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Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) populations from the Emscher River terrace open air hyena den near Bottrop and other sites in NW Germany: Their bone accumulations along rivers in lowland mammoth steppe environments and scavenging activities on woolly rhinoceros

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A B S T R A C T

Crocuta crocuta spelaea (Goldfuss, 1823) remains (NISP = 50) are present in the early to middle Upper Pleistocene Emscher River terrace open air den site along the Rhine–Herne Canal near Bottrop (Westphalia, NW Germany). The population includes bones from cubs and bones with pathological features from old animals but is predominantly made up of adult hyenas (NISP = 3820) found within the glacial mammoth steppe fauna of the Münsterland Bay Lowlands. A larger quantity of woolly rhinoceros (*Coelodonta antiquitatis*) bones (NISP = 1601) are present than in other bone-rich open air hyena den sites, of which about 67% are damaged. This damage can be shown to have resulted mainly from hyena activities, and shows repetitions of the same three stages of destruction on the massive woolly rhinoceros bones. Those bone shafts that the hyenas were unable to break were left with irregular jagged margins. The taphonomy of bones from the Bottrop open air site indicates that the rhinoceros body parts had only been transported over short distances, in contrast to those from the Perick Caves hyena den where longer transport distances resulted in a higher proportion of limbs compared to other body parts. The large woolly rhinoceros was an important second megafauna prey for hyenas in the lowland areas (after the woolly mammoth), in contrast to the nearby Sauerland Karst mountain areas that are rich in hyena dens and their associated bone assemblages, although the higher proportions of rhinoceros bones present is also to some extent a result of the incomplete destruction of their massive bones. The proportions of woolly mammoth and woolly rhinoceros remains in the hyena prey bone assemblages gradually decrease from the lowlands towards the nearby Sauerland Karst mountain regions. In these mountainous boreal forest regions cave bears were instead the main food source for hyenas, as result of the scarcity or absence of mammoth steppe fauna. The large bone accumulations along the Emscher River terraces near Bottrop can mostly be attributed to the activities of hyenas, which were responsible for the repeated incomplete state of bone preservation. The bone accumulations are predominantly of leg bones and include a relatively high proportion of hyena bones which, together with the faunal composition and the size of the accumulations, indicate a mixed long-term use of the terraces along the Emscher River as an extensive communal hyena den and prey storage site, and also probably somewhere in the area, as a birth den. Some of the bone material may also have been accumulated by natural processes, or even by Neanderthals.

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1. Introduction

Upper Pleistocene hyena den sites had already been recorded 200 years ago in a number of central European caves, such as in the Zoolithen Cave (D) by Cuvier (1805), Buckland (1823), and Goldfuss (1823), in the Lindenthal Cave at Gera (D, Liebe, 1876), the Sandford Hill Cave and Wookey Hole Cave, GB (Reynolds, 1902), and the Teufelsluken Cave (A, Ehrenberg et al.,1938). Several new cave and open air sites have been identified and reported in central Europe during the last century, in France, Italy, and the Czech Republic (e.g. Musil, 1962; Fosse et al., 1998; Tournepiche and Couture, 1999; Stiner, 2004; Diedrich and Žák, 2006). Recent reviews carried out within the “European Ice Age Spotted Hyena Program” have also

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identified many new hyena dens in Germany and the Czech Republic. This program focussed on the Upper Pleistocene spotted hyena populations, bone assemblages, interactions with prey, and the antagonism between hyenas and lions, as well as their different types of den sites (Diedrich, 2004, 2005, 2006, 2007a–c, 2008a–c, 2009a–d, 2011c–d). This revue of the open air site near Bottrop (in Westphalia, NW Germany) provides an important contribution to the palaeoecological understanding of the last hyenas of Europe and their interactions with the megafauna. Upper Pleistocene open air hyena remains in NW Germany were first described from a few specimens found at Herne, Herten-Stuckenbusch, Lipperode, and Bottrop, in the Münsterland Bay Lowlands (Fig. 1, Heller, 1960; Diedrich, 2004). However, not all of the material from Bottrop, the richest of these sites, was studied, nor was any of it studied in detail, and hence this material now forms the subject of this contribution.

Several thousands of bones were collected from a 3 km stretch of the Rhein–Herne Canal, in the Emscher River valley near Bottrop, between 1958 and 1976; they were collected on secondary position from the "floating fields" and included the

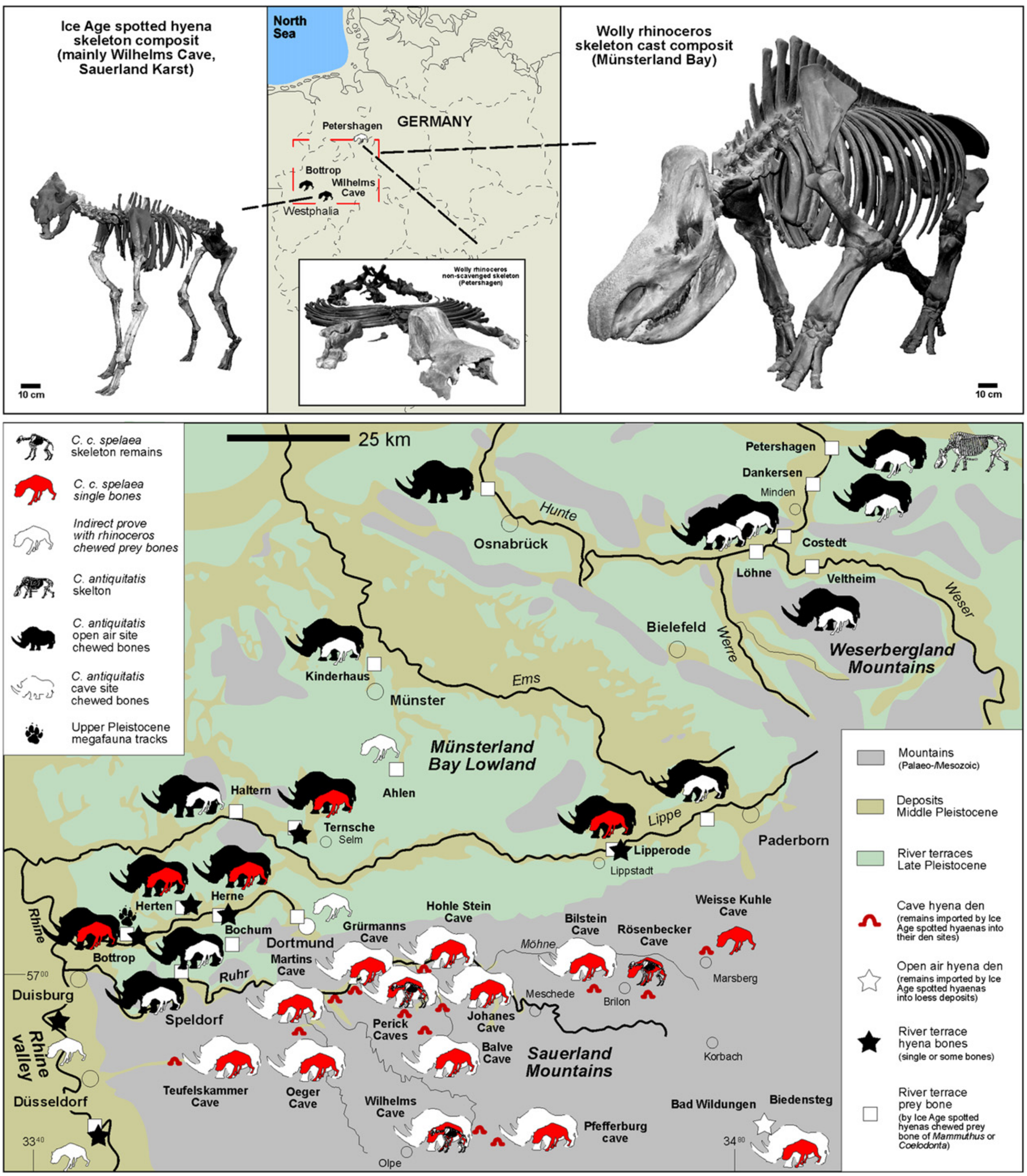

Fig. 1. Topographic position of the Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) open air Emscher River Terrace Bottrop open air den and other hyena den sites in NW Germany. Hyena skeleton in the coll. of the GPIM, Woolly rhinoceros skeleton in the MNUB (composed after Diedrich, 2005, 2006a,b, 2008c, 2010c,f; Diedrich, 2011f, and new results).

remains of hyenas (Heinrich, 1983, 1987). In addition to these faunal remains some middle Palaeolithic Neanderthal artefacts such as hand axes and flakes were also recovered during the construction of the canal, but not from any systematic archaeological excavation and so they have no stratigraphic context in relation to the recovered bones (Heinrich, 1983, 1987), which anyway lack any clearly identifiable marks from cuts or blows. Some additional bones were excavated from Bottrop-

