Review Article

Recycling of Badger/Fox Burrows in Late Pleistocene Loess by Hyenas at the Den Site Bad Wildungen-Biedensteg (NW, Germany): Woolly Rhinoceros Killers and Scavengers in a Mammoth Steppe Environment of Europe

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The Late Pleistocene (MIS 5c-d) Ice Ages spotted hyena open air den and bone accumulation site Bad Wildungen-Biedensteg (Hesse, NW, Germany) represents the first open air loess fox/badger den site in Europe, which must have been recycled by *Crocuta crocuta spelaea* (Goldfuss, 1823) as a birthing den. Badger and fox remains, plus remains of their prey (mainly hare), have been found within the loess. Hyena remains from that site include parts of cub skeletons which represent 10% of the megafauna bones. Also a commuting den area existed, which was well marked by hyena faecal pellets. Most of the hyena prey bones expose crack, bite, and nibbling marks, especially the most common bones, the woolly rhinoceros *Coelodonta antiquitatis* (NISP = 32%). The large amount of woolly rhinoceros bones indicate hunting/scavenging specializing on this large prey by hyenas. Other important mammoth steppe hyena prey remains are from *Mammuthus primigenius*, *Equus caballus przewalskii*, *Bison/Bos*, *Megaloceros giganteus*, *Cervus elaphus*, and *Rangifer tarandus*. The few damaged bone remains of a scavenged cave bear *Ursus spelaeus* subsp. are unique for an open air situation. Abundant micromammal, frog, and some fish remains were concentrated in “pellets” that contain mainly mammoth steppe micromammals and also frog and fish remains that seem to originate from the nearby river/lake.

1. Introduction

Late Pleistocene European bone assemblages have been produced mainly by late Ice Age spotted hyena *Crocuta crocuta spelaea* [1] and were first recognized by Buckland [2] in the “Kuhloch Cave” (König-Ludwigs Cave, Bavaria, Germany) and the Kirkdale Cave (Kent, England). More recent studies provide information on the hyena prey bone assemblages (e.g., [3–10]) as well as on the new subdivided fossil hyena den types (e.g., [11]). These identifications of three classified Ice Age den forms are particularly important also to distinguish bone accumulations made by hyenas from those accumulated by Middle Palaeolithic humans (e.g., [9, 12–15]).

Few contemporary used hyena and Neanderthal sites have been described from hyena dens in mammoth steppe lowlands and adjacent cave-rich region environments of north-central Europe, in England and Germany [9, 16]. The degree of prey bone damage and presence/absence of “nibbling sticks” and faecal pellets or hyena population structure and their individual amount allow the reconstruction, much better, of the ethology of the last hyenas of Europe. The discussions for nonarchaeological sites no longer focus only on the human/carnivore origin discussion. Although hyena cave-den sites predominate in the European fossil record (e.g., Germany in [17]), open air sites may have been much more common throughout the mammoth steppe lowlands of Europe, but have been overlooked or not identified as such (cf. Westeregeln or Bottrop sites in [10, 18]).

Open air hyena den sites in loess deposits without human impact are not analyzed in Germany, as yet, whereas other bone accumulation sites on river terraces have been analyzed along the Emscher River near Bottrop in the Westphalian mammoth steppe lowland [10]. Recently many open air hyena den sites (loess, gypsum karst, river terraces: Saalfeld, Bottrop, Westeregeln, Sewecken-Berge, Thiede, and others) from Germany have been described [17, 19–21], whose density...
overlaps with the Middle Palaeolithic Neanderthal occupation and open air and cave sites in Germany, even in the famous Neanderthal valley [22, 23]. Additionally, the review of lion localities in northern Germany [24] demonstrates not only quite hard competition conditions about megafauna prey between those two top predators killing and consuming each other, but also competition with human Neanderthals during the Late Pleistocene. In Germany, additionally, mostly hyena den sites have been described and newly identified, also partly overlapping with human camp sites, for example, Balve Cave [17, 22, 23, 25–27]. The herein reviewed hyena den site Bad Wildungen-Biedensteg is not far from a Middle Palaeolithic site Buhlen (Micoquien to Late Mousterien: [28]), but has no evidence of human impact.

History of the Bad Wildungen Hyena Den Site. First Ice Age fauna remains in the clay pit site “Ziegeleigrube Biedensteg” in Bad Wildungen-Biedensteg of northern Hesse (Central Germany, Figure 1, GPS coordinates: long. 9°8′24.32″E, lat. 51°7′16.44″N) were discovered in 1932 by the hobby palaeontologist/archaeologist Pusch, who excavated and rescued many macromammal bones. In 1952 Jacobshagen and Lorenz found a micromammal-rich “pellet horizon” and two hyena skulls [29]. Jacobshagen described in 1963, briefly, this fauna, but wrote mainly about the micromammas. Huckriede and Jacobshagen [30] published the first section, which was studied with an addition of new sedimentological results by Semmel [31] and Kulick [32]. The last micropalaeontological research was performed by Storch [33] on pellet material. First thoughts about hyena gnawing and bone deposits were mentioned by Jacobshagen [34] with new research being published about the hyenas, woolly rhinoceros, and cave bears [35]. Here, the complete megafauna and hyena den site analyses are presented in more broad comparisons to many other new analyzed Late Pleistocene hyena dens studied these past years in Germany and Czech Republic (Figure 1).

2. Material and Methods

The main collection (including coll. Pusch, coll. Lorenz) is owned by the Rudolf-Lorenz-Stiftung (coll. no. Bl-52/1-237) and was partly presented in the “Stadt museum of Bad Wildungen.” Additionally, a few macromammal bones from the collection in the “University of Marburg” were integrated in this study, which was also mentioned in the article of Jacobshagen [34]. This collection was partly rediscovered by Dr. Fichter, who kindly helped by donating the important micromammal collection to the “Kur museum Bad Wildungen.” Only Kulick [32] made a small systematic excavation at the site, which produced mainly micromammals from pellets.

Comparative bone material was used in many different collections. The most important is the woolly rhinoceros skeleton from Petershagen (NW-Germany) in the Museum Natur und Mensch Bielefeld (MNMB). Another mounted skeleton cast in the Museum für Ur- und Ortsgeschichte Eisezithalle Quadrat Bottrop (EMOB) was used for the skeleton redrawing and comparison of the bone positions in the skeleton of the Bad Wildungen-Biedensteg material. Skeletons of the extinct Przewalski horse (Equus caballus przewalskii) were studied in the Julius-Kühn Museum Halle/Saale (JKMH; see also [36]), reindeer (R. tarandus) and arctic fox (V. lagopus) skeletons in the collection of the University of Alberta Department of Biological Sciences (UADBS); mammoth (M. primigenius) remains and cave bear (U. spelaeus) and red fox (V. vulpes) bones were compared to skeletal material in the Geologisch-Paläontologische Museum der Westfälischen Wilhelms-Universität Münster (GPIM). Finally, recent badger (M. meles) or common hare (L. europaeus) and the Pleistocene hyena materials from the Srbsko-Chlum were used in the collection of the National Museum Prague (NMP) and from the Perick Caves of the Staatliche Naturhistorische Sammlungen Dresden (SNSD). The open air gypsum karst site Westeregeln material was studied in the Martin-Luther-University Halle/Saale (MLU,IFG) and the Natural History Museum of the Humboldt-University Berlin (MB).

3. Sedimentary Geology, Paleoenvironment, and Dating

The geological situation at the hyena site “Lehmgrube Biedensteg” was published by Huckriede and Jacobshagen [30], Semmel [31], and Kulick [32]. The overview of the redrawn sketch of the outcrop section, with a combination of all published results and new interpretations about the hyena deposits, is presented in Figure 2.

The Wilde River gravels at the base of the section are of the Eemian Interglacial period. They consist of Red Bunter sandstone and claystone, llydite, quartz, or diabase pebbles. These deposits are overlain by a palaeosol resulting from solifluction. In this “Eemien Soil” the river pebbles are resedimented with reddish-brown loess. The “Lower Loess” is from the early to middle Lower Weichselian (MIS 5c-d), and after Semmel [31], a product of the first part of the glaciation (early Late Pleistocene, Figure 2), where, in this mountainous region, loess was deposited in a mammoth steppe environment. Some snails were found in the Lower Loess by Jacobshagen [34], the mentioned loess soil snail Pupilla muscorum (Müller) fitting to the cold period climatic and environmental mammoth steppe interpretation.

In the middle and at the end of the Late Pleistocene a climatic stagnation resulted in a palaeosol along the Wilde River gravels which were, at that time, on the shore of a small lake. This lake was caused by subsurface salt dissolution and positioned in a large-scaled sinkhole structure. The lake was filled up by the Wilde River, indicated by the presence of many aquatic vertebrate species, such as frogs (Rana agiloides Brunner), but mainly by salmonid fish (cf. [34]) that lived in fluent water.

