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By Ice Age Spotted Hyenas Removed, Cracked, Nibbled and Chewed Skeleton Remains of *Coelodonta antiquitatis* (BLUMENBACH 1799) from the Lower Weichselian (Upper Pleistocene) Freeland Prey Deposit Site Bad Wildungen-Biedensteg (Hessia, NW Germany)

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Eighty percent of 74 fragmentary cranial and postcranial bones of the Upper Pleistocene woolly rhinoceros *Coelodonta antiquitatis* (BLUMENBACH 1799) from the Lower Weichselian (65.000-90.000 BP, OIS 5, Upper Pleistocene) ice age spotted hyena open air prey deposit site Biedensteg at Bad Wildungen (Hessia, NW-Germany) exhibit crack, bite and nibbling marks. The skeletal remains represent at least five woolly rhinoceros individuals. Individual carcasses of an early adult female and a calf have been identified. Both show carcass disrupting and destruction by the hyenas in form of partly articulated bones, bone cracking, nibbling and chewing. Articulated parts of the skeletons were removed from the carcass and were stored in mud pits with other prey bones. The long bones, which are filled completely by the bone spongiosa, were generally not cracked, but are always gnawn intensively starting from the joints, while the hyenas mostly left the bone shaft intact. Such bone spongiosa was also not uncommon in hyena coprolites at the site. Typical bone destruction stages are represented. Those described in detail here include the cranium, scapula, humerus, ulna, radius, femur, tibia, pelvis but also vertebrae and costae. The woolly rhinoceros bones at the Bad Wildungen-Biedensteg freeland prey deposit site take 53% of the prey animal bones of *Crocuta crocuta spelaea* (Goldfuss 1823) and prove with other prey bones a mixed feeding onto all huge ice age mammals. Remains of *Mammuthus antiquitatis*, *Bison priscus*, *Equus ferus przewalskii*, *Megaloceros giganteus*, *Rangifer tarandus*, *Ursus spelaeus* and *C. c. spelaea* itself are included in the hyeana-modified fauna with 5-12% each showing signs of scavenging. The high percentage of the *Coelodonta* bones results more of the fact, that those are, such as mammoth bones, the most massive ones of ice age animals. The taphonomic comparison of *C. antiquitatis* carcasses and bones of Westphalian cave and freeland hyena den and prey deposit sites indicate the most important destruction impact of woolly rhinoceros carcasses by the Upper Pleistocene spotted hyena.

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Introduction

The first bones in the clay pit site "Ziegeleigrube Biedensteg" in Bad Wildungen of northern Hessia (Central Germany, fig. 1, coordinates R: 35,1058, H: 56,6550) were discovered in 1932 by F. Pusch who collected and excavated many bones, especially of macromammals. In 1952 E. Jacobshagen and R. Lorenz found snow owl pellets in a "pellet horizon," but also recovered two hyena skulls from this horizon. Jacobshagen (1963) initially described this fauna, focusing on the micromammals, whereas Huckriede & Jacobshagen (1963) published the first investigated section with additional new results presented by Semmel (1968) and Kulick (1973). The last palaeontological research was conducted by Storch (1969) on snow owl pellet material. Since then, the macrofauna was forgotten and not studied in detail. Therefore a very important ice age hyena prey deposit open air site in Europe was not understood, although initial observations about hyena gnawing and bone deposits were mentioned by Jacobshagen (1963).

With the "European Ice Age Spotted Hyena project" the macromammal material of Biedensteg are emphasized. Before the rediscovery of this old material in 2005, the only recently studied hyena den sites are from the Sauerland cave-rich region of north-western Germany (Diedrich, 2005d).

Analysis of Biedensteg allows the first comparison of an open air bone deposit site to cave sites and to produce a more complete and detailed picture of the palaeoecology of the most important ice age carnivore, the ice age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823). In addition, the role of the woolly rhinoceros as a very important prey for the hyenas and the *Coelodonta antiquitatis* (Blumenbach 1799) carcass and bone taphonomy for caves and freeland sites is clarified. Finally the hyena influence of the bone destruction is of importance for the interpretation of archaeological human sites, of which the animals sometimes were removing bones (cf. Diedrich, 2005d) or consumed bone rubbish left by the middle Palaeolithic Neandertals or modern human groups of the early Joungpalaeolithic (cf. Koenigswald, 2002).

The macromammal bone collection was prepared for the study the first time by the company PaleoLogic. Many broken bones were repaired and only excavation-induced damage marks were refilled. The bones were finally conserved with the nitro based lack CLOU L1. Samples for radiocarbon isotope analysis were not taken, given the age of the deposits in excess of 65,000 years (the Lower Weichselian period). A few bone fragments, which were marked as such, are not conserved for different geochemical studies in future.

The main collection (including coll. Pusch, coll. Lorenz) is owned by the Rudolf-Lorenz-Stiftung (coll.-No. Bi-52/1-224) and was partly presented in the "Heimatmuseum of Bad Wildungen." In addition a few macromammal bones from the collection in the "University of Marburg" were integrated into this study. The later had been previously noted in Jacobshagen's article (1963). This

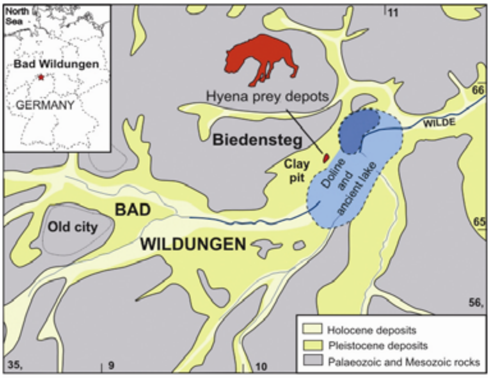

Figure 1. Topographical position of the Ice Age spotted hyena prey deposit site Bad Wildungen-Biedensteg (Hessia, NW-Germany). The prey was deposited at the margin of an ancient small lake and muddy area created by the old Wilde River that filled up a doline depression during the Weichsel ice age period (Graphics Paleologic).

collection was rediscovered by Dr. J. Fichter of the Naturkundemuseum Kassel who kindly helped to donate the important micromammal collection of the pellet horizon to the "Kurmuseum Bad Wildungen." In the Stadtmuseum Bad Wildungen a new presentation of the hyena prey deposit site and the Weichsel fauna is under construction and will be opened in 2007.

Comparative woolly rhinoceros material was consulted in different collections. The most important is the articulated skeletal remain from Petershagen (NW Germany) in the collection of the Museum Natur und Mensch Bielefeld (see. also Diedrich, 2005a, and submitted). This is one of the few non chewn skeletons with excellent

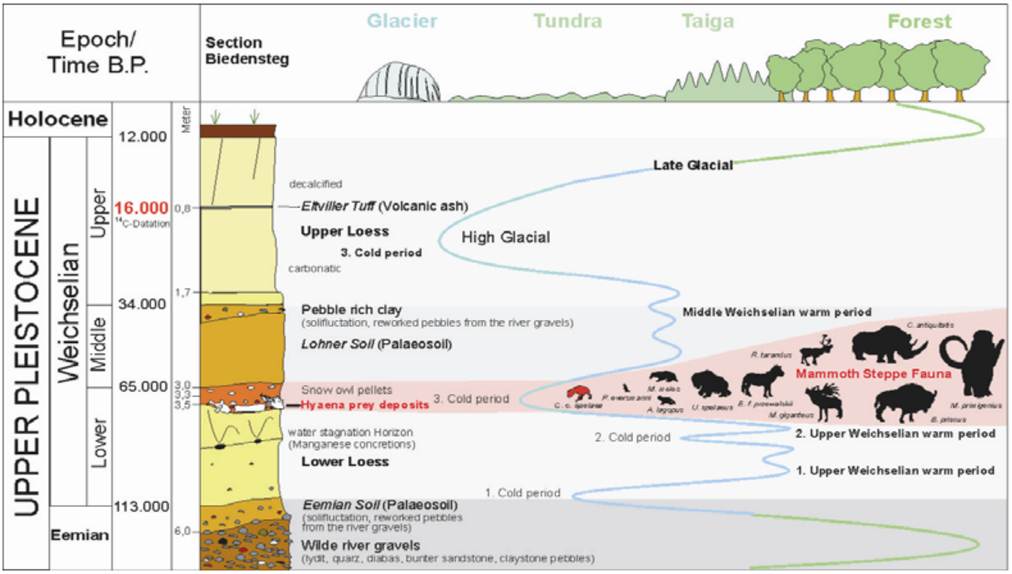

Figure 2. Generalized section at the Ice Age spotted hyena prey deposit site Biedensteg (Bad Wildungen, Hess, NW-Germany). The macrofauna deposited by the hyenas during the Lower Weichsel are dominated by woolly rhinoceros bones, while the rest of the prey fauna is a typical mammoth steppe mammal fauna consisting of *M. primigenius*, *C. antiquitatis*, *B. priscus*, *M. giganteus*, *R. tarandus*, *E. f. przewalskii*, *U. spelaeus*, *A. lagopus*, *M. meles*, *P. eversmanni* and *C. crocuta spelaea*.

well preserved ribs and postcranial bones. The mounted skeleton cast in the Museum für Ur- und Ortsgeschichte Eiszeithalle Quadrat Bottrop (fig. 19) was used for the skeleton redrawings (fig. 4) and comparison of the bone positions in the skeleton of the Bad Wildungen-Biedensteg material.

Geology and Dating

The geological situation at the hyena deposit site "Lehmgrube Biedensteg" was published by Huckriede & Jacobshagen (1963), Semmel (1968) and Kulick (1973). The overview of the redrawn sketch of the outcrop section with the addition of all published results and interpretations derived from the present investigation about the hyena deposits presented here (fig. 2).

The Wilde river gravels at the base of the section are of the Eem interglacial period. They consist of red bunter sandstone- and claystone-, lydit-, quartz-, diabas-pebbles. These deposits are overlain by a paleosol resulting from solifluctation. In this "Eem-Soil" the river pebbles are resedimented with reddish-brown loess. The Lower Loess is from the early to middle Lower Weichselian (OIS 5) and a product of the first maximum Glaciation (fig. 2) where in this mountainous region Loess was deposited in a mammoth steppe environment. Some snails were found in the Lower Loess by Jacobshagen (1963) and the loess soil snail *Pupilla muscornum* (Müller) conforms to the climatic and environment interpretation.

In the middle and at the end of the Lower Weichselian a climatic stagnation produced a paleosol on the Wilde river gravels, which were at that time on the shore of a small lake. This lake was formed by subsurface salt dissolution and positioned within a sinkhole. The lake was filled by the Wilde River, that is evidenced by the presence of many aquatic species such as frogs (*Rana agiloides* Brunner, 1951) but mainly by salmonid fish (cf. Jacobshagen, 1963) that required flowing water. The muddy area at the Wilde River or lake shore was used by the Ice Age spotted hyenas as prey deposit sites. Bones from animals of the mammoth steppe macro fauna was deposited here, which were mentioned as "bone nests" in the publication of Jacobshagen (1963). The sedimentary depression structures in the bone rich Loess horizon described by Kulick (1973) as "cryoturbation and channels" also could be at least partially the result of bioturbation and were possibly caused by the hyenas who deposited animal prey remains during summer, when the permafrost soil was soft in the upper part. As described here, the he main bones are from *Coelodonta antiquitatis* (Blumenbach). Other animals such as the woolly mammoth *Mammuthus primigenius* (Blumenbach), the giant deer *Megaloceros giganteus* (Blumenbach), the reindeer *Rangifer tarandus* (Linné), the Przewalski horse *Equus ferus przewalskii* (Poljakoff), the steppe bison *Bison priscus* (Bojanus), the cave bear *Ursus spelaeus* (Rosenmüller), the arctic fox *Alopex lagopus* (Linné) or the steppe iltis *Putorius eversmanni* (Lesson) are present in the first maximum glaciation fauna. Additionally there are many steppe environment typical rodents such as *Lemmus lemmus* (Linné), *Dicrostonyx henseli* (Hinton), *Microtus gregalis* (Pallas), *Alactaga saliens* (Gmelin) or birds such as *Lagopus lagopus* (Linné) listed with many other species by Jacobshagen (1963). The hyena *Crocuta*

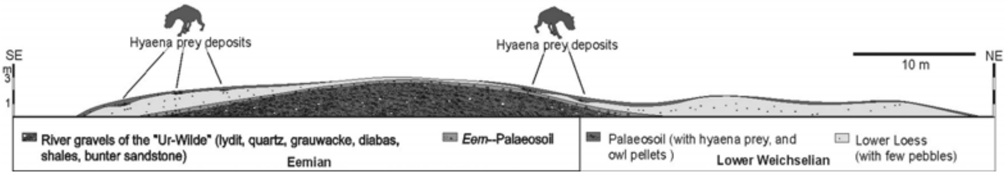

Figure 3. Clay pit outcrop section at the Ice Age spotted hyena prey deposit site Biedensteg (Bad Wildungen, Hess, NW-Germany). The macrofauna was deposited by the hyenas during the Lower Weichsel in Loess mud pits at the margins of the Ur-Wilde river gravels (see. fig. 2, Graphics PaleoLogic).

crocuta spelaea (Goldfuss 1823) remains from Biedensteg is present with skulls, postcranial bones and many coprolites (Diedrich, submitted b). The bioturbation interpretation would fit into the “hyena prey deposit site”, but cannot be evaluated directly because the clay pit Biedensteg do not allow access to the deposits. In the section (fig. 2) such depressions are labled as hyena bone deposits. It is also possible that subsequent 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.