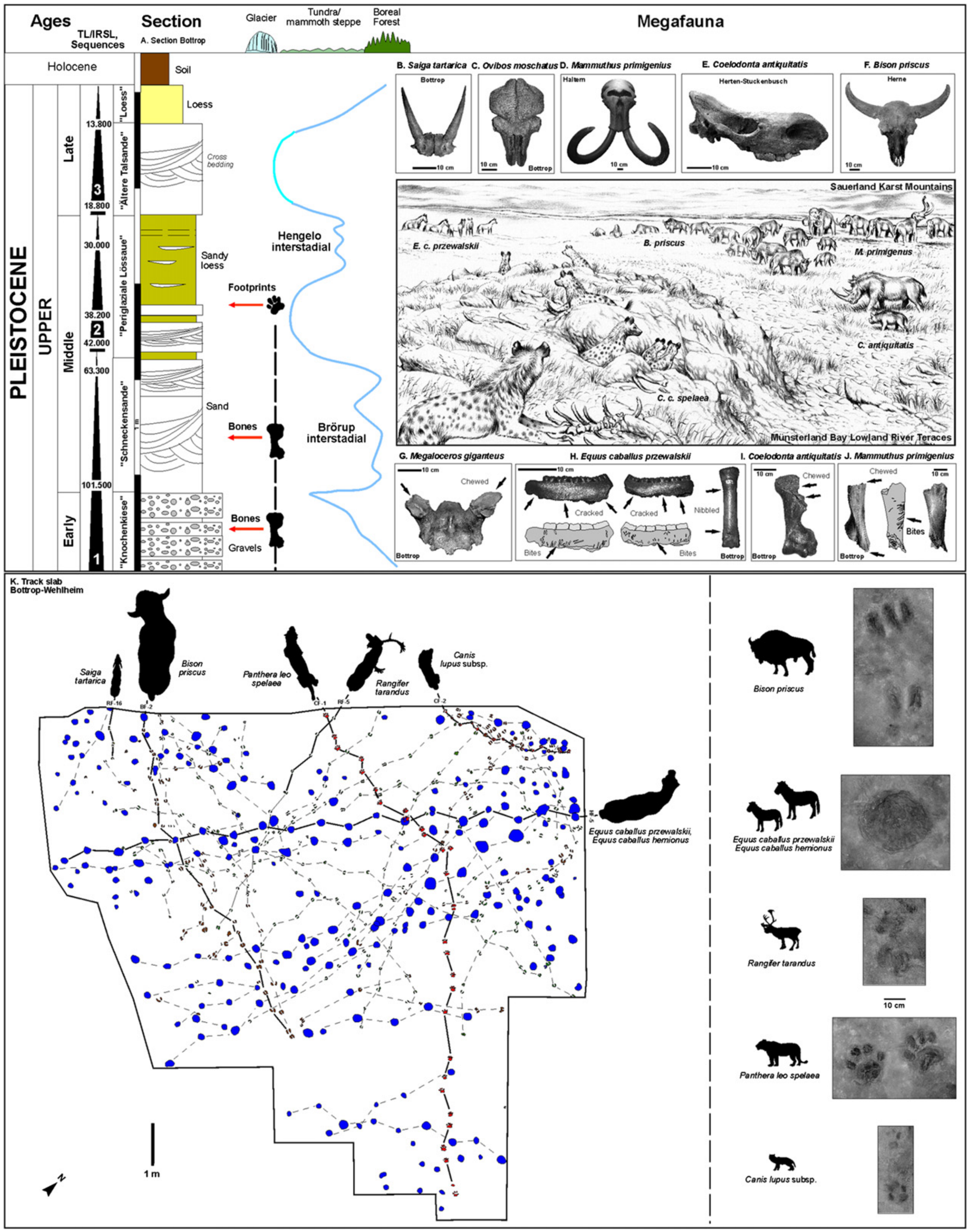

Fig. 2. A. Stratigraphy at the Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) open air Emscher River Terrace Bottrop site, and megafauna skulls from NW Germany. B. Saiga antelope skull from Bottrop (coll. MFUOB), C. Musk ox skull from Bottrop (coll. MFUOB). D. 40 years old mammoth bull skull from Haltern ((coll. MFUOB), E. Female woolly rhinoceros skull from Herten-Stuckenbusch (coll. GPIM), F. Male steppe bison skull from Herne (coll. GPIM). G. Cold period megafauna around an open air hyena den in the Münsterland Bay Lowlands with the Sauerland Karst Mountains in the background (Illustration G. “Rinaldino” Teichmann, TL/IRSL and section data based on Frechen 1995).

Welheim in 1995, and their stratigraphic context recorded (Koenigswald and Walders, 1995; Fig. 2A).

Despite the early descriptions of glacial mammoth steppe megafauna and the recording of the large open air bone site (including hyena remains) along the Rhine-Herne Canal (Fig. 1) near Bottrop (Heinrich, 1983, 1987), detailed faunal analyses only started at this locality following the new bone and track discoveries from the Bottrop-Welheim site (Fig. 2), which is also situated on the Emscher River terraces (Koenigswald and Walders, 1995). Investigations into the various animal groups represented have continued since then, starting with an analysis of the cave bear bones (Diedrich, 2009b) and the steppe lion *Panthera leo spelaea* population, including an ichnological taxonomy of the steppe lion tracks of Bottrop-Welheim (Diedrich, 2011a). The megafauna taphonomy and the origins of the bone accumulations are discussed herein within the broader context of late Pleistocene localities in the Münsterland Bay Lowlands of NW Germany, which was probably a mammoth steppe environment in the early to middle Upper Pleistocene, with typical woolly mammoth, woolly rhinoceros, steppe bison, musk ox, Przewalski horse, Ice Age donkey, saiga, giant deer, and reindeer fauna, all of which are well known in the area not only from many skulls (Fig. 2B–F) but also from large quantities of postcranial bones (about 4000 in total).

The review of the Bottrop bone material in the context of hyena activities started with the misidentified “giant deer mask of Neanderthals” (Heinrich, 1983), all three examples of which were revised simply to be simply hyena scavenged *Megaloceros* skull remains (Fig. 2G), being similar to material illustrated from the Balve Cave hyena den in the Sauerland Karst (Fig. 1, Diedrich, 2011f). Dropped and chewed *Megaloceros* antlers, cracked and chewed horse mandibles, chewed metapodials (Fig. 2H–I), scavenged mammoth bones (Fig. 2), and damaged woolly rhinoceros bones (Fig. 2I), provide the first obvious indications of strong hyena activity. The identification of bone accumulations from the Bottrop area as having been from human prey or emplaced by floods was too simplistic, as was also the case for at the Balve Cave site where the partly damaged megafauna bones have recently been identified as being mostly the imported remains of hyena prey (Diedrich, 2011f).

The majority of bones recovered from the Münsterland Bay Lowlands, including the finds from near Bottrop and have not been recovered by systematic excavations. Bones were collected from many river terrace gravel pits. Only the megafauna and tracks from Bottrop-Welheim and some of the bones described herein have been mapped and their stratigraphic context analysed in detail (Koenigswald et al., 1995; Koenigswald and Walders, 1995; cf. Fig. 2A).

The large mammal bones from Bottrop are often damaged, partly as a result of the modern damage by machines, but also possibly as a result of fluvial transport (Heinrich, 1987). The modern damage can usually be clearly distinguished from damage by carnivores. The damage to animal bones and the large bone accumulations is suggested herein to have resulted predominantly from the activities of large predators, in particular the Ice Age spotted hyenas (*Crocuta crocuta spelaea*) that were common at that time in the mountainous areas of the Sauerland Karst (Fig. 1, Diedrich, 2010c, 2011f). The palaebiogeography and palaeoecology of the Münsterland Bay Lowland steppe lions of NW Germany, including the Bottrop lion population, are well known, as are the differences between their prey in the lowland areas (Diedrich, 2004b, 2011a) and in the caves of Sauerland Karst mountainous areas (Diedrich, 2009a, 2011b). Lions are, however, not considered to be likely destroyers of woolly rhinoceros carcass bones because they did not have a suitable dentition to cause that sort of damage, nor did they have the ability to dismember the carcass of their largest prey (cf. Diedrich, 2010e). Some of the bite marks may certainly be attributable to lions consuming the intestines, inner organs and meat, but not the sort of damage that can be seen to the massive bones of the woolly rhinoceros.

In this paper a preliminary description and review of the hyena bone material from Bottrop, as well as the small quantity of Upper Pleistocene material available from the other NW German open air sites (Fig. 1), is presented in a review, together with a contribution to the taphonomy of the large quantity of woolly rhinoceros bones from Bottrop. The *Coelodonta antiquitatis* bones from Bottrop and other sites, and their repetitive patterns of damage, have recently been recognised as very useful indicators for the identification of late Pleistocene hyena den sites in northern Europe (cf. Diedrich and Žák, 2006; Diedrich, 2006b, 2008d, 2011f), as will be discussed here through comparisons with the well studied hyena den cave sites of the Sauerland Karst mountain areas (Fig. 1), in which woolly rhinoceros remains with identical stages of damage have been commonly found in several hyena den caves (cf. Diedrich, 2008d, 2011f).

2. Material and methods

The studied and illustrated megafauna material from the Münsterland Bay Lowland sites consists of about 5500 bones (3820 from Bottrop), which are housed in the main collections in the Geologisch-Paläontologische Museum der Westfälischen-Wilhelms-Universität Münster (**GPIM**), in particular material from the Herten-Stuckenbusch and Selm-Ternsche sites. Additional material from Herne was studied in the Emschertalmuseum Herne collection (**EH**). This was found mainly during work on the Rhine-Herne Canal, as was material deposited in the Natural History Museum of the Humboldt-University Berlin (**MB**). The main finds described and analysed herein are from (1) the Bottrop river terraces of the Rhine-Herne Canal constructions, and (2) the Bottrop-Welheim construction site, most of which are housed with the largest Münsterland Bay Lowland late Pleistocene bone collection and the track slab mold in the Museum für Ur- und Ortsgeschichte Quadrat, Bottrop (**MUOB**). A single woolly rhinoceros skull and a little other additional material was studied in the Bergbaumuseum Bochum collection (**BMB**). Osteological comparisons were made between the woolly rhinoceros bones and the almost complete skeleton from Petershagen, stored in the Museum Natur und Umwelt Bielefeld (**MNUB**). Attention in this study has focused on the hyena population from Bottrop (Bottrop material: NISP = 50) and their interactions with one of their largest prey, the woolly rhinoceros (Bottrop material: NISP = 1601). An important comparison to the Sauerland Karst hyena den cave and material has also been included.