The muddy area at the Wilde River or lake shore was used by the Ice Age spotted hyenas as prey deposit sites [35]. Bones from animals of the mammoth steppe macrofauna were deposited here, whereas “bone nests” were mentioned in the publication of Jacobshagen [34]. The sedimentary depression structures in the bone-rich loess horizon described by Kulick [32] as “cryoturbation and channels” also could be partially of bioturbation origin and were possibly caused by the hyenas who deposited animal prey remains in the soft soil, only in...
Figure 1: (a) Topographic position of the Ice Age spotted hyena *Crocuta crocuta spelaea* birth and commuting den site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (b) The prey was deposited at the margin of an ancient small lake and muddy area of the Pre-Wilde River that filled up a doline during the Late Pleistocene. (c) Generalized section at the Ice Age spotted hyena *C. c. spelaea* prey deposit site Biedensteg (Bad Wildungen, Hesse, NW-Germany).
Figure 2: Remains of the Ice Age spotted hyena *Crocuta crocuta spelaea* from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) High adult female deformed skull (no. Bi-10at), (a) lateral, (b) occipital, (c) ventral, (d) dorsal, (e) frontal. (2) Early adult female skull (no. Bi-52/45), (a) lateral, (b) occipital, (c) ventral, (d) dorsal, (e) frontal, (f) redrawing (pmx: premaxillary, mx: maxillary, pa: palatine, ba: basis occipital, oc: occipital, j: jugal, tmp: temporal). (3) Brain case of a very young cub (no. Bi-10ev), (a)-(b) lateral, (c) caudal, (d)-(e) dorsal. (4) Left cracked mandible of an adult female, (b) dorsal, (c) labial (no. Bi-52/51). (5) Left radius of a young cub (no. Bi-10ew), cranial. (6) Axes of an adult animal (no. Bi-52/234), lateral. (7) Left femora of a young cub cranial (no. Bi-10em). (8)–(17) Coprolites from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (8) Two large pellets, partly encrusted by caliche (no. Bi-52/221). (9) Large oval pellet, partly encrusted by caliche at which originally another pellet was attached (no. Bi-52/213). (10) Three articulated pellets of different shape, partly encrusted by caliche (no. Bi-52/214). (11) Four partly articulated pellets, encrusted by caliche. Pellet D is broken; the end exposes a small prey bone fragment (no. Bi-52/210). (12) Two articulated pellets. In pellet B a bone fragment is present (no. Bi-52/219). (13) Sigmoid drop shaped and pointing single pellet (no. Bi-52/209). (14) Cone shaped and basal flat single pellet, that was originally attached to another pellet (no. Bi-52/220). (15) Irregular u-shaped pellet that was originally attached to other pellets (no. Bi-52/207). (16) Irregular shaped pellet that was originally attached to other pellets (no. Bi-52/212). (17) Small flat drop shaped pellet (no. Bi-52/218). (11) Small drop shaped single pellet (no. Bi-52/211). (18) Bone remains (red are represent) from an adult female, an early juvenile cub of few weeks of age and coprolites from the hyena freeland prey deposit site Bad Wildungen-Biedensteg near Hesse (NW-Germany).
summer times, when the permafrost soil was soft in the upper parts.

The bioturbation interpretation would fit into the “hyena commuting/prey storage site,” but can no longer be studied because of the nonopen loess pit Biedensteg. In this section (Figure 2) such depressions are figured as hyena prey depots. Possibly, a later cryoturbation, a result of permafrost soils fitting into the environment and climatic situation of that time, was responsible for secondary overprint of the primary sediment structures. Bioturbation by mammoths on lake shores, which left depressions of their footprints, must be taken into account, as is discussed for other sites (cf. [37]).

The “pellet horizon” is figured differently in the publications (of Jacobsen et al., 1963, [32]). The section of Kulick [32] indicates that the pellets and the macromammal bones are mixed in a single horizon. Proof for that might be caliche concretions around hyena coprolites in which micromammal bones and teeth are also cemented in. The “hyena prey depot site” and the “pellet horizon” are from the same period and are dated relatively (no absolute data) into the late Middle Late Pleistocene or Weichselian (65.000–90.000 BP, MIS 5c-d, Figure 2).

The bone-rich horizon is overlain by another palaeosol, the “Lohner Soil,” which can be found in the region at different sections [31, 32]. After their interpretations a solifluction of Loess and Wilde river gravel material took place in the middle Late Pleistocene warm period (Figure 2). V. vulpes and M. meles were the dominating faunal elements, besides L. europaeus. This fauna fits to Meles/Vulpes den burrow sites in loess soils, in front of which they often left some prey bones.

Finally the upper loess was deposited within the LGM, and after, the upper part was decalcified during the Holocene period. The “Eltviller Tuff” is a one to two centimeter thin layer in the upper loess and the only absolute dated horizon with an age of around 16.000 BP ([31], Figure I(c)).

4. Small Carnivore Fox Den and Mustelid Bone Assemblage

Meles meles (Linneé 1758) (Figure 4(13)–(32)) (Table 5) is known by one skull of an adult male (Figure 4(13)) and a second brain case of a juvenile. Several postcranial bones consist of the forelimb (Figure 4(14)–(20)) and hind limb bones (Figure 4(21)–(29)), although vertebrae are missing (cf. Table 1).

Vulpes vulpes (Linneé 1758) (Figure 4(1)–(9)) remains consist of 13 common fox bones (Table 3) including a skull. This skull is incomplete, as most of the anterior part with its dentition is missing. The last three teeth are in the left maxillary (Figure 4(1)). From a right forelimb the scapula, humerus, and radius were found, which seem to belong to one individual (Figure 4(2)–(4)). From a hind limb, not only the left femur shaft and incomplete tibia but also a right calcaneus and a metatarsus III are represented (Figure 4(5)–(8)). A fragment of a metapodial is missing its proximal joint. Finally a lumbar vertebra and one rib are preserved. The pelvis is missing its left part (Figure 4(9)). A second pelvis fragment is again incomplete. Material from two individuals is present, indicated by the pelvis remains. Possibly most of the bones belong to only one individual. All postcranial bones show a complete fuse of the symphyses and are from either a single animal or several adult animals.

Vulpes lagopus (Linneé 1758) (Figure 4(10)–(12)) (Table 4) was found with a nearly complete skull, without the jugal arches, but with the right mandible (Figure 4(10)–(11)). The skull sutures are not fully fused and teeth are barely used; therefore it was a young adult individual, as only a single individual can be estimated from the bone material. The postcranial material is present with a femur shaft and pelvic fragment (Figure 4(12)).

Mustela putorius Linnaeus 1758 (Figure 4(33)) (Table 6) is present with a single half skull (Figure 4(33)) of which the anterior part with most of the dentition is preserved.

Lepus europaeus/timidus Linneé 1758 (Figure 14(1)–(9)) (Table 14) is represented by 28 bones which are cranial fragments, two are mandibles and the rest are postcranial bones (Table 13). There is an articulated pedal skeleton (Figure 14(9)) and an articulated pelvis with lumbar vertebral column (Figure 14(5)). The figured material (Figure 14) seems to be from one individual, which is indicated by the bone preservation and articulations. Another argument is the individual adult’s age and the fresh fractures of the humerus, radius, the right femur and left tibia, or some processes of the vertebrae, which were caused during the excavations. Bones from other individuals of young and adult age are also preserved and have been completely disarticulated. 25% of the remains are from young animals; 75% are from adult hares. Three animals can be estimated by the tibia as minimum individual number.

5. The Hyena Population and Coprolite Remains

The Ice Age spotted hyena Crocuta crocuta spelaea [1] (Figure 2) skeletal remains consist of four skulls, three mandibles, one radius, and a femur (Table I). Additionally, there are 16 coprolites which were rescued.

From the first skull (Figure 2(1)) deformations do not allow exact metric data. The second skull (Figure 2(2)) is 290 mm in total length and measures 265 mm between the incisive and condyle. The largest height is behind the frontal processes (114 mm). The distances between the canines and P₄ are about 68 mm. The width of the frontals (zygomatic processes) measures 90 mm. Finally the outer distance between the canines is 58 mm. The largest diameter of the canines in the middle of the tooth is 18 mm. The brain case symphyse of the third animal (Figure 2(3)) is slightly fused and articulated. The parietal, frontal, palatine, and temporal are incomplete. The maximum width measured, between the temporal, 73 mm, whereas it is preserved in 76 mm in length.

One left mandible (Figure 2(4)) is of an adult animal and might belong to one of both individual adult skulls, which show a similar tooth use stage. The jaw was cracked by hyenas between the P₂ and P₃; the P₃,4 and M₁ are present. The ramus was damaged during excavations.

A few postcranial bones are represented with one axis of an adult animal exposing bite damage marks (Figure 2(6)).
A left radius and a left femur (Figure 2(5) and (7)) are from one very young cub, both being incomplete as a result of scavenging activities by large carnivores.

**Coprolite Material.** The hyena coprolites are generally white inside and the pores are filled with iron and manganese minerals. The coprolites show a moderate variability and even bone contents (Figure 2(8)–(17)). The largest one (Figure 2(8)) is a double pellet being connected by caliche incrustations. It seems to represent a fossilized, originally softer and humid, faecal pellet. The other pellets have repeating shapes and have attached 3–5 smaller pellets (Figure 2(9)–(12)), representing possibly more dry dung. Single pellets have often defined shapes. The most represented one is the “drop shaped pellet” (Figure 2(13)–(15)). They can point to both sides or can end round to flat on one side as a result of attachment to another pellet. Other pellets are “unshaped” and irregular. These were often found in the non-spindle-like pellet aggregations (Figure 2(10)). In the material from Biedensteg each coprolite contains several bone fragments, which are often visible on the surfaces (Figure 2(11)–(12)). These are small pieces, well rounded by stomach acid, and are mainly from the bone compacta, but also are isolated pieces of bone spongiosa. This spongiosa is very thin walled and should have been completely dissolve. These spongiosa pieces are most comparable to the bone spongiosa of the woolly rhinoceros, but might also refer to other megamammals.
6. Hyena Megafauna Prey Remains

*Ursus spelaeus* Rosenmüller 1794 subsp. (Figure 3) is represented by four cave bear bones and fragments. The left scapula (Tables 2 and 3(1)), which lacks all distal parts seems to be destroyed by hyenas. Large carnivore gnawing and bite marks are visible at the glenoid. A right humerus shaft (Figure 3(2)) is missing the joints as a result of heavy carnivore chewing. At the shaft ends and in the lower middle, bite marks are present. The diameter of the bone shaft is small, being only 49 mm. From one left incomplete ulna (Figure 3(3)) the distal joints were chewed and also some bite marks are visible. The 50 mm maximum width ulna has, again, small proportions.

Finally, a fragment of a femur shaft (Figure 3(4)) with heavy chewing damage indicate the cracking and further use of the bone fragment as a typical hyena “nibbling stick” (for teething purposes of hyena cubs).

*Mammuthus primigenius* (Blumenbach 1799) (Figure 12 (1)–(3)) is represented by three remains consisting of a tooth lamella fragment from a juvenile animal, a thoracic vertebra neural arch and centrum fragment, and a long bone fragment used as a nibbling stick (Table 7). The material is from adolescent elephants.

