neanderthal camp site, a new picture has emerged of the megafauna and palaeoenvironment. The site is situated in a gypsum karst area in the middle of the Westergeln surrounding Magdeburger-Börde lowland, which was a mammoth steppe environment during the early to middle Upper Pleistocene. It had a typical "mammoth steppe micro- and megafauna", comprising herbivores such as mammoth, wholly rhinoceros, steppe bison, aurochs, przewalskii horse, reindeer, rare cave bear and "steppe/boreal forest carnivores" with steppe lion, Ice Age spotted hyenas and wolves. The "karst cavity fauna" is dominated by small carnivores with badgers common and arctic foes, but also martens. Medium-sized rodent mammals such as *A. saliens*, *S. refuscens* and *M. bobac*, as well as various micromammals, also fit to the glacial steppe palaeoenvironment fauna typical of loess soil regions. All date into the early to middle Upper Pleistocene. This aging is also supported by new, 8 m deep, excavations and detailed stratigraphic work in doline fill, on the edge of the Berling gypsum quarry from which most of the described bones were collected historically, together with Middle Palaeolithic artefacts. Hyenas would have mainly used this strategic outlook as a commuting den, to which large quantities of prey remains were carried or dragged in order to avoid conflicts, especially with lions. These remains were mainly from woolly rhinoceroses and Przewalksi horses, and were predominantly the limbs of these animals. A large clan or repeated use by hyenas must have been mainly responsible for the bone accumulation over a long period of time, and hyena cubs were probably also raised at this site periodically. The bone accumulation contains few incomplete bones, which is typical of hyena dens, but not of human camp sites where bones are more fragmented and broken into pieces. The predominance of rhinoceros bones, which in several cases have damage stages that are very typical of hyena activities, is a result of the indestructible nature. Although the mammoth remains were also almost impossible for hyenas to destroy, the predominance of mammoth teeth may suggest Neanderthal activities in which the large mammoth bones served as "bone coal". The single tusk seems to have been imported by humans. Other megafauna bones would have been more easily crushed by hyenas, while horse remains must have been imported as a main food source for the hyenas, often as articulated limbs rather than vertebral columns. Many distal parts of horse limbs remained untouched, with no gnaw/chew damage, as is also the case with zebra limbs left by modern hyenas in Africa. The high proportions of rhinoceros and horse remains compares well with many other European Late Pleistocene mammoth steppe hyena dens with their hyena bone accumulations and suggests scavenging rather than hunting of woolly rhinoceros calves, but hunting of large numbers of mainly adult horses. Two other possible factors have to be taken in account concerning the bone taphonomy of those two main prey animals: 1 "schlepp effect" and 2. the greater durability of rhino over horse bones. Shed reindeer antlers were also collected by hyenas from time to time and transported to the den (but few amounts, and male antlers only), leaving only the bases with strong evidence of gnaw damage. There are controversal large quantities of smaller shed antler fragments from female reindeer or their calves, which can only be explained as being due to human selection and shamanic antler storage, which is only typical of more modern humans and therefore possibly indicates Magdalénian use of this as an important mystic site at a much later time. Several of the herein figured small antlers were found together in another doline outside the Berling quarry, therefore those seem to be not connected to the "hyena bone assemblage". No carnivore (hyena or wolf) collects selected small reindeer antlers or causes larger "depots", weather in caves, not to expect at open air sites such as Westeregeln. At least 80% of the total historical collected bone material must relate to hyena activity, representing the remains of large carnivore prey that were carried or dragged to the hill on the gypsum karst by hyenas rather than the "kitchen refuse" of Neanderthals.

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References

Aldhouse-Green, S., Scott, K., Schwarcz, H., Grün, R., Housley, R., Rae, A., Bevins, R., Redknap, M., 1995. Coygan Cave, Laugharne, 1995. South Wales, a Mousterian Site and Hyaena den: A Report on the University of Cambridge Excavations. In: Proceedings of the Prehistoric Society London, vol. 61, 37–80 pp.

Arribas, A., Palmqvist, P., 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). Geobios 31 (Suppl.), 3–47.

Avery, G., Avery, D.M., Braine, S., Loutit, R., 1984. Bone accumulation by hyenas and jackals a taphonomic study. South African Journal of Science 80, 186–187.

Baales, M., 1996. Umwelt und Jagdökonomie der Ahrensburger Rentierjäger im Mittelgebirge. Römisch-Germanisches Zentralmuseum Monographien 38, 1–364.