3. Geology and dating

The open air sites at Bottrop, Herten-Stuckenbusch, and Selm-Ternsche, as well as other sites on the Emscher and Lippe rivers of NW Germany (Fig. 1), have yielded many kinds of bones, predominantly from Ice Age megamammals (mainly from *Mammuthus primigenius* and *C. antiquitatis*) which are indirectly ascribed a biostratigraphic date through their association with mammoth steppe megafauna into the Upper Pleistocene Weichselian/Wuermian, or OIS 3–5 (Siegfried, 1983; Heinrich, 1983; Koenigswald and Walders, 1995; Diedrich, 2008c; Fig. 2). Other gravel pit sites on the Weser, Werre, and Elbe rivers have also produced a typical Upper Pleistocene glacial mammoth steppe fauna (Henke, 1969; Diedrich, 2005l). Geological studies of the river terraces, especially those of the Werre, Lippe and Ems, date most bone remains that have not been reworked into the “Niederterrassen” of the Upper Pleistocene, which include the “Knochenkies”, “Schneckensande”, “Periglaziale Lössaue”, “Ältere Talsande”, and in some areas, loess deposits (e.g. Henke, 1969; Heinrich, 1983; Skupin et al., 1993; Skupin et al., 1995; Jansen and Drozdzewski, 1986; Frechen, 1995). The best known

Table 1
Bone material list of *Crocuta crocuta spelaea* (Goldfuss, 1823) from the Late Pleistocene hyena open air Emscher River terrace site Bottrop (NW Germany).

No	Inv.-No.	Bone type	Commentary	Left	Right	Individual age	Sex	Bite marks	Collection
1	RHK 1979 - 4/323	Cranium	Brain case			Adult			Eiszeithalle Quadrat Bottrop
2	RHK 1979 - 4/7290	Cranium	Brain case			Adult			Eiszeithalle Quadrat Bottrop
3	RHK 1970 - 4/7293	Cranium	Saggital crest			Adult		x	Eiszeithalle Quadrat Bottrop
4	RHK 1970 - 4/7292	Cranium	Saggital crest			Adult			Eiszeithalle Quadrat Bottrop
5	RHK 1979 - 4/7294	Cranium	Occipital			Juvenile			Eiszeithalle Quadrat Bottrop
6	RHK 1979 - 4/7297	Cranium	Occipital			?Juvenile			Eiszeithalle Quadrat Bottrop
7	RHK 1979 - 4/7295	Cranium	Squamosal, Proc. glenoideus, sin.			?Juvenile			Eiszeithalle Quadrat Bottrop
8	RHK 1979 - 4/7301	Mandible	With P3-4	x		Hoch Adult			Eiszeithalle Quadrat Bottrop
9	RHK 1979 - 4/7302	Mandible	With P2-4, M1	x		Früh Adult			Eiszeithalle Quadrat Bottrop
10	RHK 197912825	Mandible	Ramus		x	Adult			Eiszeithalle Quadrat Bottrop
11	RHK 1979 - 4/7298	Maxillary	With P2, roots of P3	x		Adult			Eiszeithalle Quadrat Bottrop
12	RHK 1979 -4/7.324	Maxillary	With C, P2-4		x	Adult			Eiszeithalle Quadrat Bottrop
13	RHK 1979 - 4/7299	Premaxillary	With P3, roots of P3		x	Juvenil			Eiszeithalle Quadrat Bottrop
14	RHK 1979 - 4/7300	Tooth				Adult			Eiszeithalle Quadrat Bottrop
15	RHK 1979 - 4/7315	Scapula	Distal incomplete		x	Adult			Eiszeithalle Quadrat Bottrop
16	RHK 1979 - 4/8964	Scapula	Nearly complete			Juvenile			Eiszeithalle Quadrat Bottrop
17	RHK 1970 - 4/7318	Humerus, distal 54 mm	Distal joint		x	Adult	Male	cracked	Eiszeithalle Quadrat Bottrop
18	RHK 1970 - 4/7317	Humerus, distal 59 mm	Distal joint	x		Adult	Female		Eiszeithalle Quadrat Bottrop
19	RHK 1970 - 4/7316	Humerus, distal 60 mm	Nearly complete	x		Adult	Female	x	Eiszeithalle Quadrat Bottrop
20	RHK 1975 - 4/7321	Ulna	Without distal joint	x		Adult			Eiszeithalle Quadrat Bottrop
21	RHK 1975 - 4/7319	Ulna	Without distal joint		x	Adult			Eiszeithalle Quadrat Bottrop
22	RHK 1975 - 4/7320	Ulna	Without distal joint		x	Adult		x	Eiszeithalle Quadrat Bottrop
23	RHK 1975 - 4/7322	Radius	Without distal joint	x		Adult			Eiszeithalle Quadrat Bottrop
24	RHK 1975 - 4/7333	Metacarpus	V		x	Adult			Eiszeithalle Quadrat Bottrop
25	RHK 1970 - 4/7309	Cervical vertebra	Atlas			Adult			Eiszeithalle Quadrat Bottrop
26	RHK1976 - 4/8966	Cervical vertebra	Axes			Juvenile			Eiszeithalle Quadrat Bottrop
27	RHK 1970 - 4/7308	Cervical vertebra	C4			Adult			Eiszeithalle Quadrat Bottrop
28	RHK 1970 - 4/7303	Cervical vertebra	?			Juvenile			Eiszeithalle Quadrat Bottrop
29	RHK 1970 - 4/7307	Cervical vertebra	C6			Adult			Eiszeithalle Quadrat Bottrop
30	RHK 1970 - 4/7305	Cervical vertebra	C7			Adult			Eiszeithalle Quadrat Bottrop
31	RHK 1970 - 4/7306	Cervical vertebra	C7			Adult			Eiszeithalle Quadrat Bottrop
32	RHK 1962 - 4/7310	Thoracic vertebra	T1			Adult			Eiszeithalle Quadrat Bottrop
33	RHK 1970 - 4/7311	Thoracic vertebra	T1			Adult			Eiszeithalle Quadrat Bottrop
34	RHK 1970 - 4/7312	Thoracic vertebra	T6-7			Adult			Eiszeithalle Quadrat Bottrop
35	RHK 1970 - 4/7313	Thoracic vertebra	T14			Adult			Eiszeithalle Quadrat Bottrop
36	RHK 1962 - 4/7314	Lumbar vertebra	L1			Adult			Eiszeithalle Quadrat Bottrop
37	RHK 1970 - 4/8963	Pelvis	Acetabulum	x		Adultl			Eiszeithalle Quadrat Bottrop
38	RHK 1970 - 4/8962	Pelvis, Acetabulum joint diameter 36 mm	Half	x		Adultl			Eiszeithalle Quadrat Bottrop
39	RHK 1976 - 4/7324	Femur, distal width 55 mm	Distal joint	x		Adultl	Male		Eiszeithalle Quadrat Bottrop
40	RHK 1976 - 4/7323	Femur, distal width 60 mm	Distal joint	x		Adultl	Female		Eiszeithalle Quadrat Bottrop
41	RHK 1970 - 4/7322	Tibia	Without proximal joint	x		Adult			Eiszeithalle Quadrat Bottrop
42	RHK 1970 - 4/7329	Tibia	Without proximal joint		x	Adult			Eiszeithalle Quadrat Bottrop
43	RHK 1970 - 4/7327	Tibia	Without proximal joint	x		Adult	Male	cracked	Eiszeithalle Quadrat Bottrop
44	RHK 1970 - 4/7328	Tibia	Without proximal joint	x		Adult, pathological			Eiszeithalle Quadrat Bottrop
45	RHK 1970 - 4/7325	Tibia, length 192 mm, distal width 53 mm	Complete	x		Adult, pathological	Male		Eiszeithalle Quadrat Bottrop
46	RHK 1975 - 4/12833	Tibia	Proximal joint	x		Juvenile			Eiszeithalle Quadrat Bottrop
47	RHK 1970 - 4/7326	Tibia	Distal joint	x		Adult	Female		Eiszeithalle Quadrat Bottrop
48	RHK 1970 - 4/7330	Calcaneus	Complete		x	Adult			Eiszeithalle Quadrat Bottrop
49	RHK 1970 - 4/7332	Calcaneus	Complete		x	Adult			Eiszeithalle Quadrat Bottrop
50	RHK 1970 - 4/7331	Calcaneus	Complete			Juvenile			Eiszeithalle Quadrat Bottrop

stratigraphy is from the Emscher River terraces, presented here in a new generalized “Niederterrassen” section with three sedimentary sequences (Fig. 2A).

3.1. Early Weichselian “Knochenkiese”

The oldest Emscher River terrace gravel and sand layers are the bone-rich horizons that have been named the “Knochenkiese” (“bone gravels”). Those bonebeds have been dated into the early Upper Pleistocene, being older than 101.5 Ka (Jansen and Drozdzewski, 1986; Frechen, 1995, Fig. 2A). The material described herein from the Rhine-Herne Canal seems to be mainly from these horizons and includes the following glacial megafauna (Fig. 2): *M. primigenius*, *C. antiquitatis*, *Bison priscus*, *Ovibos moschatus*, *Megaloceros giganteus*, *Cervus elaphus*, *Rangifer tarandus*, *Equus caballus przewalskii*, *Equus caballus hemionus*, *Saiga tartarica*, *Canis lupus* subsp., *Panthera leo spelaea* and *Ursus* cf. *spelaeus* (Koenigswald von Walders, 1995; Diedrich, 2009, 2011a), as well as the *Crocuta crocuta* *spelaea* presented herein. Important climatic indicators and mammoth steppe environment megafauna finds include the skull remains of *O. moschatus* and *Saiga tartarica* (cf. Koenigswald von Walders, 1995, Fig. 2B–C), while other mammoth steppe megafauna are also well known but also from several skulls recovered from various Münsterland Bay Lowland localities (Fig. 2D–F).