The “pellet horizon” is figured differently in the publications (cf. Jacobshagen et al., 1963, Kulick, 1973). For sure the pellets are not only from snow owls, because they are not feeding on anures or fishes. Such remains could be remains of consumption by the steppe iltis *Putorius eversmanni* (Lesson). The iltis is active along small rivers or lakes focusing on fishes, frogs and other animals (Claußen, 1986). Certainly the large numbers of frog bones must have resulted from some other large water birds and other predators that also left pellets and bone remains at the river and along the lake. The section of Kulick (1973) indicates that the pellets and the macromammal bones are mixed within a single horizon. Verification of this is provided by caliche concretions around hyena coprolites in which many of the micromammal bones and teeth are embedded. The “hyena prey deposit site” and the “pellet horizon” are hence considered to be from the same period and are dated relatively into the late Lower Weichselian (65.000-90.000 BP, OIS 5a-d, fig. 2). Therefore the complete micro- and macrofauna and its taphonomy has to be studied anew to understand the lake or muddy swamp area and its surrounding and climatic situation of a mammoth steppe and permafrost environment.

The large bone accumulation is a product of the combined activities of the Ice Age spotted hyena and smaller macromammals by *A. lagopus* whereas fish and anures mainly are remains of prey from *P. evernsmanni* or large predator water birds (cf. Claußen, 1986). Micromammals were introduced mainly by the snow owl *Nyctea scandiaca* (Linné) pellets.

The bone rich horizon is overlain by another paleosol, in that case the “Lohner Soil”, which can be found in the region at different sections described by Semmel (1968) and Kulick (1973). Based their interpretations, a solifluctation of Loess and Wilde river gravel material took place in the Middle Weichselian warm period (fig. 2). It seems, that some mammal species, which are also described from the "bone rich horizon" are from that time. *Vulpes*

vulpes is the dominating faunal element besides *Lepus europaeus*. These warm period faunal elements conform to expectations of *Vulpes* den sites in loess soils, in front of which they often left some prey bones. The large cave/burrow systems are often up to several meters deep and would have therefore reached the "bone rich horizon" of the hyena prey deposits. It is possible, that such *Meles/Vulpes* cave systems have caused a faunal mixing of the arctic and warm period mammal fauna, which was not excavated and documented in detail. This problem was not discussed in Jacobshagen (1963). Regardless, the preservation of the *M. meles* bone material matches the Ice Age mammal bones, whereas the red fox and maybe hare bones are from the warmer period, but for sure from the Weichsel and not of Holocen age.

Finally the Upper Loess was sedimented, and subsequently the upper part was decalcified during the Holocene. The “Eltviller Tuff” is a one to two centimetres thick layer in the Upper Loess and the only dated horizon with an age of 18.000 BP (Semmel, 1968). This confirms an interpretation of the Upper Loess of its sedimentation during the maximum glaciation (fig. 2).

Palaeontology

Family Rhinocerotidae OWEN 1845
Genus *Coelodonta* BRONN 1831
***Coelodonta antiquitatis* (BLUMENBACH 1799)**

The material consists of a few cranial and mainly postcranial bones of five woolly rhinoceros individuals (table 1). The remains of a young, less than one year old calf with milk dentition, an early adult female animal, and a few remains of a male adult skeleton are identified. (fig. 4). Besides these partially preserved skeletons, other skeletal elements, mainly forelimbs, from other individuals are represented.

Males and females exhibit sexual dimorphism, which is not well studied and described for *C. antiquitatis*. Comparisons of some long bones such as the ulna and radius, but also the tibiae, from Bad Wildungen-Biedensteg indicate strong sexual dimorphism (see figs. 8, 9, 11).

All bones have distinct nibbling, chewing and gnawing marks, mainly produced by the Ice Age spotted hyenas (e.g. fig. 18A). On one pelvic fragment (Fig. 12), two different bite mark types were found. These were caused by animals other than the hyenas. At the acetabular region, thin and long scratches indicate a scavenging origin of a smaller carnivore such as the wolf *Canis lupus* or the arctic fox *Alopex lagopus* (fig.18B). Similar scratches were also found at the top skull of an early juvenile animal (fig. 5.1b). Many parallel and flat quadratic shaped scratches at the margin of the ilium must have been caused by rodents such as mice (fig. 18C). Scratches deep into the spongiosa of the joints, e.g. the femora (Figs. 10.1, 11.1, 19.A) are very typical of hyena origin and can be found at many other open air and cave sites (e.g., Diedrich, 2004, 2007).

The cranial material consists of a middle part of a top skull from a calf. The connection between the maxillas was restored by the earlier preparation and was not removed during the new preparation because of a problematic possible destabilisation. Originally the maxillary margins between the teeth were also damaged by hyenas. All four pm^{1-4} milk

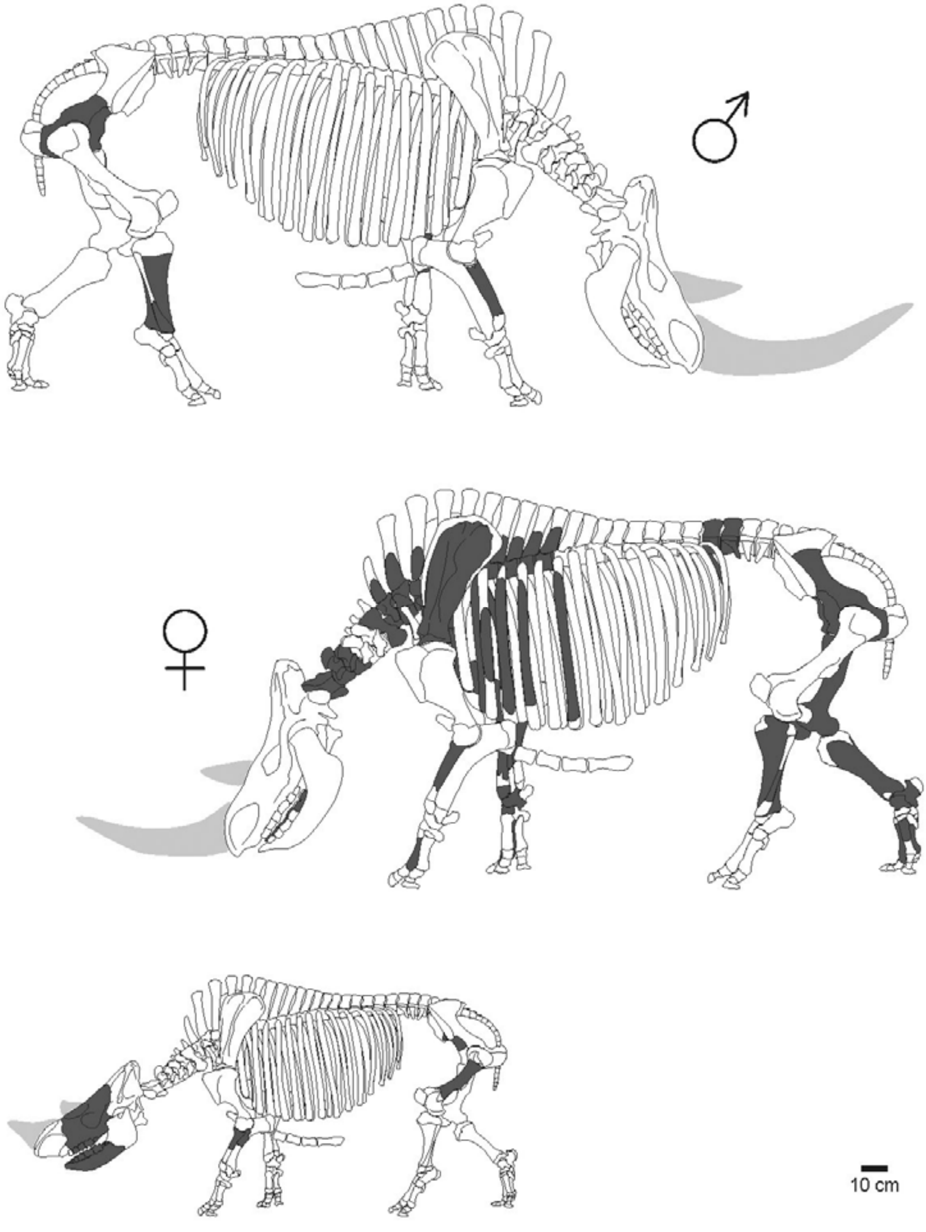

Figure 4. Skeletal elements represented (red) from adult male, female, and a juvenile individual from the hyena open air deposit at Bad Wildungen-Biedensteg near (Hessia, NW-Germany) (Graphics PaleoLogic).

teeth on both sides are present (fig. 5.1c). Both pm4's are breaking through the jaw, whereas the M^1's were unerupted. These molars are not present but the alveolar groves are well visible. The stage of dental development indicates an individual age of about a one year old calf. This top skull was heavily damaged by the hyenas, especially at the front and the braincase. The latter shows a very interesting brain case opening from the occipital. The hyenas have cracked the skull from the posterior to successfully reach the brain. In addition to the bite marks resulting of the hyenas, there are also a series of thin, parallel long scratch marks on the right maxilla in the height of the pm_{2-4} that could be the result of other carnivores such as wolf or the arctic fox.

Both lower jaws (fig. 5.1d) correspond to the top skull which is proved by the identical milk dentition of the pm_{1-4} and the eruption state of the M_1. Both mandibles were cracked in the symphysis area by hyenas and show old fractures encrusted by caliche. Additionally they are lacking the rami and have very extensive typical chewing and gnawing marks (fig. 5.1e, g). The left mandible (fig. 5.1e-f) contains the pm_{1-4} and the M_1. The right mandible (fig. 5.1g-h) was damaged by the excavations which damaged the anterior part including the pm_{1-2}. The missing rami and the preservation of the top skull without the jugals is a result of the hyena activity. The Ice Age spotted hyena cracked the lower jaws out of the joints, whereas the jugals and the rami were destroyed later.

Other cranial material was described and partly figured by Jacobshagen (1963). He illustrated several lower jaw teeth of one individual (right P_{3-4}, M_1, and left M_{2-3}). The limited occlusal surface wear of the M^3 indicate an early adult animal. Therefore it is suggested, that these teeth belonged to the skeleton of the early adult female individual (see. fig. 4). It seems that the hyenas have cracked the lower jaws of this individual completely, while it is unclear what happened to the top skull. This pattern of isolated teeth of rhinoceros and other prey animals, especially horse, is common at cave den sites and is often attributed to complete upper and lower jaw destruction by hyenas. The only skeleton material hyenas can not digest are the teeth, therefore these were not destroyed by consumption.

Scapulae are represented by a single nearly complete left shoulder blade (fig. 6). Some left margins of the glenoid fossa that were destroyed by hyenas were restored. Bite marks were found only distally. Here the 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 different in preservational state and may have originated in a lower horizon. Chewing can not be documented on this second scapula.

One humerus is described by Jacobshagen; however, this can not be relocated. It was a right humerus that was chewn on the proximal articular end.

