Hindawi Publishing Corporation
Journal of Geological Research
Volume 2013, Article ID 190795, 31 pages
http://dx.doi.org/10.1155/2013/190795

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

Cajus Diedrich

PaleoLogic Private Research Institute, Petra Bezruce 96, 26751 Zdice, Czech Republic

Correspondence should be addressed to Cajus Diedrich; cdiedri@gmx.net

Received 15 September 2012; Accepted 27 January 2013

Academic Editor: Atle Nesje

The Late Pleistocene (MIS 5c-d) Ice Age 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 cave 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 Moustérien: [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 paleontologist/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 micromammals. 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. Bi-52/1-237) and was partly presented in the "Stadtmuseum 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 "Kurmuseum 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 Eiszeithalle 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, lydite, quartz, or diabase pebbles. These deposits are overlain by a palaeosoil resulting from solifluction. In this "Eemian 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 palaeosoil 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

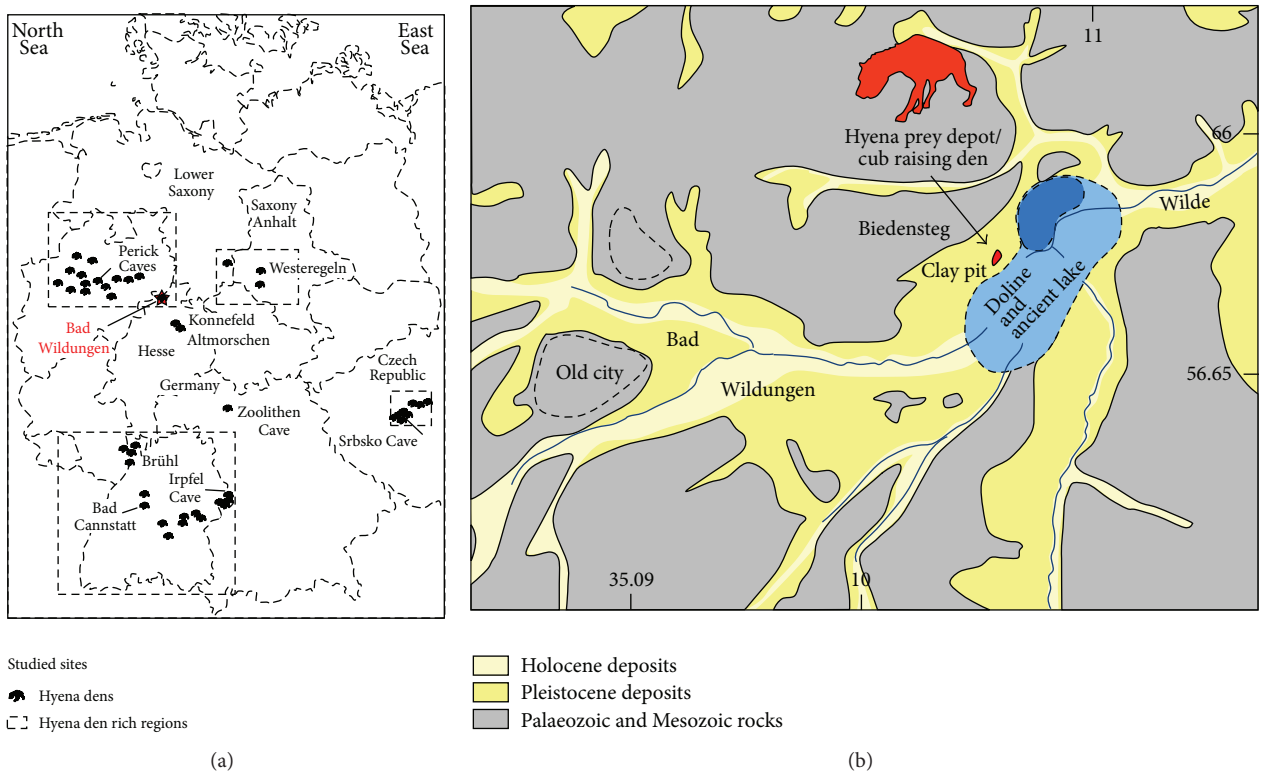


Figure 1: (a) Topographic position of the Ice Age spotted hyena *Crocuta crocuta spelaea* birth and commuting den site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (b) The prey was deposited at the margin of an ancient small lake and muddy area of the Pre-Wilde River that filled up a doline during the Late Pleistocene. (c) Generalized section at the Ice Age spotted hyena *C. c. spelaea* prey deposit site Biedensteg (Bad Wildungen, Hesse, NW-Germany).

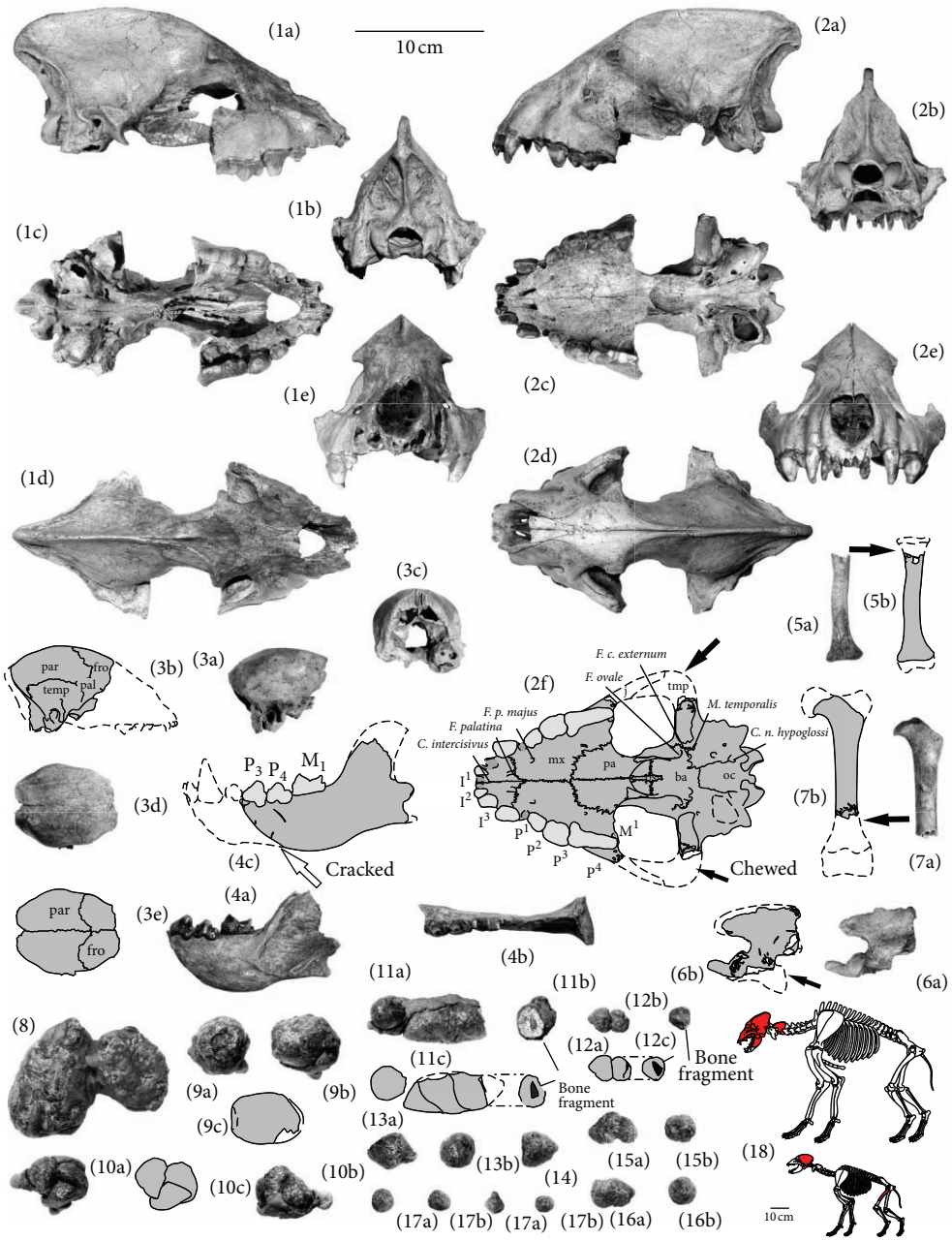


Figure 2: Remains of the Ice Age spotted hyena *Crocuta crocuta spelaea* from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) High adult female deformed skull (no. Bi-10at), (a) lateral, occipital, (c) ventral, (d) dorsal, (e) frontal. (2) Early adult female skull (no. Bi-52/45), (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), craniolateral. (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 Jacobshagen 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 palaeosoil, 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 1(c)).

4. Small Carnivore Fox Den and Mustelid Bone Assemblage

Meles meles (Linné 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 (Linné 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 (Linné 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 Linné 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 1). 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 P^4 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 P_2 and P_3; the $P_{3\text{-}4}$ and M_1 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)).