*Coelodonta antiquitatis* (Blumenbach 1799) (Figures 5–11) is the most abundant, listed in Table 8. The cranial elements consist of a middle part of a skull from a young calf (Figure 9).
Figure 4: Small carnivores from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1)–(9) *Vulpes vulpes*: (1) incomplete skull (no. Bi-52/39), (a) lateral, (b) caudal, (c) ventral. (2) Right scapula (no. Bi-52/235), lateral. (3) Right humerus (no. Bi-52/10), cranial. (4) Right radius (no. Bi-52/24), cranial. (5) Left femur without joints (no. Bi-52/104), cranial. (6) Left tibia (no. Bi-52/105a), cranial. (7) Left calcaneus (no. Bi-52/238), cranial. (8) Right metatarsus III (no. Bi-52/239), cranial. (9) Incomplete pelvis (no. Bi-52/127), lateral. (10)–(12) *Vulpes lagopus*: (10) nearly complete skull with right lower jaw (no. Bi-10bh), (a) lateral, (b) dorsal, (c) ventral, (d) frontal, (e) occipital. (11) Right mandible (no. Bi-52/243), lateral. (12) Pelvis, acetabulum (no. Bi-10bn), lateral. (13)–(32) *Meles meles*: (1) skull with lower jaw (no. Bi-10ah), (a) lateral, (b) occipital, (c) dorsal, (d) frontal, (e) ventral, (f) lower jaw dorsal. (14) Left Humerus (no. Bi-10ap), cranial. (15) Left ulna shaft (no. Bi-10ao), lateral. (16) Right ulna (no. Bi-10av), lateral. (17) Left radius (no. Bi-10aw), lateral. (18) Right radius (no. Bi-10ao), lateral. (19) Left mt III (no. Bi-10bf), dorsal. (20) Left mt V (no. Bi-10bb), dorsal. (21) Left tibia (no. Bi-52/85), cranial. (22) Right calcaneus (no. Bi-10an), cranial. (23) Left calcaneus (no. Bi-10at), cranial. (24) Right astragal (no. Bi-BadW-2), dorsal. (25) Left astragal (no. Bi-10ay), dorsal. (26) Right mt IV (no. Bi-BadW-5), dorsal. (27) Right mt I (no. Bi-BadW-8), dorsal. (30) Phalanx II (no. Bi-BadW-2), dorsal. (31) Phalanx II (no. Bi-BadW-3), dorsal. (32) Phalanx II (no. Bi-BadW-4), dorsal. (33) *Mustela putorius*, anterior part of a skull (no. Bi-10bs), (a) lateral, (b) frontal, (c) dorsal, (d) ventral.

Table 2: Bones of *Ursus spelaeus* subsp. Rosenmüller 1794 from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type    | Commentary       | Left | Right | Age | Bite marks | Collection              |
|-----|-----------|--------------|------------------|------|-------|-----|------------|-------------------------|
| 1   | 52/227    | Scapula      | Without distal part | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung  |
| 2   | 52/2      | Humerus      | Shaft            | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung  |
| 3   | 52/241    | Ulna         | Incomplete       | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung  |
| 4   | 52/242    | Femur        | Fragment         | ?    |       | Adult | x          | Rudolf-Lorenz-Stiftung  |
The connection in-between the maxillae were restored in former times. Originally, the maxillary part between the teeth was damaged by hyenas. All three \( m_1^{1-3} \) milk teeth on both sides are present (Figure 6(1a)–(1d)). Both \( m_1 \)'s are breaking through, whereas the \( m_2 \)'s were still in the maxillary.

These are not present, but the alveolar grooves are preserved. This skull was badly damaged by the hyenas, especially at the anterior part and the brain case. The latter shows a very interesting large carnivore brain case opening. There are some bite marks, but thin parallel long scratch
Figure 6: *Coelodonta antiquitatis* remains of a less than half-year-old calf with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Skull with brain case opening (no. Bi-10ac), (a) and (c) dorsal, (b) ventral, (d) lower jaw (no. Bi-52/37 and 38), dorsal, (e)-(f) lateral left, (g)-(h) lateral right. (2) Articulated left ulna and radius from calf (no. Bi-52/47 and 42), lateral. (4) Left femur from calf (no. Bi-52/43), cranial. (3) (1) Left ileum remain of a calf (no. Bi-52/13), lateral.

Table 3: Bones of *Vulpes vulpes* 1758 from the open air prey deposit site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 52/39     | Cranium   | Incomplete |      |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 2   | 52/35     | Scapula   | Nearly complete | x |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 3   | 52/10     | Humerus   | Complete   |      |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 4   | 52/24     | Radius    | Complete   |      |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 5   | 52/104    | Femur     | Nearly complete | x |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 6   | 52/105a   | Tibia     | Complete   | x    |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 7   | 52/238    | Calcaneus | Complete   | x    |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 8   | 52/127    | Pelvis    | Nearly complete |     |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 9   | 52/128    | Pelvis    | Fragment   |     |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 10  | 52/239    | Metatarsus III | Complete | x |       | Adult|            | University of Marburg |
| 11  | 52/240    | Metatarsus | Without proximal joint | x |       | Adult|            | University of Marburg |
| 12  | 52/21     | Lumbar vertebra | Nearly complete | x |       | Adult|            | Rudolf-Lorenz-Stiftung |
| 13  | 52/105b   | Costa     | Nearly complete | x |       | Adult|            | Rudolf-Lorenz-Stiftung |

marks on the right maxillary in the high of the dm$^{2-3}$ could have resulted from other smaller carnivores or hyena cubs. Both mandibles of the lower jaw (Figure 6(e)–(h)) fit to the skull by the identical milk dentition of the dm$^{1-3}$ and the tooth rising of the m$_1$. Both jaws were cracked in the symphyses area and have old fractures. Additionally, they are lacking the rami and have large carnivore chewing and gnawing marks (Figure 6(e)–(h)). The left jaw possesses the dm$^{1-3}$ and the m$_1$. The right mandible was damaged by the excavations and because of this is lacking the anterior part, including the dm$^{1-2}$. Other cranial material was described and partly refigured by Jacobshagen [34]. He refigured some lower jaw teeth of one individual (right P$_{3-4}$, M$_1$, and left M$_{2-3}$). The little use of the M$_3$ indicates an origin of an early adult animal. It is suggested here that these belonged most probably to the skeleton of an early adult female individual (Figure 5(b)). Scapulae are preserved with one nearly complete left shoulder blade (Figure 7(1)). Some parts from the left side and joint area, destroyed by the excavations, were restored. Bite marks were found only distally. Here, hyenas left typical chewing marks in the very soft scapula. The margin is therefore typically irregular, resulting from cracked bone material. The scapula seemed to belong to the female skeleton. A second fragment of a scapula is
Figure 7: *Coelodonta antiquitatis* fore leg remains of adolescent and grown up animals with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left scapula from an adult individual (no. Bi-52/20), lateral. (2) Scapula fragment (no. Bi-52/88), lateral. (3) Right humerus (no. Bi-180c), caudal. (4) Left radius from an adult male individual (no. Bi-52/30), cranial. (5) Right radius from an adult male individual (no. Bi-52/44), cranial. (6) Right distal radius joint from an early adult female individual (no. Bi-52/224), (a) cranial, (b)-(c) ventral. (7) Left radius from an adult female individual (no. Bi-52/49), cranial.