Ulnae are represented by four bones (figs. 7, 8) from different aged animals. The most juvenile, a neonate to early young animal, left ulna must have been articulated to a radius (Fig. 7.1). This allows comparison to an articulated right ulna/ radius from an early-adult to adult animal whose articular ends exhibits similar destruction by gnawing (fig. 7.2). This second articulation could belong to the female early adult rhinoceros, of which

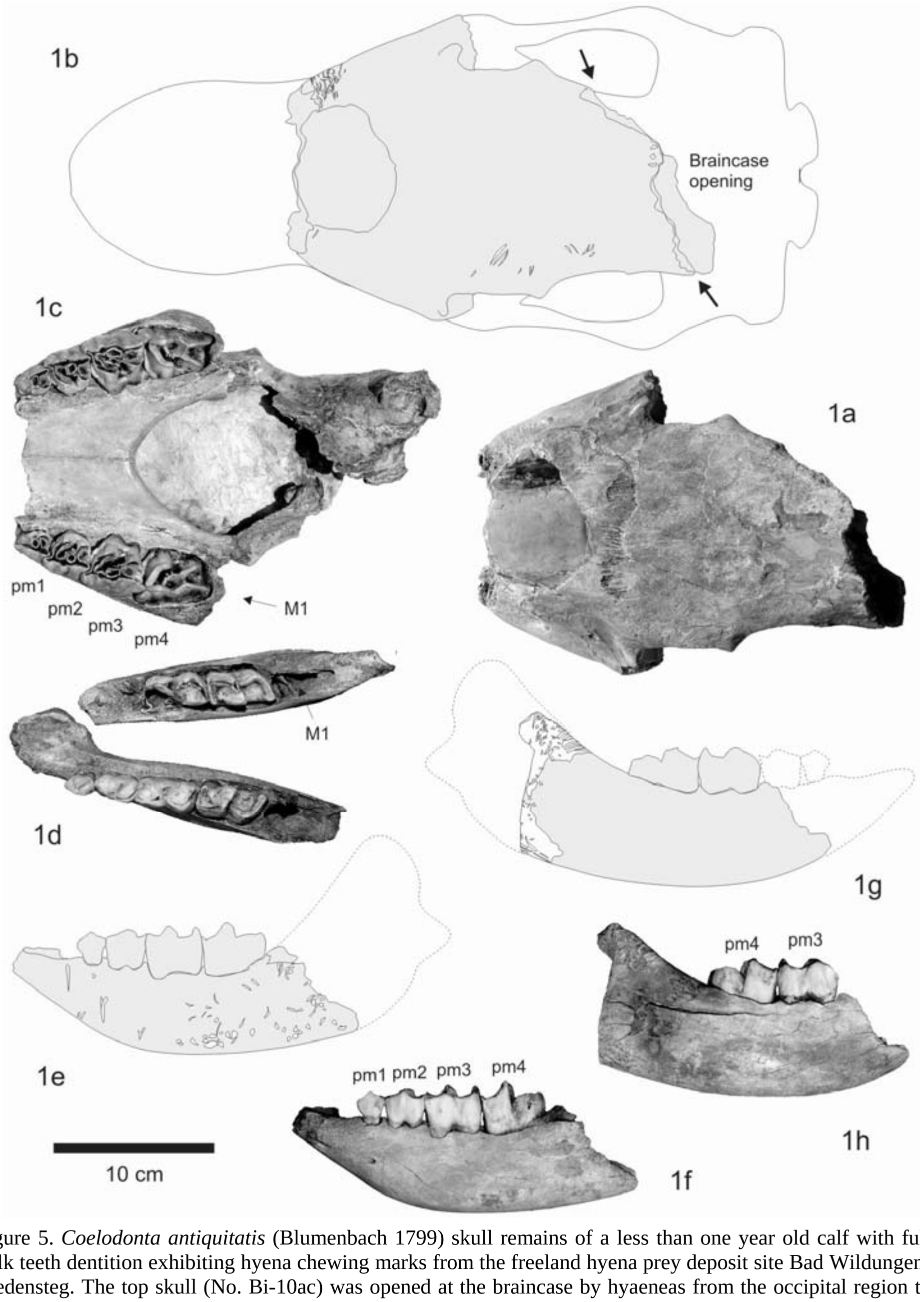

Figure 5. *Coelodonta antiquitatis* (Blumenbach 1799) skull remains of a less than one year old calf with full milk teeth dentition exhibiting hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. The top skull (No. Bi-10ac) was opened at the braincase by hyaeneas from the occipital region to reach the brain. 1a, c, d, h, and f. Photo. 1b, g, and e. Redrawing, 1a-c. Top skull, a-b. Dorsal, c. Ventral. 1d-f. Lower jaws (No. Bi-52/37 and 38), d. Dorsal, e-f. Lateral labial.

other bones were also found partly articulated.

The number of rhinoceros individuals at Biedensteg is estimated based on frequency of the radius (figs. 8, 9). At least seven radii were found, of which four are from an early adult to adult animals and the last from the calf. Five *C. antiquitatis* individuals can be demonstrated to have been utilized by carnivores or scavengers. One unfused, distal epiphysis, (fig. 9.4) could belong to a radius from the female animal.

Three femora are preserved, of which one is a fragment, a second from a juvenile animal (fig. 10.2), and a third from an adult *C. antiquitatis* (fig. 10.1). A fourth, heavily gnawed fragment may be part of the same individual, female early adult woolly rhinoceros, as the third. As described in Jacobshagen (1963) there was a right femur found in articulation with a tibia.

Only one nearly complete left patella (fig. 10.3) was excavated and could also belong to the female skeleton.

The tibia, which must belong to the femur and the female animal (fig. 11.1) has very typical nibbling marks and is in an early stage of destruction. Also this fits well to the partly articulated female skeleton, which was disrupted in connected body parts. Another tibia is very massive and has a robust shaft (fig. 11.2). Comparison suggests sexual dimorphic size differences with the stronger males and therefore the limb bones are more massive. The third tibia, from an adult female is comparable and shows similar destruction stage to the element illustrated in Figure 11.1, and therefore not illustrated here. The regularity in woolly rhinoceros long bone destruction, especially at the tibia, is notable. The proximal and the distal joints are initially gnawed cranially. Usually, the proximal end was consumed first. The distal end of the shaft in a middle stage of destruction exhibits two zones of destruction on the lateral and medial margins all three tibiae (fig. 11.1-2).

Two fibulae fragments are represented. One (fig. 11.3) is missing the proximal end as a result of the excavations. It was articulated to a tibia that also exhibited hyena chewing and could also belong to the female animal carcass. The distal part clearly shows long scratches. The second fibula was cracked away from a tibia and was heavily gnawed. Hyenas only left the middle shaft with bite marks on both ends (fig. 11.4).

Only single specimens of the astragalus and calcaneus are in the material (fig. 11.5-6). They clearly articulate, which is confirmed by many hyena scratch marks that cross both bones.

Here it is suggested that the bones, which must have been articulated by tendons and meat during its embedding belonged to the articulated hind leg of the female carcass.

Based on the descriptions in Jacobshagen (1963) there were three complete metatarsals (2-4) that would conform to the female skeleton, but it is unclear if they are from the right or left side.

The four pelvis remains are typical of hyena feeding (fig. 12). The acetabulum and surrounding areas were unmodified in three cases. Two of these acetabular fragments are from different animals. The one figured (fig. 12.4) has nice hyena and also arctic fox (?) or wolf (?) gnawing, and even nibbling marks of rodents (figs. 19B-C). The fourth pelvis is only a part of the ilium (fig. 12.1) and seems to belong to the

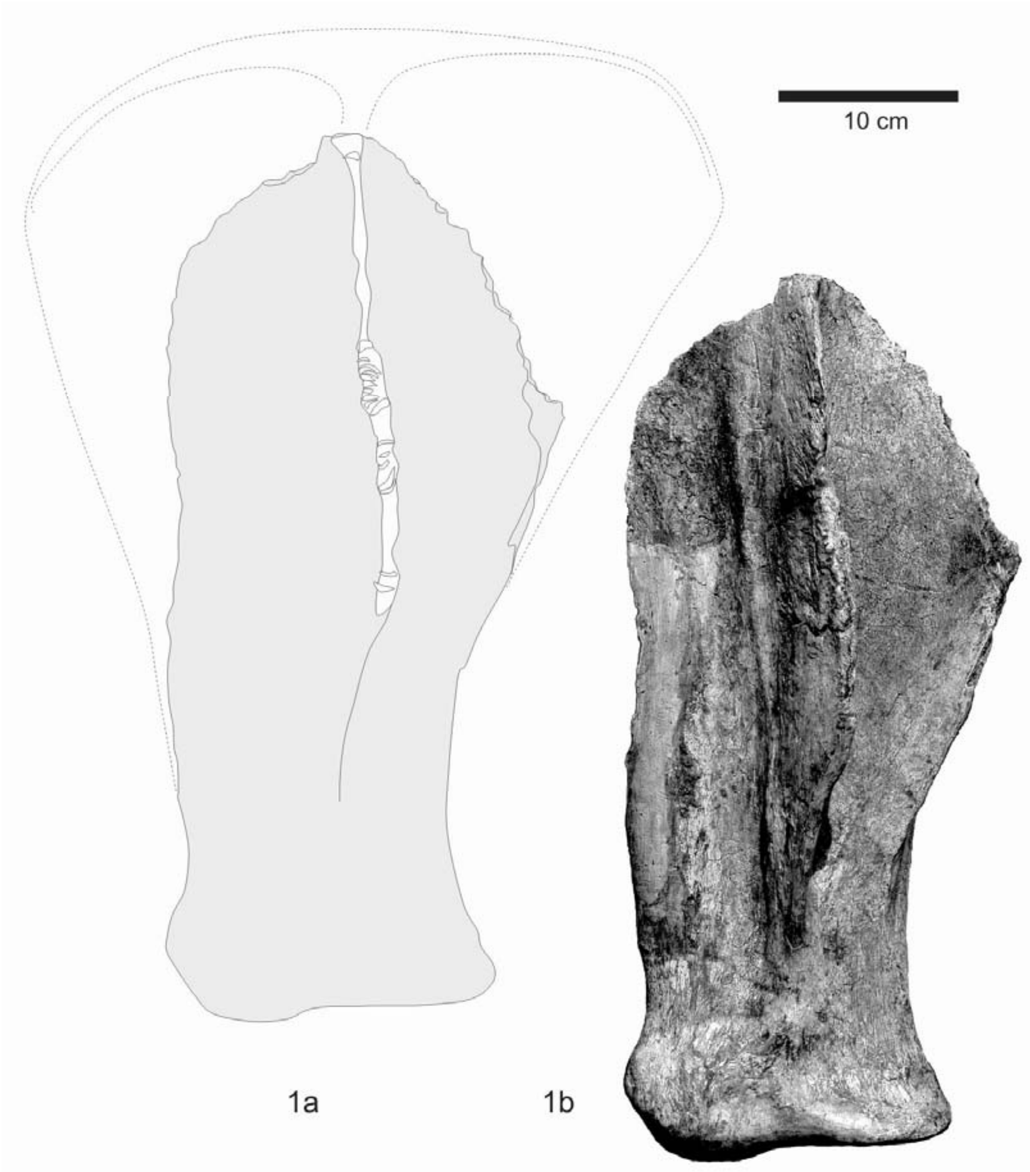

Figure 6. *Coelodonta antiquitatis* (Blumenbach 1799) scapula remains with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Left scapula from an adult individual (No. Bi-52/20), lateral, 2. First Phalanx of an adult animal (No. Bi-52/101), cranial view (Photos and graphics Paleologic).

juvenile animal, because it is also gnawn from the acetabular region, which is easy if the ileum, is not fused to the ischium and pubis. In young animals the soft articulation can be chewn away and produce the pattern illustrated by this bone. It is also strongly chewn at the soft distal part. The bites left a very irregular margin.

All vertebrae show the typical hyena chewing by the lacking of nearly all processes. They are all from one individual which is proved by different position, partly articulations and the similar degree of non-fusing of the caudal vertebra centrum discs. The cranial disc, in contrast, is fused completely in all recovered vertebrae. The first three cervical vertabra were found articulated (fig. 13.5). Atlas (fig. 13.1), axis (fig. 13.2) and the third cervical vertebra (fig. 13.3) have clearly defined bite marks on the heavily damaged transverse processes.

The next articulated group includes three vertebrae from the sixth cervical to the first thoracic (fig. 14.1) (this articulation includes cervical vertebra 6 [fig. 13.], 7 [fig. 14.1], and first thoracic vertebra [fig. 14.2]). They also lack most of their processes, especially the dorsal spines. The irregular margins, which are similar to other soft bone parts such as the scapula or the ilium margins, are show typical carnivore grawing damage. Two additional vertebrae discovered in articulation are the second (fig. 14.4) and third (fig. 14.5) thoracic vertebrae, both of which are heavily gnawed. (fig. 14.7). The fourth thoracaic vertebra (fog. 14.6) is represented by a centrum that was found dissarticulated. It was extensively modified by gnawing, with the neural arch having been completely consumed by hyenas. Parts on the left side were cut away by the excavation activities. The largest articulated vertebral segment consists of the sixth to ninth thoracic vertebrae (these four vertebrae are show in fig. 15.5). Typical of hyena scavenging, the dorsal spines of each of these is damaged (fig. 15.1-4). This is the result of feeding on the back musculature (M. spinalis, M. longissimus, M. cervicalis, and M. multifidus thoracalis, or M. errectus). With the destruction of this musculature it was possible to disarticulate parts of the vertebral column. Finally, the last thoracic (fig. 15.6) and first lumbar (fig. 15.7) vertebra were found in articulation (fig. 15.8). The first lumbar vertebra is lacking parts of the proc. transversi as a result of hyena feeding activities.

The ribs generally have no hyena bite marks, but obviously they were cracked out of the carcass thorax (fig. 16). All ribs have cracking fractures at both ends, therefore all articular surfaces are lacking. Such rib fragments are typical of carcasses in which hyenas entered the thoracic region to reach the intestines. At least one small rib fragment (fig. 16.8) has additional small bite marks on the distal end. Nibbling by a small carnivore such as a young hyena, a wolf or arctic fox is suggested by the pointed distal end. A small fragment was chewed by hyenas (fig. 16.9). The extensive feeding damage to the middle thorax area is demostrated by the paucity of the ribs (see fig. 4) from this area of the carcass. The rib fragments represented are from the anterior part around the forelimb, in addition to only a few from the last thoracic vertebrae.