Table 1: Bones of *Crocuta crocuta spelaea* (Goldfuss 1823) from the open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

No.	Coll.-No.	Bone type	Commentary	Left	Right	Age	Bite marks	Collection
1	52/45	Skull	Nearly complete, female			Early adult	x	Rudolf-Lorenz-Stiftung
2	10at	Skull	Nearly complete, female			High adult	x	Rudolf-Lorenz-Stiftung
3	/	Skull	—			?		(Mentioned in [34], missing)
4	10ev	Skull	Brain case			Cub	x	Rudolf-Lorenz-Stiftung
5	52/51	Mandibula	—	x		Early adult	x	Rudolf-Lorenz-Stiftung
6	?	Mandibula	—			?		(Mentioned in [34], missing)
7	?	Mandibula	—			?		(Mentioned in [34], missing)
8	52/234	Cervical vertebra	Axes			Adult	x	Rudolf-Lorenz-Stiftung
9	10ew	Radius	Without joints	x		Cub	x	Rudolf-Lorenz-Stiftung
10	52/249	Thoracic vertebra	Disc			Cub		Rudolf-Lorenz-Stiftung
11	10em	Femur	Without joints	x		Cub	x	Rudolf-Lorenz-Stiftung
12	52/209	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
13	52/220	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
14	52/207	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
15	52/210	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
16	52/212	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
17	52/206	Coprolite	Single pellet, with prey bone fragment					Rudolf-Lorenz-Stiftung
18	52/218	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
19	52/226	Coprolite	Single pellet, with prey bone fragment					Rudolf-Lorenz-Stiftung
20	52/208	Coprolite	Single pellet, with prey bone fragment					Rudolf-Lorenz-Stiftung
21	52/225	Coprolite	Single pellet, with prey bone fragment					Rudolf-Lorenz-Stiftung
22	52/211	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung
23	52/214	Coprolite	Three articulated pellets					Rudolf-Lorenz-Stiftung
24	52/213	Coprolite	Single large pellet					Rudolf-Lorenz-Stiftung
25	52/219	Coprolite	Two articulated pellets, with prey bone fragment					Rudolf-Lorenz-Stiftung
26	52/221	Coprolite	Two large articulated pellets					Rudolf-Lorenz-Stiftung
27	52/237	Coprolite	Single pellet					Rudolf-Lorenz-Stiftung

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 dissolute. These spongiosa pieces are most comparable to the bone spongiosa of the woolly rhinoceros, but might also refer to other megamammals.

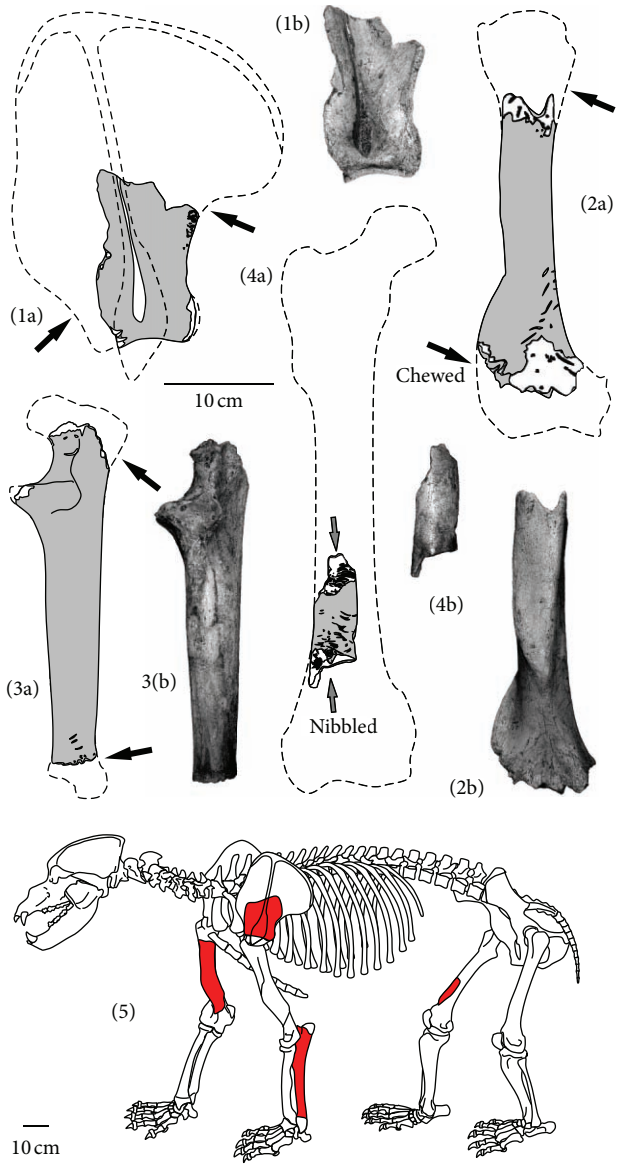


Figure 3: *Ursus spelaeus* subsp. bones from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). The bones seem to belong to one adult female individual. (1) Left scapula fragment (no. Bi-52/227), lateral. (2) Right humerus shaft (no. Bi-52/2), cranial. (3) Left ulna shaft (no. Bi-52/241), lateral. (4) Right femora shaft fragment and "nibbling stick" (no. Bi-52/242), cranial. (5) Present bones (red) of an adult female *Ursus* cf. *spelaeus* Rosenmüller, 1794, from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany).

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).

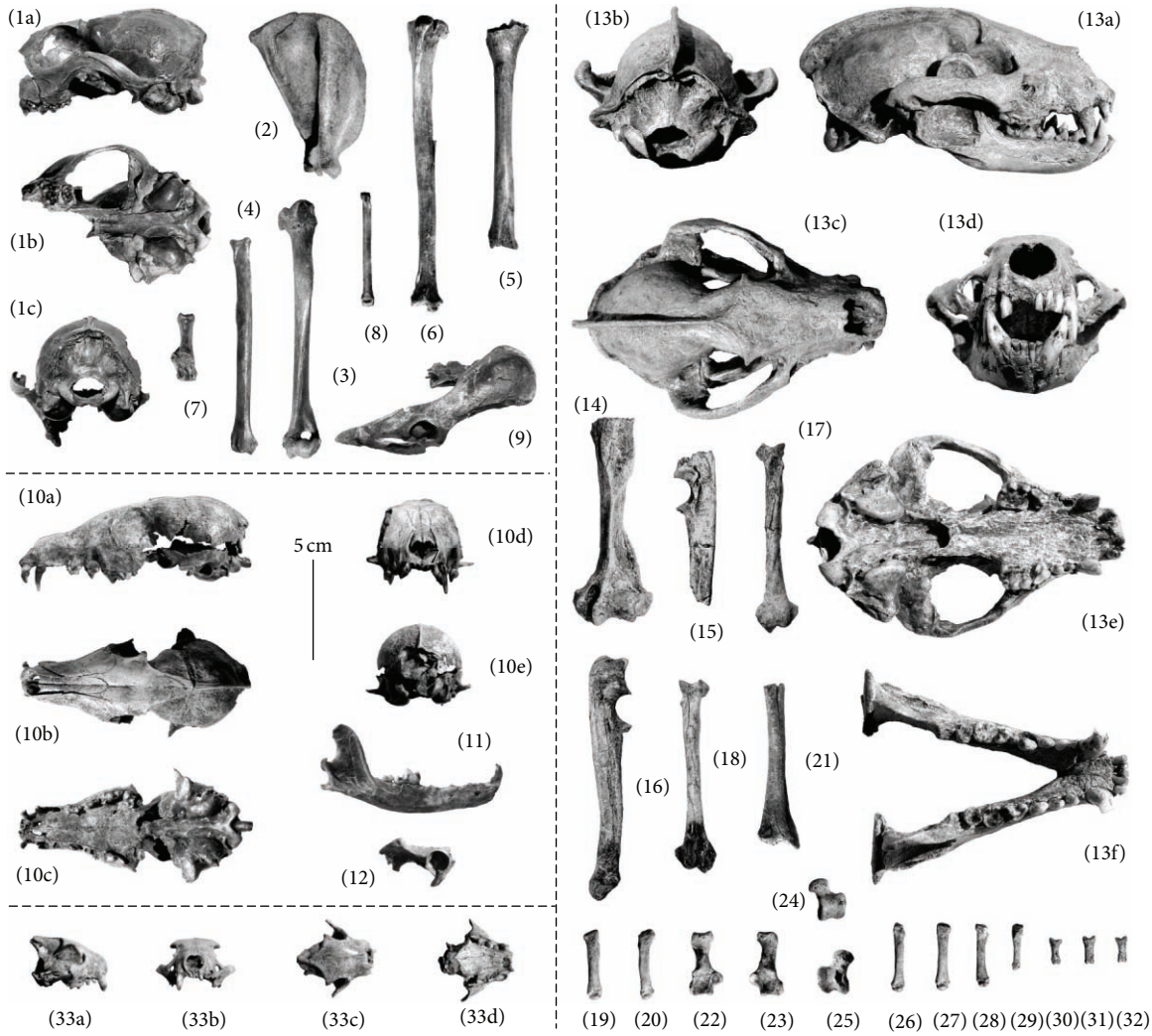


Figure 4: Small carnivores from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1)–(9) *Vulpes vulpes*: (1) incomplete skull (no. Bi-52/39), (a) lateral, (b) caudal, (c) ventral. (2) Right scapula (no. Bi-52/235), lateral. (3) Right humerus (no. Bi-52/10), cranial. (4) Right radius (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) Rigth astragal (no. Bi- BadW-2), dorsal. (25) Left astragal (no. Bi-10ay), dorsal. (26) Rigth mt IV (no. Bi- BadW-5), dorsal. (27) Rigth mt I (no. Bi- BadW-8), dorsal. (30) Phalanx II (no. BadW-2), dorsal. (31) Phalanx II (no. BadW-3), dorsal. (32) Phalanx II(no. 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