Bearder, S.K., Randall, R.M., 1978. The use of fecal marking sites by spotted hyaenas and civets. Carnivore 1, 32–48.

Behrensmeyer, A.K., Boaz, D., 1980. The recent bones of Amboseli Park Kenya in relation to East African paleoecology. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 72–92.

Bignon, O., Eisenman, V., 2006. Western European late glacial horses diversity and its ecological implications. In: Equids in Time and Space. Oxbow Books, Mashkour, pp. 161–171.

Bleicher, W., 1993. Die Oeger-Höhle eine Kultstätte alsteinzeitlicher Rentierjägergruppen. Hohenlimburger Heimatblätter 93 (9), 309–323.

Bosinski, G., 1979. Die Ausgrabungen in Gönnersdorf 1968–1976 und die Siedlungsbefunde der Grabung 1968. In: Der Magdalenien Fundplatzz Gönnersdorf, 3. Franz Steiner Verlag, Wiesbaden.

Bosinski, G., 1992. Eiszeitjäger im Neuwieder Becken. Archäologie am Mittelrhein und Mosel 1, 1–148.

Boydston, E.E., Kapheim, K.M., Holekamp, K.E., 2006. Patterns of den occupation by the spotted hyaena (*Crocuta crocuta*). African Journal of Ecology 44, 77–86.

Boyle, K.V., 1997. Late Magdalenian carcase management strategies, the Périgord data. Anthropozoologica 25/26, 287–294.

Brain, C.K., 1980. Some criteria for the recognition of bone collecting agencies in African caves. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the Making:

Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 107–130.

Buckland, W., 1823. Reliquiae Diluvianae, or Observations on the Organic Remains Contained in Caves, Fissures, and Diluvial Gravel, and Other Geological Phenomena, Attesting the Action of a Universal Deluge. J. Murray, London.

Capitan, L., Breuil, H., Peyrony, D., 1910. La caverne de Font-de-Gaume aux Eyzies (Dordogne). Monaco.

Chauvet, J.-M., Deschamps, B.E., Hillaire, C., 1995. Grotte Chauvet. Altsteinzeitliche Höhlenkunst im Tal der Ardèche. In: Thorbecke Speläo 1. Sigmaringen.

Cooper, S.M., 1993. Denning behavior of spotted hyaenas (*Crocuta crocuta*) in Botswana. African Journal of Ecology 31, 178–180.

Cooper, S.M., 2008. The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. African Journal of Ecology 28 (2), 131–141.

Cramer, B., 2002. Morphometrische Untersuchungen an quartären Pferden in Mitteleuropa. Tübingen: Unpublished Dissertation.

Di Silvestre, I., Novelli, O., Bogliani, G., 2000. Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal. African Journal of Ecology 38, 102–107.

Diedrich, C.G., Žák, K., 2006. Upper Pleistocene hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) prey deposit and den sites in horizontal and vertical caves of the Bohemian Karst (Czech Republic). Bulletin of Geosciences 81 (4), 237–276.

Diedrich, C.G., Weber, T., Wansa, S., 2010. Neanderthalercamp und Hyänenhorst – Neue Untersuchungen im pleistozänen Gipskarst von Westeregeln, Salzlandkreis (Sachsen-Anhalt), Abstract 52th meeting of the Hugo Obermaier-Gesellschaft, Leipzig, 21–22 pp..

Diedrich, C.G., Weber, T., The Neanderthal artefacts and bone assemblage from an overlapping Middle Palaeolithic Neanderthal camp and hyena open air den gypsum karst site in Westeregeln Germany, Saxony Anhalt (Central Germany). Journal of Archaeological Science, in press

Diedrich, C., 2005a. Eine oberpleistozäne Population von *Crocuta crocuta spelaea* (Goldfuss, 1823) aus dem eiszeitlichen Fleckenhyänenhorst Perick-Höhlen von Hemer (Sauerland, NW Deutschland) und ihr Kannibalismus. Philippia 12 (2), 93–115.

Diedrich, C., 2005b. Von eiszeitlichen Fleckenhyänen eingeschleppte Reste des Steppenwisents *Bison priscus* Bojanus, 1827 aus dem oberpleistozänen Fleckenhyänenhorst des Perick-Höhlensystems (NW Deutschland). Philippia 12 (1), 21–30.