3.2. Middle Weichselian "Schneckensande" and "Periglaziale Lößaue"

The base of the snail-rich cross-bedded sands of the "Schneckensande" is no older than 101.5 Ka and it continues until 63.3 Ka (Frechen, 1995, Fig. 2A). The track slab from the Emscher River terrace fluvial deposits of Bottrop-Welheim (Fig. 2K) are of middle Upper Pleistocene age and have been ascribed an age of about 38.2 Ka by thermoluminescence (IRSL), as have some other glacial megafauna bones (Koenigswald von Walders, 1995) of the periglacial layer covering the "Schneckensand" of the Emscher River terraces (Frechen, 1995). Bone shaft remains from the woolly mammoth exhibiting hyena bite marks (cf. Koenigswald von Walders, 1995; Fig. 2I) and woolly rhinoceros bones damaged by hyenas have also been found in this layer, together with the above-mentioned megafauna.

3.3. Upper Weichselian "Ältere Talsande"

The oldest cross-bedded fluvial sands covering the "Schneckensande" horizons (Fig. 2A) have IRSL thermoluminicence dates of 18.8–13.8 Ka, placing them into the Bölling Interstadial to Older Dryas (Speetzen, 1980; Frechen, 1995). No megafauna remains have been recorded from these sands deposited in the coldest, high glacial period, but only in the loess layers that are sometimes equivalent to the sands, especially outside the terraces.

4. Palaeontology

4.1. Hyena remains

Family Hyaenidae Gray 1821
Genus *Crocuta* Kaup 1828
Species *Crocuta crocuta* Erxleben 1777
Crocuta crocuta spelaea (Goldfuss 1823)

Fifty bones are from *Crocuta crocuta spelaea*, from Bottrop (Table 1), and a few more bones from Selm-Ternsche, Herten-

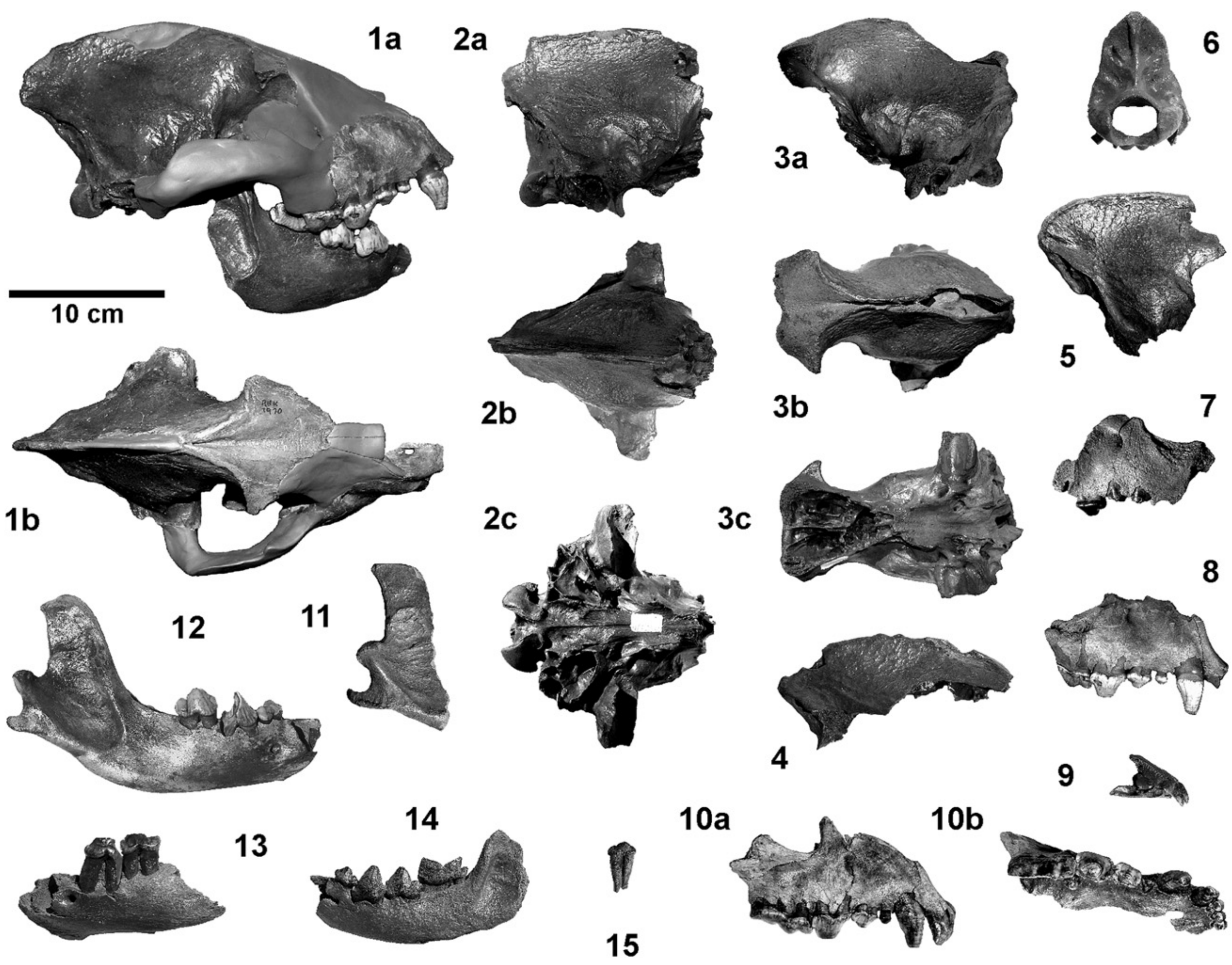

Fig. 3. *Crocuta crocuta spelaea* (Goldfuss 1823) cranial remains from Late Pleistocene hyena open air sites of NW-Germany. 1. Skull composed of different parts and animals (brain case, maxillary and lower jaw; in the exhibition; MFUOB without No.), a. lateral, b. dorsal. 2, Brain case of a grown up animal of Bottrop (MFUOB No. RHK 4/7.290), a. dorsal, b. lateral, c. ventral. 3. Brain case of a grown up animal from Bottrop (MFUOB No. RHK 4/7.323), a. dorsal, b. lateral, c. ventral. 4. Brain case fragment of a grown up animal from Bottrop (MFUOB No. RHK 4/7.293), lateral. 5. Brain case fragment of an adult animal from Bottrop (MFUOB No. RHK 4/7.292), lateral. 6. Occipital of a cub skull from Bottrop (MFUOB No. RHK 4/7.294), occipital. 7. Right maxillary of an adult animal from Bottrop (MFUOB No. RHK 4/7.298), lateral. 8. Right maxillary of an adult animal from Bottrop (MFUOB No. RHK 4/7.324), lateral. 9. Right premaxillary of a cub from Bottrop (MFUOB No. RHK 4/7.299), lateral. 10. Right upper jaw of an early adult animal from Herne (EMH No. Herne-1), a. lateral, b. ventral. 11. Left mandible ramus from Bottrop (MFUOB No. RHK 12825), lateral. 12. Right mandible from the Lippe River Terrace site Lipperode (GPIM No. A 5F1234), lateral. 13. Left mandible of a high adult animal from Bottrop (MFUOB No. RHK 4/7.301), lateral. 14. Left mandible of a young adult animal from Bottrop (MFUOB No. RHK 4/7.302), lateral. 15. Left lower jaw P_2 from Bottrop (MFUOB No. RHK 4/7.300), a. labial.