Table 4: Bones of *Vulpes lagopus* 1758 from the open site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type  | Commentary                  | left | right | Age     | Bite marks | Collection                  |
|-----|-----------|------------|-----------------------------|------|-------|---------|------------|-----------------------------|
| 1   | 10bh      | Cranium    | Nearly complete with right lower jaw |      |       | Senile  |            | Stadtuseum Bad Wildungen    |
| 2   | 52/243    | Mandible   | Fragment with P4            | x    |       | Adult   |            | University of Marburg       |
| 3   | 10eh      | Femur      | Shaft                       | x    |       |         |            | Stadtuseum Bad Wildungen    |
| 4   | 10bn      | Pelvis     | Fragment, acetabulum        | x    |       | Adult   |            | Stadtuseum Bad Wildungen    |
in preservation and could be found in a lower horizon. One humerus is described by Jacobshagen [34], which can no longer be located. It was a right humerus that was chewed on the proximal joint. Ulnae are present with five bones (Figure 8(1)–(4)) from different old animals. The most juvenile, a neonate to young, animal’s left ulna must have been articulated to one radius (Figure 6(2)). This result is from the comparison to an articulated right ulna/radius from a young adult to adult animal whose joints are chewed away in the same way (Figure 8(1)). The latter might belong to the young adult female rhinoceros (Figure 5(b)), of which also other bones were found partly articulated. At least seven radii (Figure 7(4)–(6), MNI = 7) were found, of which four are from young adult to adult animals and the last from the neonate to very young individual. The four pelvis remains are typical rests of hyena feeding activities (Figure 10(1)–(3)). The acetabular and surrounding two acetabular fragments are from different animals. The one figured (Figure 10(1)) has not only hyena, but also arctic fox, wolf or hyena cub, and even small rodent nibbling marks. The fourth pelvis remain is only a part of the ileum (Figure 6(3)) and seems to belong to the juvenile animal, because it is also chewed from the acetabular region. It is also heavily chewed at the soft distal part with irregular margin. Four femora are preserved, of which one is a fragment, a second is from a juvenile animal (Figure 6(4)), and a third and fourth are from an adult C. antiquitatis (Figure 10(4)–(5)). Another fragment is of an adolescent, with strong chewing marks (Figure 10(6)). As described by Jacobshagen [34], there was a right femur (Figure 10(4)) found in articulation with a tibia (Figure 11(2)). Only one nearly complete left patella (Figure 11(9)) was excavated and might belong also to the female skeleton’s hind leg (Figure 5(b)). The tibia has very typical hyena caused damages and is in an early stage (stage 1) of destruction. Also this fits well with the partly articulated female skeleton carcass. Three tibiae are very massive and have a strong width in the shaft (Figure 11(3)–(5)). All tibiae compared indicate a sexual dimorphism with males being stronger and more massive in their bones. Mostly the proximal joint was chewed away first, although at the distal part in a middle stage (stage 2 of three) of bone feeding, two grooves were left, which is documented at all three tibiae (Figure 11(3)–(5)). Two fibula
Figure 9: *Coelodonta antiquitatis* thoracic remains, all of which are most probably from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) First cervical vertebra (atlas) (no. Bi-52/9), caudal. (2) Second cervical vertebra (axes) (no. Bi-52/1), cranial. (3) Third cervical vertebra (no. Bi-52/11), cranial. (4) First three cervical vertebrae (no. Bi-52/107/1 to 3), lateral. (5) Sixth cervical vertebra (no. Bi-52/107/1), cranial. (6) Seventh cervical vertebra (no. Bi-52/107/2), cranial. (7) Articulated last cervical to second thoracic vertebrae (no. Bi-52/107/1 to 3), lateral. (8) First thoracic vertebra (no. 108-3), cranial. (9) Third thoracic vertebra (no. Bi-52/10m), cranial. (10) Fourth thoracic vertebra (no. Bi-52/152), cranial. (11) Second thoracic vertebra (no. Bi-52/10j). (12) Articulated second and third thoracic vertebrae (no. Bi-52/10) to m, lateral. (13) Sixth thoracic vertebra (no. Bi-52/107-1), cranial. (14) Seventh thoracic vertebra (no. Bi-52/107-2), cranial. (15) Eighth thoracic vertebra (no. Bi-52/107-3), cranial. (16) Ninth thoracic vertebra (no. Bi-52/107-4), cranial. (17) All four articulated sixth to ninth thoracic vertebrae (1)–(4) (no. Bi-52/107/1 to 4), lateral. (18) Articulated last thoracic and first lumbar vertebra (no. Bi-52/10l and 10h), lateral. (19) Lumbar vertebra neural arch (no. Bi without no.), cranial. (20) Posterior right costa fragment (no. Bi-10ad). (21) Anterior costa fragment (no. Bi-10v). (22) Middle right costa fragment (no. Bi-52/2). (23) Anterior left costa fragment (no. Bi-10z). (24) Anterior right costa fragment (no. Bi-52/100). (25) Middle left costa fragment (no. Bi-52/15). (26) Middle left costa fragment (no. Bi-52/156). (27) Upper costa fragment with chewing marks (no. Bi-52/3). (28) Anterior right costa fragment, distally chewed (no. Bi-52/3a), cranial.
remains are in the material, with one (Figure 11(7)) being proximally incomplete as a result of the excavations. That one was articulated to one tibia in the stage of hyena chewing and seems to belong to the female carcass (Figure 5(b)). The distal part shows long bite scratches. The second fibula was cracked away from a tibia and was left with the middle shaft with bite marks at both ends (Figure 11(6)). Only one astragalus and calcaneus are in the material (Figure 11(8)) also most probably belonging to the hind leg of the female skeleton (Figure 5(b)). They fit perfectly together, indicated additionally by overlapping bite scratch marks which are crossing both bones. After the descriptions by Jacobshagen [34] there were three complete metatarsals (2–4) that also fit for the female skeleton (Figure 5(b)), although it is unclear whether they are from the right or left side. All vertebrae show the typical hyena chewing by the lack of nearly all processes. They seem to be all from one nearly adult individual, indicated by a series of articulation and the similar degree of nonfusing of the caudal vertebra centrum disc. The cranial disc, in contrast, is already fused completely at all vertebrae. From the vertebral column, the first three cervical vertebrae were found connected (Figure 9(4)). Atlas (Figure 9(1)), axes (Figure 9(2)), and the third cervical vertebra (Figure 9(3)) have bite marks on the damaged processes. The next articulated vertebral column part is the vertebra from the sixth cervical to the first thoracic (Figure 9(7)). Articulated cervical vertebrae no. 6 (Figure 9(5)) and no. 7 (Figure 9(6)) and thoracic vertebra no. 1 (Figure 9(8)) are also lacking most of their processes, especially the dorsal ones. Two more articulated vertebrae are the second (Figure 9(9)) and third (Figure 9(11)) thoracic vertebra which are heavily chewed (Figure 9(12)). The fourth thoracic vertebra (Figure 9(10))
Coelodonta antiquitatis hind limb remains partly from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left tibia from a female individual (no. Bi-10c), cranial. (2) Right tibia from a female individual (no. Bi-52/7), cranial. (3) Right tibia from a female individual (no. Bi-10e), cranial. (4) Right tibia from a male individual (no. 52/9), cranial. (5) Right tibia from a male individual (no. Bi-52/201), cranial. (6) Left fibula shaft (no. Bi-52/4), lateral. (7) Left fibula fragment (no. Bi-52/16), lateral. (8) Articulated right calcaneus and astragal (no. Bi-10f, g), (a)-(b) dorsal, (c)-(d) lateral. (9) Right patella from an early adult to adult animal (no. Bi-52/228), cranial. (10) Right metatarsus III (no. Bi-140b), cranial. (11) First phalanx of an adult animal (no. Bi-52/101), cranial.

was only a centrum that was found in nonarticulation with other vertebrae. The complete neural arch was eaten. Parts of the left side were cut by excavation activities. The longest articulated vertebral column part exists from the sixth to ninth thoracic vertebrae (Figure 9(17)). Typical for the hyena scavenging activities are the chewed dorsal spines. Finally, the articulated last thoracic and first lumbar vertebra were found connected (Figure 9(18)). Also, the first lumbar vertebra is lacking parts of the proc. transversus. The ribs generally have no hyena bite marks, but obviously they were removed from the carcass (Figure 9(20)–(28)). All costae have cracking fractures at both ends; all joints are lacking. Only one small rib fragment (Figure 9(28)) has distally small bite marks. Nibbling by a small carnivore, such as a young hyena, wolf, or arctic fox, has caused a pointed distal end. A small fragment was used for nibbling by young hyenas ("nibbling stick" no. 3, Figure 9(27)). The present rib fragments are from the anterior part around the forelimb, and a few are from the last thoracic vertebrae.

Bison/Bos (Figure 12(4)–(9)) remains consist of 13 bones (Table 9), two of which are teeth, the others being postcranial bones, which are all incomplete as a result of large carnivore activities. Most bones are limb bones, especially from the hind limbs. The teeth are two M1’s, one from the upper and the other from the lower jaw. The strong tooth use indicates an individual of adult to older adult age. From the forelimb a metacarpal fragment (Figure 12(4)) was found. The metacarpal shows a typical hyena cracking preservation; the distal part has sharp edges. Most bones are from the hind limbs. Both femora were cracked in the middle of the shaft but also the distal joints were heavily eaten and nibbled (Figure 12(5)-(6)). One middle shaft of a cracked tibia
and one proximally chewed calcaneus (Figure 12(8)) and two femur fragments seem to originate of the right hind limb of one animal. Finally, there is one thoracic vertebra centrum (Figure 12(9)) and one cervical vertebra (Figure 12(10)). The processes were chewed, and also some deep scratch bite marks can be found ventrally. All bones belonged to one, or possibly a few adult individuals.

Equus caballus przewalskii Poljakoff 1881 (Figure 13(4)–(15)) consists of 19 bones, of which two are mandible fragments, one cranial fragment and a single tooth, although mainly leg remains are represented (Table 10). The one metacarpus is 236 mm in length and distally 50 mm in width (Figure 13(8)) and falls within the small Przewalskii horse metapodial osteometry (cf. [9–11, 18, 37–44]). The same is for one complete metatarsus (Figure 13(15)) with its 257 mm length and 53 mm distal width. Also, there is the nearly complete lower jaw of a male horse (Figure 13(4)), as well as other small-sized bones from the smaller Przewalskii horse. There are bones from young horses (21%), with all others being from adult individuals (79%).

Megaloceros giganteus (Blumenbach 1799) (Figure 13(1)) was found with only seven bones, including one mandible fragment and three teeth, all from adult animals (Table 11). The material described and figured from Jacobshagen [34] is lost.

