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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 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).

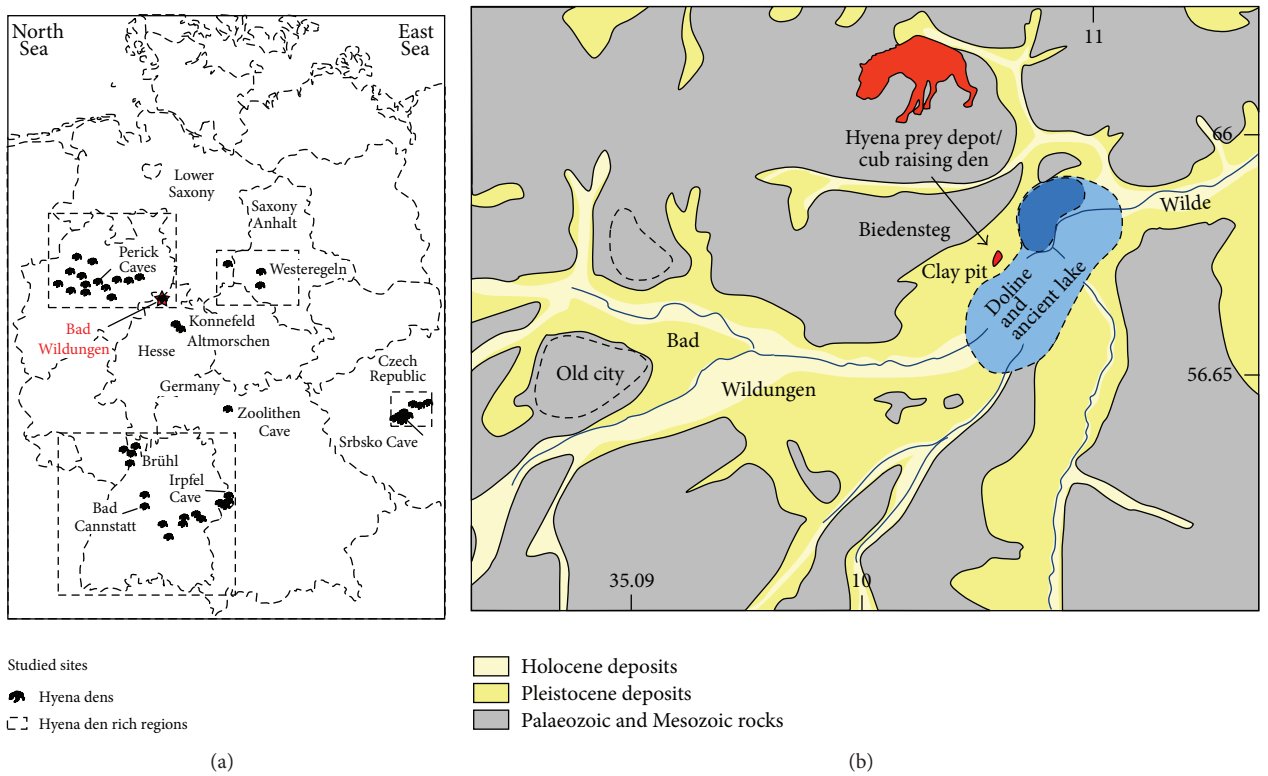
3. Sedimentary Geology, Paleoenvironment, and Dating