Diedrich, C., 2005c. Von oberpleistozänen Fleckenhyänen gesammelte, versteckte, verbissene, zerknackte Knochen und Geweihe des Riesenhirsches *Megaloceros giganteus* (Blumenbach, 1799) aus den Perick-Höhlen im Nordsauerland (NW Deutschland). Philippia 12 (1), 31–46.

Diedrich, C., 2005d. Benagte und zerknackte Knochen des eiszeitlichen Pferdes *Equus ferus przewalskii* Poljakoff 1881 aus einem oberpleistozänen Fleckenhyänenhorst des Nordsauerlandes und westfälischen Freilandfundstellen. Philippia 12 (1), 47–62.

Diedrich, C., 2005e. Von eiszeitlichen Fleckenhyänen benagte *Mammuthus primigenius* (Blumenbach, 1799)-Knochen und -Knabbersticks aus dem oberpleistozänen Perick-Höhlenhorst (Sauerland) und Beitrag zur Taphonomie von Mammutkadavern. Philippia 12 (1), 63–84.

Diedrich, C., 2006a. The *Crocuta crocuta spelaea* (Goldfuss, 1823) population from the early Upper Pleistocene hyena open air prey deposit site Biedensteg near Bad Wildungen (Hess, NW Germany) and the contribution to their phylogenetic position, coprolites and prey. Cranium 23 (2), 39–53.

Diedrich, C., 2006b. By ice age spotted hyenas protracted, cracked, nibbled and chewed skeleton remains of *Coelodonta antiquitatis* (Blumenbach, 1807) from the Lower Weichselian (Upper Pleistocene) open air prey deposit site Bad Wildungen-Biedensteg (Hessia, NW Germany). Journal of Taphonomy 4 (4), 173–205.

Diedrich, C., 2007. The Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) population and its prey from the gypsum karst den site Westeregeln near Magdeburg (Middle Germany). Abhandlungen und Berichte für Naturkunde 30, 57–83.

Diedrich, C., 2008a. Eingeschleppte und benagte Knochenreste von *Coelodonta antiquitatis* (Blumenbach, 1807) aus dem oberpleistozänen Fleckenhyänenhorst Perick-Höhlen im Nordsauerland (NW Deutschland) und Beitrag zur Taphonomie von Wollnashornknochen in Westfalen. Mitteilungen der Höhlen und Karstforscher 2008 (4), 100–117.

Diedrich, C., 2008b. Late Pleistocene hyenas *Crocuta crocuta spelaea* (Goldfuss, 1823) from Upper Rhine valley open air sites and the contribution to skull shape variability. Cranium 25 (2), 31–42.

Diedrich, C., 2009. Steppe lion remains imported by Ice Age spotted hyenas into the late Pleistocene Perick caves hyena den in Northern Germany. Quaternary Research 71 (3), 361–374.

Diedrich, C., 2010a. The *Crocuta crocuta spelaea* (Goldfuss, 1823) population and its prey from the late Pleistocene Teufelskammer cave hyena den besides the famous Paleolithic Neanderthal cave (NRW, NW Germany). Historical Biology 23 (2–3), 237–270.

Diedrich, C., 2010b. Specialized horse killers in Europe – foetal horse remains in the Late Pleistocene Srbsko Chlum-Komín Cave hyena den in the Bohemian Karst (Czech Republic) and actualistic comparisons to modern African spotted hyenas as zebra hunters. Quaternary International 220 (1–2), 174–187.

Diedrich, C., 2010c. Späteiszeiliche Fleckenhyänen-Fressstrategien und Steppenlöwen an ihrer größte Beute – dem Waldelefanten *Palaeoloxodon antiquus* Falconer and Cautley, 1845 in Neumark-Nord. Archäologie in Sachsen-Anhalt Sonderband 62, 449–459.

Diedrich, C., 2010d. Die späteiszeitlichen Fleckenhyänen und deren Exkremente aus Neumark-Nord. Archäologie in Sachsen-Anhalt Sonderband 62, 440–448.

Diedrich, C., 2011a. Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) footprints and bone remains from open air sites in northern Germany – evidence of hyena-lion antagonism in Europe. Quaternary Science Reviews 30, 1883–1906.

Diedrich, C., 2011b. The Late Pleistocene spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) population from the Zoolithen Cave at Gailenreuth (Bavaria, South Germany) – a hyena cub raising den of specialized cave bear scavengers in Boreal Forest environments of Central Europe. Historical Biology 23 (4), 335–367.