Cervus elaphus Linné 1758 (Figure 13(2)–(3)) is present with only two remains (Table 13). From the cranium, a right maxillary fragment with two $M^1$–$M^2$ shows the $M^2$ not in a developed state, although, the $M^3$ alveolar is opened and the tooth is in change. Another remain is a metatarsus...
Figure 13: (1)-(2) Cervid and Equid remains from the hyena open air den site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (a) Redrawing, (b) photo. (1) *Megaloceros giganteus* tibia fragment (no. Bi-52/32), cranial. (2) (3) *Cervus elaphus*. (2) Maxillary of a young animal (no. Bi-10ep), ventral. (3) Metatarsus of a young animal (no. Bi-52-113-1), cranial. (4)-(15) *Equus caballus przewalskii*. (4) Nearly complete lower jaw with both mandibles from an adult male. This jaw was broken into some pieces as a result of sediment pressure and not of hyena cracking activities (no. Bi-52/204), (a) lateral right mandibula, (b) dentition dorsal. (5) Anterior symphyseal part of a lower jaw from a juvenile less than one-year-old male (no. Bi-52-27), dorsal. (6) Radius-ulna of an adult animal (no. Bi-10aa), cranial. (7) Radius-ulna of an adult animal (no. Bi-52/50), caudal. (8) Metacarpus of an adult animal (no. Bi-52/112), cranial. (9) Phalanx 1 of an adult animal (no. Bi-52/14), cranial. (10) Phalanx 2 of an adult animal (no. Bi-52/78), cranial. (11) Lumbar vertebra no. 4 of a juvenile animal (no. Bi-10eg), cranial. (12) Anterior part of the sacrum of a juvenile animal, belonging to the vertebra of Figure 9 (no. Bi-10ad), dorsal. (13) Right pelvis remain (ileum, ischium) of an adult animal (no. Bi-10i), lateral. (14) Tibia fragment (no. Bi-52/51), caudal. (15) Metatarsus of an adult animal (no. Bi-10lt), cranial. (16)-(25) *Rangifer tarandus*. (16) Antler base of an adult animal (no. Bi-52/41). (17) Antler base of an adult animal (no. Bi-52/40). (18) Antler base of an adult animal (no. Bi-52/33), all cranial. (19) Right scapula (no. Bi-52/132), lateral. (20) Left scapula (no. Bi-52/126), lateral. (21) Left tibia (no. Bi-52/10), cranial. (22) Right tibia (no. Bi-52/151), cranial. (23) Articulated metatarsal bones (no. Bi-52/115-4, 5, 7, 8), cranial. (24) Forelimb phalanx II of a juvenile (no. BI-52/246), dorsal. (25) Hind limb phalanx II (BI-52/246), dorsal.
Table 5: Bones of *Meles meles* Linné 1758 from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age  | Bite marks | Collection          |
|-----|-----------|-----------|------------|------|-------|------|------------|---------------------|
| 1   | 10ah      | Cranium   | Skull with lower jaws | Senile |       |      |            | Rudolf-Lorenz-Stiftung |
| 2   | BadW-1    | Cranium   | Skull with lower jaws | Juvenile |   |   |            | Rudolf-Lorenz-Stiftung |
| 3   | 64/1      | Humerus   | Without joints |       |       | Juvenile |            | Rudolf-Lorenz-Stiftung |
| 4   | 10ap      | Humerus   | Without proximal joint | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 5   | 10ao      | Ulna      | Incomplete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 6   | 10av      | Ulna      | complete  |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 7   | 10aw      | Radius    | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 8   | 52/84     | Radius    | Without joints |       | Juvenile |   |            | Rudolf-Lorenz-Stiftung |
| 9   | 10ao      | Radius    | complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 10  | 52/87     | Radius    | Without joints |       | Juvenile |   |            | Rudolf-Lorenz-Stiftung |
| 11  | 10bd      | Pisiform  | Complete   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 12  | 52/86     | Femur     | Without joints | x | Juvenile |   |            | Rudolf-Lorenz-Stiftung |
| 13  | 52/85     | Tibia     | Without joints, half | x | Juvenile |   |            | Rudolf-Lorenz-Stiftung |
| 14  | 10aq      | Tibia     | Fragment   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 15  | 10at      | Calcaneus | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 16  | 10an      | Calcaneus | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 17  | 10ay      | Astragal  | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 18  | BadW-2    | Astragal  | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 19  | 10qr      | Astragal  | Complete   | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 20  | 10lm      | Intermid  | Complete   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 21  | 10bf      | Metatarsus | III, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 22  | 10bb      | Metatarsus | V, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 23  | BadW-5    | Metatarsus | IV, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 24  | BadW-6    | Metatarsus | III, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 25  | BadW-7    | Metatarsus | II, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 26  | BadW-8    | Metatarsus | I, complete | x | Adult |       |            | Rudolf-Lorenz-Stiftung |
| 27  | BadW-2    | Phalanx II| Complete   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 28  | BadW-3    | Phalanx II| Complete   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 29  | BadW-4    | Phalanx II| Complete   |   |       | Adult |            | Rudolf-Lorenz-Stiftung |

Table 6: Bones of *Mustela putorius* Linnaeus 1758 from the open air prey deposit site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age  | Bite marks | Collection          |
|-----|-----------|-----------|------------|------|-------|------|------------|---------------------|
| 1   | 10bs      | Cranium   | Nearly complete | Senile |       |      |            | Stadtuseum Bad Wildungen |
| 2   | 52/247    | Pelvis    | Fragment   | Adult |       |      |            | University of Marburg |

(Figure 13(3)). All remains are from possibly a single calf, approximately 1.5 years old.

*Rangifer tarandus* Linné 1758 (Figure 13(16)–(25), Table 12) is more common, with 24 remains. The rest of the bone material, such as a right metatarsus, a phalanx 1 and phalanx 2 proximal joint disc, and a right radius distal joint fit in the nonfusing of the joints to one young animal. The dropped antlers are from males and are all from sheds, which must have been collected by hyenas. Similar damages are present on the distal ends where large triangular-oval bite impact marks and elongated scratches indicate large carnivore damage (Figure 13(15)–(17)).

7. Discussion

7.1. The Badger/Fox Types and Den Micromammals and Pellet Accumulators. At open air badger den sites, typically, most skulls and massive long bones were found, although such long-term used badger loess den systems are described [45]. In those, bone accumulations are dominated by skull remains, being figured, for example, for the Schneehalle Cave (South Germany, [46]). Commonly, badgers die in their dens [46–48], explaining their bone accumulations in burrows and caves. The amount of bones, mainly of senile and very young badgers of Bad Wildungen, fit into such a scheme. Bite marks
Table 7: Bones of *Mammuthus primigenius* (Blumenbach 1799) from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 10ex      | Dens      | Fragment of lamella | Early juvenile |   |      |   | Rudolf-Lorenz-Stiftung |
| 2   | 52/116    | Thoracic vertebra | Neural arch | ? Adult | x |      |   | Rudolf-Lorenz-Stiftung |
| 3   | 52/149    | Thoracic vertebra | Centrum | ? Adult | x |      |   | Rudolf-Lorenz-Stiftung |
| 4   | 52/222    | Long bone | Fragment, "nibbling stick" | x | Adult | x |           | Rudolf-Lorenz-Stiftung |

![Figure 14: (1)–(9). *Lepus europaeus/timidus* remains from the hyena open air prey deposit site Bad Wildungen-Biedensteg (Hesse, NW-Germany) possibly belonging to one individual. (1) Left maxillary with dentition (no. Bi-63h), ventral. (2) Right humerus fragment (no. Bi-63g), cranial. (3) Right radius fragment (no. Bi-63f), cranial. (4) Pelvis (no. Bi-63a), lateral. (5) Pelvis of Figure 4 with five articulated lumbar vertebrae (no. Bi-63a), dorsal. (6) Right femur (no. Bi-63b), cranial. (7) Right tibia (no. Bi-63d), cranial. (8) Left femur fragment (no. Bi-63c), cranial. (9) Right incomplete pedal skeleton (no. Bi-63e), cranial. (10) *Spermophilus rufescens*, skull with lower jaw (52/257), (a) dorsal, (b) lateral. (11)–(13) Pellets with frog and micromammal remains (Bi-52/243, 52/244, 52/245).](image)

and missing joints in a humerus and tibia might be the result of badger cannibalism [47] or even hyena activities. The skull and postcranial material can be referred to the Asian species *Meles meles* cf. *leucurus* (cf. [49, 50]), and the skull seems to be of male origin (cranial sexual dimorphism; see [51]). This is so far important, because this subspecies seem to have immigrated to Europe from Asia during the Late Pleistocene, where it is nowaday’s extinct [50]. The badger, with its diet (cf. [52]), was not responsible for the bone accumulations of medium-sized mammals and anures, or reptiles, but of micromammals (cf. [53]), also at the Bad Wildungen-Biedensteg open sit site.

Foxes (*V. lagopus* and *V. vulpes*) might have reused the badger burrows [48]. Fox bones and skulls are typically found at those fox den sites and would explain, additionally, the presence of smaller mammal fox prey remains, especially hares and the micromammal pellets generally found at modern fox dens (cf. [48]).

Quaternary small mustelids in central Europe are rare in the fossil record outside caves (cf. [54, 55]). Their pellets can contain anure or fish bones. Frog or fish remains from Bad Wildungen seem to be partly of prey deposits of *Mustela putorius*. The small marten type is storing along small rivers or lakes, fishes, frogs, and other animals [48].

A especially high amount of frog bones must have resulted, additionally, from other large water birds and/or other predators which also left pellets and bone remains at the river and along the lake.