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



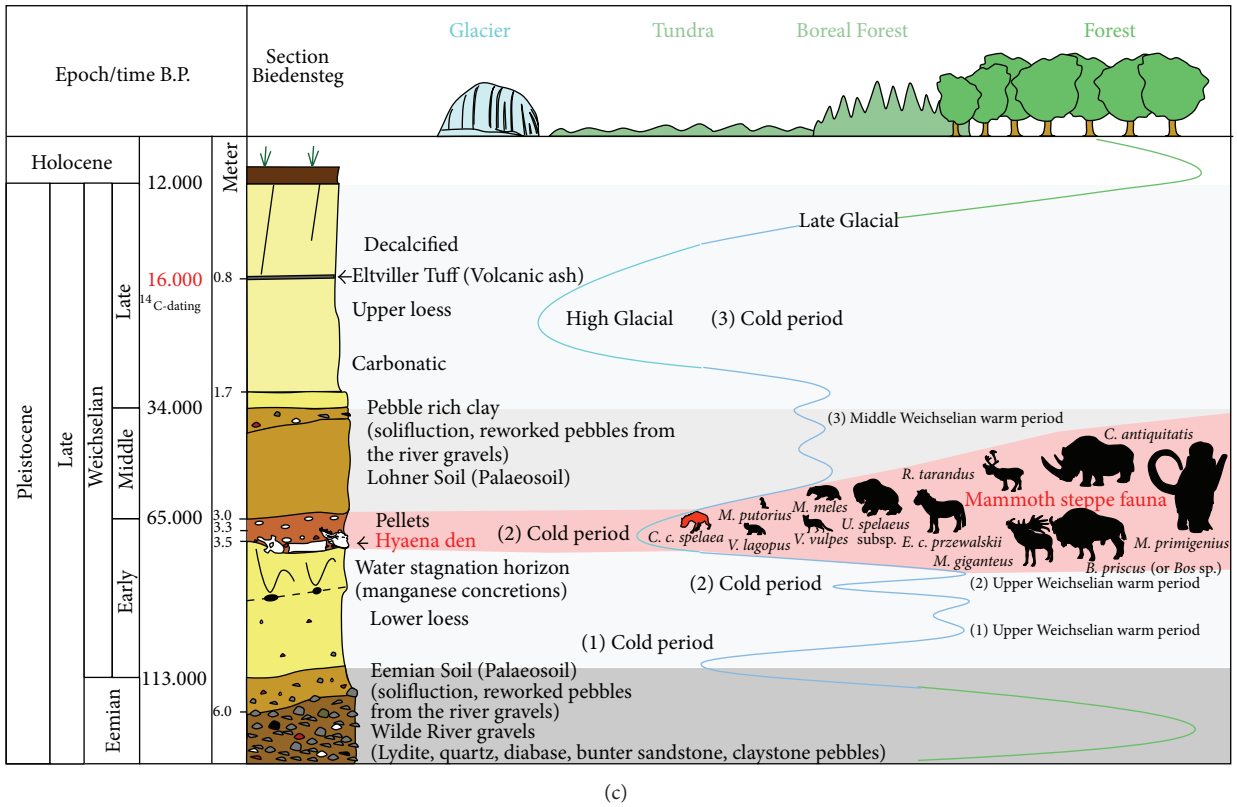


Figure 1: (a) Topographic position of the Ice Age spotted hyena *Crocuta crocuta spelaea* birth and commuting den site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (b) The prey was deposited at the margin of an ancient small lake and muddy area of the Pre-Wilde River that filled up a doline during the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

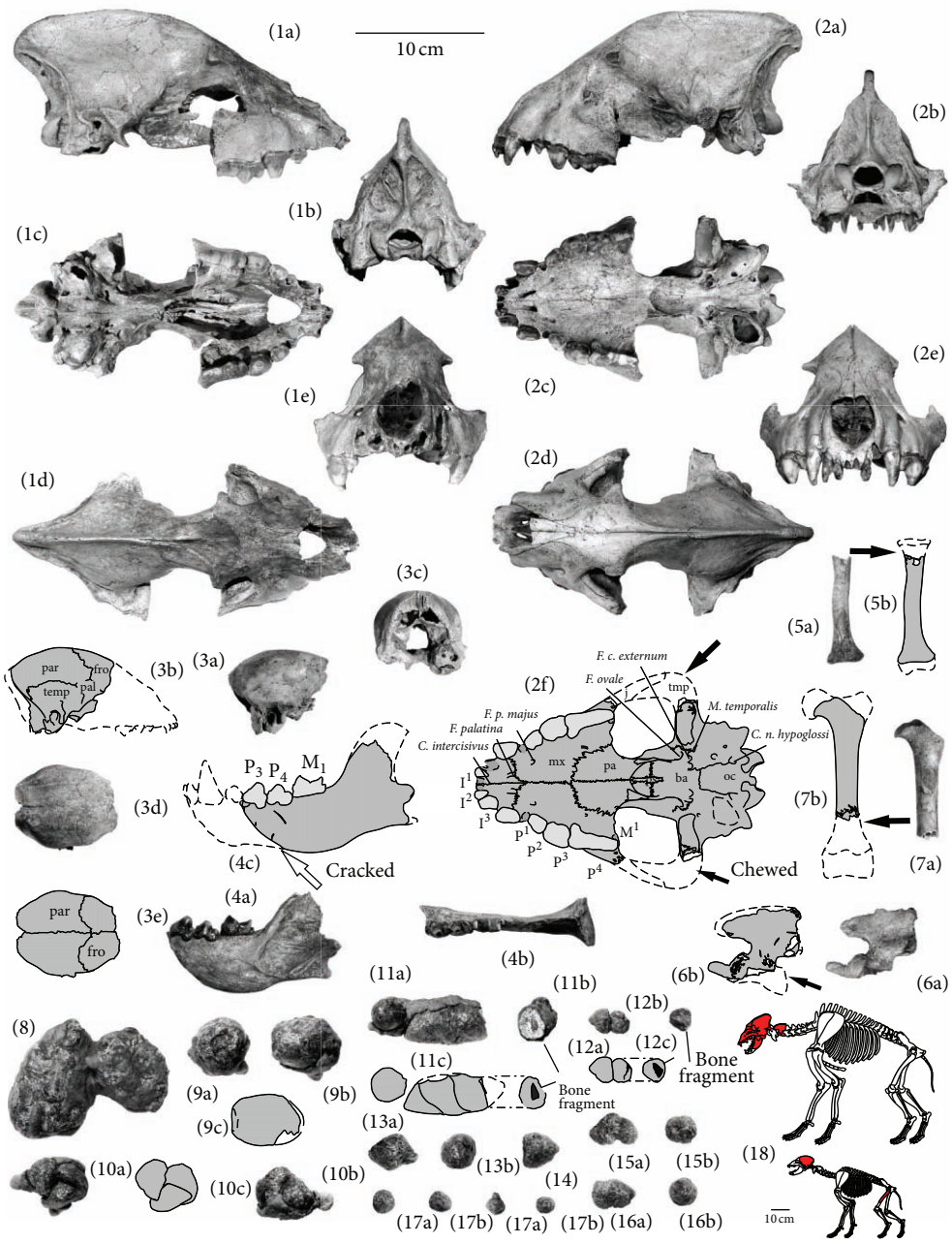


Figure 2: Remains of the Ice Age spotted hyena *Crocuta crocuta spelaea* from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) High adult female deformed skull (no. Bi-10at), (a) lateral, occipital, (c) ventral, (d) dorsal, (e) frontal. (2) Early adult female skull (no. Bi-52/45),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