Diedrich, C., 2011c. Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) remains from the Balve Cave (NW Germany) - a cave bear, hyena den and Middle Palaeolithic human cave, and review of the Sauerland Karst lion sites. Quaternaire 22 (2), 105–127.

Diedrich, C., 2011d. Periodical use of the Balve Cave (NW Germany) as a Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) den: hyena occupations and bone accumulations vs. human Middle Palaeolithic activity. Quaternary International 233, 171–184.

Diedrich, C., 2011e. One of Europe`s last glacial *Crocuta crocuta spelaea* (Goldfuss, 1823) clans from the Rösenbeck Cave hyena den (Germany) and contribution to cranial shape variability. Biological Journal of the Linnean Society London 103, 191–220.

Diedrich, C., 2011f. Seltene Freilandfunde der späteiszeitlichen Fleckenhyäne *Crocuta crocuta spelaea* (Goldfuss, 1823) in Sachsen-Anhalt und Beitrag zu Horsttypen der letzten Hyänen im Jung-Pleistozän von Mitteldeutschland. Zeitschrift für Mitteldeutsche Vorgeschichte 93, in press-a.

Diedrich, C., 2012a. The Late Pleistocene Crocuta crocuta spelaea (Goldfuss, 1823) population from the Emscher River terrace hyena open air den Bottrop and other sites in NW-Germany – woolly rhinoceros scavengers and their bone accumulations along rivers in lowland mammoth steppe environments. Quaternary International. doi:10.1016/j.quaint.2011.07.046.

Diedrich, C., 2012b. The Ice Age spotted *Crocuta crocuta spelaea* (Goldfuss, 1823) population, their excrements and prey from the Late Pleistocene hyena den Sloup Cave in the Moravian Karst; Czech Republic. Historical Biology 24 (2), 161–185.

Diedrich, C., 2012c. Europe's first Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) skeleton from the Koněprusy Caves – a hyena cave prey depot site in the Bohemian Karst (Czech Republic). Historical Biology 24 (1), 63–89.

East, M.L., Hofer, H., Türk, A., 1989. Functions of birth dens in spotted hyaenas (*Crocuta crocuta*). Journal of Zoology London 219, 690–697.

Ehrenberg, K., Sickenberg, O., Stifft-Gottlieb, A., 1938. Die Fuchs-oder Teufelslucken bei Eggenburg, Niederdonau. 1 Teil. Abhandlungen der Zoologisch–Botanischen Gesellschaft 17 (1), 1–130.

Faith, J.T., 2007. Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. Journal of Archaeological Science 34, 1601–1609.

Feustel, R., 1980. Magdalénienstation Teufelsbrücke II, Paläontologischer Teil. Weimarer Monographien zur Ur- und Frühgeschichte 3, 1–71.

Forsten, A., 1987. The small caballoid horse of the Upper Pleistocene and Holocene. Journal of Animal Breeding Genetics 105, 161–176.

Fosse, P., Brugal, J.P., Guadelli, J.L., Michel, P., Tournepiche, J.F., 1998. Les repaires d' hyenes des cavernes en Europe occidentale: presentation et comparisons de quelques assemblages osseux. In: Economie Prehistorique: Les comportements de substance au Paleolithique. 44–61. XVIII Rencontres internationales d' Archeologie et d' Historie d' Antibes. Editions APDCA, Sophia Antipolis.

Frank, L.G., 1986. Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. Animal Behavior 34, 1510–1527.

Frank, L.G., 1994. When hyenas kill their own. New Scientist 141, 38–41.

Giebel, C.G., 1850a. Mitteilungen über das Vorkommen der diluvialen Knochen in der Provinz Sachsen. Jahresberichte der Naturwissenschaftlichen Vereinigung Halle 3, 12–21.

Giebel, C.G., 1850b. Beiträge zur Osteologie des *Rhinoceros*. In: Jahresberichte der Naturwissenschaftlichen Vereinigung Halle 3, 72–157 pp.

Giebel, C.G., 1851. Die antediluvialianische Saeugethierfauna Deutschlands. In: Jahresberichte der Naturwissenschaftlichen Vereinigung Halle 1852, 219–236 pp.

Goldfuss, G.A., 1823. Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt. VI. Ueber die Hölen-Hyäne (*Hyäna spelaea*). Nova Acta Physico-Medica Academiea Caesarae Leopoldino-Carolinae Naturae Curiosorum 3 (2), 456–490.