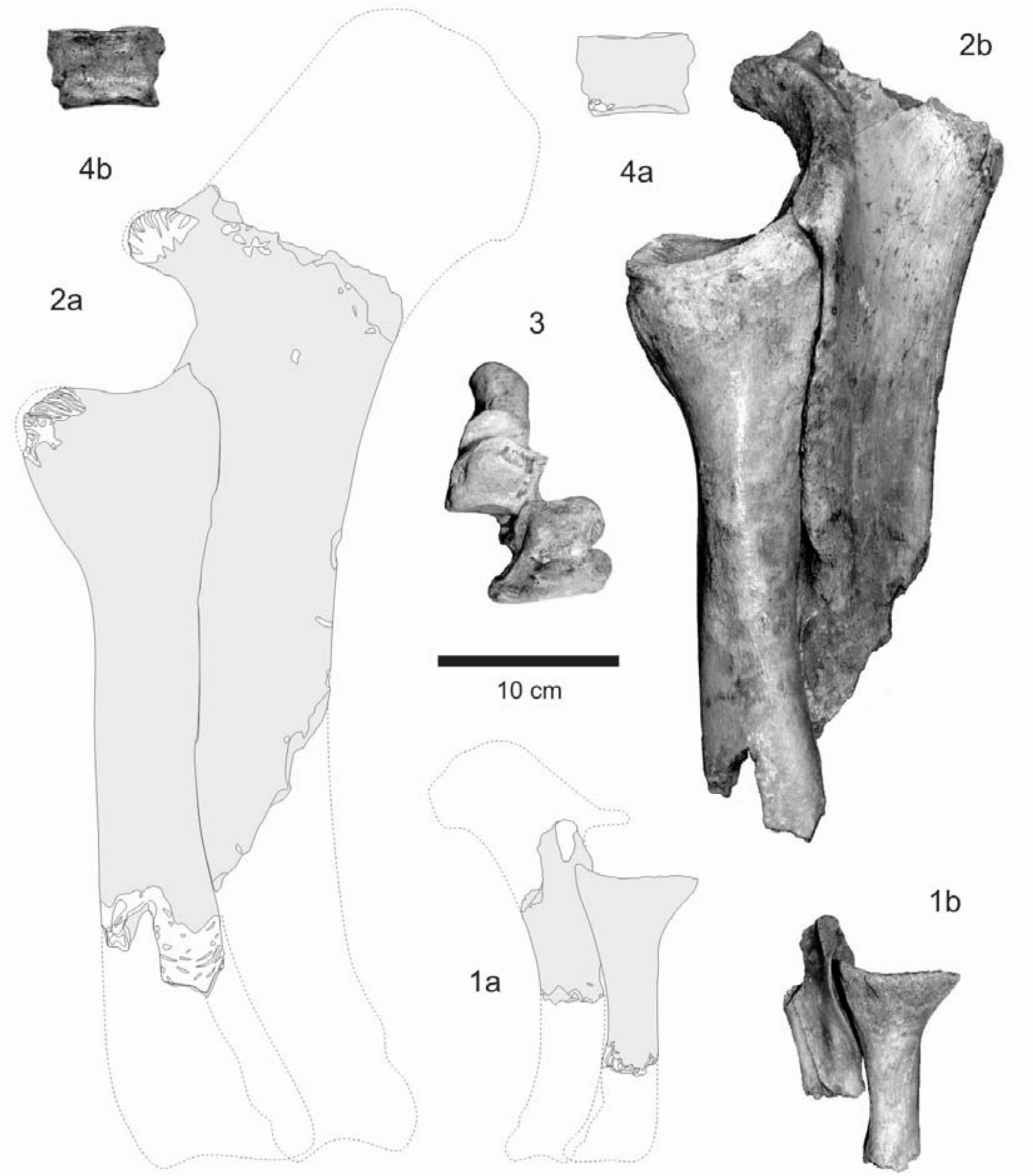

Figure 7. *Coelodonta antiquitatis* (Blumenbach 1799) forelimb remains with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Articulated left radius-ulna from a few months year young individual, possibly the calf (No. Bi-52/47 and 42), lateral. 2. Articulated right radius- and radius from an early adult female individual (No. Bi-52/111 and 116), lateral view (Photos and graphics Paleologic).

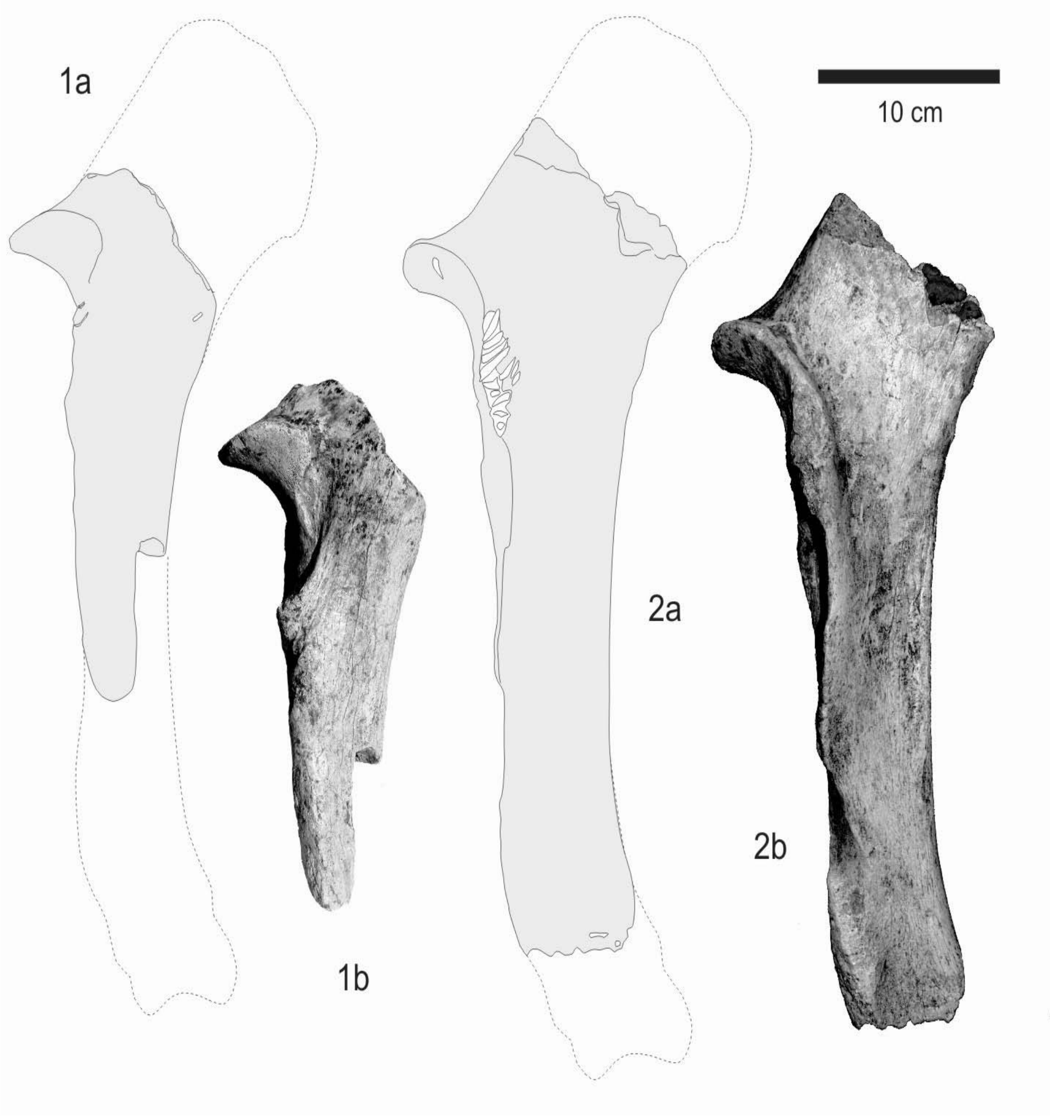

Figure 8. *Coelodonta antiquitatis* (Blumenbach 1799) forelimb remains (ulna) with hyena chewing marks from the open air hyena prey deposit site Bad Wildungen-Biedensteg.
a. redrawing, b. photo. 1. Right ulna from an adult female individual (No. Bi-10a), lateral. 2. Right ulna from an adult female individual (No. Bi-52/53), lateral (Photos and graphics Paleologic).

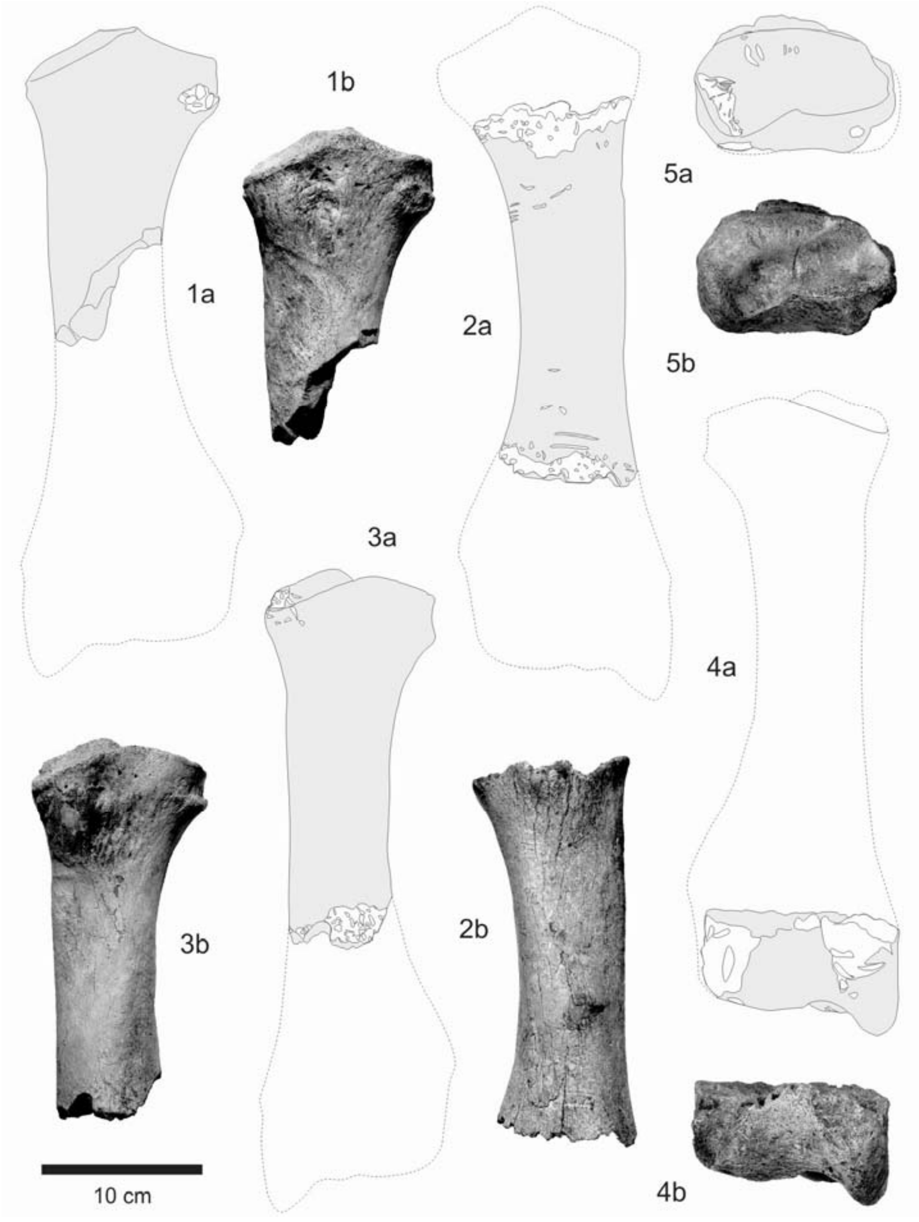

Figure 9. *Coelodonta antiquitatis* (Blumenbach 1799) forelimb remains with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Left radius from an adult male individual (No. Bi-52/30), cranial. 2. Right radius from an adult male individual (No. Bi-52/44), cranial. 3. Left radius from an adult female individual (No. Bi-52/49), cranial. 4. Right radius from an early adult female individual (No. Bi-52/224), cranial. 5. as 4, but in ventral view (Photos and graphics Paleologic).