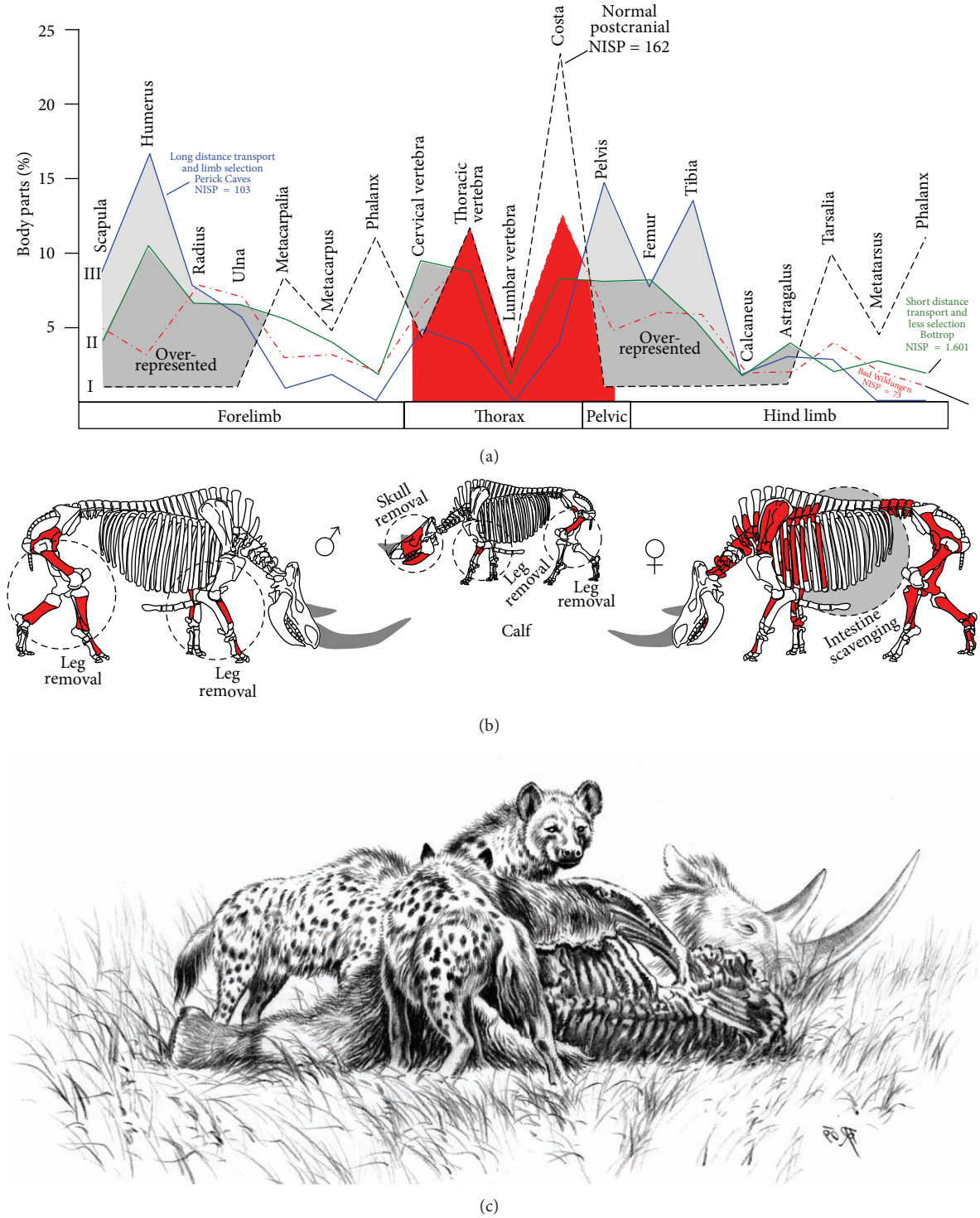


FIGURE 5: Present bone material of one (or several) male, a female skeleton remain, and calf skeleton remain of the woolly rhinoceros *Coelodonta antiquitatis* from Bad Wildungen-Biedensteg (Hesse, NW-Germany) open air hyena den.

The connection in-between the maxillas were restored in former times. Originally, the maxillary part between the teeth was damaged by hyenas. All three dm^{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

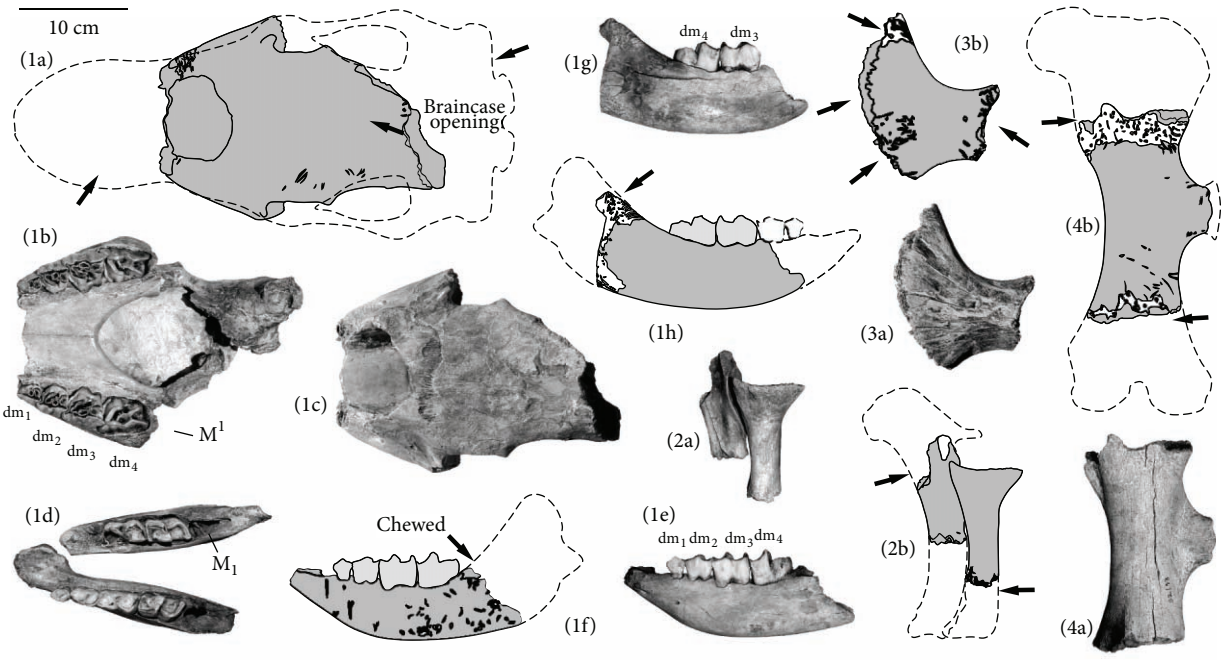


Figure 6: *Coelodonta antiquitatis* remains of a less than half-year-old calf with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Skull with brain case opening (no. Bi-10ac), (a) and (c) dorsal, (b) ventral, (d) lower jaw (no. Bi-52/37 and 38), dorsal, (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		x	Adult		Rudolf-Lorenz-Stiftung
4	52/24	Radius	Complete		x	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		x	Adult		Rudolf-Lorenz-Stiftung
10	52/239	Metatarsus III	Complete		x	Adult		University of Marburg
11	52/240	Metatarsus	Without proximal joint			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(1e)–(1h)) 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(1e)–(1h)). 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