Grönnow, B., 1987. Meiendorf and Stellmoor revisited. An analysis of late Palaeolithic render exploitation. Acta Archaeologica 56, 131–161.

Heinrich, A., 1987. Geologie und Vorgeschichte Bottrops. Geschichte Bottrops I. Historische Gesellschaft Bottrop.

Heinrich, W.-D., 2003. Rodentier-Biostratigraphie und Altersstellung pleistozäner Säugetier-Fundstätten Mitteldeutschlands. Veröff. Landesamt. Archaeologie in Sachsen-Anhalt 57 (1), 237–244.

Henschel, J.R., Tilson, R., Von Blottnitz, F., 1979. Implications of a spotted hyaena bone assemblage in the Namib Desert. South African Archaeological Bulletin 34, 127–131.

Hill, A., 1980. A Modern Hyena Den in Amboseli National Park, Kenya, Nairobi. In: Proceedings of the 8th Pan-African Congress on Prehistory and Quaternary Studies, 137–138 pp.
Hill, A., 1989. Bone modification by modern spotted hyenas. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, pp. 169–178.
Hofer, H., East, M., 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: Sinclair, A.R.E., Arcese, P. (Eds.), Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, Chicago, pp. 332–363.
Hofer, H., 1998. The biology of the spotted hyaena. In: Mills, M.G.L., Hofer, H. (Eds.), Hyaenas of the World: Status Survey and Action Plan. IUCN, Gland, pp. 29–38.
Klinghardt, F., 1931. Vergleichende Untersuchungen über das Gehirnrelief einiger rezenter und fossiler Raubtiere. Palaeontographica A 74, 135–176.
Koenigswald, W. von, 2002. Lebendige Eiszeit – Klima und Tierwelt im Wandel. Theiss-Verlag, Wissenschaftliche Buchgesellschaft, Darmstadt.
Kruuk, H., 1966. Clan-system and feeding habits of spotted Hyaenas (*Crocuta crocuta*, Erxleben). Nature 209 (5029), 1257–1258.
Kruuk, H., 1970. Interactions between populations of spotted hyaenas (*Crocuta crocuta*, Erx.) and their prey species. In: Watson, A. (Ed.), Animal Populations in Relation to Their Food Resources. Blackwell, Oxford, pp. 359–374.
Kruuk, H., 1972. The Spotted Hyena. A Story of Predation and Social Behavior. The University of Chicago Press, Chicago.
Kuhn, B.F., Berger, L.R., Skinner, J.D., 2008. Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyaenas. International Journal of Osteoarchaeology 20 (1), 15–35.
Lam, Y.M., 1992. Variability in the behavior of spotted hyaenas as taphonomic agents. Journal of Archaeological Science 19, 389–406.
Lansing, S.W., Cooper, S.W., Boydston, E.E., Holekamp, K.E., 2007. Taphonomic and zooarchaeological implications of spotted hyena (*Crocuta crocuta*) bone accumulations in Kenya: a modern behavioral ecological approach. Paleobiology 35 (2), 289–309.
Leroi-Gourhan, A., 1971. Préhistoire de l' art occidental. Ars Antiqua 1, 1–601.
Liebe, K.T., 1876. Die Lindentaler Hyänenhöhle und andere diluviale Knochenfunde in Ostthüringen, vol. 9. Archiv des Anthropologischen Organs der deutschen Gesellschaft für Anthropologie, Ethnographie und Urgeschichte, 1–55 pp.
Mills, M.G.L., Mills, M., 1977. An Analysis of Bones Collected at Hyaena Breeding Dens in the Gemsbok National Parks. In: Annales of the Transvaal Museum, vol. 30. 145–155.
Musil, R., 1962. Die Höhle "Sveduv stůl", ein typischer Höhlenhyänenhorst. Anthropos N.S 5 (13), 97–260.
Nehring, A., 1875. Ausgrabungen diluvialer Tiere zu Westeregeln bei Oschersleben. Verhandlungen der Berliner Gesellschaft für Anthropologie, Ethnographie und Urgeschichte. 206–208.
Nehring, A., 1876. Ausgrabungen bei Thiede und Westeregeln. Verhandlungen der Berliner Gesellschaft für Anthropologie, Ethnographie und Urgeschichte, 206–209 pp.
Nehring, A., 1878a. Die quaternären Faunen von Thiede und Westeregeln nebst Spuren des vorgeschichtlichen Menschen I. Archaeologie und Anthropologie 10, 359–398.