7.2. Hyena Population and Cannibalism. The hyena skulls from Bad Wildungen-Biedensteg are from female hyenas which are similar to many other skulls of central Europe (cf. [17]) and are anatomically interesting in their dentition (partly absence of M1), but fall into the variability of *C. c. spelaea*. A brain case, two incomplete limb bone shafts, a left radius, and a left femur are fitting for a single cub, which are very small in their proportions. They also have bite marks and must have been chewed, as compared to other cannibalistic damaged hyena long bone finds from Europeans caves (cf. [11, 22, 23, 25, 27, 56]). Their proportions fit best for a very young cub, maybe only of a few days or weeks in age, compared to the cub material from the Srbsko-Chlum-Komin Cave, Czech Republic [11]. The young hyena was possibly eaten cannibalistically, possibly by another cub, due to competition (cf. modern African hyenas in [57–59]). All bones of the Bad Wildungen hyena population and even the skulls have nibbling, chewing, and cracking marks of hyenas. The lack of the jugals and temporal parts of the skulls is the result of cracking the lower jaws from their joints, which is demonstrated for many skull finds in Europe (cf. [17]). The scavenging of their own species leaves dominantly cranial remains at not only den sites, such as the skulls, lower jaws, and teeth, but also the long bones (e.g., modern spotted hyenas, [60, 61]). Scavenging of their own is best documented in the Srbsko-Chlum-Komin Cave [11]. The dominance of cranial material at Bad Wildungen hyena den site is comparable not only to the German Perick Caves and Rösenbeck Cave and other Sauerland Karst hyena dens, but also to other caves, such as the Czech Sloup Cave, Výpustek, in the Bohemian and Moravian Karst regions [7, 17, 56]. Vertebræ and rib bones are underrepresented at most hyena den sites (especially at birthing dens and prey storage den types), the exceptions being where complete articulated skeletons are found at prey storage sites, such as were found
Table 8: Bones of *Coelodonta antiquitatis* (Blumenbach) from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 10ac      | Cranium   | Middle part with dm\(^1\)-\(^3\), M\(^1\) dentition | Early juvenile | x     | x   | Rudolf-Lorenz-Stiftung |
| 2   | 52/37     | Mandible  | Milk dentition, with dm\(^3\), M\(^1\) | Early juvenile | x | Rudolf-Lorenz-Stiftung |
| 3   | 52/38     | Mandible  | Milk dentition, with dm\(^1\)-\(^3\), M\(^1\) | Early juvenile | x | Rudolf-Lorenz-Stiftung |
| 4   | Ma 1      | Dens      | Milk tooth, upper jaw | Early juvenile | University of Marburg |
| 5   | Ma 2      | Dens      | Milk tooth, upper jaw | Early juvenile | University of Marburg |
| 6   | Ma 3      | Dens      | Milk tooth, upper jaw | Early juvenile | University of Marburg |
| 7   | Ma 4      | Dens      | P3 | Early adult | University of Marburg |
| 8   | Ma 5      | Dens      | P4 | Early adult | University of Marburg |
| 9   | Ma 6      | Dens      | M1 | Early adult | University of Marburg |
| 10  | Ma 7      | Dens      | M2 | Early adult | University of Marburg |
| 11  | Ma 8      | Dens      | M3 | Early adult | University of Marburg |
| 12  | 10l       | Scapula   | Fragment | ? Adult | x | Rudolf-Lorenz-Stiftung |
| 13  | 52/20     | Scapula   | Without distal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 14  | 52/200    | Scapula   | Incomplete | ? Adult | x | Rudolf-Lorenz-Stiftung |
| 15  | 52/88     | Scapula   | Fragment | ? Adult | Universit\(y\) of Marburg |
| 16  | 180c      | Humerus   | Incomplete | Adult | x | (Mentioned in [34], missing) |
| 17  | 10v       | Humerus   | Incomplete | Adult | x | Rudolf-Lorenz-Stiftung |
| 18  | 52/47, 42 | Ulna/radius | Shafts, articulated | Juvenile | x | Rudolf-Lorenz-Stiftung |
| 19  | 52/116, 111 | Ulna/radius | Shafts, articulated | ? Adult | x | Rudolf-Lorenz-Stiftung |
| 20  | 52/143    | Ulna      | Shaft | ? Adult | x | Rudolf-Lorenz-Stiftung |
| 21  | 10p       | Ulna      | Shaft | ? Adult | x | Rudolf-Lorenz-Stiftung |
| 22  | 52/53     | Ulna      | Shaft | Adult | x | Rudolf-Lorenz-Stiftung |
| 23  | 10a       | Ulna      | Shaft | Adult | x | Rudolf-Lorenz-Stiftung |
| 24  | 52/49     | Radius    | Without distal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 25  | 52/44     | Radius    | Shaft | Adult | x | Rudolf-Lorenz-Stiftung |
| 26  | 52/30     | Radius    | Proximal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 27  | 52/224    | Radius    | Distal joint | Early adult | x | Rudolf-Lorenz-Stiftung |
| 28  | 10a       | Radius    | Proximal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 29  | 52/235    | Intermediate | Nearly complete | Adult | x | Rudolf-Lorenz-Stiftung |
| 30  | 52/34     | Carpale 3 | Nearly complete | Adult | x | Rudolf-Lorenz-Stiftung |
| 31  | Ma 11     | Metacarpale 3 | Nearly complete | Adult | University of Marburg |
| 32  | Ma 12     | Metacarpale 3 | Nearly complete | Adult | University of Marburg |
| 33  | 52/101    | Phalanx   | Complete | Adult | | Rudolf-Lorenz-Stiftung |
| 34  | 52/43     | Femur     | Shaft | Juvenile | x | Rudolf-Lorenz-Stiftung |
| 35  | 52/153    | Femur     | Shaft, fragment | x | Rudolf-Lorenz-Stiftung |
| 36  | 10ab      | Femur     | Incomplete | Adult | x | Rudolf-Lorenz-Stiftung |
| 37  | 10ea      | Femur     | Shaft | Early adult | x | Rudolf-Lorenz-Stiftung |
| 38  | 10aya     | Femur     | Shaft | Early adult | x | Rudolf-Lorenz-Stiftung |
| 39  | 52/228    | Patella   | Complete | Adult | x | Rudolf-Lorenz-Stiftung |
| 40  | 52/7      | Tibia     | Incomplete | Adult | x | Rudolf-Lorenz-Stiftung |
| 41  | 52/201    | Tibia     | Without proximal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 42  | 10c       | Tibia     | Incomplete | Adult | x | Rudolf-Lorenz-Stiftung |
| 43  | 52/9      | Tibia     | Without proximal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 44  | 10t       | Tibia     | Without proximal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 45  | 52/4      | Fibula    | Distal joint | Adult | x | Rudolf-Lorenz-Stiftung |
| 46  | 52/16     | Fibula    | Shaft | Adult | x | Rudolf-Lorenz-Stiftung |
### Table 8: Continued.
| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 47  | 10f       | Calcaneus | Incomplete | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 48  | 10g       | Astragalus| Incomplete | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 49  | 52/140b   | Metatarsus| III, complete | x |       | Adult |            | Rudolf-Lorenz-Stiftung |
| 50  | Ma 13     | Metatarsale 2 | Proximal joint |       |       | Adult |            | University of Marburg |
| 51  | Ma 14     | Metatarsale 3 | Nearly complete |       |       | Adult |            | University of Marburg |
| 52  | Ma 15     | Metatarsale 4 | Nearly complete |       |       | Adult |            | University of Marburg |
| 53  | 52/48     | Pelvis    | Incomplete | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 54  | 52/82     | Pelvis    | Incomplete | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 55  | 52/13     | Pelvis    | Ilium, fragment | x   |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 56  | 10e       | Pelvis    | Incomplete | x    |       | Adult | x          | Rudolf-Lorenz-Stiftung |
| 57  | 52/9      | Cervical vertebra | Atlas | Early adult | x | Rudolf-Lorenz-Stiftung |
| 58  | 52/1      | Cervical vertebra | Axes | Early adult | x | Rudolf-Lorenz-Stiftung |
| 59  | 52/11     | Cervical vertebra | No. 3 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 60  | 52/18     | Cervical vertebra | No. 5 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 61  | 52/107-1  | Cervical vertebra | No. 6 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 62  | 52/107-2  | Cervical vertebra | No. 7 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 63  | 52/107-3  | Thoracic vertebra | No. 1 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 64  | 10m       | Thoracic vertebra | No. 2 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 65  | 10j       | Thoracic vertebra | No. 3 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 66  | 52/152    | Thoracic vertebra | Centrum, No. 4 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 67  | 52/108-1  | Thoracic vertebra | No. 6 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 68  | 52/108-2  | Thoracic vertebra | No. 7 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 69  | 52/108-3  | Thoracic vertebra | No. 8 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 70  | 52/108-4  | Thoracic vertebra | No. 9 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 71  | 10l       | Thoracic vertebra | No. 18 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 72  | 10h       | Lumbar vertebra | No. 1 | Early adult | x | Rudolf-Lorenz-Stiftung |
| 73  | 10r       | Lumbar vertebra | Neural arch | Early adult | x | Rudolf-Lorenz-Stiftung |
| 74  | 52/3      | Costa     | Fragment | ? | x | Rudolf-Lorenz-Stiftung |
| 75  | 52/5      | Costa     | Fragment | ? | x | Rudolf-Lorenz-Stiftung |
| 76  | 52/156    | Costa     | Fragment | Early adult | x | Rudolf-Lorenz-Stiftung |
| 77  | 52/58     | Costa     | Anterior, 2, distally incomplete | x | Early adult | Rudolf-Lorenz-Stiftung |
| 78  | 52/57     | Costa     | Middle, approx. 6 to 8 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 79  | 52/52     | Costa     | Middle, approx. 4–6 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 80  | 52/15     | Costa     | Middle, approx. 7–9 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 81  | 52/100    | Costa     | Anterior, approx. 2–3 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 82  | 52/3a     | Costa     | Anterior, approx. 3-4 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 83  | 10q       | Costa     | Anterior, approx. 4–6 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 84  | 10v       | Costa     | Anterior, approx. 3-4 | x | Early adult | Rudolf-Lorenz-Stiftung |
| 85  | 10ad      | Costa     | Posterior | x | Early adult | Rudolf-Lorenz-Stiftung |

at the Czech Výpustek Cave, Koněprusy Cave and Srbsko-Chlum-Komin Cave [9, 40].

7.3. Hyena Den Type and Recycling of Badger/Fox Dens. Hyena dens are identified starting in the Pliocene to Middle Pleistocene (e.g., [12, 62, 63]). In the Late Pleistocene the hyena den site record is much higher (e.g., [3–6, 8, 17, 64–66]) and more details about the “den type” can be studied. The large bone enrichment at Bad Wildungen was already identified as a product of the activities of C. c. spelaea [35]. The comparison of different Late Pleistocene C. c. spelaea hyena cave and open air den sites in Europe allows a classification of the den type, by separating three main age classes: (1) cubs, (2) adolescents, and (3) adult-senile individuals (Figure 15). The high presence of cubs indicates, similarly as in modern spotted hyenas [57, 67–69], birthing dens. Other
Table 9: Bones of *Bison priscus* (Bojanus 1827) from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | /         | Dens      | M1, upper jaw |      |       |     | (Mentioned in [34], missing) |            |
| 2   | /         | Dens      | M1, lower jaw |      |       |     | (Mentioned in [34], missing) |            |
| 3   | BadW-9    | Scapula   | Proximal half | Adult |       |     | Rudolf-Lorenz-Stiftung |            |
| 4   | 10af      | Metacarpus| Proximal joint | x    | Adult | x   | Rudolf-Lorenz-Stiftung |            |
| 5   | /         | Carpale 3 + 4 | | | | | (Mentioned in [34], missing) | |
| 6   | 52/205    | Femur     | Distal joint and shaft fragment | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 7   | 10o       | Femur     | Shaft | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 8   | 10k       | Femur     | Distal joint, fragment | x | Adult | x | Stadtmuseum Bad Wildungen | |
| 9   | 52/236    | Tibia     | Without proximal joint | x | Adult | x | Museum Korbach, (Stadtmuseum Bad Wildungen) | |
| 10  | 52/12     | Calcaneus | Nearly complete | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 11  | 52/17     | Thoracic vertebra | Centrum | Adult |       |     | Rudolf-Lorenz-Stiftung | |