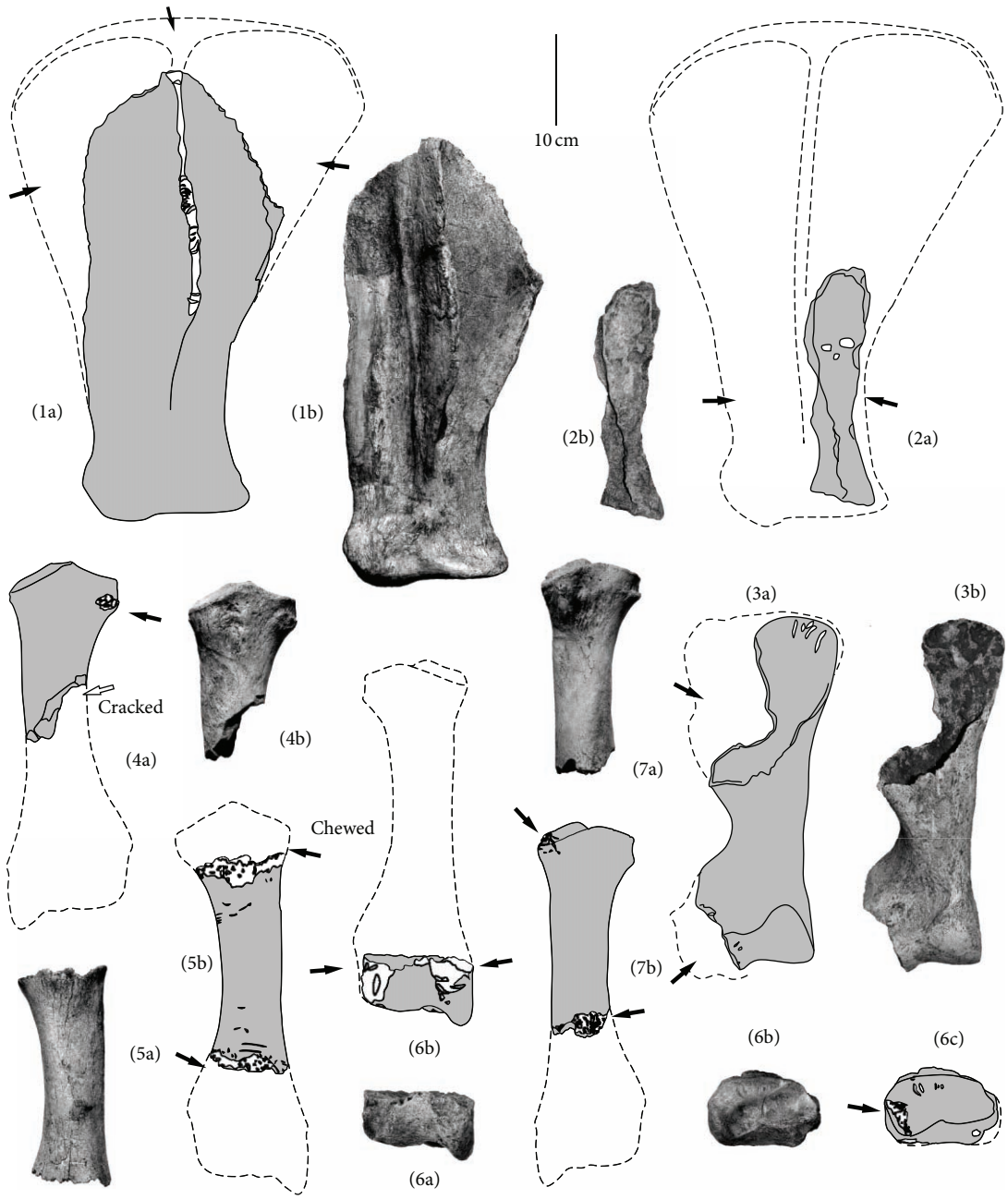


Figure 7: *Coelodonta antiquitatis* fore leg remains of adolescent and grown up animals with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left scapula from an adult individual (no. Bi-52/20), lateral. (2) Scapula fragment (no. Bi-52/88), lateral. (3) Rigth 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		Stadtmuseum Bad Wildungen
2	52/243	Mandibula	Fragment with P4	x		Adult		University of Marburg
3	10eh	Femur	Shaft	x				Stadtmuseum Bad Wildungen
4	10bn	Pelvis	Fragment, acetabulum	x		Adult		Stadtmuseum Bad Wildungen

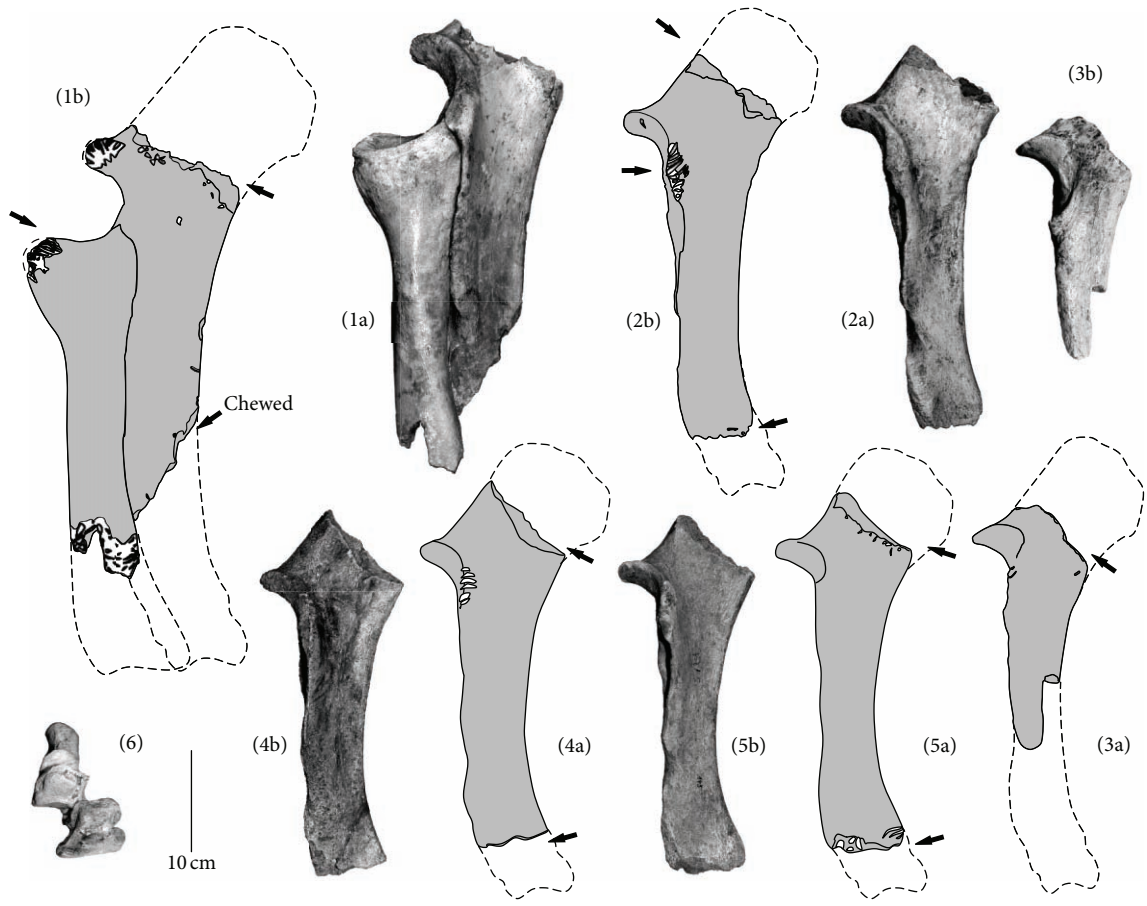


Figure 8: *Coelodonta antiquitatis* fore leg remains of grown up animals with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Articulated right ulna and radius from an early adult female individual (no. Bi-52/111 and 116), lateral. (2) Right ulna from an adult female individual (no. Bi-52/53), lateral. (3) Right ulna from an early adult female individual (no. Bi-10a), lateral. (4) Right ulna from an adolescent/adult individual (no. 10p), lateral. (5) Right ulna from an adolescent/adult female individual (no. 52/143), lateral. (6) Articulated intermedium and carpale 3 from an adult individual (no. Bi-52/34 and 235), cranial.

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 groves were left, which is documented at all three tibiae (Figure 11(3)–(5)). Two fibula