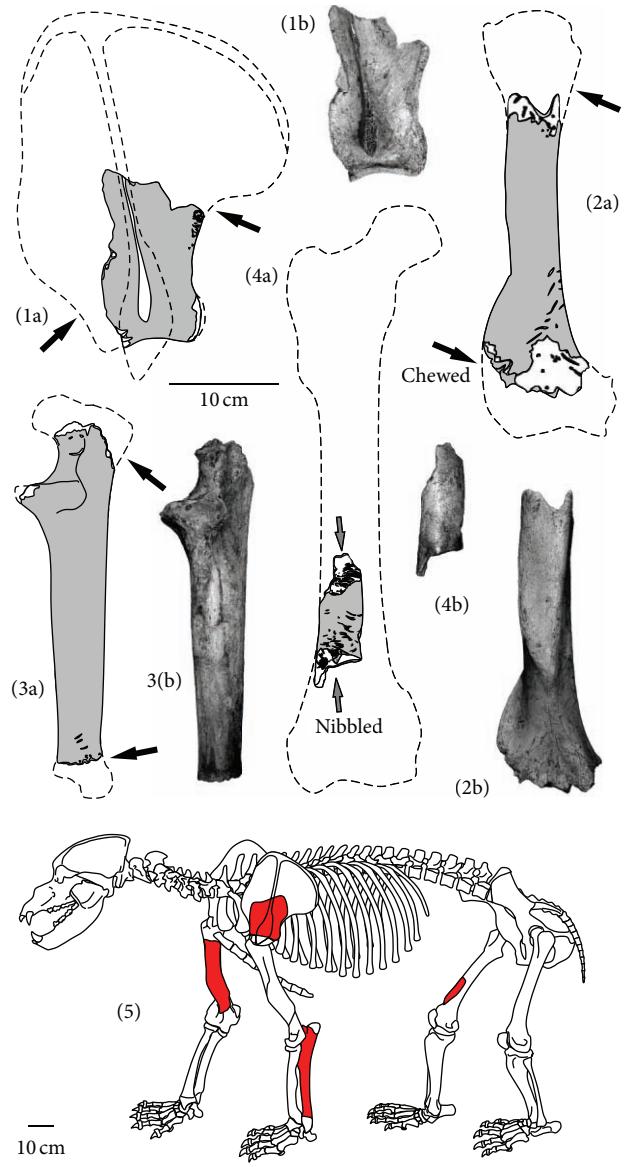


Figure 3: *Ursus spelaeus* subsp. bones from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). The bones seem to belong to one adult female individual. (1) Left scapula fragment (no. Bi-52/227), lateral. (2) Right humerus shaft (no. Bi-52/2), cranial. (3) Left ulna shaft (no. Bi-52/241), 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).