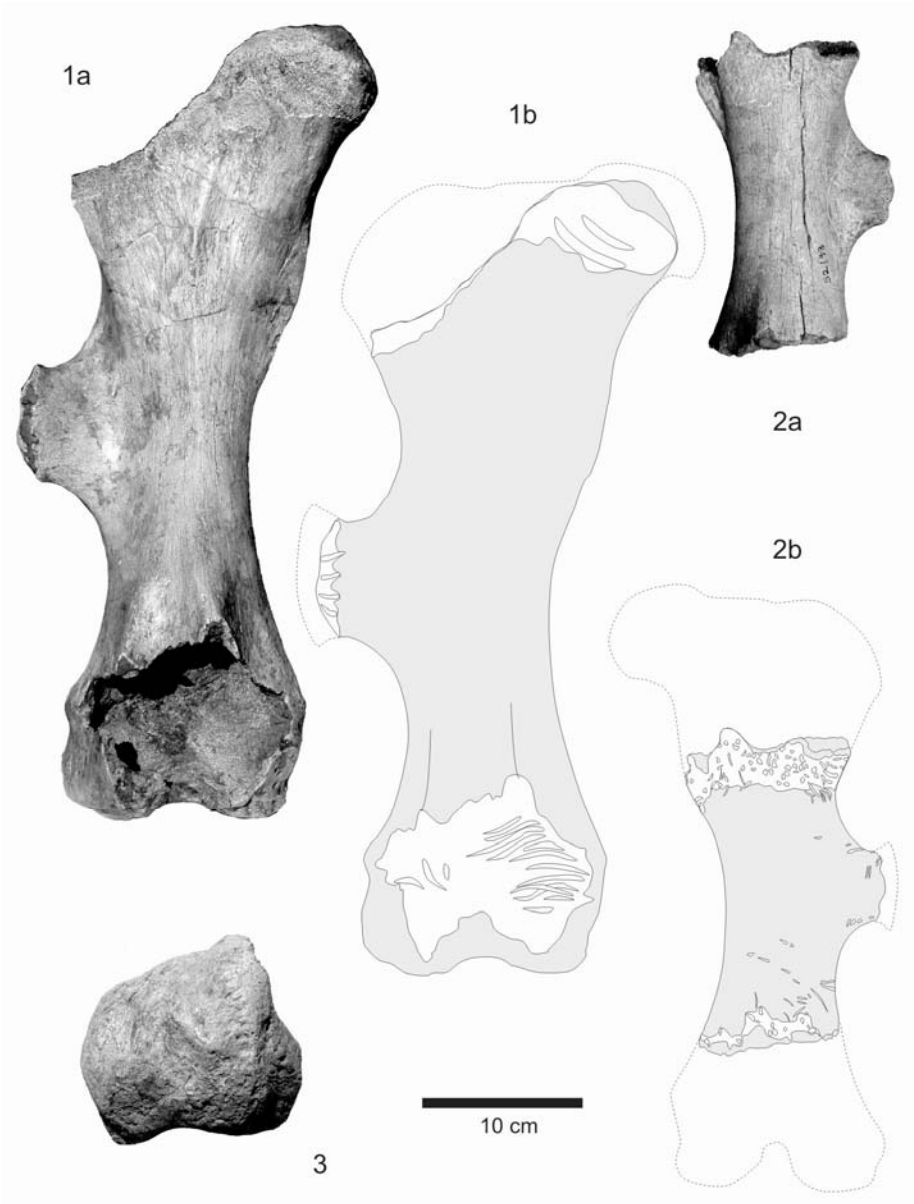

Figure 10. *Coelodonta antiquitatis* (Blumenbach 1799) hindlimb remains with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Right femur from an early adult to adult animal (No. Bi-10ab), 2. Left femur from a calf (No. Bi-52/43), 3. Right patella from an early adult to adult animal (No. Bi-52/228), all cranial (Photos and graphics Paleologic).

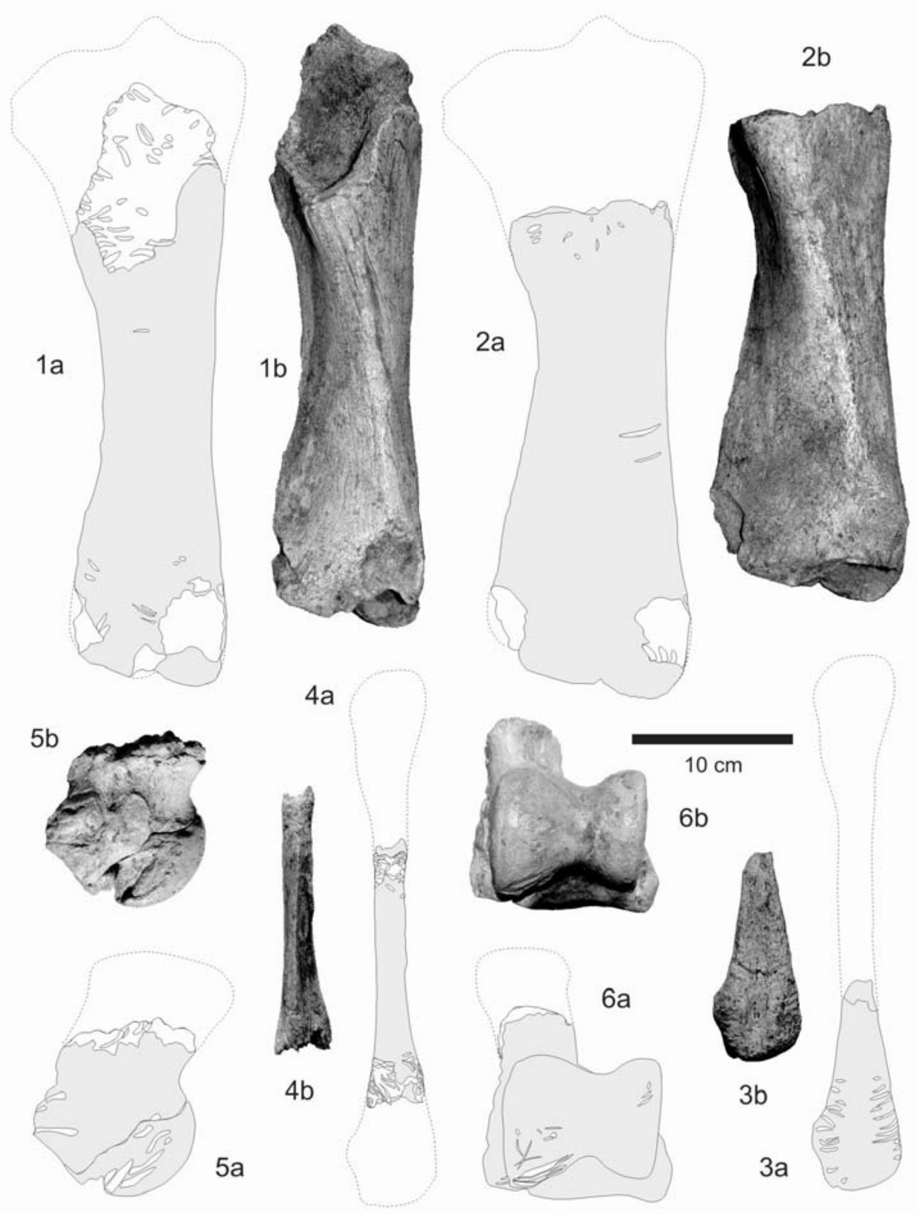

Figure 11. *Coelodonta antiquitatis* (Blumenbach 1799) hindlimb remains from an early adult to adult individual with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Right tibia from a female individual (No. Bi-52/7), cranial. 2. Right tibia from a male individual (No. Bi-52/201), cranial. 3. Left fibula (No. Bi-52/4), lateral. 4. Left fibula (No. Bi-52/16), lateral. 5 and 6. Articulated right calcaneus and astragalus (No. Bi-10f, g), 5. Lateral, 6. Dorsal (Photos and graphics Paleologic).

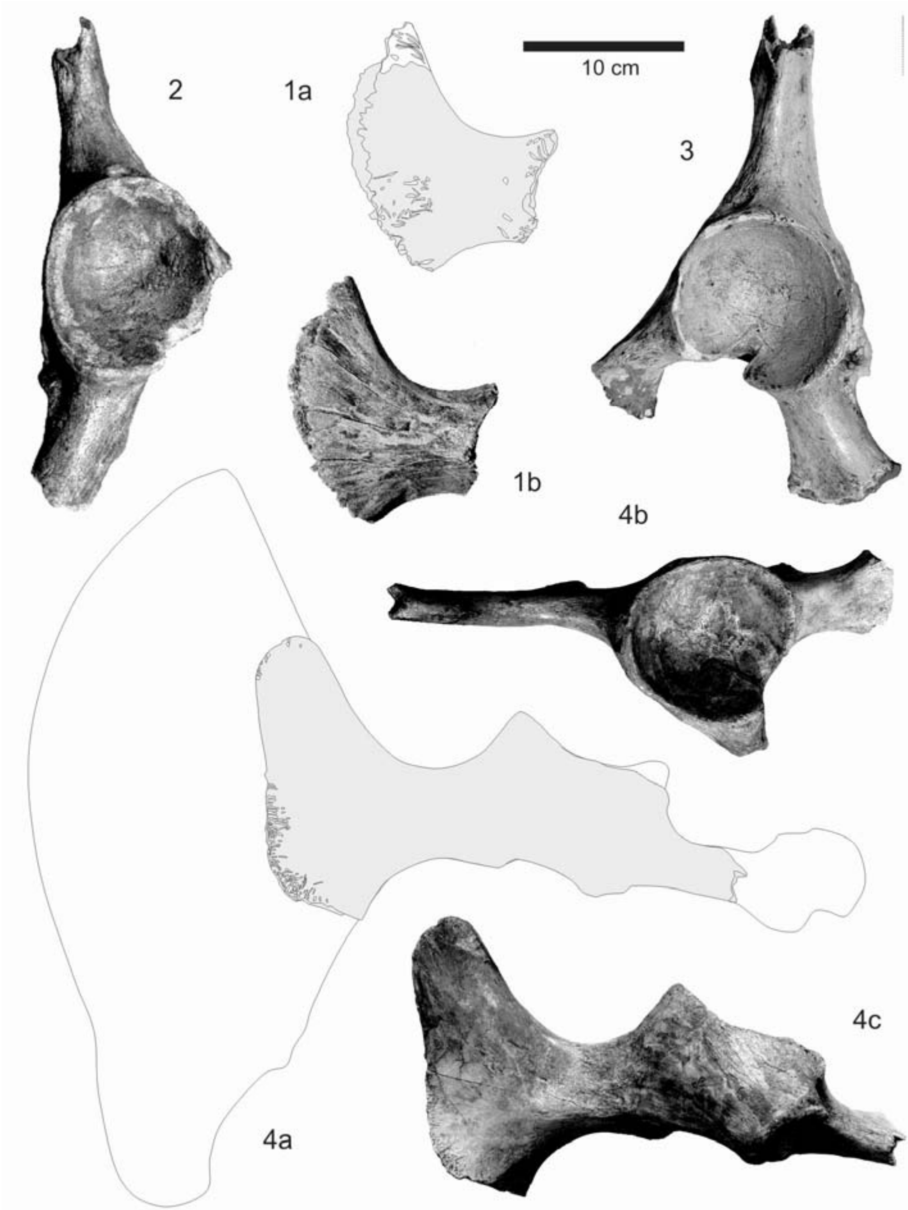

Figure 12. *Coelodonta antiquitatis* (Blumenbach 1799) pelvis remains with hyena chewing marks from the free-land hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Left ilium remain of a calf (No. Bi-52/13), lateral. 2. Right ilium remain of an adult individual (No. Bi-52/82), acetabular. 3. Left pelvic ilium remain of an adult individual (No. Bi-52/10e), acetabular. 4. Left pelvic remain with acetabulum of an early adult to adult individual (No. Bi-52/48), b. Acetabular, c. Lateral (Photos and graphics Paleologic).

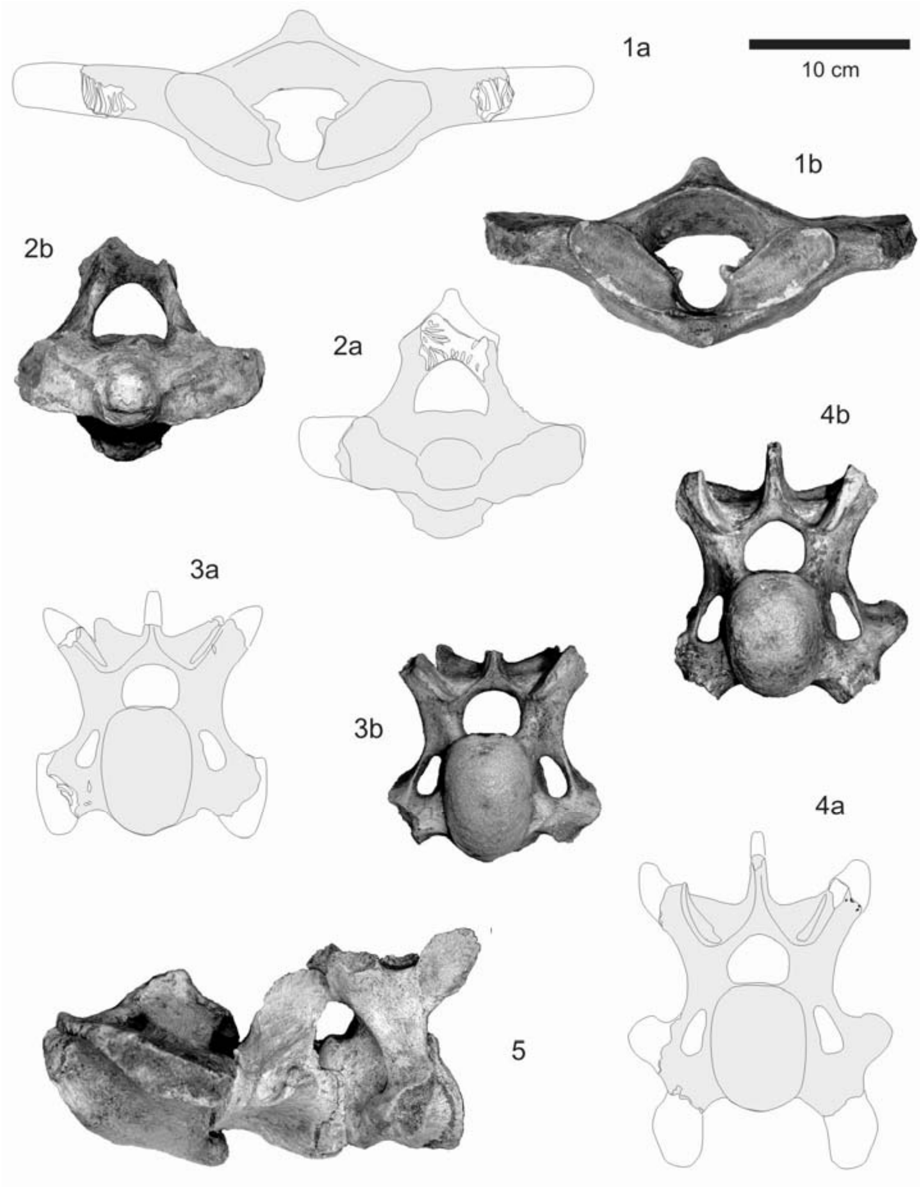

Figure 13. *Coelodonta antiquitatis* (Blumenbach 1799)-skeleton cervical vertebrae of an early adult individual with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. First cervical vertebra (atlas) (No. Bi-52/9), caudal. 2. Second cervical vertebra (axis) (No. Bi-52/1), cranial. 3. Third cervical vertebra (No. Bi-52/11), cranial. 4. Sixth cervical vertebra (No. Bi-52/107-1), cranial. 5. First to third articulated cervical vertebrae (No. Bi-52/9, 1, and 11), lateral (Photos and graphics Paleologic).