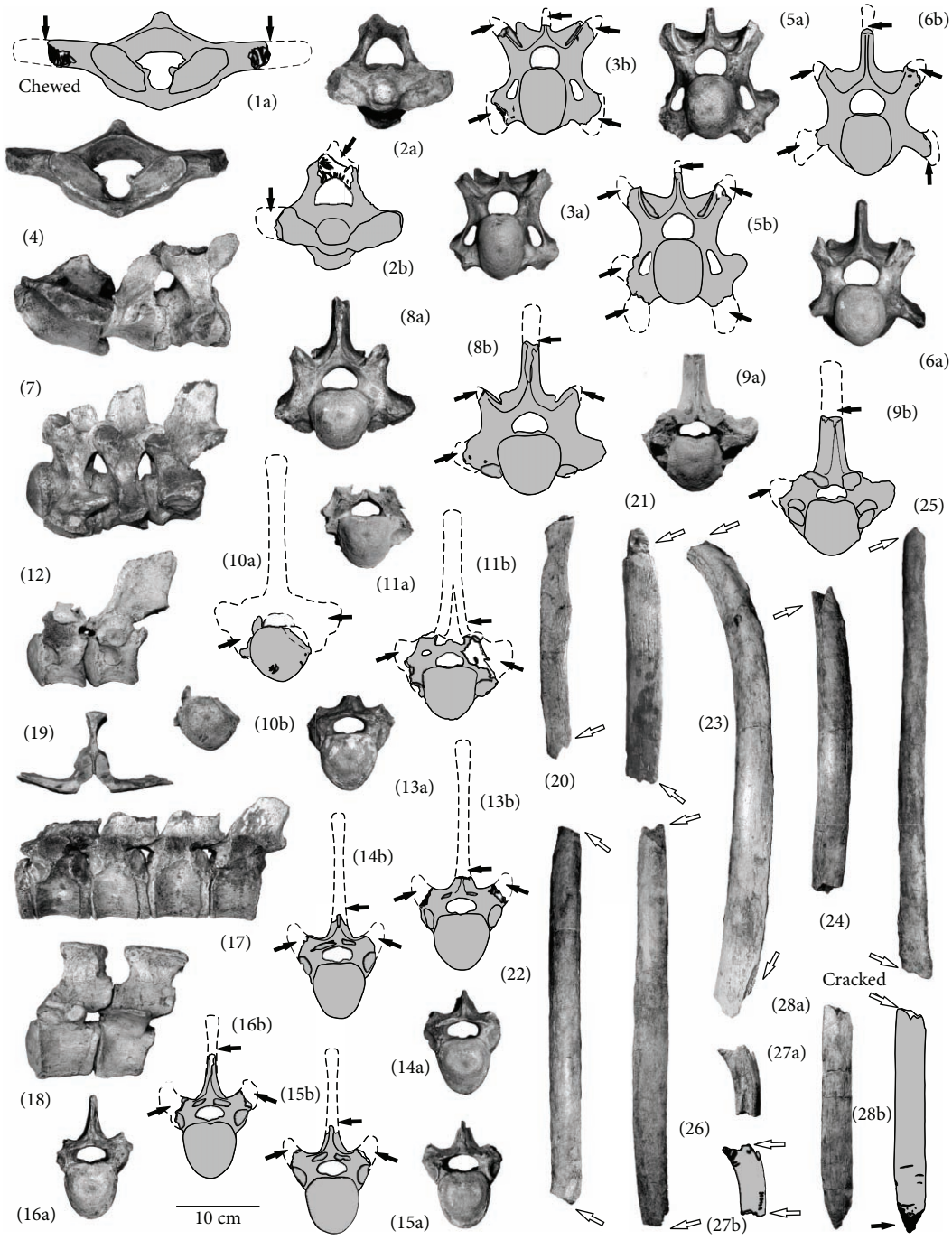


Figure 9: *Coelodonta antiquitatis* thoracic remains, all of which are most probably from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) First cervical vertebra (atlas) (no. Bi-52/9), caudal. (2) Second cervical vertebra (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-52/10j 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-52/52). (23) Anterior left costa fragment (no. Bi-10q). (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.

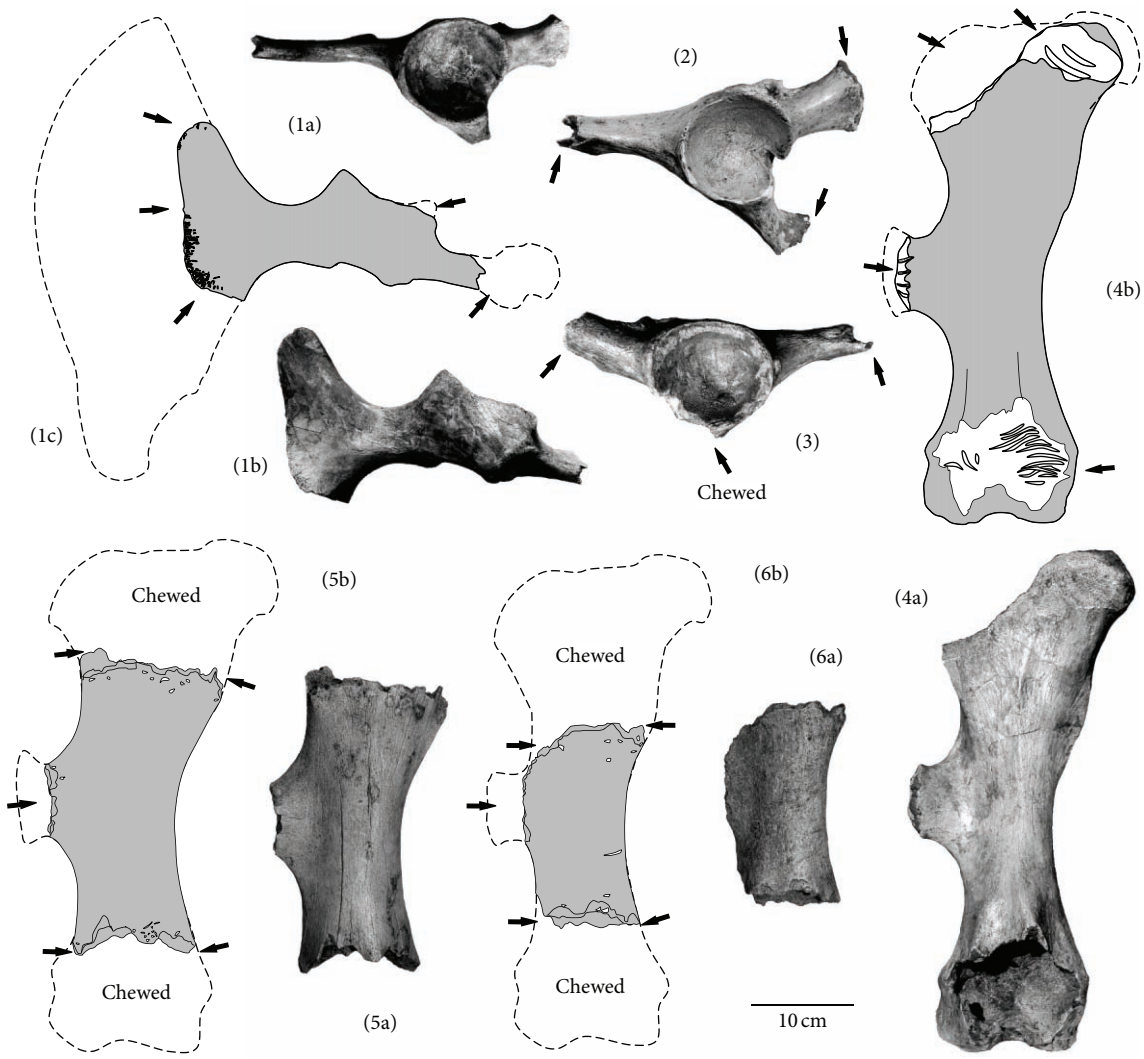


Figure 10: *Coelodonta antiquitatis* thoracic remains partly from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left pelvic acetabulum of an early adult to adult individual (no. Bi-52/48), (b) acetabular, (c) lateral. (2) Right pelvic ileum and acetabulum of an adult individual (no. Bi-52/82), acetabular. (3) Left pelvic ileum remain of an adult individual (no. Bi-52/10e), acetabular. (4) Right femur from an early adult to adult animal (no. Bi-10ab), cranial. (5) Left femur shaft of a grown-up animal (no. Bi-10aya), cranial. (6) Left femur shaft of an adolescent animal (no. Bi-10ea), 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 vertebrae which are heavily chewed (Figure 9(12)). The fourth thoracic vertebra (Figure 9(10))