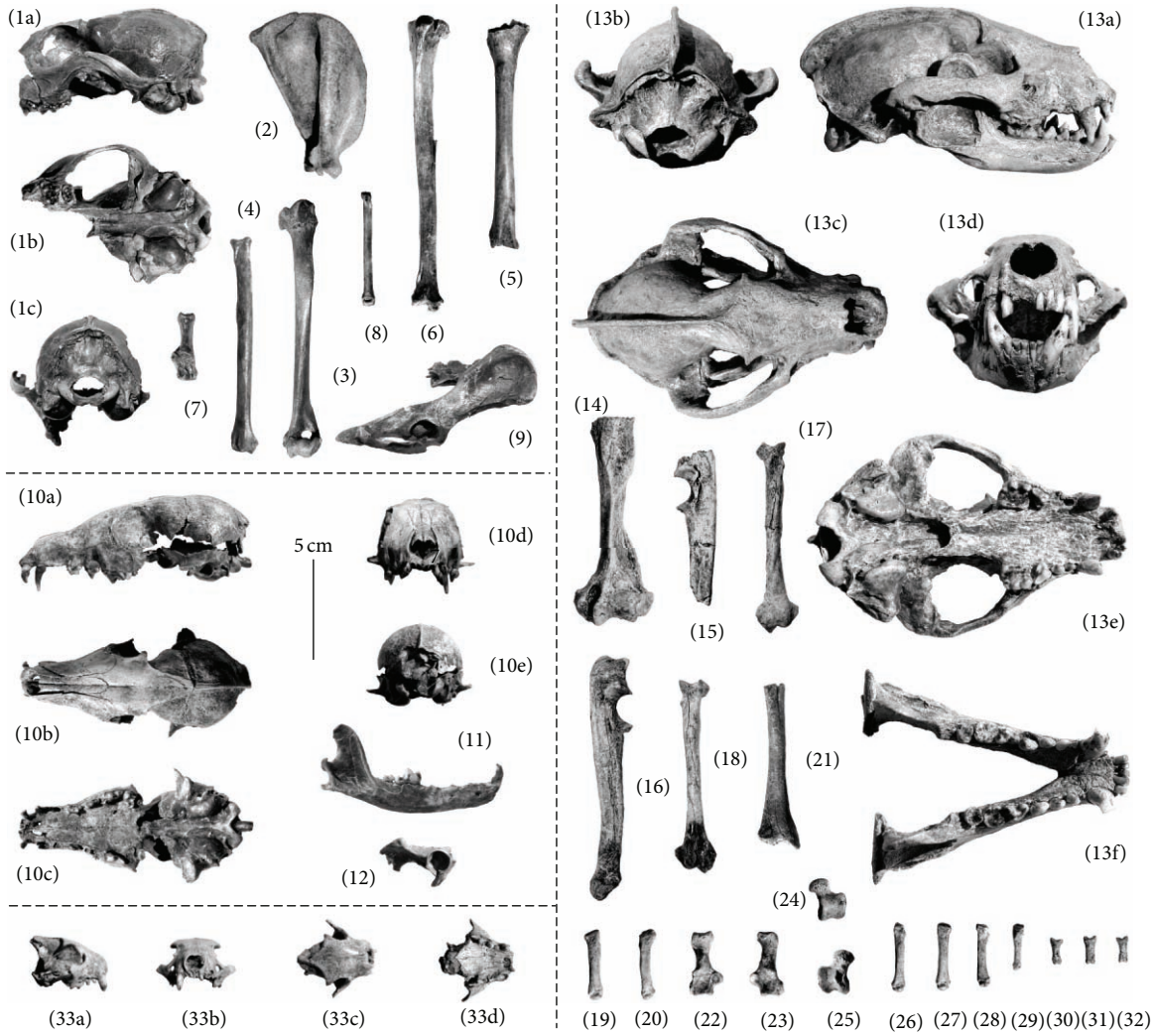


Figure 4: Small carnivores from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1)–(9) *Vulpes vulpes*: (1) incomplete skull (no. Bi-52/39), (a) lateral, (b) caudal, (c) ventral. (2) Right scapula (no. Bi-52/235), lateral. (3) Right humerus (no. Bi-52/10), cranial. (4) Right radius (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

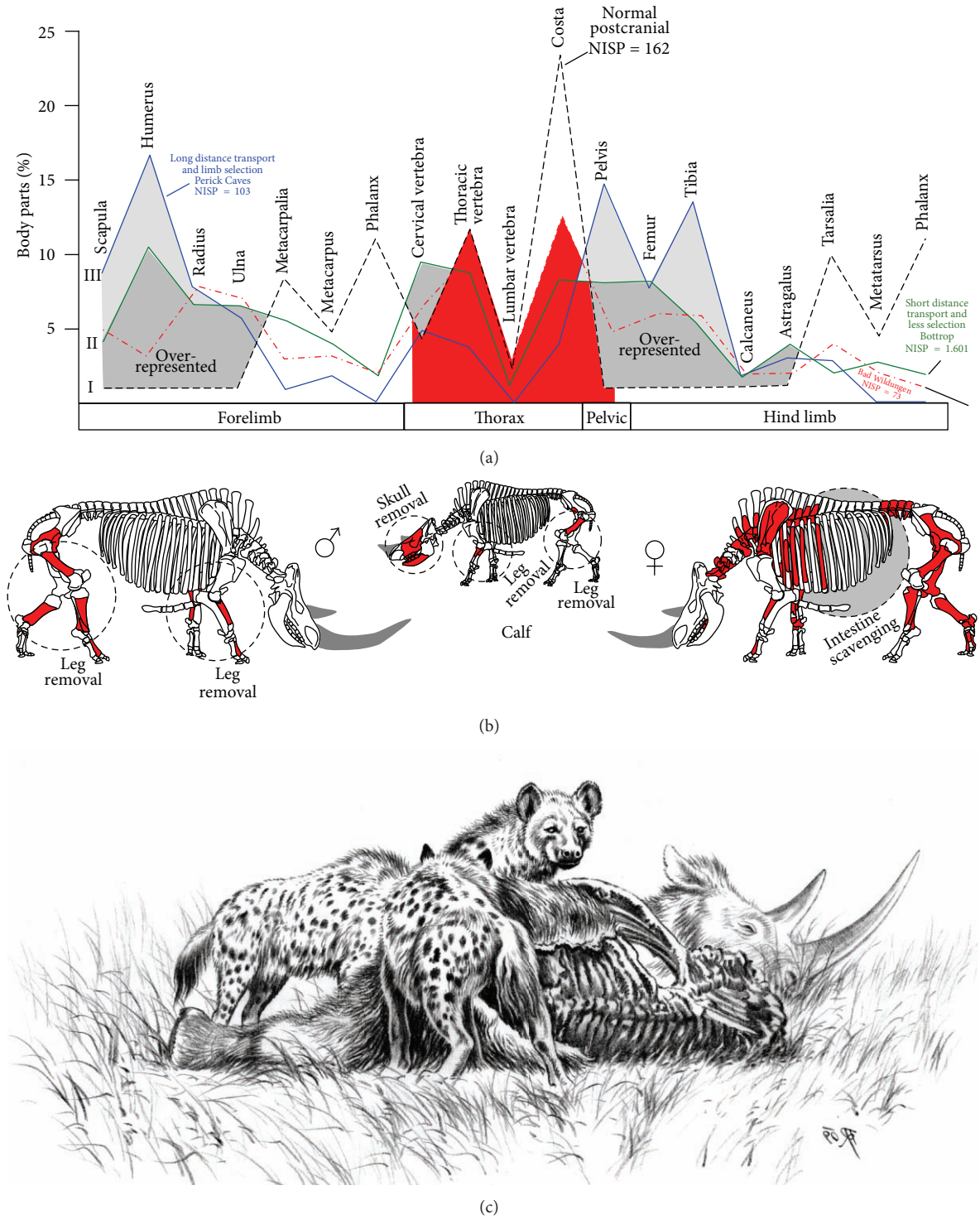


FIGURE 5: Present bone material of one (or several) male, a female skeleton remain, and calf skeleton remain of the woolly rhinoceros *Coelodonta antiquitatis* from Bad Wildungen-Biedensteg (Hesse, NW-Germany) open air hyena den.