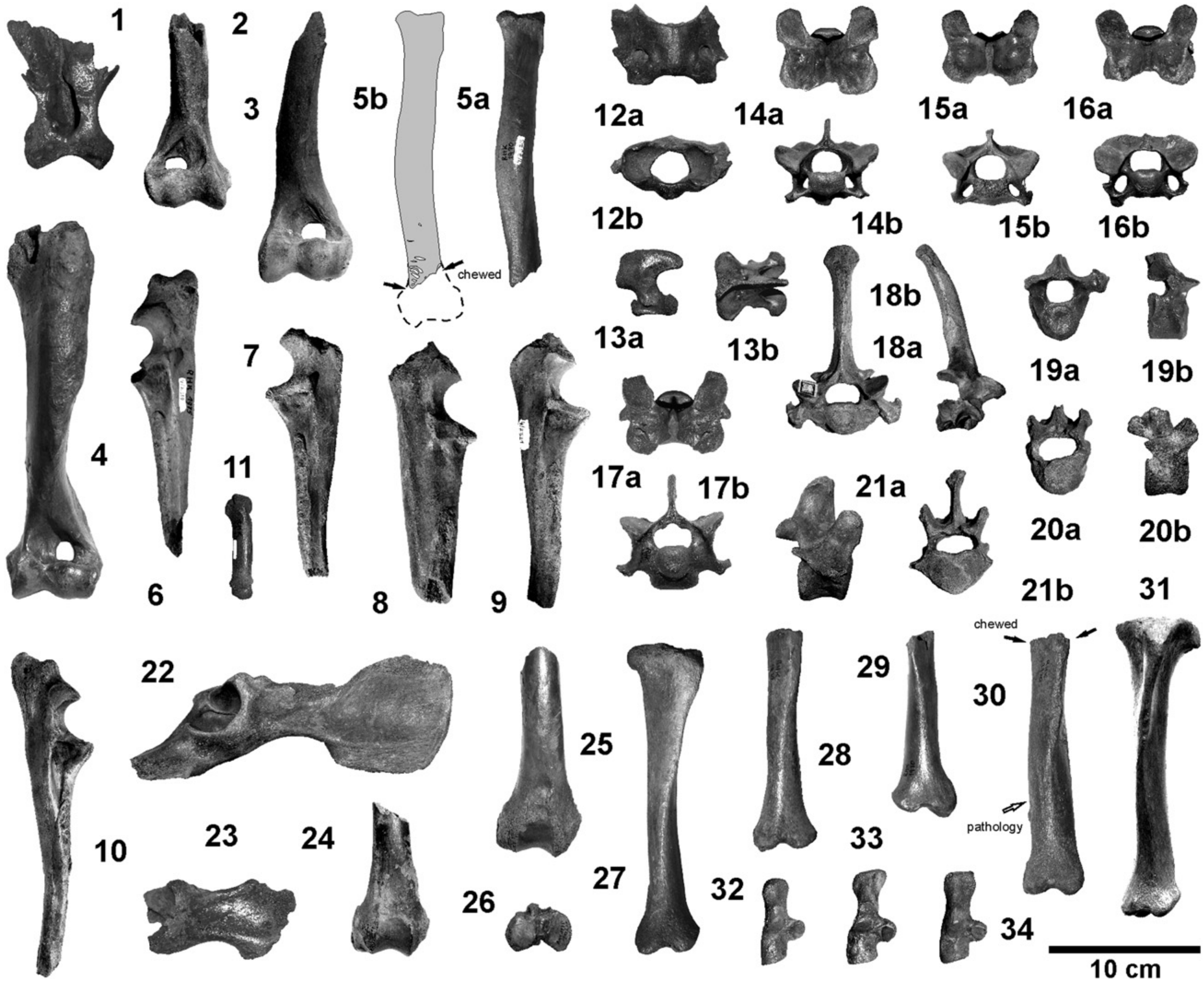

Fig. 4. *Crocuta crocuta spelaea* (Goldfuss 1823) postcranial bones from Late Pleistocene hyena open air sites of NW-Germany. 1. Right scapula of a grown up animal from Bottrop (MFUOB No. RHK 4/7.315), lateral. 2. Right half humerus of a grown up male animal from Bottrop (MFUOB No. RHK 4/7.318), cranial. 3. Right half humerus of a grown up female animal from Bottrop (MFUOB No. RHK 4/7.317), cranial. 4. Right humerus of a grown up animal from Bottrop (MFUOB No. RHK 4/7.316), cranial. 5. Left radius of a grown up animal from Bottrop (MFUOB No. RHK 4/7.322), lateral. 6. Right ulna of a grown up animal from Bottrop (MFUOB No. RHK 4/7.319), lateral. 7. Right ulna of a grown up animal from Bottrop (MFUOB No. RHK 4/7.320), lateral. 8. Left ulna of a grown up animal from Bottrop (MFUOB No. RHK 4/7.285), lateral. 9. Left ulna of a grown up animal from Bottrop (MFUOB No. RHK 4/7.321), lateral. 10. Right metacarpus V of a grown up animal from Bottrop (MFUOB No. RHK 4/7.333), dorsal. 10. Right ulna of a grown up animal from Selm-Ternsche (GPIM No. A 5.244), lateral. 11. Right Mc V of a grown up animal from Bottrop (MFUOB No. RHK1975 4/7.333), cranial. 12. Atlas of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.309), a. dorsal, b. cranial. 13. Axes of a cub from Bottrop (MFUOB No. RHK1976 4/8.966), a. lateral, b. dorsal. 14. Cervical vertebra no.4 of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.308), a. dorsal, b. cranial. 15. Cervical vertebra ? no.4 of a cub from Bottrop (MFUOB No. RHK 1970 4/7.303), a. dorsal, b. cranial. 16. Cervical vertebra no.6 of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.307), a. dorsal, b. cranial. 17. Cervical vertebra no.7 of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.305), a. dorsal, b. cranial. 18. Thoracic vertebra no.1 of a grown up animal from Bottrop (MFUOB No. RHK 1962 4/7.310), a. cranial, b. lateral. 19. Thoracic vertebra ?no.6-7 of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.312), a. cranial, b. lateral. 20. Thoracic vertebra no. 14 of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/7.313), a. cranial, b. lateral. 21. Lumbar vertebra 1 of a grown up animal from Bottrop (MFUOB No. RHK 1962 - 4/7314), a. lateral, b. cranial. 22. Coxa of a grown up animal from Bottrop (MFUOB No. RHK 1970 – 4/8963), lateral. 23. Coxa fragment of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/8962), lateral. 24. Left distal femur fragment of a grown up animal from Bottrop (MFUOB No. RHK 1976 4/7324), cranial. 25. Left distal fragment of a grown up animal from Bottrop (MFUOB No. RHK 1976 4/7323), cranial. 26. Left tibia proximal joint of an early adult animal from Bottrop (MFUOB No. RHK 1975 4/12833), dorsal. 27. Left tibia of a grow up animal from Bottrop (MFUOB No. RHK 1970 4/7325), cranial. 28. Left tibia of a grow up animal from Bottrop (MFUOB No. RHK 1970 4/7327), cranial. 29. Right tibia of an early adult animal from Bottrop (MFUOB No. RHK RHK 1970 4/7329), cranial. 30. Left pathological tibia of a senile animal from Bottrop (MFUOB No. RHK RHK 1970 4/7328), cranial. 31. Left tibia of a grown up animal from Selm-Ternsche (GPIM No. A 5.41), cranial. 32. Right calcaneus of a cub from Bottrop (MFUOB No. RHK 1970 4/7331), cranial. 33. Right calcaneus of a grow up animal from Bottrop (MFUOB No. RHK 1970 4/7330), cranial. 34. Right calcaneus of a grow up animal from Bottrop (MFUOB No. RHK 1970 4/7332), cranial.

Stuckenbusch and Lipperode are also included, representing all the known hyena material from the studied area.

4.1.1. Cranium

Several skull fragments are present from Bottrop, mostly from adult hyenas but also from cubs (Fig. 3.1–9, Table 1). The illustrated skull was compiled from various skull fragments for exhibition purposes (Fig. 3.1), but the brain-case, right maxillary/premaxillary, and the mandible are from adult animals. The dentition in the upper and lower jaws is similar in having moderately worn teeth. There are also four more brain cases and fragments from adult hyenas (Fig. 3.2–5). One occipital (Fig. 3.6) is from a cub's skull. Additional skull fragments from Bottrop include two right maxillaries (Fig. 3.7,8) from adult animals with moderately worn teeth, and one right premaxillary from a cub (Fig. 3.9). There is also one right maxillary with premaxillary and a full dentition in a moderate stage of wear from the Emscher River terrace site at Herne (Fig. 3.10a–b). Only four mandible fragments are preserved from Bottrop, one is a ramus (Fig. 3.11), two others (Figs. 3.3 and 13) are from adult animals with moderately worn teeth, and a final fragment is from an older cub with un-polished teeth in the small mandible (Fig. 3.14). There is also a single left P^2 tooth (Fig. 3.15). One lower jaw with a damaged anterior part (Fig. 3.12) was collected from the Lippe River terrace site at Lipperode.

4.1.2. Postcranium

Bones from all body parts are represented (Table 1), but most of the material is again from adult hyenas and the fragmentation does not allow any well founded metric analyses to be made, but only overall population statistics. Some measurements are presented in Table 1.

The fore limb remains consist of a single right scapula (Fig. 4.1) and three incomplete right and left humeri (Fig. 4.2–4) that appear to be from adult (possibly early adult) animals. The left radius (Fig. 4.5) has been distally chewed, as indicated by oval-triangular bite mark depressions around the margin on both sides. Four ulnae from Bottrop are all missing the distal parts; in some cases the incompleteness on the proximal joint could possibly be the result of carnivore damage (Fig. 4.6–9). Another ulna fragment came from the Lippe River terrace site at Selm-Ternsche (Fig. 4.10). A single right metacarpus V (Fig. 4.11) is the only paw bone.

The axial skeleton is represented by several vertebrae, such as the atlas of an adult animal (Fig. 4.12), the axis from a cub (Fig. 4.13), and cervical vertebrae from adult hyenas (Figs. 3.14,3.16,3.17) and from a cub (Fig. 4.15), but these are from different neck positions. A completely preserved no. 1 thoracic vertebra (Fig. 4.18), incomplete vertebrae of unclear exact (middle to posterior) thoracic positions (Fig. 4.19,20), and a lumbar vertebra (Fig. 4.21) are all from adult animals. Two coxae and other fragments are again from adult hyenas (Fig. 4.22,23).

The hind limb bone material contains two half femora (Fig. 4.24,25) from adult hyenas and a single distal joint from a cub (Fig. 4.26). Most of the bones are tibiae. Only one is complete and useful for metric sex comparisons to tibiae from other localities (length: 192 mm, distal width: 53 mm), such as another complete, slightly larger tibia from the Lippe River terrace site at Selm-Ternsche (Fig. 4.31: length: 203 mm, distal width: 51 mm). The other three illustrated tibiae from Bottrop have their proximal parts missing; in one case, the tibia shows unusual pathologic thickening at the distal end and was obviously damaged and chewed by a carnivore (Fig. 4.21). Of three calcanei one is from a cub (Fig. 4.32) and the other two are from adult hyenas (Fig. 4.33,34). There are no pedal bones present.

4.2. Woolly rhinoceros remains

Bones and fragments from *C. antiquitatis* (1601 NISP) have been identified from the Bottrop site. Only the best examples and most typical patterns of damage are discussed and illustrated to any great extent herein, with all other material being used for statistical analyses.