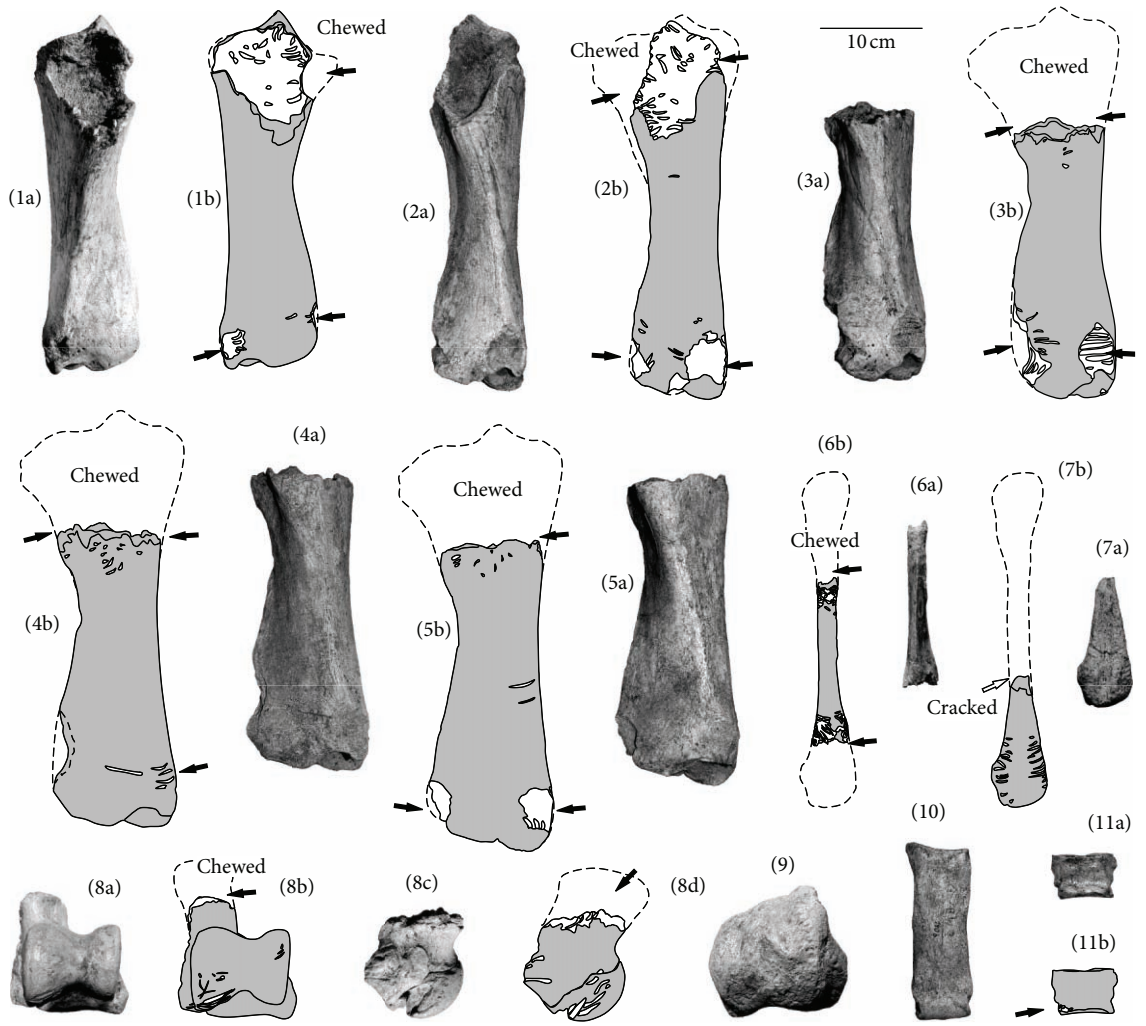


Figure 11: *Coelodonta antiquitatis* hind limb remains partly from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left tibia of a female individual (no. Bi-10c), cranial. (2) Right tibia from a female individual (no. 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

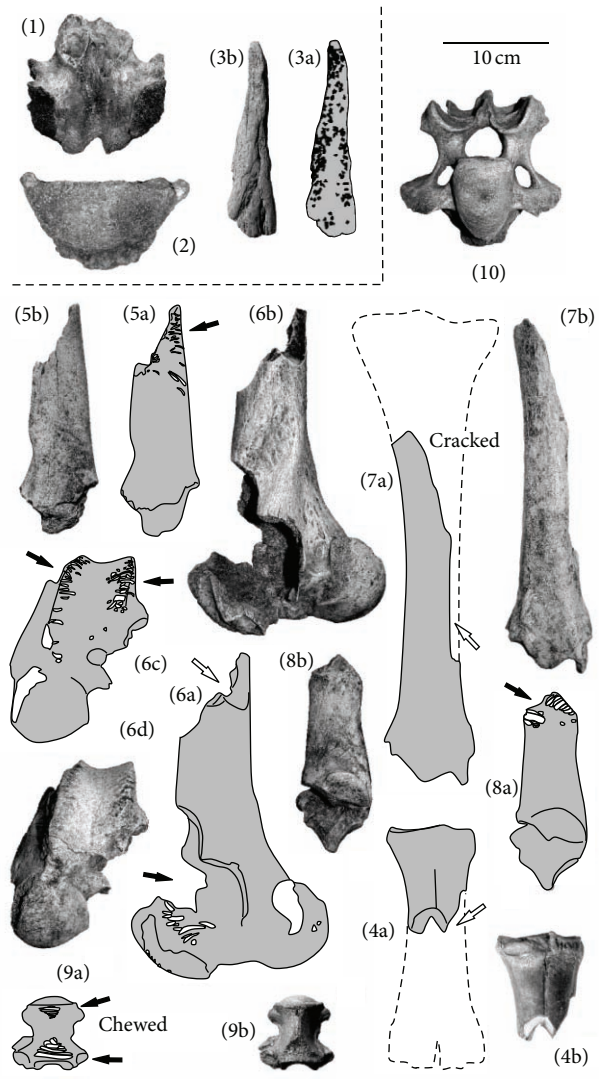


Figure 12: Elephant and bison/bos remains of adult animals from the hyena open air prey deposit site Bad Wildungen-Biedensteg near Hesse (NW-Germany). (a) Redrawing, (b) photo. (1)–(3) *Mammuthus primigenius*. (1) Dorsal vertebra neural arch (no. Bi-52/116), ventral. (2) Thoracic vertebra centrum (no. Bi-52/149), cranial. (3) Long bone fragment nibbling stick (no. Bi-52/222). (4)–(10) *Bos/Bison*. (4) Left metacarpal (no. Bi-10af), cranial. (5) Right femur shaft (no. Bi-10o), lateral. (6) Left distal femur (no. Bi-52/205), lateral, ventral. (7) Right tibia (no. Bi-52/236), cranial. (8) Right calcaneus (no. Bi-52/12), lateral. (9) Thoracic vertebra centrum (no. Bi-52/17), ventral. (10) Middle cervical vertebra (no. Bi without no.).

and one proximally chewed calcaneus (Figure 12(8)) and two femur fragments seem to originate of the rigth 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 $M^{1\text{-}2}$ 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

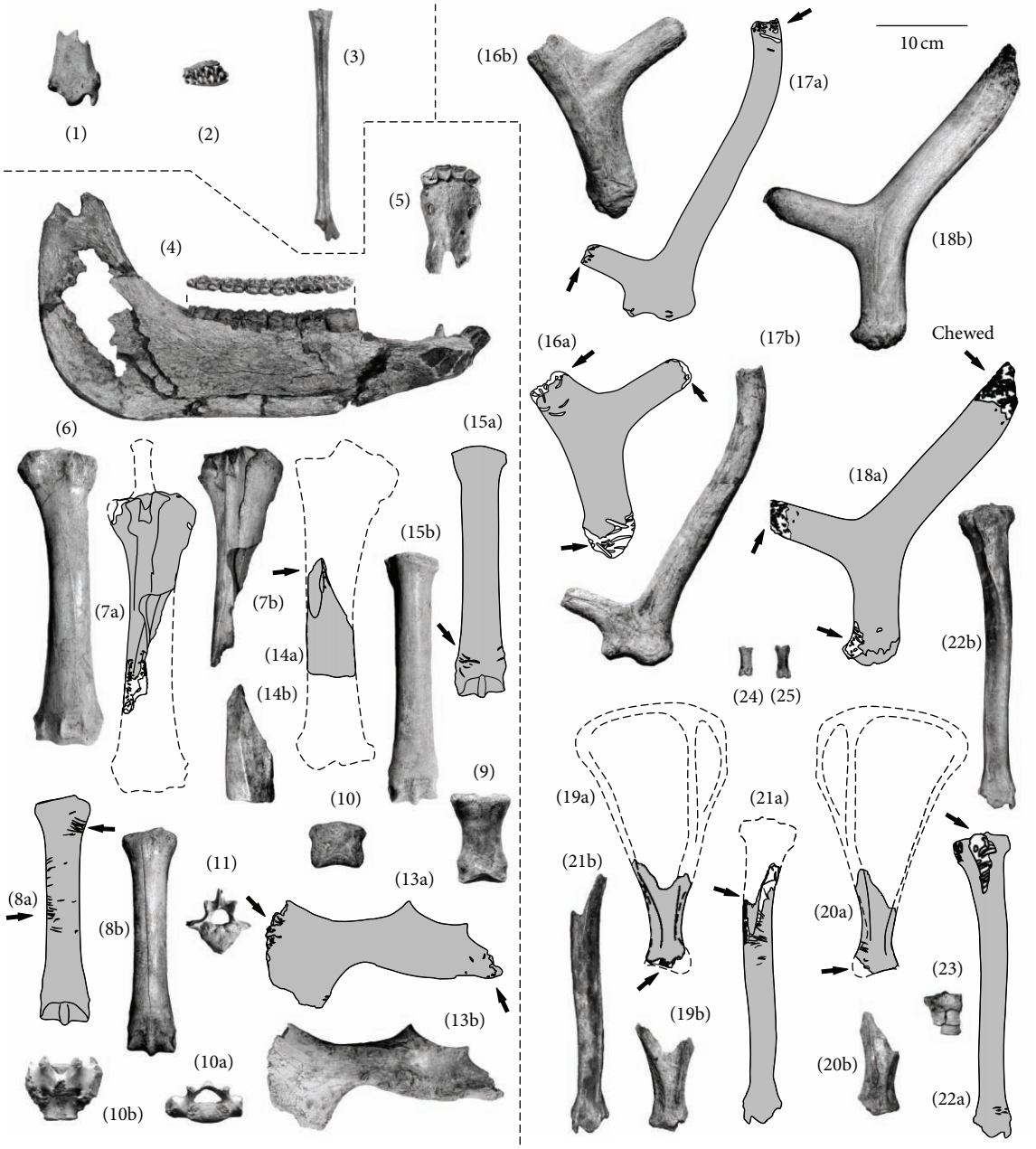


Figure 13: (1)-(2) Cervid and Equiid remains from the hyena open air den site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (a) Redrawing, (b) photo. (1) *Megaloceros giganteus* tibia fragment (no. Bi-52/32), cranial. (2)-(3) *Cervus elaphus*. (2) Maxillary of a young animal (no. Bi-10ep), ventral. (3) 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-10eq), 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 craniolateral. (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 metatarsalia 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		x	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	Intermedium	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		Stadtmuseum 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