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

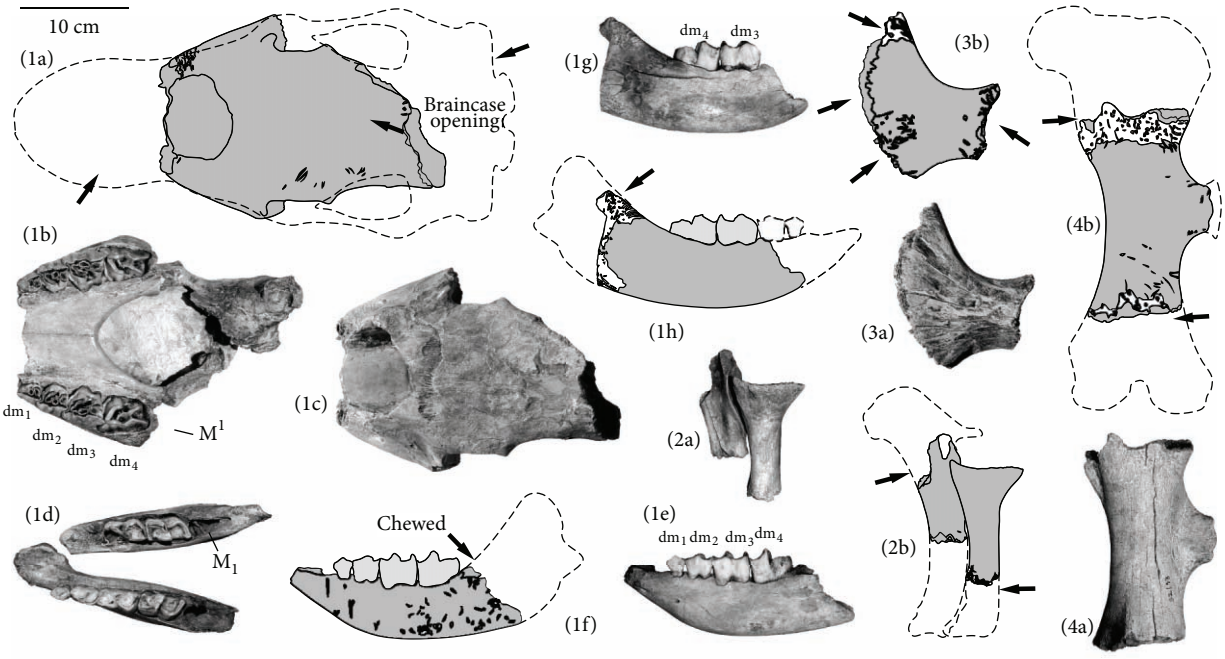


Figure 6: *Coelodonta antiquitatis* remains of a less than half-year-old calf with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Skull with brain case opening (no. Bi-10ac), (a) and (c) dorsal, (b) ventral, (d) lower jaw (no. Bi-52/37 and 38), dorsal, (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