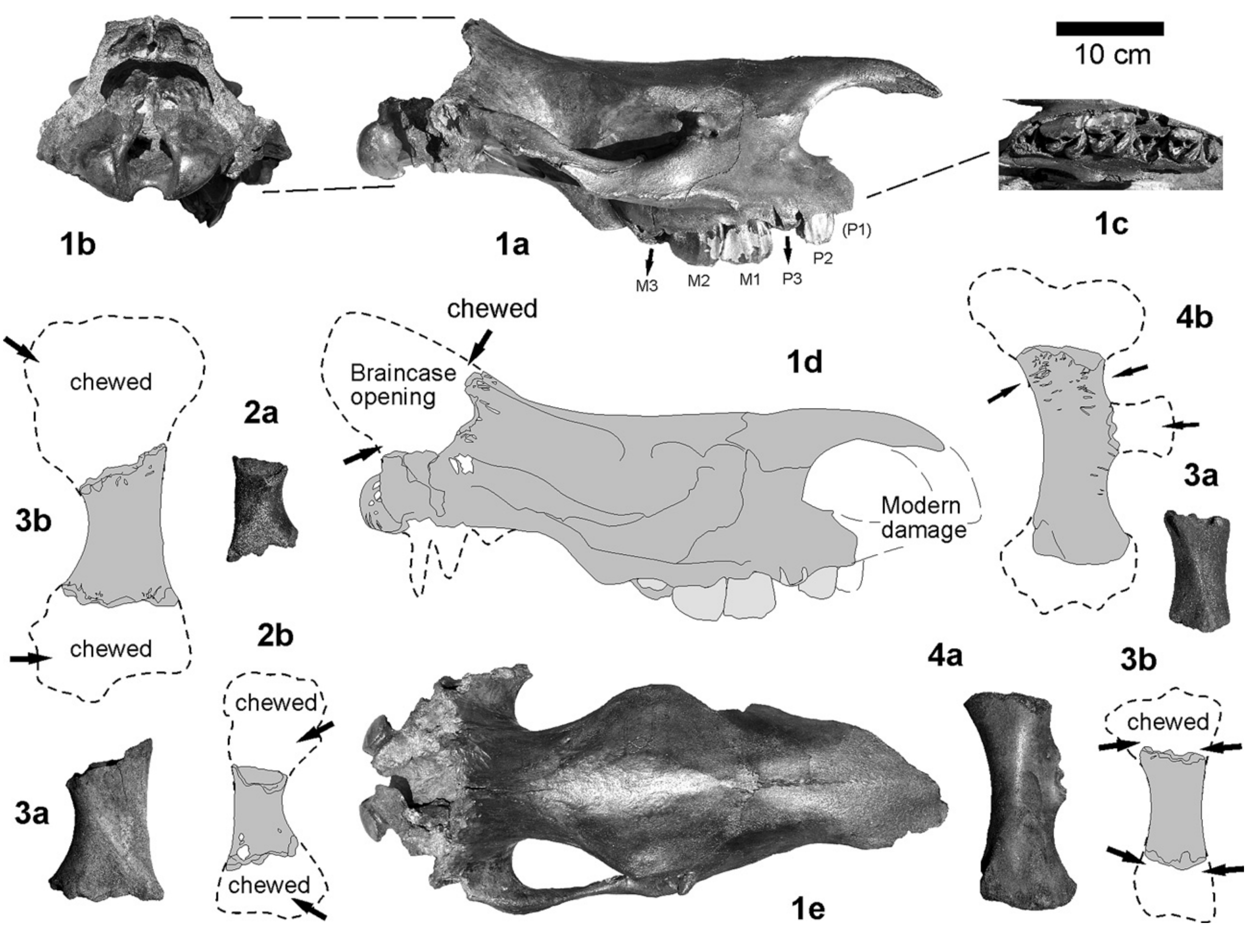

Fig. 5. *Coelodonta antiquitatis* (Blumenbach 1799) damaged cranium and postcranial longbones of neonates, calves to early adolescents from Late Pleistocene open air sites in NW-Germany. 1. Skull of a calf from Selm-Ternsche with hyena bite damages (GPIM No. A5N 780), and d. lateral, b. occipital, c. ventral right dentition, e. dorsal. 2. Right humerus shaft of a neonate or calf from Bottrop (MFUOB without No. RHK), cranial. 3. Left humerus shaft of an adolescent animal from Bottrop (MFUOB No. RHK 1970 4/2.627), cranial. 4. Right tibia shaft of a young calf from Bottrop (MFUOB No. RHK 1975 4/2.691), cranial. 4. Left femur shaft of a calf from Bottrop (MFUOB No. RHK 1970 4/2.748), cranial.

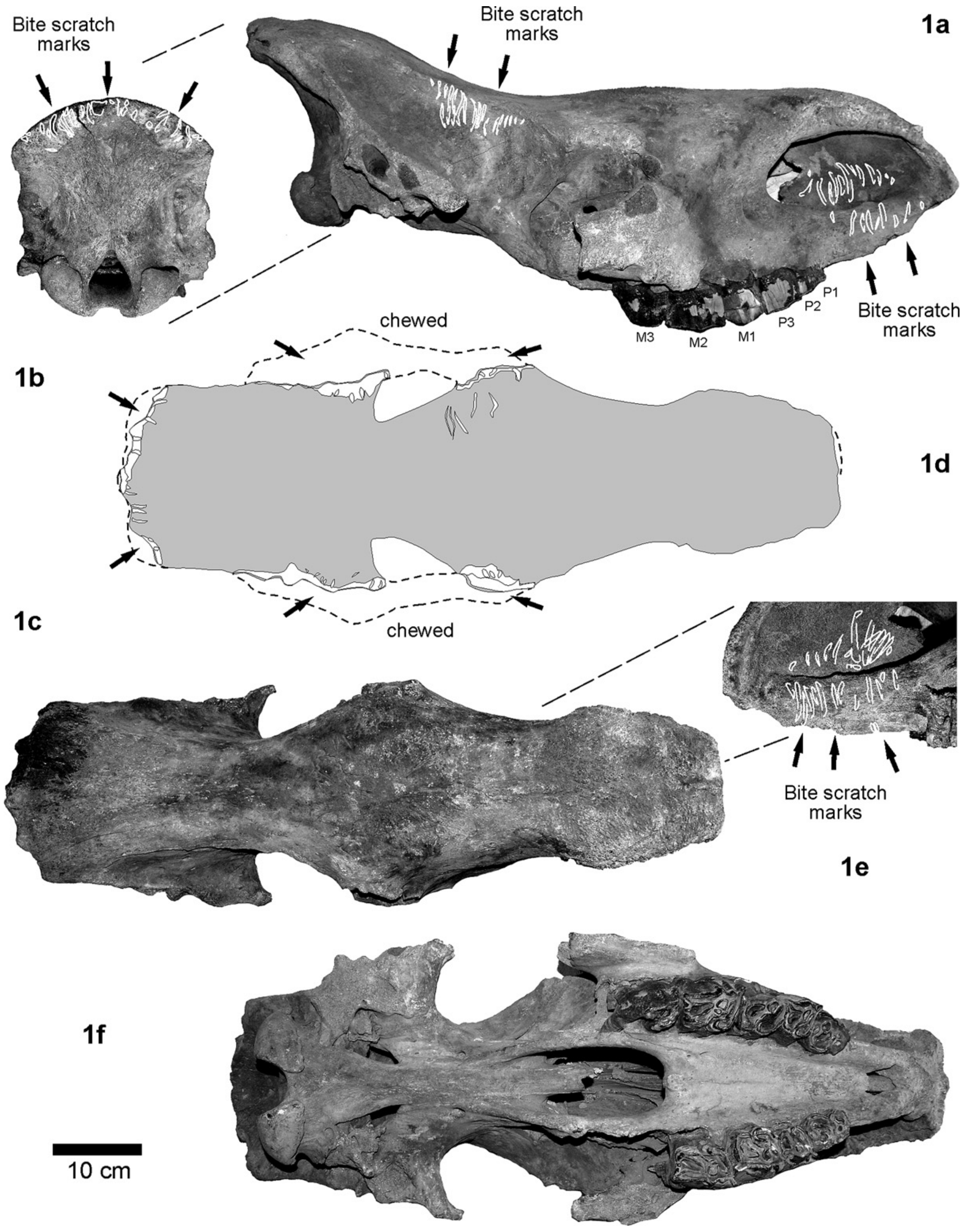

Fig. 6. *Coelodonta antiquitatis* (Blumenbach 1799) damaged cranium of adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Skull of and adult from Bochum (NW-Germany) with hyena bite damages (BMB No. Pleist1), a. lateral, b. occipital, c–d. dorsal, e. left nasal enlarged, f. ventral. The jugal arches are chewed for the lower jaw removements.

4.2.1. Cranium

Many skulls have been studied but only two were found with good evidence of scavenging by a large carnivore out of the several collections investigated from sites in NW Germany. An older calf skull (Fig. 5.1) from Selm-Ternsche is a quite unique find, with a brain case opening that has a jagged margin and bite marks around the opened brain case, on the parietals and other brain-case bones. In this skull only the left jugal arch has been chewed. The skull of an adult *C. antiquitatis* from Bochum (Fig. 6) shows an initial stage of damage, with 4–5 mm wide elongate tooth scratch marks on the parietal and on both sides of the anterior nasal region. There are also signs of bite damage and tooth marks along the occipital margin, and the jugal arches have both been chewed off.