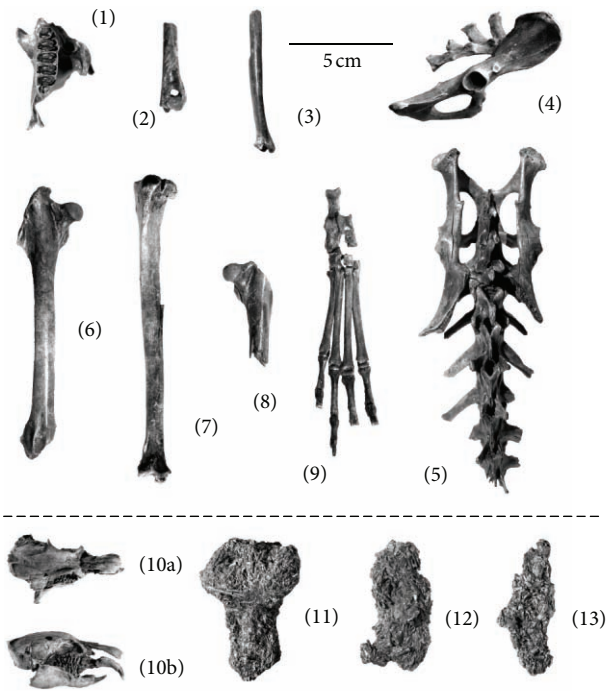


Figure 14: (1)–(9). *Lepus europaeus/timidus* remains from the hyena open air prey deposit site Bad Wildungen-Biedensteg (Hesse, NW-Germany) possibly belonging to one individual. (1) Left maxillary with dentition (no. Bi-63h), ventral. (2) Right humerus fragment (no. Bi-63g), cranial. (3) Right radius 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).

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 sir 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 M^1), 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]. Vertebrae 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	Rudolf-Lorenz-Stiftung
2	52/37	Mandible	Milk dentition, with dm_3, M_1		x	Early juvenile	x	Rudolf-Lorenz-Stiftung
3	52/38	Mandible	Milk dentition, with dm_{1-3}, M_1	x		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		x	Early adult		University of Marburg
8	Ma 5	Dens	P4		x	Early adult		University of Marburg
9	Ma 6	Dens	M1		x	Early adult		University of Marburg
10	Ma 7	Dens	M2	x		Early adult		University of Marburg
11	Ma 8	Dens	M3	x		Early adult		University of Marburg
12	10l	Scapula	Fragment	x		? Adult	x	Rudolf-Lorenz-Stiftung
13	52/20	Scapula	Without distal joint	x		Adult	x	Rudolf-Lorenz-Stiftung
14	52/200	Scapula	Incomplete		x	? Adult		Rudolf-Lorenz-Stiftung
15	52/88	Scapula	Fragment			? Adult		Rudolf-Lorenz-Stiftung
16	180c	Humerus	Incomplete		x	Adult	x	(Mentioned in [34], missing)
17	10v	Humerus	Incomplete	x		Adult	x	Rudolf-Lorenz-Stiftung
18	52/47, 42	Ulna/radius	Shafts, articulated	x		Juvenile	x	Rudolf-Lorenz-Stiftung
19	52/116, 111	Ulna/radius	Shafts, articulated		x	Early adult	x	Rudolf-Lorenz-Stiftung
20	52/143	Ulna	Shaft		x	? Adult	x	Rudolf-Lorenz-Stiftung
21	10p	Ulna	Shaft		x	? Adult	x	Rudolf-Lorenz-Stiftung
22	52/53	Ulna	Shaft		x	Adult	x	Rudolf-Lorenz-Stiftung
23	10a	Ulna	Shaft		x	Adult	x	Rudolf-Lorenz-Stiftung
24	52/49	Radius	Without distal joint	x		Adult	x	Rudolf-Lorenz-Stiftung
25	52/44	Radius	Shaft		x	Adult	x	Rudolf-Lorenz-Stiftung
26	52/30	Radius	Proximal joint	x		Adult	x	Rudolf-Lorenz-Stiftung
27	52/224	Radius	Distal joint		x	Early adult	x	Rudolf-Lorenz-Stiftung
28	10a	Radius	Proximal joint		x	Adult	x	Rudolf-Lorenz-Stiftung
29	52/235	Intermedium	Nearly complete		x	Adult		Rudolf-Lorenz-Stiftung
30	52/34	Carpale 3	Nearly complete		x	Adult		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	x		Juvenile	x	Rudolf-Lorenz-Stiftung
35	52/153	Femur	Shaft, fragment	x				Rudolf-Lorenz-Stiftung
36	10ab	Femur	Incomplete		x	Adult	x	Rudolf-Lorenz-Stiftung
37	10ea	Femur	Shaft	x		Early adult	x	Rudolf-Lorenz-Stiftung
38	10aya	Femur	Shaft	x		Early adult	x	Rudolf-Lorenz-Stiftung
39	52/228	Patella	Complete		x	Adult		Rudolf-Lorenz-Stiftung
40	52/7	Tibia	Incomplete		x	Adult	x	Rudolf-Lorenz-Stiftung
41	52/201	Tibia	Without proximal joint		x	Adult	x	Rudolf-Lorenz-Stiftung
42	10c	Tibia	Incomplete	x		Adult	x	Rudolf-Lorenz-Stiftung
43	52/9	Tibia	Without proximal joint		x	Adult	x	Rudolf-Lorenz-Stiftung
44	10t	Tibia	Without proximal joint		x	Adult	x	Rudolf-Lorenz-Stiftung
45	52/4	Fibula	Distal joint	x		Adult	x	Rudolf-Lorenz-Stiftung
46	52/16	Fibula	Shaft	x		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		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	52/1808-2	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			?		Rudolf-Lorenz-Stiftung
76	52/156	Costa	Fragment			Early adult		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	x	Rudolf-Lorenz-Stiftung
79	52/52	Costa	Middle, approx. 4–6		x	Early adult	x	Rudolf-Lorenz-Stiftung
80	52/15	Costa	Middle, approx. 7–9	x		Early adult	x	Rudolf-Lorenz-Stiftung
81	52/100	Costa	Anterior, approx. 2–3		x	Early adult	x	Rudolf-Lorenz-Stiftung
82	52/3a	Costa	Anterior, approx. 3-4		x	Early adult	x	Rudolf-Lorenz-Stiftung
83	10q	Costa	Anterior, approx. 4–6	x		Early adult	x	Rudolf-Lorenz-Stiftung
84	10v	Costa	Anterior, approx. 3-4	x		Early adult	x	Rudolf-Lorenz-Stiftung
85	10ad	Costa	Posterior		x	Early adult	x	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	/	Scapula						(Mentioned in [34], missing)
4	BadW-9	Scapula	Proximal half			Adult		Rudolf-Lorenz-Stiftung
5	10af	Metacarpus	Proximal joint	x		Adult	x	Rudolf-Lorenz-Stiftung
6	/	Carpale 3 + 4						(Mentioned in [34], missing)
7	52/205	Femur	Distal joint and shaft fragment	x		Adult	x	Rudolf-Lorenz-Stiftung
8	10o	Femur	Shaft		x	Adult	x	Rudolf-Lorenz-Stiftung
9	10k	Femur	Distal joint, fragment		x	Adult	x	Stadtmuseum Bad Wildungen
10	52/236	Tibia	Without proximal joint		x	Adult	x	Museum Korbach, (Stadtmuseum Bad Wildungen)
11	52/12	Calcaneus	Nearly complete		x	Adult	x	Rudolf-Lorenz-Stiftung
12	52/17	Thoracic vertebra	Centrum			Adult	x	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			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, length = 236 mm, distal width = 50 mm	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, length = 257 mm, distal width = 53 mm	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			Adult		Rudolf-Lorenz-Stiftung
16	52/202	Cervical vertebra	Fragment, neural arch			Adult	x	Rudolf-Lorenz-Stiftung
17	10eq	Lumbar vertebra	No. 4, without processi			Juvenile	x	Rudolf-Lorenz-Stiftung
18	10ad	Pelvis	Sacrum, incomplete			Juvenile	x	Rudolf-Lorenz-Stiftung
19	52/157	Costa	Fragment				x	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	/	Mandibula	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			Juvenile		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	Carpale	Complete		x	Juvenile		Rudolf-Lorenz-Stiftung
13	52/115-7	Carpale 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

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	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 14: Bones of *Lepus* sp. 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	x	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	x	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	x	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	x	Adult		Rudolf-Lorenz-Stiftung
28	52/255	Tarsalia	2 complete		x	Adult		Rudolf-Lorenz-Stiftung

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 Magdalénian [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