Nehring, A., 1878b. Die quaternären Faunen von Thiede und Westeregeln nebst Spuren des vorgeschichtlichen Menschen II. Archaeologie und Anthropologie 11, 1–24.
Nehring, A., 1884. Fossile Pferde aus deutschen Diluvial-Ablagerungen und ihre Beziehung zu den lebenden Pferden. Landwirtschaftliches Jahrbuch, 81–160 pp.
Nehring, A., 1890. Übersicht über 24 mitteleuropäische Quartär-Faunen. Zeitschrift der deutschen geologischen Gesellschaft 32, 468–509.
Pickering, T.R., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. International Journal of Osteoarchaeology 12, 127–141.
Pokines, J.T., Kerbis, Peterhans, J.C.K., 2007. Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. Journal of Archaeological Science 34, 1914–1931.
Schroeder, H., 1930. Über *Rhinoceros mercki* und seine nord- und mitteldeutschen Fundstellen. In: Abhandlungen der Preußischen Geologischen Landersanstalt Neue Folge 1927. 1–124.
Scott, L., Klein, R.G., 1981. A hyena accumulated bone assemblage from late holocene deposits at Deelpan, Orange Free State, South Africa. Annales of the South African Museum 86, 217–227.
Skinner, J.D., Henschel, J.R., Jaarsveld van, A.S., 1986. Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. South African Journal of Zoology 21, 303–308.
Spöttel, W., 1926. *Equus przewalskii* Poljakov 1881 mit besonderer Berücksichtigung der im Tierzuchtinstitut der Universität Halle gehaltenen Tiere, vol. 11. Kühn Archiv, 89–137 pp.
Springhorn, R., 2003. A wild horse (*Equus przewalskii* Poljakov, 1881) of Mesolithic age from Kempen (Germany, Northrhine-Westphalia, Lippe County). Eiszeitalter und Gegenwart 52, 40–46.
Stiner, M.S., 2004. Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy. Revue de Paléobiologie 23 (2), 771–785.
Sutcliffe, A.J., 1970. Spotted Hyaena: crusher, gnawer, digester and collector of bones. Nature 227, 110–113.
Thenius, E., 1961. Hyänenfraßspuren aus dem Pleistozän von Kärnten. Carinthia II. Naturwissenschaftliche Beiträge zur Heimatkunde Kärntens 151 (71), 88–101.
Toepfer, V., 1966. Westeregeln – ein klassischer Fundplatz für die Forschungsgeschichte des mitteldeutschen Pleistozäns. Jahresschriften für Mitteldeutsche Vorgeschichte 50, 1–20 pp.
Tournepiche, J.F., Couture, C., 1999. The hyena den of Rochelot cave (Charente, France). Monographien des Römisch-Germanischen Zentralmuseums 42, 89–101.
Tromnau, G., 1980. Den Rentierjägern auf der Spur – 50 Jahre Eiszeitforschung im Ahrensburger Tunneltal. Karl-Wachholtz Verlag, Neumünster.
Vialou, D., 1986. L'art des grottes en Ariège Magdalénienne. CNRS, Paris.
Virchow, R., 1878. Vorlage von Manufakten aus dem Diluvium von Thiede und Westregeln. In: Correspondenzblatt der deutschen Geselschaft für Anthropologie, Ethnographie und Urgeschichte 11, 149–151 pp.
Volf, J., 1996. Das Urwildpferd *Equus przewalskii*, Bd. 249. Neue Brehm-Bücherei, Wittenberg.
Weber, T., 2004. Der Faustkeil – das Universalgerät des Altsteinzeitmenschen? In: Meller, H. (Ed.), Paläolithikum und Mesolithikum Kataloge zur Dauerausstellung des Landesmuseums für Vorgeschichte in Halle 1, pp. 167–174.
Weinstock, J., 2000. Late Pleistocene reindeer populations in middle and Western Europe. Bio Archaeologica 3, 1–307.
Wernert, P., 1968. Beutestücke der Höhlenhyänen im anatomischen Verband aus Achenheimer Lössen. Quartär 19, 55–64.
Winterfeld, F., 1885. Über quartäre Mustelidenreste Deutschlands. Zeitschrift der deutschen Geologischen Gesellschaft 37, 826–864.
Zapfe, H., 1939. Lebensspuren der eiszeitlichen Höhlenhyäne. Palaeobiologie 7, 111–146.