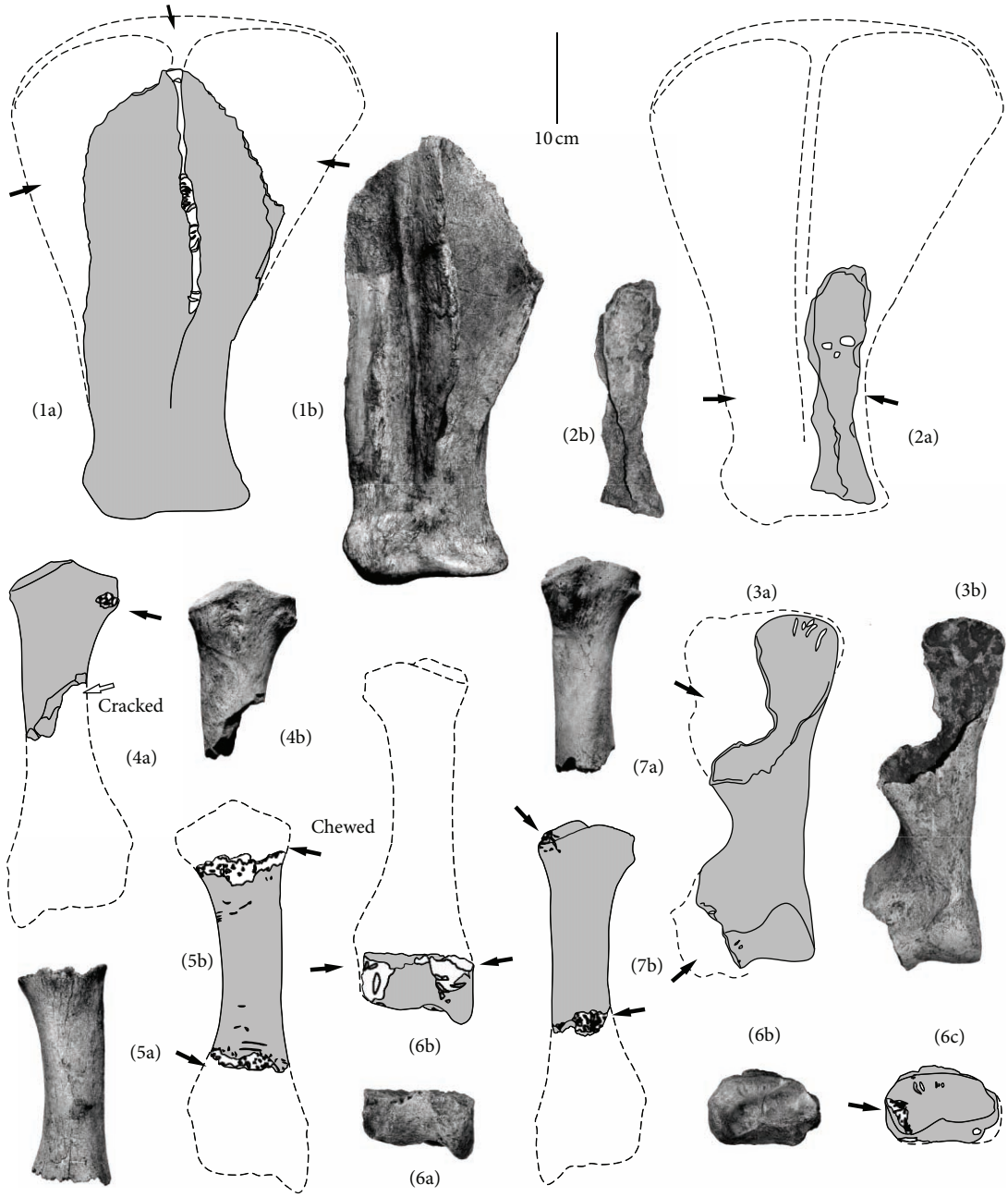


Figure 7: *Coelodonta antiquitatis* fore leg remains of adolescent and grown up animals with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left scapula from an adult individual (no. Bi-52/20), lateral. (2) Scapula fragment (no. Bi-52/88), lateral. (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

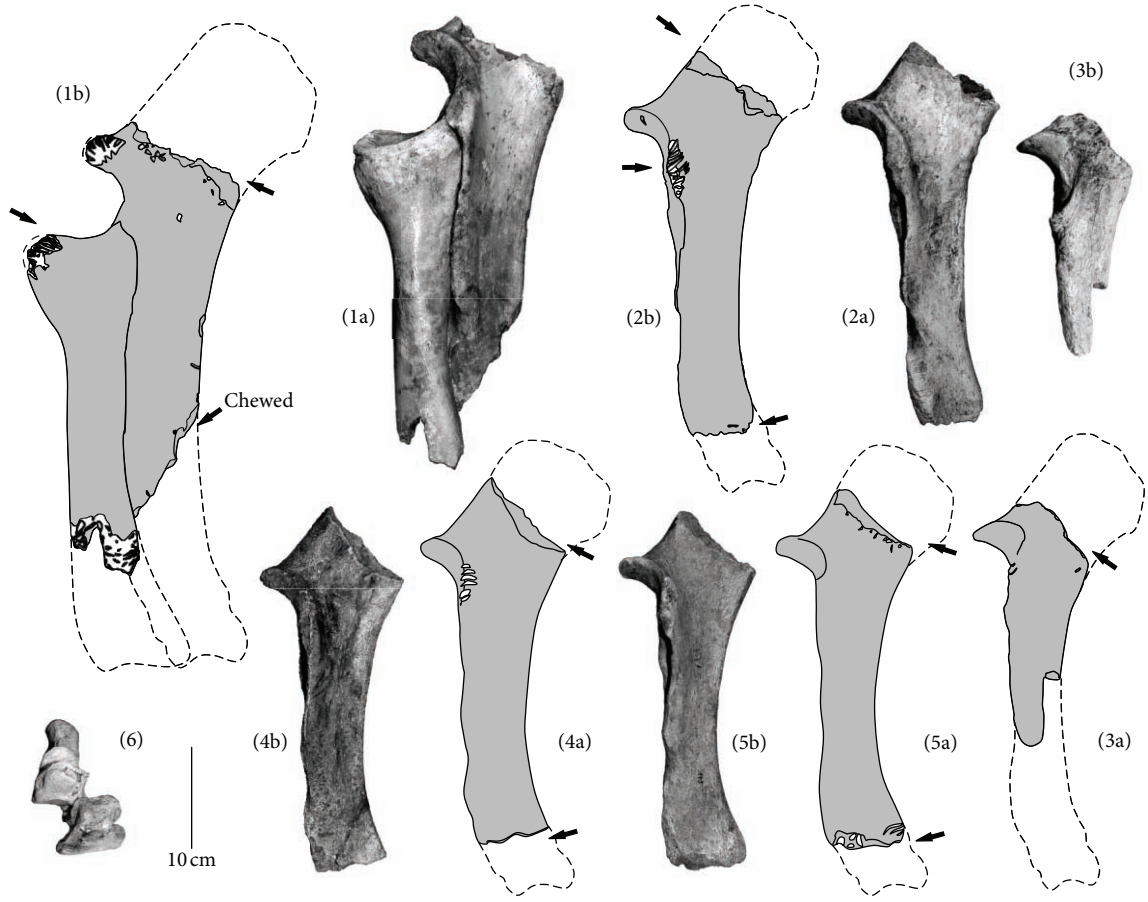


Figure 8: *Coelodonta antiquitatis* fore leg remains of grown up animals with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Articulated right ulna and radius from an early adult female individual (no. Bi-52/111 and 116), lateral. (2) Right ulna from 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