Table 10: Bone material list of *Equus caballus przewalskii* Poljakoff 1881 from the open air prey deposit site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 52/221    | Mandibula | Nearly complete | x | Adult |     | Rudolf-Lorenz-Stiftung | |
| 2   | 52/27     | Mandibula | Anterior part, male |      | Juvenile | | Rudolf-Lorenz-Stiftung | |
| 3   | 52/203    | Cranium   | Occipital, fragment |      |       | | Rudolf-Lorenz-Stiftung | |
| 4   | 52/147    | Dens      | C, male | x | Adult | | Rudolf-Lorenz-Stiftung | |
| 5   | 52/50     | Ulna/radius | Incomplete | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 6   | 10aa      | Ulna/radius | Nearly complete | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 7   | 52/112    | Metacarpus | Nearly complete | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 8   | 52/155    | Metacarpus | Distal joint | x | Adult | | Rudolf-Lorenz-Stiftung | |
| 9   | 52/14     | Phalanx 1  | Complete | | | | Rudolf-Lorenz-Stiftung | |
| 10  | 52/78     | Phalanx 2  | Complete | | | | Rudolf-Lorenz-Stiftung | |
| 11  | 10lt      | Metatarsus | Complete | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 12  | 52/51     | Tibia     | Fragment | x | | | Rudolf-Lorenz-Stiftung | |
| 13  | 52/28     | Pelvis    | Fragment, ilium | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 14  | 10i       | Pelvis    | Fragment, ilium | x | Adult | x | Rudolf-Lorenz-Stiftung | |
| 15  | 52/131    | Cervical vertebra | Fragment, neural arch | | | | Rudolf-Lorenz-Stiftung | |
| 16  | 52/202    | Cervical vertebra | Fragment, neural arch | | | | Rudolf-Lorenz-Stiftung | |
| 17  | 10eq      | Lumbar vertebra | No. 4, without processi | Juvenile | x | | Rudolf-Lorenz-Stiftung | |
| 18  | 10ad      | Pelvis    | Sacrum, incomplete | | | | Rudolf-Lorenz-Stiftung | |
| 19  | 52/157    | Costa     | Fragment | | | | Rudolf-Lorenz-Stiftung | |

indicators for such birthing dens are “nibbling sticks.” At Bad Wildungen there are three such chewed bone fragments: one of a mammoth, whose bone fragments are found at birthing dens [70] for teething purposes of hyena cubs [7]; the other nibbling sticks are from *Coelodonta* and *Ursus* bone fragments. These birthing dens are generally recycled from medium-sized carnivore, such as porcupines, or by hyenas own excavated burrows, which can be situated nearby commuting dens (cf. modern in [71]). Bad Wildungen must have also been this type of den, where higher amounts of prey remains were accumulated, or even stored (prey storage den type). Similar large bone accumulations at commuting den sites have been reported in Africa from *C. c. crocuta* (cf. [61, 68, 71–81]).
### Table 11: Bones of *Megaloceros giganteus* (Blumenbach 1799) from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type        | Commentary                  | Left | Right | Age | Bite marks | Collection                     |
|-----|-----------|------------------|-----------------------------|------|-------|-----|------------|---------------------------------|
| 1   | /         | Mandible         | Fragment with M1–3          | x    |       |     |            | (Mentioned in [34], missing)    |
| 2   | /         | Dens             | P1, upper jaw               |      |       |     |            | (Mentioned in [34], missing)    |
| 3   | /         | Dens             | M2, upper jaw               | x    |       |     |            | (Mentioned in [34], missing)    |
| 4   | /         | Dens             | M3, upper jaw               | x    |       |     |            | (Mentioned in [34], missing)    |
| 5   | /         | Cervical vertebra| Atlas                       |      |       |     |            | (Mentioned in [34], missing)    |
| 6   | /         | Cervical vertebra| Axes                        |      |       |     |            | (Mentioned in [34], missing)    |
| 7   | 52/32     | Tibia            | Distal joint                | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |

### Table 12: Bones of *Rangifer tarandus* Linné 1758 from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type         | Commentary                  | Left | Right | Age | Bite marks | Collection                     |
|-----|-----------|-------------------|-----------------------------|------|-------|-----|------------|---------------------------------|
| 1   | /         | Dens              | —                           |      |       |     |            | (Mentioned in [34], missing)    |
| 2   | /         | Dens              | —                           |      |       |     |            | (Mentioned in [34], missing)    |
| 3   | 52/40     | Antler            | Dropped antler with base, fragment | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |
| 4   | 52/41     | Antler            | Dropped antler with base, fragment | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |
| 5   | 52/33     | Antler            | Dropped antler with base, fragment | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |
| 6   | 52/132    | Scapula           | Incomplete                  | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |
| 7   | 52/126    | Scapula           | Incomplete                  | x    | Adult | x    | Rudolf-Lorenz-Stiftung          |
| 8   | 52/115-1  | Ulna              | Proximal joint              |       |       |     | Rudolf-Lorenz-Stiftung          |
| 9   | 52/115-3  | Radius            | Distal joint                | x    | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 10  | 52/115-4  | Radiale           | Complete                    | x    | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 11  | 52/115-5  | Intermedium       | Complete                    | x    | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 12  | 52/115-8  | Carpalx           | Complete                    | x    | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 13  | 52/115-7  | Carpalx 4         | Complete                    | x    | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 14  | 52/117    | Metacarpus        | Distal joint                |       | Juvenile |    | Rudolf-Lorenz-Stiftung          |
| 15  | 52/52     | Pelvis            | Acetabulum, fragment        |       | Adult  |     | Rudolf-Lorenz-Stiftung          |
| 16  | 52/57     | Pelvis            | Acetabulum, fragment        |       | Adult  |     | Rudolf-Lorenz-Stiftung          |
| 17  | 52/115-2  | Phalanx 1         | Without proximal joint, forelimb | Juvenile |         | Rudolf-Lorenz-Stiftung          |
| 18  | 52/115-6  | Phalanx 2         | Proximal joint, forelimb    | Juvenile |         | Rudolf-Lorenz-Stiftung          |
| 19  | 52/74     | Tibia             | Fragment, distal            | Juvenile |         | Rudolf-Lorenz-Stiftung          |
| 20  | 52/151    | Tibia             | Nearly complete             | x    | Adult  | x    | Rudolf-Lorenz-Stiftung          |
| 21  | 52/10     | Tibia             | Without proximal joint      | x    | Adult  | x    | Rudolf-Lorenz-Stiftung          |
| 22  | 10lz      | Phalanx 1         | Without proximal joint, hind limb | Juvenile |     | Rudolf-Lorenz-Stiftung          |
| 23  | 52/246    | Phalanx 1         | Without proximal joint, hind limb | Juvenile |     | Rudolf-Lorenz-Stiftung          |
| 24  | 4.4/54    | Phalanx 1         | Complete                    |         | Adult  |     | Rudolf-Lorenz-Stiftung          |

7.4. *Hyena Den Marking*. In most cases, pellets of the Late Pleistocene spotted hyenas have repeating shapes, which were found recently at several reported den sites [3, 5–7, 11, 22, 41, 82]. Exact documented excrement markings on a gypsum karst open air den were recently published at the site Westeregeln, Central Germany [9]. A first terminology was published for the pellet shape types [44]. The hyena pellets from Bad Wildungen fall within the hyena pellet shape types. Several smaller pellets are attached to each other, forming spindle-like, or irregular accumulated aggregations, similar to modern African spotted hyena excrements [9]. Modern spotted hyenas are using faecal pellets to mark their territory, especially their den sites [83]. The Ice Age spotted hyenas must have done the same. Well documented examples are found in Germany at two open air sites: Bad Wildungen-Biedensteg [35] and the gypsum karst site Morschen-Konnefeld [84]. Similar abundant pellets are found in caves of France [6] and Czech Republic [5].

7.5. Bone Assemblage and Fauna Statistics. The high amount (10%) of hyena bone remains is typical for Late Pleistocene hyena dens (e.g., [8, 11, 65, 66]). A high percentage of hyena prey bone remains at the site Bad Wildungen-Biedensteg (Figure 16) do not represent the real percentages of the prey. It is more demonstrated, for example, at other hyena open air sites, as a result of taphonomy and selection [9]. The bones of the woolly rhinoceros are extremely massive, and, in contrast to nearly all other large
mammal bones, completely filled with the spongiosa. The long bones were difficult or impossible to crack and hyenas always left, in a last stage (stage 3), the bone shaft of long bones or massive bones which are classified in three damage stages [10]. The open air site Bad Wildungen-Biedensteg has delivered only a very few mammoth bones (2% of the prey bones) which are typical at middle high mountainous hyena dens of Europe, where mammoths seem to have been absent or rare [7]. Hyenas specialized there on cave bear scavenging ([42], Figure 16). The amount of Przewalski horse remains (8%) is as usual high. In most open air sites and middle mountainous elevated European caves the small Przewalski horse is the main or second dominant prey (up to 50%; [7, 9–11, 18, 37, 40–44]). If all the small carnivores are excluded from the statistics, then the horse remains represent the second largest prey (cf. [85]). Bones of those horses are recorded with small proportioned forms (see metapod discussion) attributed to E. c. przewalskii in Germany or Czech Republic at other hyena den sites of early to middle Late Pleistocene age [7, 85]. Late Palaeolithic archaeological sites have the youngest records from the Late Magdalenian [86] or Epipalaeolithic/Early Mesolithic [87]. Finally, trackways have been described from the German Volcanic ashes of the Laacher Volcano to be of Przewalski horse origin [37, 88]. Additionally, archaeologists have discussed intensive horse figurations in cave and mobile

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 10ep      | Cranium   | Maxillar, with M1-2 | x    |       | Juvenile | Rudolf-Lorenz-Stiftung |
| 2   | 52-113-1  | Metatarsus | Without distal joint | x    |       | Juvenile | Rudolf-Lorenz-Stiftung |