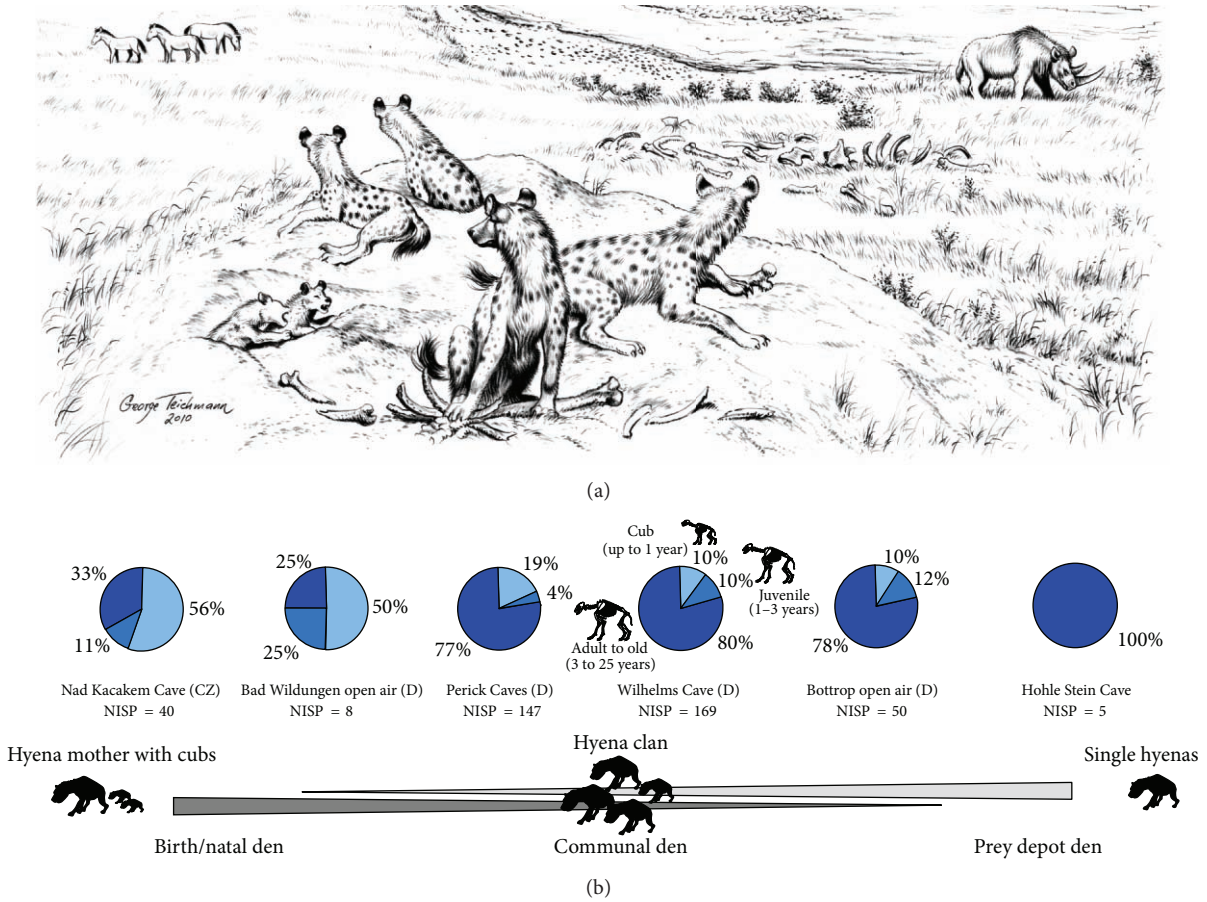
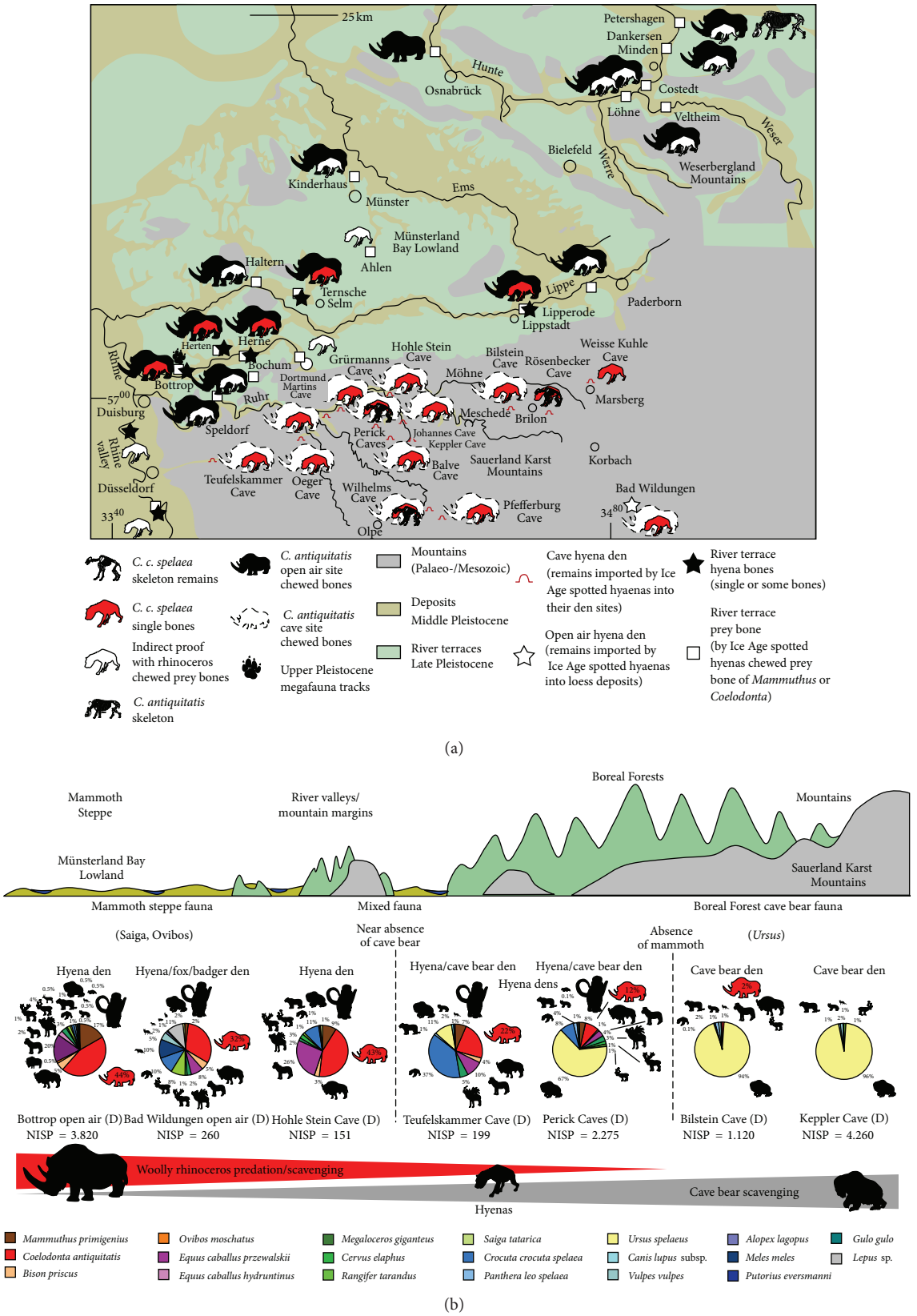


Figure 15: (a) Late Pleistocene spotted hyena clan at the birth/natal den at the open air loess site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (b) Population structure comparisons of hyena den sites of central Europe in which Bad Wildungen falls intermediately within the birth/natal den and communal sites.

art and identified also the horses by the unique "M-sign" (resulting from fur colour and fur change) and "uplifted mane" (only in those horses, not in modern present horses) to represent obviously Przewalski horses within the Late Palaeolithic times (cf. e.g., [86, 89]) and especially within the cold periods of the Late Pleistocene.

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]).



(a)

(b)

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 spongiosa remains of woolly rhinoceros 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 rhinoceros (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 Age 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 saliens* (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 iltis and large carnivore water birds, or owls. Nearby, a badger/fox den 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 spongiosa fragments from woolly rhinoceros 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).

Acknowledgments

The work is dedicated in the memory of L. Lorenz and her husband R. Lorenz (in former times running the Rudolf-Lorenz-Stiftung), who both supported much rescuing material from the locality, research financing, and care keeping of the collection, which is housed in the Heimatmuseum of the City Bad Wildungen. For the kind hosting during the studies the author thanks Mrs. L. Lorenz, and for the cooperation Dr. V. Brendow, the museums head of the Kurmuseum Bad Wildungen. Dr. I. Wrazlido (Leader Museum Natur und Mensch Bielefeld) kindly allowed the comparison of the woolly rhinoceros skeleton from Petershagen. The author thanks Dr. J. Fichter very much for the help in the donation of the collection that was housed partly in the University of Marburg (coll. E. Jacobshagen). The research and project "Hyena open air prey deposit site Bad Wildungen-Biedensteg" was financially supported by the Rudolf-Lorenz-Stiftung, the Sparkassenstiftung of Bad Wildungen, and the PaleoLogic. Sadly, the responsible Ministry of Culture of Hesse and the office for palaeontological monument survey Wiesbaden did not take care of the site, which was damaged further by

a newer house construction, where many finds have been destroyed in the late 90s. Finally the author thanks the reviewers, especially Prof. Dr. Müller-Beck, for their supporting critics of the first paper draft. And last, the author would like to thank S. Stevens for the spell check.

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