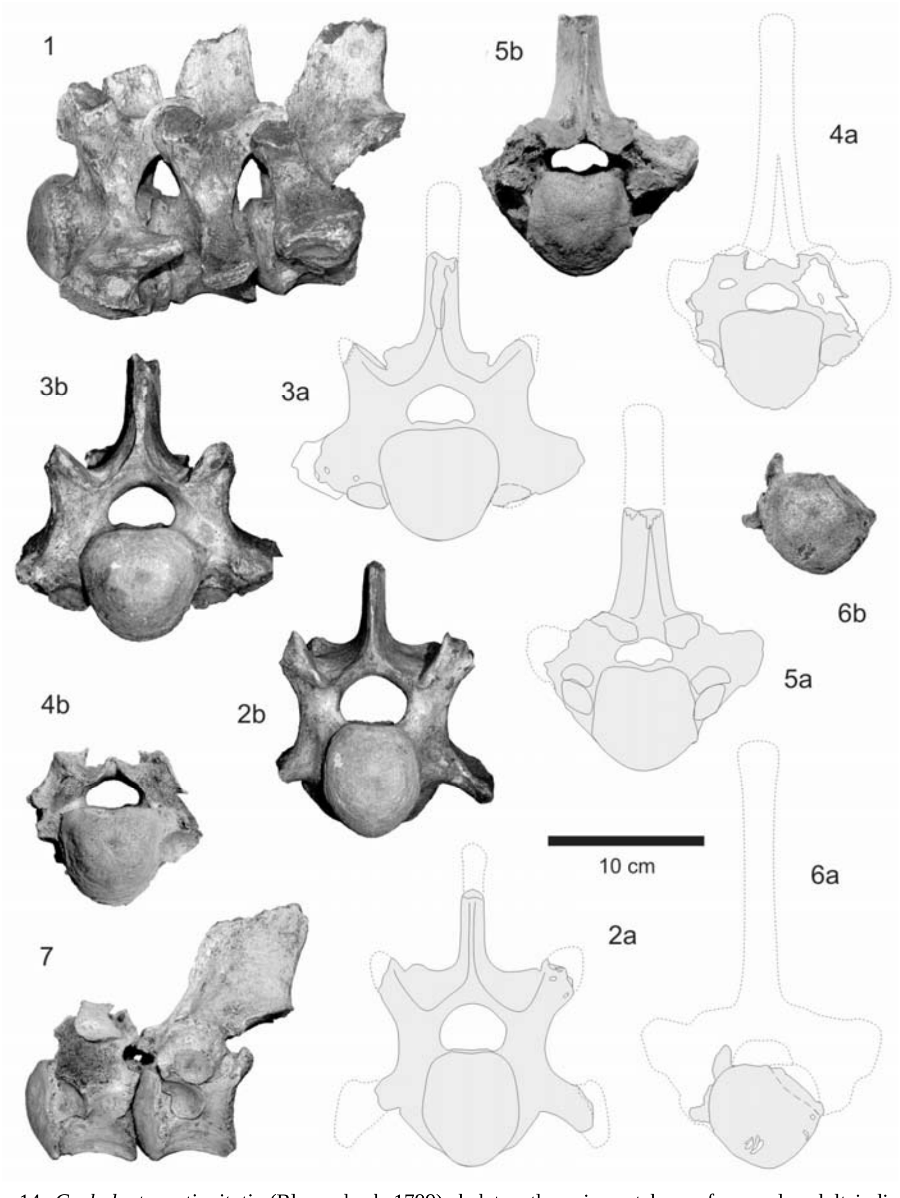

Figure 14. *Coelodonta antiquitatis* (Blumenbach 1799)-skeleton thoracic vertebrae of an early adult individual with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Articulated sixth cervical vertebra to first thoracic verteba (No. Bi-52/107-1 to 3), lateral. 2. Seventh cervical vertebra (No. Bi-52/107-2), 3. First thoracal vertebra (No. 108-3). 4. Second thoracic vertebra (No. Bi-52/10j). 5. Third thoracic vertebra (No. Bi-52/10m). 6. Fourth thoracal vertebra (No. Bi-52/152), all cranial. 7. Articulated second and third thoracic vertebrae (No. Bi-52/10j and m), lateral (Photos and graphics Paleologic).

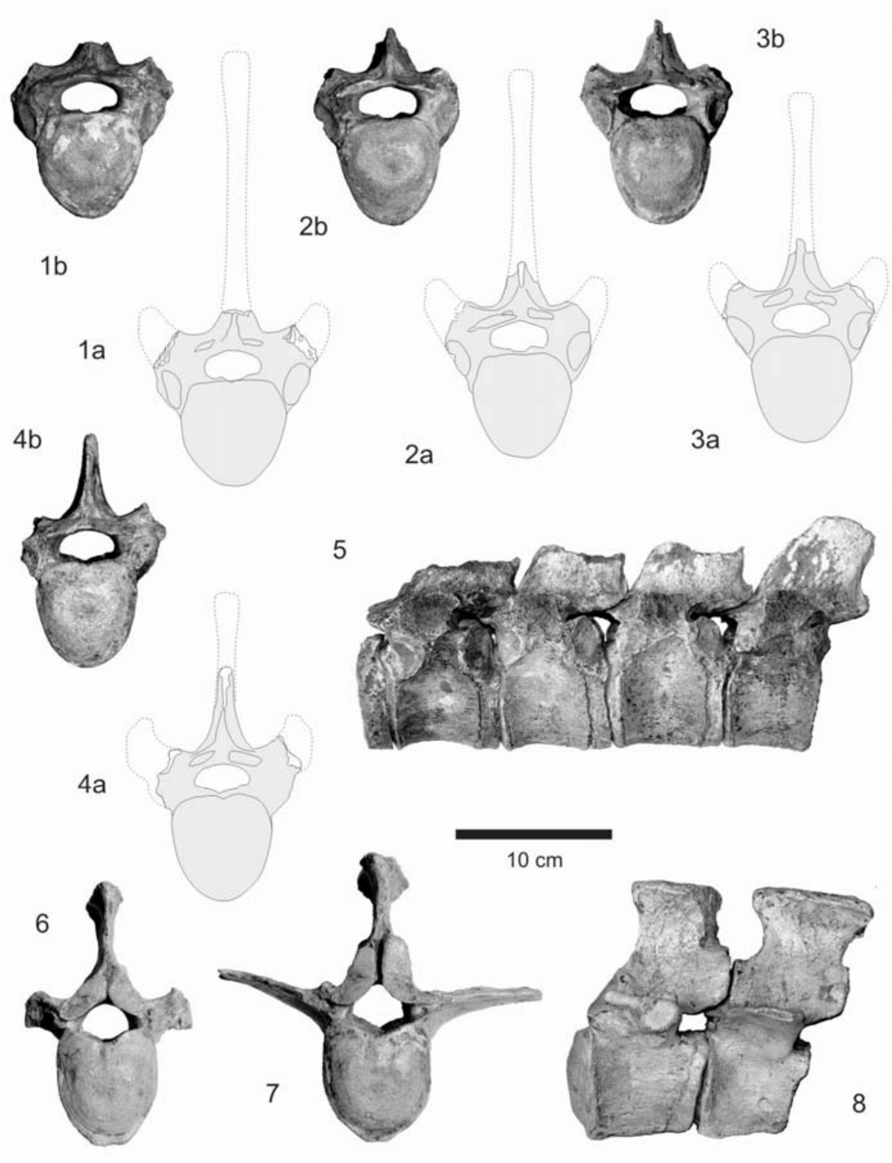

Figure 15. *Coelodonta antiquitatis* (Blumenbach 1799)-skeleton thoracic and lumbar vertebrae of an early adult individual with hyena chewing marks from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Sixth thoracic vertebra (No. Bi-52/107-1), cranial. 2. Seventh thoracic vertebra (No. Bi-52/107-2), cranial. 3. Eigth thoracic vertebra (No. Bi-52/107-3), cranial. 4. Ninth thoraic vertebra (No. Bi-52/107-4), cranial. 5. All four articulated sixth to ninth thoracic vertebrae of fig 1-4 (No. Bi-52/107-1 to 4), lateral, 6. Last thoracic vertebra (No. Bi-52/10l), cranial. 7. First lumbar vertebra (No. Bi-10h), cranial. 8. Articulated last thoracic and first lumbar vertebrae (No. Bi-52/10l and 10h), lateral (Photos and graphics Paleologic).

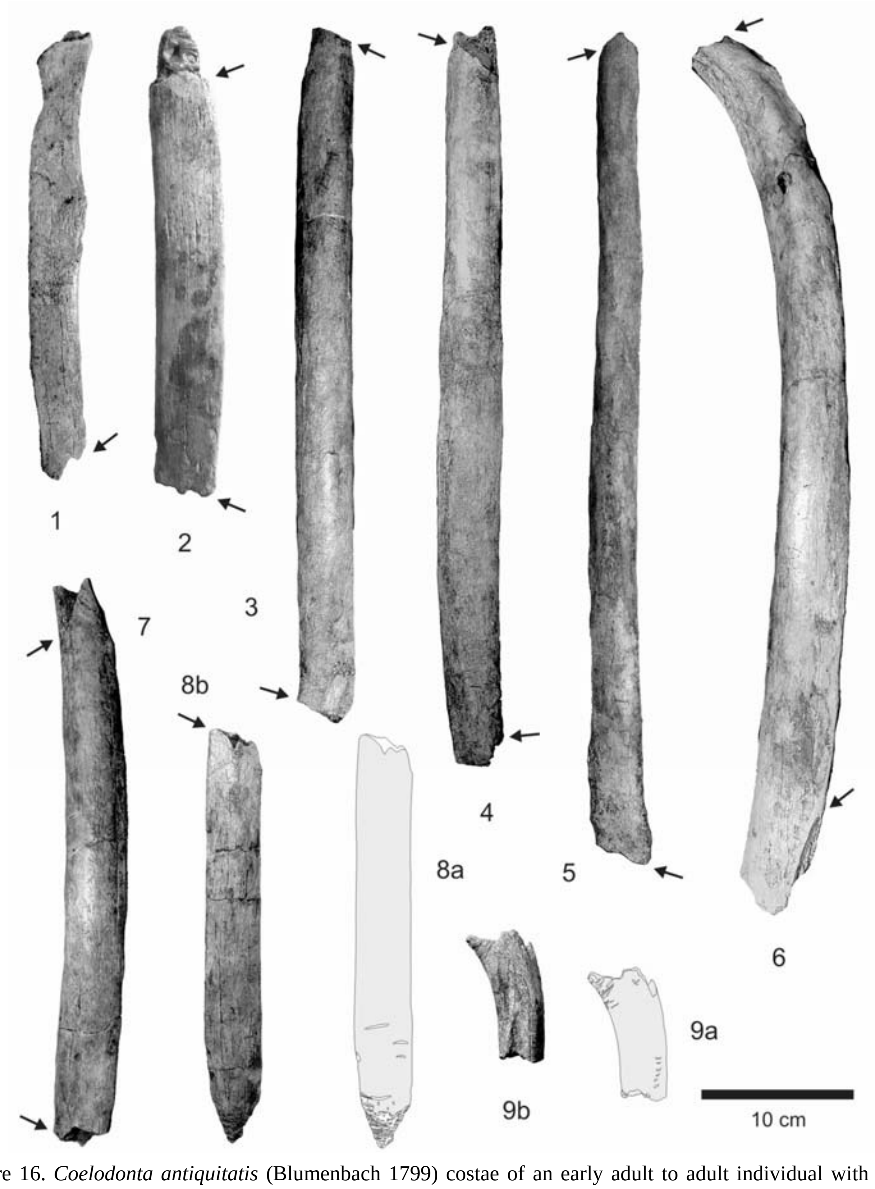

Figure 16. *Coelodonta antiquitatis* (Blumenbach 1799) costae of an early adult to adult individual with hyena cracking (arrows) and chewing marks of juvenile hyenas or other small carnivores from the freeland hyena prey deposit site Bad Wildungen-Biedensteg. a. redrawing, b. photo. 1. Posterior right rib fragment (No. Bi-10ad). 2. Anterior rib fragment (No. Bi-10v). 3. Middle right fragment (No. Bi-52/52). 4. Middle left fragment (No. Bi-52/156). 5. Middle left fragment (No. Bi-52/15). 6. Anterior left costa fragment (No. Bi-10q). 7. Anterior right rib fragment (No. Bi-52/100). 8. Anterior right rib fragment, distally chewn (No. Bi-52/3a). 9. Proximal rib fragment with chewing marks, (No. Bi-52/3) (Photos and graphics Paleologic).