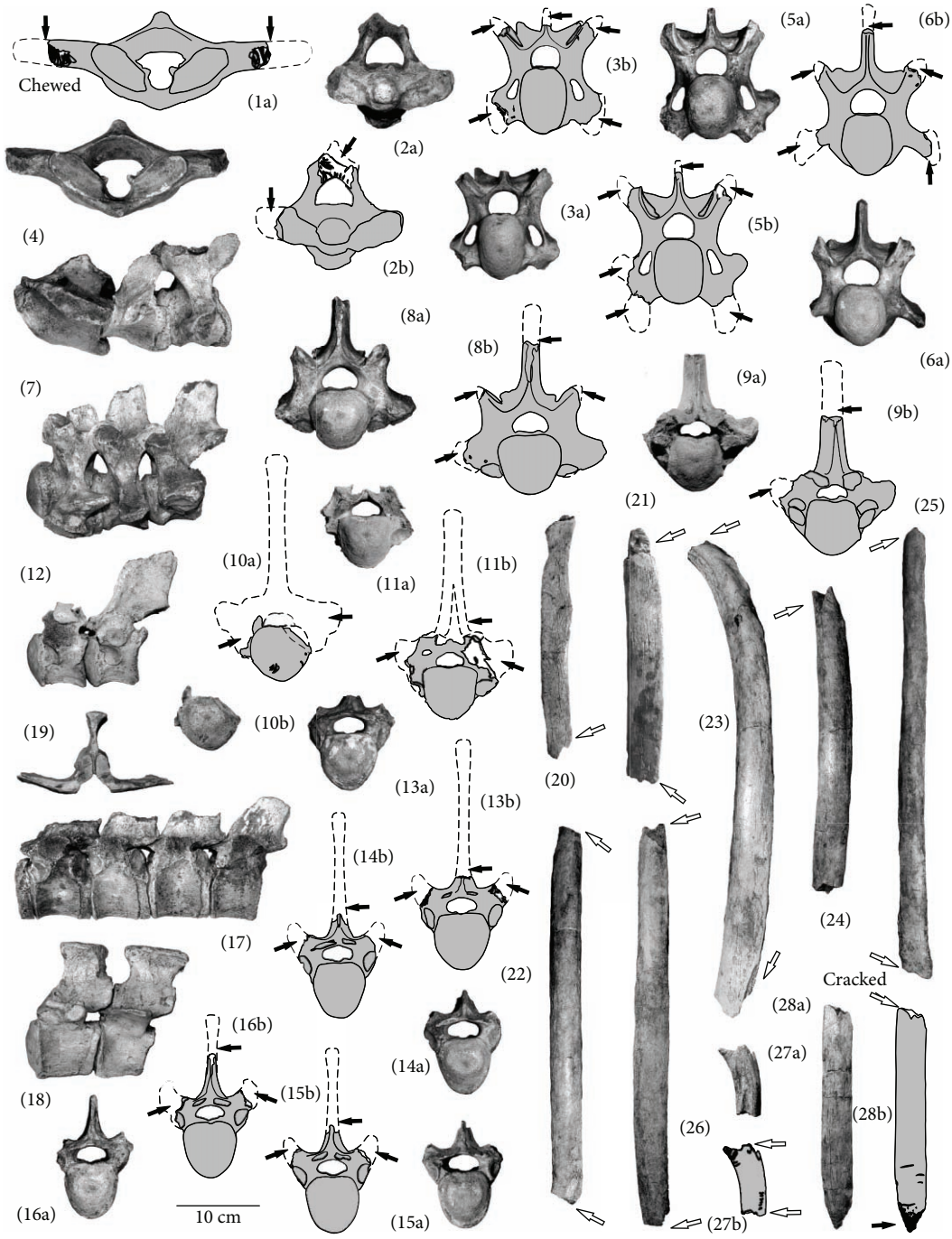


Figure 9: *Coelodonta antiquitatis* thoracic remains, all of which are most probably from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) First cervical vertebra (atlas) (no. Bi-52/9), caudal. (2) Second cervical vertebra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