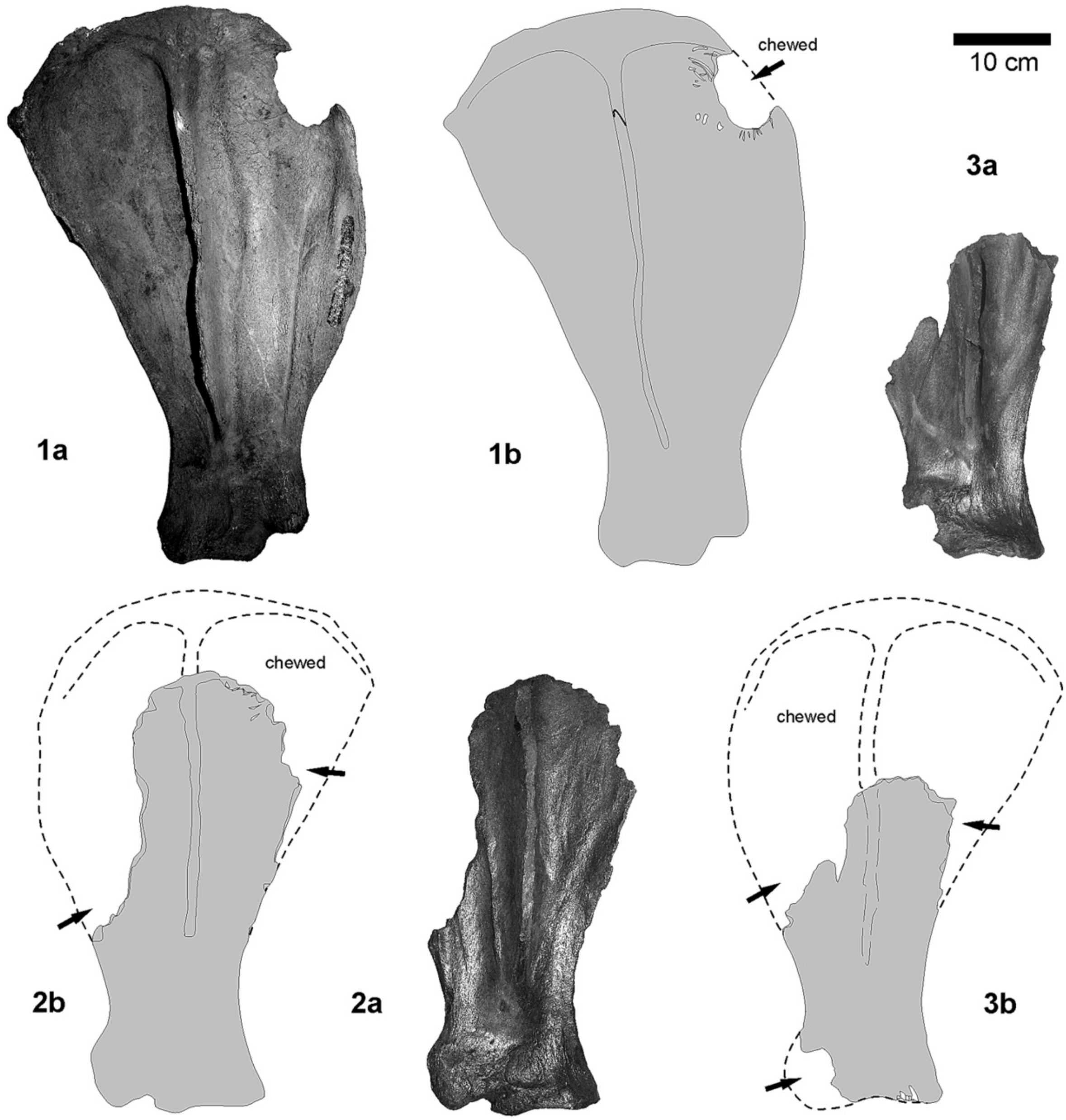

Fig. 7. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb scapulae bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right scapula from Herne, Rhine-Herne Canal (MB No. Ma.43216), lateral. 2. Left scapula from Herne, Rhine-Herne Canal (MB No. 504), lateral. 3. Left scapula from Selm-Ternsche (NMD No. A5H 771), lateral.

4.2.2. Postcranium

The fore leg long bones (humerus, ulna, and radius) from Bottrop and other open air sites of NW Germany show various stages of damage, and important repetitions of damage patterns. Scapula damage starts at the distal margin (Fig. 7.1, Stage I) and the damage then extends all around the distal end (Fig. 7.2, Stage II). Further damage is then typically on the anterior part of the glenoid (Fig. 7.3, Stage III). The chewing of humeri always started with the proximal joint (Fig. 8.2, Stage I). The distal joint is only repeatedly chewed on one side (the outer lateral side) and never on the opposite side (Fig. 8.3–7, 9.1–5, 9.8, Stage II), which demonstrates a systematic pattern due to carnivores. In some cases (Stage III) only the shafts remain (Figs. 9.6,7, 10.1–3). In the radii from Bottrop the damage starts at the distal joint, either on just one or on both sides (Fig. 10.5–7, Stage I) and in most cases the distal joint has been completely eaten (Figs. 10.8–10, 11.1–3, Stage II). In the next stage of bone damage the proximal joint is also chewed repeatedly from the inner side (Fig. 11.4–6). In several instances only the shafts have remained untouched (Fig. 11.7,8, Stage III). In contrast, damage to ulnae starts at the proximal end (Figs. 11.10,11, 12.1,2, Stage I). The distal joints are then chewed (Fig. 12.3, Stage II). The penultimate stage of bone damage has only the middle bone shaft remaining (Figs. 12.4–10). Some metacarpi (here two mc III) have had their distal ends eaten (Figs. 12.12,13).

The pelvis is typically only represented by remains of the acetabulum. Those are chewed at all three distally parts and expose jagged margins and bite mark impressions. These acetabulum remains illustrated herein are in damage Stage II and are from adolescent to adult animals (Figs. 13.1–7).

The hind leg femora and tibia also have repeated patterns of damage. The femora exhibit three main stages of destruction. In

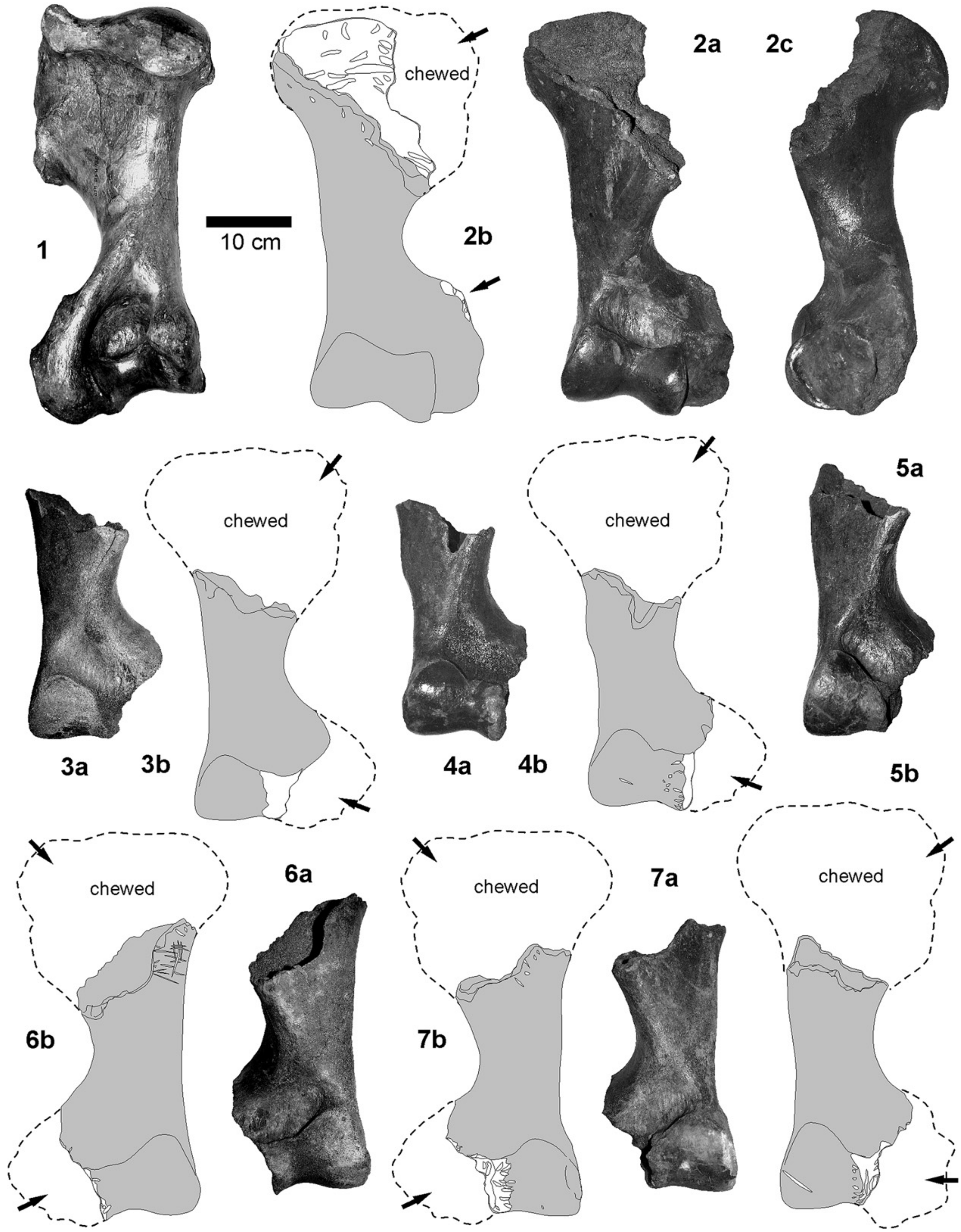

Fig. 8. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb humeri bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Complete left humerus from Selm-Ternsche (GPIM No. A5H 730), caudal. 2. Left humerus from Bottrop (MFUOB No. RHK 1970 4/2.515), cranial. 3. Left humerus from Bottrop (MFUOB No. RHK 1970 4/2.544), cranial. 4. Left humerus from Bottrop (MFUOB No. RHK 1974/75 4/2.595), cranial. 5. Left humerus from Bottrop (MFUOB No. RHK 1958 4/2.536), cranial. 6. Left humerus from Bottrop (MFUOB No. RHK 1974/75 4/2.551), cranial. 7. Left humerus from Bottrop (MFUOB No. RHK 1970 4/9.629), cranial.