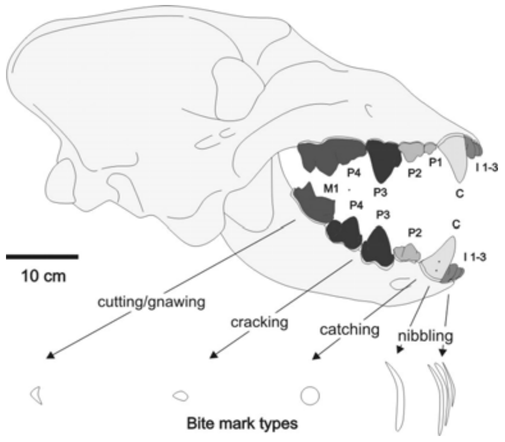

Figure 17. The dentition of the ice age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) and the resulting bite marks on prey bones. Long parallel scratches were found mainly in the spongiosa of the longbones. At the end of gnawed bone shafts boomer-ang and oval shaped grooves can be observed at the Biedensteg woolly rhinoceros bones (Graphics Pa-leologic).

Discussion

The freeland prey deposit site Bad Wildungen-Biedensteg must have been located at the margin of an ancient small lake and the Wilde River in a permafrost tundra or mammoth steppe landscape during the first maximum glaciation (Lower Weichsel, 65.000-90.000 BP). This flat lake or at least muddy area was in the centre of a large sinkhole structure, which was caused by subsurface dissolution of Zechstein salt. The sinkhole got freshwater influence by the early Wilde river. This is proved by some river freshwater fish remains, but also some other animals such as the common occurrence of frogs or water birds in the bone record (cf. Jacobshagen, 1963) which support a flat lake scenario. Such lakes were clearly important places, especially in summertimes of the arctic climate. In winter they were frozen completely and hyenas had no chance to deposit prey remains into the soil, or to get them out. The finds of juveniles such as the rhinoceros calf or the few weeks old hyena allow estimation of the hunting and main prey depositing activity time of the hyenas at Biedensteg as the late spring and short summer. At that time many animals used that area, which was muddy only in that season by the melting of the upper permafrost soil. The shallow lake was used by a variety of animals, such as the woolly rhinoceros, Przewalski horses, and other carnivores like cave bears for a water resource. The steppe iltis *Putorius eversmanni* mainly lived close to the water and seemed to have created prey deposits of fish, frogs and other animals around the lake, which could partly explain the rich anure microfauna.

The macrofauna of Biedensteg is dominated (53%) be the bones of the woolly rhinoceros *C. antiquitatis*. Isolated bone remains of woolly rhinoceros skeletons of the Upper Pleistocene are well known all over Europe from gravel pits close to rivers. They were also found submarine on the Doggerbank of the North Sea (e.g. Wüst, 1922, Borsuk-Bialynicka, 1973, Siegfried, 1983). Carcass remains, such as frozen animals in the permafrost floors of the Wrangle Islands or wax impregnated in Ukraina are very special finds (e.g. Tikhonov et al., 1999; Koenigswald, 2002). Most details of *Coelodonta antiquitatis* skeletons, skins and horns were known by the carcasses of the grounding wax impregnated animals from Ukraina (Kowalski, 2000). At least a skull find from the permafrost in Jacutia in the museum of St. Petersburg, and horns from Jakutsk have delivered anatomical details of

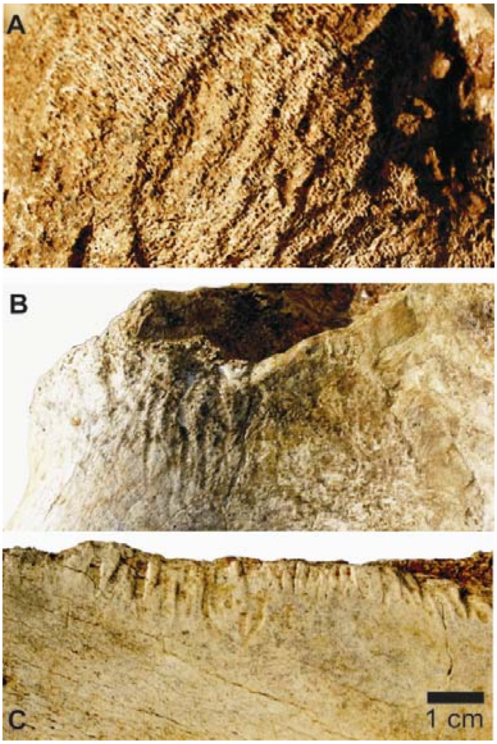

Figure 18. Bite mark types at the bones from Bad Wildungen-Biedensteg. **A.** Hyena bite scratches at the distal joint of a *C. antiquitatis* femur (No. Bi-10ab), **B.** Young hyena or artic fox scratch marks on the *C. antiquitatis* pelvis (No. Bi 52-48), **C.** Parallel and quadratic rodent nibbling marks on the same pelvis like B.

this extinct giant (cf. Koenigswald, 2002).

Articulated skeleton remains are relatively poorly represented in central Europe as a result of the carcass destruction by humans, animals, and fluvial transport by rivers. Two articulated skeletons from Belgium are displayed in the Museum of Natural History Bruxelles, a half skeleton of a juvenile individual from a Netherlands site can be found in the collections and exhibition of the Enschede Museum. Finally there was an incomplete skeleton of one adult rhinoceros excavated in Pohlitz (Löscher, 1906) that is not mounted in the Museum für Naturkunde Gera and as yet undescribed in detail. The one illustrared from Munich (in Kahlke, 1955) was lost during the World War 2. A mounted skeleton is displayed in Germany with original bones of different individuals and mixed *Bison* bones from the Westphalian sites Selm-Ternsche and Herten-Stuckenbusch in the Geologisch-Paläontologisches Museum der Westfälischen Wilhelms-Universität Münster. An anatomically correct cast was built up in the Museum für Ur- und Ortsgeschichte, Eiszeithalle Quadrat Bottrop by M. Walders (Fig. 19).

Recent descriptions of a nearly complete skeleton remain with well preserved ribs from a northern German site gave new detailed anatomical information (Diedrich, submitted a). An interesting feature of this skeleton is a partially healed rib fracture in the middle of the thoracic region, which could indicate fights between the rhinoceroses (Diedrich, 2005a) rather than carnivore attack.

However, articulated skeletons of *C. antiquitatis* are rare, as are even complete and well preserved isolated bones. The most important non-humanly induced woolly rhinoceros skeleton destruction is caused by the Ice Age spotted hyena *Crocuta crocuta spelaea*. In a first detailed study of a hyena *C. c. spelaea* cave den site, the Perick Caves in north-western Germany, the bone destruction and the importance of woolly rhinoceros as the prey of the hyenas was described (Diedrich, 2005b-h, 2006). The hyenas destroyed partially articulated carcass remains and every kind of bone, including top skulls, and moved legs and thoracal parts into their

Figure 19. Mounted composite skeleton cast of an Upper Pleistocene woolly rhinoceros *Coelodonta antiquitatis* (BLUMENBACH 1799) on display in the Museum für Ur- und Ortsgeschichte, Eiszeithalle Quadrat Bottrop. The original bones are from several Westphalian sites in Northwest Germany (especially the sites Herten-Stuckenbusch, and Selm-Ternsche) (Photo Paleologic).

cave den.

From freeland hyena deposit sites such bone destruction was not studied yet, and can be described and compared to the hyena cave dens in detail here for the freeland site Bad Wildungen-Biedensteg in comparison to the Perick caves.

It seems as if the bones of the two found partial skeletons of a calf and an early adult female *C. antiquitatis* (fig. 4) were deposited where the animals died, at the ancient Biedensteg Lake and muddy swamp. In contrast to other rhinoceros remains, the female and juvenile carcasses were destroyed by hyenas at the place. However, finally the vertebral column and other connected bones such as a right hind leg is the main argument for a woolly rhinoceros carcass, which was partly disrupted into pieces at the killing or death site. These body parts were found in different mud holes close together in the Biedensteg area. Therefore, skeletal elements such as the articulated vertebrae were not transported over long distances. Other remains of at least four more rhinoceros individuals and other prey remains were moved possibly from more far away by the Ice Age spotted hyenas. Such scenarios are described for Loess and a gypsum Karst site, at which articulated woolly rhinoceros remains with chewing marks were found (cf. Wernert 1968, Keller & Försterling 2002). The discovery positions of the bone accumulations indicate the deposit of these animal remains into soft mud along the lake shore. Biedensteg has both allochtonous (skeleton parts) and autochthonous (isolated bones) elements. One complete woolly rhinoceros carcasses of an animal that died at the lake was subsequently modified by the hyenas and other smaller carnivores were feeding on it. In other instances the hyenas moved prey remains, even collected reindeer antlers, into the mud possibly for consumption during times of lesser prey abundance.

An originally articulated right hind limb (femur and tibia fig. 10.1, tibia, astragalus and calcaneus, figs. 11.1, 11.5-6) and several articulated vertebrae (figs. 14.5, 15.1, 15.7, 16.5, 16.8) or forelimb bones such an ulna and radius (fig. 7.2) prove the original presence of one animal carcass which was dispersed. The carcass of the female *C. antiquitatis* must have lain on the right body side since more bones from that side are preserved (fig. 4). The upper skull is lacking, but it is likely that since all teeth of the lower jaw were found as isolated specimens, that the mandibles were completely destroyed by the hyenas. Maybe the upper skull was removed by the hyenas

Figure 20. Reconstruction of an Upper Pleistocene woolly rhinoceros *Coelodonta antiquitatis* (BLUMENBACH 1799) female with its joung calf in a mammoth steppe environment (production D. Luksch, Photo Paleologic).

or perhaps destroyed by the pit activities. They were feeding heavily on central carcass, where they cracked and removed all ribs and even vertebrae (cf. Fig. 4). In this area they can easily open the body to reach all internal organs, which are commonly eaten first. Other ribs were only cracked, but nearly all are lacking the proximal articular ends (fig. 17). The ribs were cracked for the opening the body cavity. The only distally chewn rib has very fine bite marks (fig. 10.8) that could have resulted from a juvenile hyena or perhaps other small carnivores such as a wolf or an arctic fox that were feeding on the carcass either before or after the hyenas. The long bone joints were not completely destroyed 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. The consumption of such a large amount of meat and bone could have taken some days, with the possibility of food utility of some bones lasting for several months.

The juvenile animal carcass was destroyed much more, or better to say mostly eaten by hyenas which left only a few longbones such as one femur and the articulated ulna/radius. The latter might also belong to another younger to few weeks old animal and not to the nearly one year old calf. The problem of an exact age at death estimate of the individual is due to the non-documantation or presence and description of neonate and very young individuals. Currenly, there is no articulated skeleton described from a neonate *Coelodonta*. However, very interesting is the braincase opening of that juvenile rhinoceros (Fig. 5.1). Prior to this cranial damage, the lower jaws were broken out of their joints. The right mandible is modified by hyenas on the ramus after the lower jaw was cracked out of the top skull (Fig. 5.1d). The braincase was opened from the occipital region to access the brain. The snout was nearly completely consumed and only the middle section of the maxillia with all teeth was left. This skull is one of the few known juvenile upper skulls in Europe with full milk dentition, and the only one which shows such a degree of hyena feeding destruction.

Certainly the active hunting of woolly rhinoceroses by packs of hyenas should be considered because at Bad Wildungen-Biedensteg the skeletal remain of a few month old animal, an early adult and, only few years old female were found, all mostly disarticulated by the carnivores, primary by hyenas. Remaining bones show, on the one hand, typical gnaw and nibbling marks of the hyaenes, but the pelvis has additionally tooth marks of the polar fox (*Alopex lagopus*) or wolf (*Canis lupus*), and also of rodents (mice etc.) which left characteristic small, parallel grooves. A hunt of young woolly rhinoceroces by the hyaenes is also discussed for the hyena den site Perick caves (Diedrich, 2007), where similar bones from a less than one year old rhinoceros were found. However, the hyenas were feeding extensively on *C. antiquitatis*, which was for sure one of the most important prey. The consumption of that prey is also documented in many small bone-spongiosa remains, which were isolated from several hyena coprolites at that site (Diedrich, submited b).