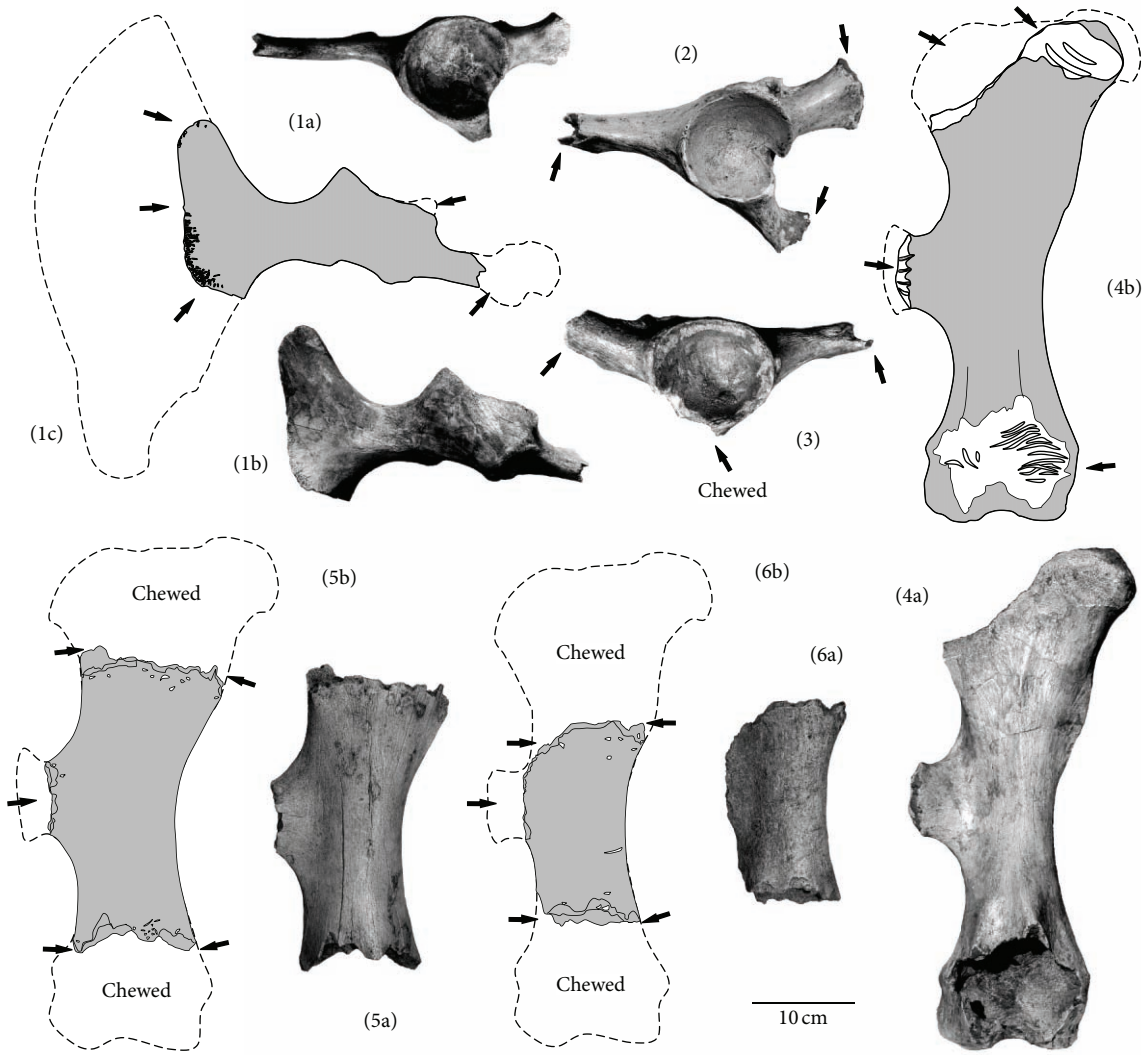


Figure 10: *Coelodonta antiquitatis* thoracic remains partly from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left pelvic acetabulum of an early adult to adult individual (no. Bi-52/48), (b) acetabular, (c) lateral. (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))

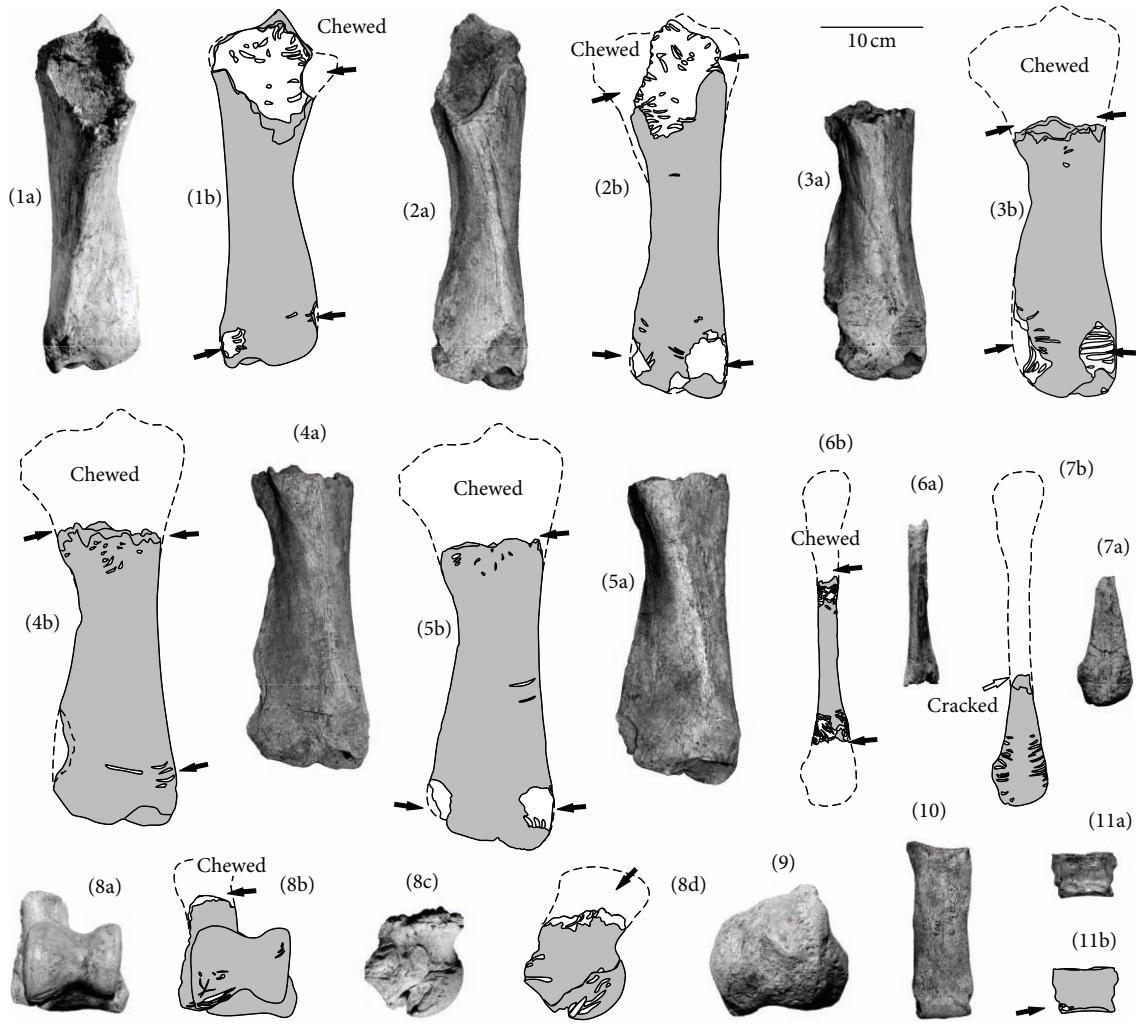


Figure 11: *Coelodonta antiquitatis* hind limb remains partly from one adolescent female animal with hyena chewing marks from the hyena open air site Bad Wildungen-Biedensteg (Hesse, NW-Germany). (1) Left tibia of a female individual (no. Bi-10c), cranial. (2) Right tibia from a female individual (no.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