Table 13: Bones of *Cervus elaphus* Linné 1758 from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

| No. | Coll.-No. | Bone type | Commentary | Left | Right | Age | Bite marks | Collection |
|-----|-----------|-----------|------------|------|-------|-----|------------|------------|
| 1   | 98        | Cranium   | Brain case, frontals, parietals, incomplete | Adult |       |       | University Marburg |
| 2   | 14        | Cranium   | Maxillar | x    |       | Adult | University Marburg |
| 3   | 63h       | Cranium   | Maxillar | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 4   | 12        | Mandibula | Incomplete | x    |       | Adult | University Marburg |
| 5   | 11        | Mandibula | Incomplete | x    | Juvenile | University Marburg |
| 6   | 63g       | Humerus   | Half, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 7   | 63f       | Radius    | Half, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 8   | 15        | Radius/ulna | Without joints | x    |       | Adult | University Marburg |
| 9   | 63b       | Femur     | Distal joint incomplete, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 10  | 63c       | Femur     | Half without distal joint, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 11  | 10        | Femur     | Without joints | x    | Juvenile | University Marburg |
| 12  | 63d       | Tibia     | Proximal joint incomplete, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 13  | 9         | Tibia     | Without proximal joint | x    | Juvenile | University Marburg |
| 14  | 13        | Tibia     | Without middle shaft | x    |       | Adult | University Marburg |
| 15  | 63e       | Pes       | Nearly complete articulated, from skeleton | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 16  | 52-105c   | Calcaneus | Complete | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 17  | 3         | Pelvis    | Fragment, acetabulum | x    |       | Adult | University Marburg |
| 18  | 5         | Pelvis    | Fragment, acetabulum | x    |       | Adult | University Marburg |
| 19  | 52/10     | Femur     | Incomplete | x    | Juvenile | University Marburg |
| 20  | 52/248    | Lumbar vertebra | Incomplete | Juvenile | University Marburg |
| 21  | 63a       | Pelvis and lumbalvertebra | Articulated from skeleton | Adult |       | Rudolf-Lorenz-Stiftung |
| 22  | 52/249    | Calcaneus | Incomplete | x    | Juvenile | Rudolf-Lorenz-Stiftung |
| 23  | 52/252    | Pes       | Incomplete, articulated | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 24  | 52/253    | Metatarsus IV | Complete | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 25  | 52/254    | Astragalus | Complete | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 26  | 52/251    | Metacarpus | 3 incomplete | Juvenile | Rudolf-Lorenz-Stiftung |
| 27  | 52/256    | Ulnar     | 2 complete | x    |       | Adult | Rudolf-Lorenz-Stiftung |
| 28  | 52/255    | Tarsalia  | 2 complete | x    |       | Adult | Rudolf-Lorenz-Stiftung |

Table 14: Bones of *Lepus* sp. from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).
7.6. Woolly Rhinoceros as Main Prey for Hyenas. Most remains are from the woolly rhinoceros (32%), which corresponds well to several other northern Germany open air hyena den sites, such as Bottrop, Westeregeln, or cave sites on the mountain slope regions, such as Hohle Stein Cave or Teufelskammer Cave ([9, 10, 22, 82], Figure 16). All bones have medium to massive nibbling, chewing, and gnawing marks, mainly produced by the Ice Age spotted hyenas, as compared to other den sites [10, 91] and modern spotted hyenas [92, 93]. Scratches deep into the spongiosa of the joints are very typical of hyena origin and can be found at many other European open air and cave sites (e.g., [11, 21–23, 25, 29, 40, 41, 82, 94, 95]). The material from Bad Wildungen consists of a few cranial and mainly postcranial bones of at least five woolly rhinoceros individuals. Remains of a young, less than one-year-old calf, a young adult female, and a few remains of a male adult skeleton can be distinguished (Figure 5(b)). Besides those, mainly forelimb bones from some other rhinoceros individuals were found. A comparison to a normal bone proportion relation analyses [10] to the material from Bottrop open air site (Figure 5(a)) shows differences mainly in the thoracic (vertebrae, costae) presence. In Bad Wildungen, those thoracic elements are more abundant, similar to those found on nonscavenged skeletons like the Petershagen skeleton [90], which indicates the scavenging of a carcass very nearby the den.

The presence of a carcass is also demonstrated by the articulated vertebral column (Figure 5(b)). To this, most probably, other elements belong. An originally articulated right hind limb (femur and tibia, astragalus, and calcaneus) or forelimb bones, such an ulna and radius, support the original presence of one animal carcass which was decomposed in parts. Such decompositions could have taken days, such as what is known for Late Pleistocene elephant carcasses [43]. The carcass of the most probable female C. antiquitatis must have laid on the right side of her body during main carcass feeding activities, because more bones from that side are preserved. The skull is lacking, but it seems as if all isolated teeth found from the lower jaw indicate the complete destruction of the mandibles by the hyenas. Isolated teeth of woolly rhinoceros are typically at hyena den sites (e.g., [10]).
Figure 16: (a) Late Pleistocene spotted hyena sites and dens and woolly rhinoceros remains in NW-Germany. (b) "Cross-section" through the mountain boreal forest cave bear dominated bone assemblages to the mammoth steppe lowland faunal assemblages (composed after [9, 10, 22, 82, 90] and new results).
Maybe the skull was cut off by the hyenas or at least destroyed. A few ribs were only cracked, and nearly all are lacking their joints. The long bone joints were not chewed off completely, because of their articulation. This indicates a fresh carcass that was not completely used by the hyenas and was left in an intermediate stage of carcass destruction (cf. Figure 5(a)). After the bone destruction stages, those are in stage 2 sensu Diedrich [10]. The spogiosa remains of woolly rhinoceroses were quite often found in the hyena coprolites at the Bad Wildungen-Biedensteg site [35]. The brain case opening of a calf is similarly figured as an adolescent rhinoceros skull from Selm-Ternsche [10], as figured from rhinoceros skull damages from other sites [96].

The finds of juveniles, such as the few-weeks-old rhinoceroses (Figures 5(b) and 6), hyena, or the neonate cave bear, fit for the hunting and main activity time of the hyenas at Biedensteg in the late spring and early summer. Other remains of at least four more rhinoceros individuals and other prey remains were imported, possibly from the Ice Ages spotted hyenas.

7.7. Hyenas as Cave Bear Scavengers. The cave bear bones might belong to one skeleton of a mature female cave bear [35]. The small diameter, 75 mm, of the scapula glenoid fits for cave bears of the smaller subspecies *U. spelaeus* subsp. of the early/middle Late Pleistocene, compared, for example, to the cave bear population of the Perick Caves in the Sauerland Karst (Figure 1; [97]) or the newer studied cave bear populations and subspecies of the Rübeland Caves [98]. Also, the other bones and femur fragments were compared to some hundred bones from the Perick and Rübeland Caves, all having again smaller proportions, excluding a *U. ingressus* cave bear type of the latest Late Pleistocene. Finally, similarly as figured with the “nibbling stick” in the Perick Caves, some cave bear femora and other bone fragment nibbling sticks are present [70], which only hyenas must have produced by teething cubs (cf. [7]). A scavenging of a cave bear carcass outside a cave is the only clear report of such a scenario [97], but is not exceptional, if compared to the hunting/feeding strategies of the Late Pleistocene spotted hyenas. It is now well known that they scavenged cave bear carcasses in the mountain regions of Europe, such as the Sauerland Caves, the Perick Caves, and Rübeland Caves, and additionally several other cave bear dens all over Europe [42, 70, 98, 99].

7.8. Fauna Biodiversity and Climatic Mammoth Steppe Indicators. The faunal statistics demonstrate (Figure 16(b)) that most megafauna bones from Bad Wildungen are related to be of hyena prey origin. Those represent a mammoth steppe megafauna with *Coelodonta antiquitatis* (cf. [29]). *Mammuthus primigenius*, *Bison/Bos*, *Megaloceros giganteus*, *Cervus elaphus*, *Rangifer tarandus*, *Equus caballus przewalskii*, and boreal mountain forest fauna of *Ursus spelaeus* subsp. (cf. [35]). Additionally, the pellets include many mammoth steppe environment rodents such as *Lemmus lemmus*, *Dicrostonyx henseli*, *Microtus gregalis*, or *Allactaga siliens* (cf. [33, 34, 100]). Represented are in higher amounts furthermore birds such as *Lagopus lagopus* and other species (cf. [34]).

8. Conclusion

The open air hyena den site Bad Wildungen-Biedensteg (NW-Germany) must have been located at the margin of an ancient small lake and the Wilde River in a mammoth steppe landscape on the eastern slopes of the Sauerland Mountains during the early to middle glaciation (early late Pleistocene or Weichselian, about “65.000–90.000 BP”, MIS 5c-d). This shallow lake margin, or at least muddy area, was in the center of a large sinkhole structure, which was caused by subsurface dissolution of Zechstein salt in the underground. The sinkhole received freshwater influence by the early Wilde River, indicated by especially freshwater fish remains, but also some other water related animals such as frogs, which were found accumulated in many pellets. Those are excrements of red/arctic foxes, steppe ilits and large carnivore water birds, or owls. Nearby, a badger/fox burrow area in loess deposits must have been present, where their bone remains and those of their prey (mainly hare, and micromammals) were accumulated, also in pellets. With Biedensteg, an open air hyena birthing and overlapping communal den with prey deposit can be presented with probably reused badger/red fox burrows for the natal den function. 10% of the NISP are *Crocuta crocuta spelaea* remains, including three grown-up animal skulls, and cranial and postcranial remains of a young cub. Abundant are hyena coprolites (mainly encrusted by caliche), which contain fragments of bones, and most probably quite abundant bone spogiosa fragments from woolly rhinoceroses bones. This corresponds to the main hyena prey *Coelodonta antiquitatis* (NISP = 32%). Another main prey is the horse *Equus caballus przewalskii* (8%). This dominance of woolly rhinoceros/horses in the Late Pleistocene bone assemblages in northern Europe was caused solely by those large carnivores and is typical of many hyena open air and cave den bone accumulation sites in northern Germany and Czech Republic (central Europe).

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