The percentage of the bone remains represented at the site Bad Wildungen-Biedensteg (Fig. 22) do not reflect the real percentages of the prey taken. It is more, such as in the Perick Caves (Diedrich 2005a-h, 2007), a result of a complex series of taphonomy pathways. The bones of the woolly rhinoceros are extremely massive, and in contrast to nearly all other large mammal bones completely filled with the spongiosa. Therefore, the long bones were difficult, or better to say impossible to crack. The hyenas always left the bone shaft of longbones or massive bones. The spongiosa itself has a high nutrition value with its bone marrow cells. Such spongiosa remains were quite often found in the *Crocuta* coprolites at the Bad Wildungen-Biedensteg site (Diedrich, submitted b). This is the main reason why hyenas preferentially consumed the joints and left deep cavities in the longbones. As a result, the spongiosa shows the best preserved scratch and bite marks of *Crocuta*. In nearly every ice age mammal bone collection, the woolly rhinoceros bones and the mammoth bones often have these distinctive hyena chewing marks.

It might be that the juvenile rhinoceros calf belonged to the early adult female -- maybe it was her calf. Why she died is unclear, but a lonely unprotected calf would have been easy prey for hyenas. Different speculations can be developed. The female was at the water place with her few weeks or months old juvenile. Given the age of the calf, it must have been late spring to early summer where both were walking to the lake or Wilde River. Here, however, the prime-aged female died. It could have been a desease. She could have fallen prey to steppe lions, or she tried to protect her calf against an attack of a large hyena clan and was the first victim. The lonely calf was then the second easy prey. Alternatively, maybe both animals are not associated and were found as carcasses on the lake shore by the *C. crocuta spelaea* as a result of separate, unrelated mortality events.

Figure. 21. Scenario of the feeding of ice age spotted hyenas on a woolly rhonoceros carcass in the mud at Bad Wildungen-Biedensteg (this illustration is of recent spoted hyena *Crocuta crocuta* feeding on a large mammal carcass).

The freeland site Bad Widlungen Biedensteg has produced only a very few mammoth bones (2% of the prey bones), which were for sure moved by hyenas. Mammoth long bones are more difficult to move over long distances, but as shown for the Perick Cave den site this prey is normally represented by high numbers of bones, only a few less than those of the woolly rhinoceros. At Biedensteg, the mammoth is very poorly represented; therefore something like a specialization on feeding onto *C. antiquitatis* can be suggested. Possibly the mammoth was not common in this middle elevation mountainous area. They preferred the flatlands and regions of large river valleys.

The second most important prey remains are from the steppe bison and Przewalski horses (fig. 22), but reindeer, red deer and giant deer are also well represented, all with 5-12% of the prey remains. Carnivores are also in the feeding spectrum of the hyenas, which is documented by the unusual find of a pregnant cave bear female that is described in detail in Diedrich (2006). Finally, the large number of *C. c. spelaea* bone remains (excluding the very common coprolites) is typical for hyena den and freeland sites. Bone fragments of the bone compacta and even of the spongiosa are frequent in the Biedensteg coprolites. The spongiosa could

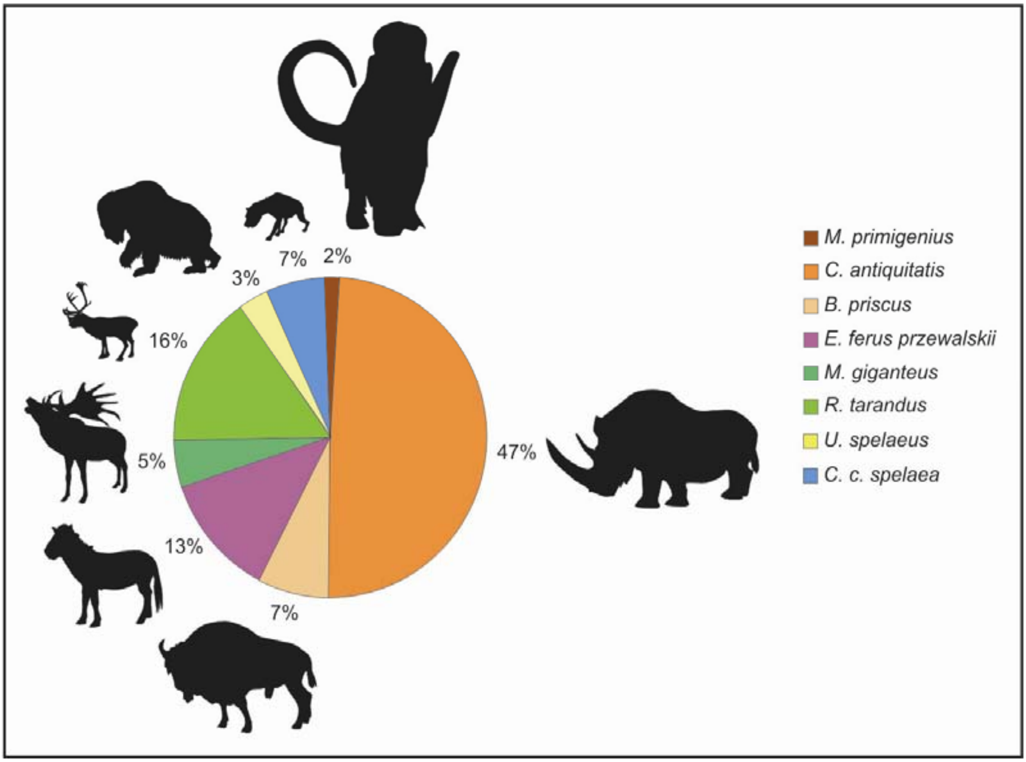

Figure 22. Percentages (n = 152 bones) of the hyena prey at Bad Wildungen-Biedensteg. Woolly rhinoceros is clearly dominant, in part a result of one calf and one female individual skeleton carcass remains, and due to the more resistant bones of *C. antiquitatis*. The hyenas are interpreted to have fed primarily on wooly rhinoceros at the Biendensteg site (Graphics PaleoLogic).

be mostly from the woolly rhinoceros bones. The result of hyena cannibalistic behaviour are indicated by the remaining cranial bones, whereas the postcranial are nearly lacking completely (Diedrich submitted b).

Bad Wildungen-Biedensteg is the first well studied freeland site at which the Ice Age spotted hyena *Crocuta crocuta spelaea* used an area with a family clan for hunting, as both a predation area and as a living zone.

Future excavations at that site should be directed toward documenting the bone taphonomy in detail to map bone accumulations, hyena excrements, and all other information to get a more detailed picture about the life of that extinct carnivore and its prey.

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No.	Coll.-No.	Bone type	Commentary	left	right	Age	Bite marks	Original	Collection
1	10ac	Cranium	Middle part with pm 1-4 dentition			Early juvenile	x	x	A
2	52/37	Lower jaw	Milk dentition, with pm 3-4		x	Early juvenile	x	x	A
3	52/38	Lower jaw	Milk dentition, with pm 1-4	x		Early juvenile	x	x	A
4	Ma 1	Dens	Milk tooth, upper jaw			Early juvenile		Mentioned in Jacobshagen 1963	B
5	Ma 2	Dens	Milk tooth, upper jaw			Early juvenile		Mentioned in Jacobshagen 1963	B
6	Ma 3	Dens	Milk tooth, upper jaw			Early juvenile		Mentioned in Jacobshagen 1963	B
7	Ma 4	Dens	P3		x	Early adult		Jacobshagen 1963	B
8	Ma 5	Dens	P4		x	Early adult		Jacobshagen 1963	B
9	Ma 6	Dens	M1		x	Early adult		Jacobshagen 1963	B
10	Ma 7	Dens	M2	x		Early adult		Jacobshagen 1963	B
11	Ma 8	Dens	M3	x		Early adult		Jacobshagen 1963	B
12	52/20	Scapula	Without distal joint	x		Adult	x	x	A
13	52/200	Scapula	Incomplete		x				A
14	52/88	Scapula	Fragment						A
15	Ma 9	Humerus			x	Adult		Mentioned in Jacobshagen 1963	B
16	52/47, 42	Ulna/Radius	Shafts, articulated	x		Juvenile	x	x	A
17	52/116, 111	Ulna/Radius	Shafts, articulated		x	Early adult	x	x	A
18	52/53	Ulna	Shaft		x	Adult	x	x	A
19	10a	Ulna	Shaft		x	Adult	x	x	A
20	52/49	Radius	Without distal joint	x		Adult	x	x	A
21	52/44	Radius	Shaft		x	Adult	x	x	A
22	52/30	Radius	Proximal joint	x		Adult	x	x	A
23	52/224	Radius	Distal joint		x	Early adult	x	x	A
24	10a	Radius	Proximal joint		x	Adult	x	x	A
25	Ma 10	Intermedium	Nearly complete			Adult		Mentioned in Jacobshagen 1963	B
26	Ma 11	Carpale 3	Nearly complete			Adult		Mentioned in Jacobshagen 1963	B
27	Ma 12	Metacarpal 3	Nearly complete			Adult		Mentioned in Jacobshagen 1963	B
28	Ma 13	Metacarpal 3	Nearly complete			Adult		Jacobshagen 1963	B
29	52/101	Phalanx	Complete			Adult		x	A
30	52/43	Femur	Shaft	x		Juvenile	x	x	A
31	52/153	Femur	Shaft, fragment	x					A

No.	Coll.-No.	Bone Type	Commentary	left	right	age	Bite marks	Original	Collection
32	10ab	Femur	Incomplete		x	Adult	x	x	A
33	52/228	Patella	Complete		x	Adult		x	A
34	52/7	Tibia	Incomplete		x	Adult	x	x	A
35	52/201	Tibia	Without proximal joint		x	Adult	x	x	A
36	10c	Tibia	Incomplete	x		Adult	x	x	A
37	52/4	Fibula	Distal joint	x		Adult	x	x	A
38	52/16	Fibula	Shaft	x		Adult	x	x	A
39	10f	Calcaneus	Incomplete		x	Adult	x	x	A
40	10g	Astragalus	Incomplete		x	Adult	x	x	A
41	Ma 14	Metatarsal 2	Proximal joint			Adult		Mentioned in Jacobshagen 1963	B
42	Ma 15	Metatarsal 3	Nearly complete			Adult		Mentioned in Jacobshagen 1963	B
43	Ma 16	Metatarsal 4	Nearly complete			Adult		Mentioned in Jacobshagen 1963	B
44	52/48	Pelvis	Incomplete	x		Adult	x	x	A
45	52/82	Pelvis	Incomplete		x	Adult	x	x	A
46	52/13	Pelvis	Ilium, fragment	x		Adult	x	x	A
47	10e	Pelvis	Incomplete	x		Adult	x	x	A
48	52/9	Cervical vertebra	Atlas			Early adult	x	x	A
49	52/1	Cervical vertebra	Axes			Early adult	x	x	A
50	52/11	Cervical vertebra	No. 3			Early adult	x	x	A
51	52/107-1	Cervical vertebra	No. 6			Early adult	x	x	A
52	52/107-2	Cervical vertebra	No. 7			Early adult	x	x	A
53	52/107-3	Thoracal vertebra	No. 1			Early adult	x	x	A
54	10m	Thoracal vertebra	No. 2			Early adult	x	x	A
55	10j	Thoracal vertebra	No. 3			Early adult	x	x	A
56	52/152	Thoracal vertebra	Centrum, No. 4			Early adult	x	x	A
57	52/108-1	Thoracal vertebra	No. 6			Early adult	x	x	A
58	52/1808-2	Thoracal vertebra	No. 7			Early adult	x	x	A
59	52/108-3	Thoracal vertebra	No. 8			Early adult	x	x	A
60	52/108-4	Thoracal vertebra	No. 9			Early adult	x	x	A
61	10l	Thoracal vertebra	No. 18			Early adult	x	x	A
62	10h	Lumbal vertebra	No. 1			Early adult	x	x	A
63	52/3	Costa	Fragment				x	x	A

No.	Coll.-No.	Bone Type	Commentary	left	right	age	Bite marks	Original	Collection
64	52/5	Costa	Fragment						A
65	52/156	Costa	Fragment			Early adult			A
66	52/58	Costa	Anterior, 2, Distally incomplete	x		Early adult			A
67	52/57	Costa	Middle, approx. 6 to 8	x		Early adult	x	x	A
68	52/52	Costa	Middle, approx. 4-6		x	Early adult	x	x	A
69	52/15	Costa	Middle, approx. 7-9	x		Early adult	x	x	A
70	52/100	Costa	Anterior, approx. 2-3		x	Early adult	x	x	A
71	52/3a	Costa	Anterior, approx. 3-4		x	Early adult	x	x	A
72	10q	Costa	Anterior, approx. 4-6	x		Early adult	x	x	A
73	10v	Costa	Anterior, approx. 3-4	x		Early adult	x	x	A
74	10ad	Costa	Posterior		x	Early adult	x	x	A

Appendix 1. Bone material list of *Coelodonta antiquitatis* (Blumenbach 1799) from the open air prey deposit site Bad Wildungen-Biedensteg (Hessia, NW-Germany).

A, Rudolf-Lorenz-Stiftung
B, University Marburg