Stage I the distal joint and caput is chewed and scratched from the dorsal side (Figs. 14.2–4, 15.1). The lateral trochanter tertius has also typically been eaten in this first stage. In Stage II only the distal half of the femur remained (Fig. 15.3), while in Stage III only the massive shaft remained after prolonged feeding by carnivores and could not be cracked any further (Figs. 15.3–5, 16.1–3, 16.6–16.7 17.1–5, 17.8), resulting in several central and short femora shafts (Figs. 16.4 and 17.6,7). A single femur from a young calf has some

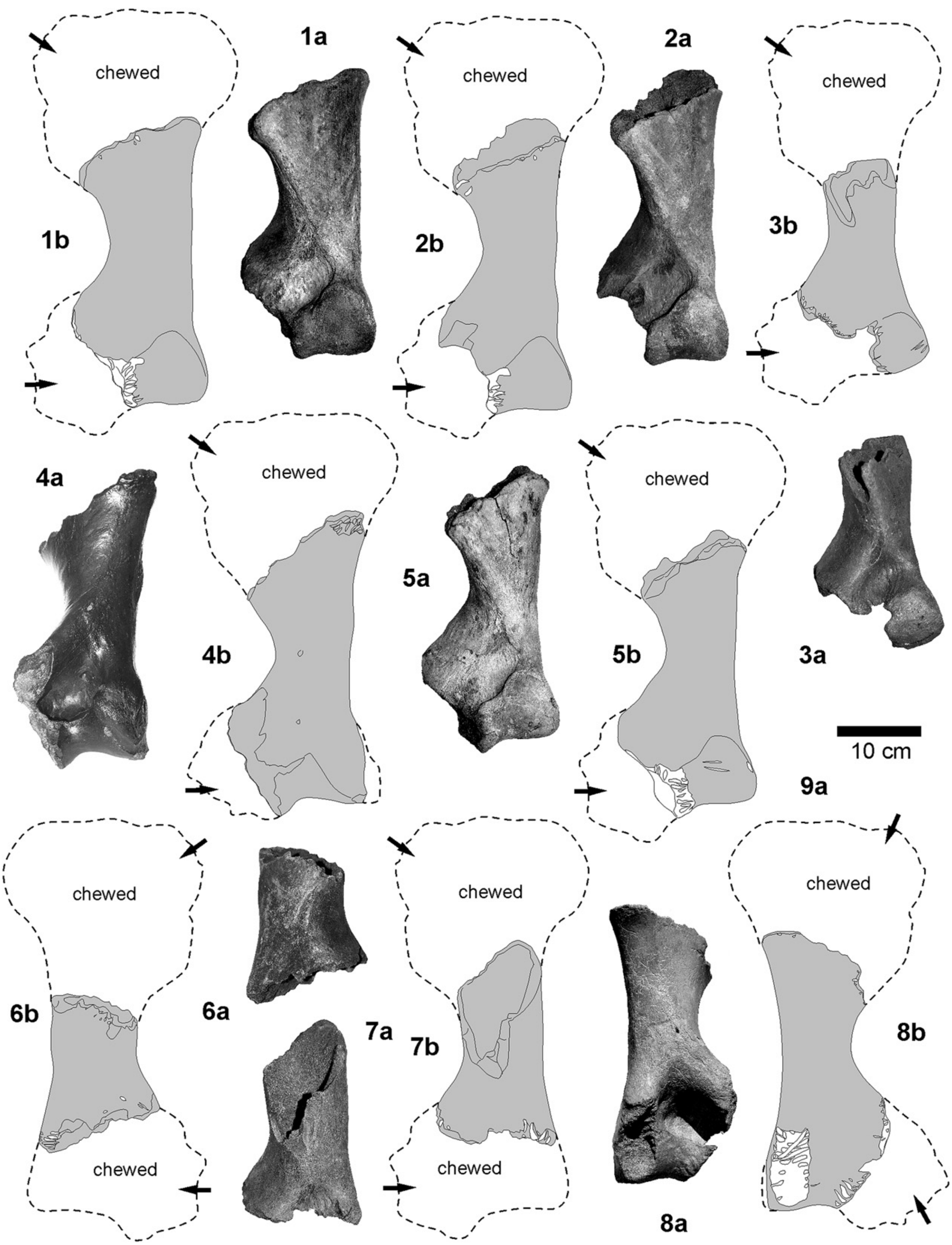

Fig. 9. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb humeri bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Left humerus from Bottrop (MFUOB No. RHK 1962 4/2.617), cranial. 2. Left humerus from Bottrop (MFUOB No. RHK 1970 4/2.206), cranial. 3. Left humerus from Bottrop (MFUOB No. RHK 1974/75 4/2.595), cranial. 4. Left humerus from Selm-Ternsche (GPIM No. A5H 716), caudal. 5. Left humerus from Herne, Rheine-Herne Canal (GPIM without No.), caudal. 6. Right humerus shaft from Bottrop (MFUOB No. RHK 1970 4/2.588), cranial. 7. Right humerus shaft from Bottrop (MFUOB No. RHK 1970 4/2.550), cranial. 8. Left humerus from Münster-Kinderhaus (GPIM without No.), caudal.

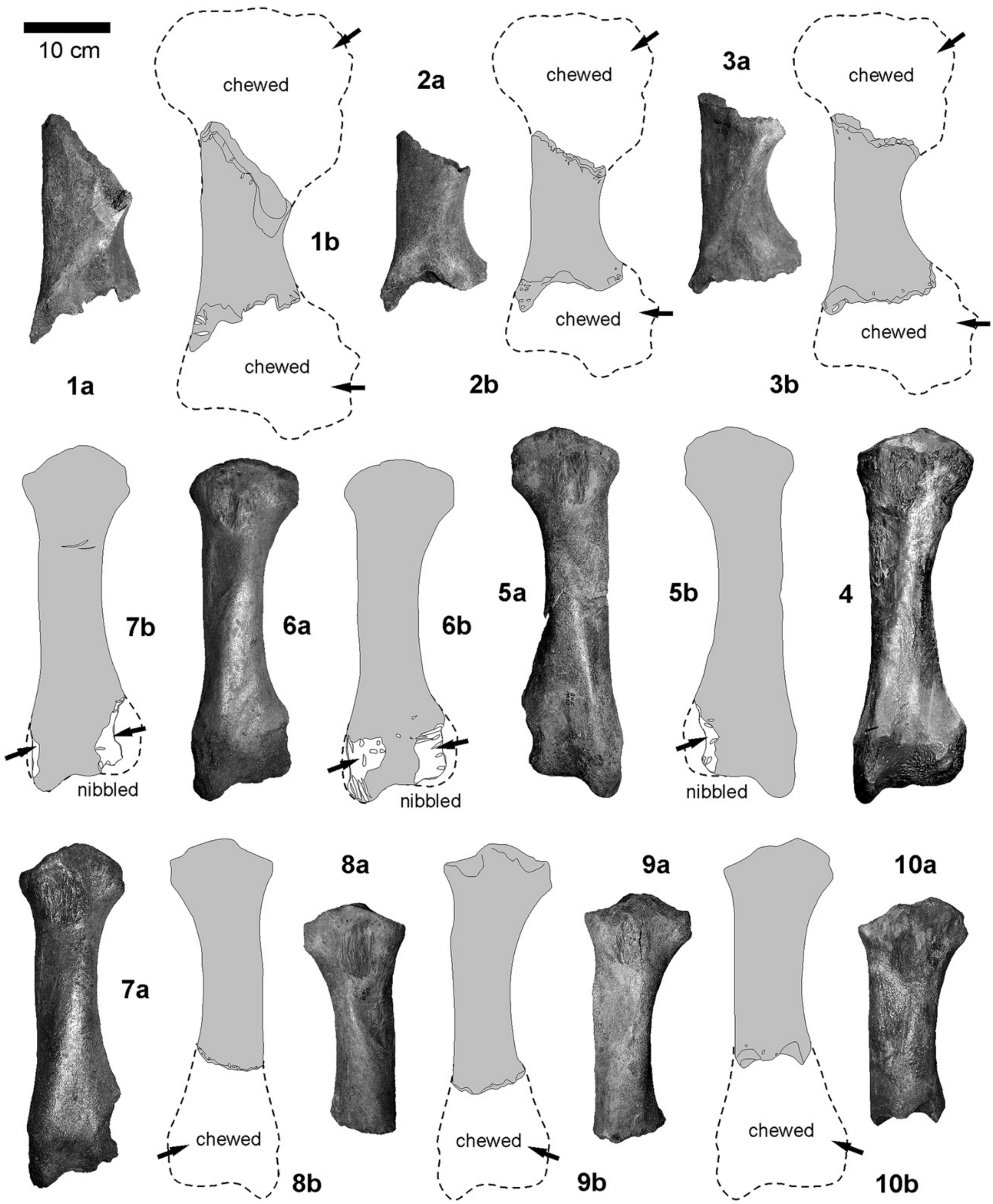

Fig. 10. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb humeri and radii bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right humerus shaft from Bottrop (MFUOB No. RHK 1970 4/2.604), cranial. 2. Right humerus shaft from Bottrop (MFUOB No. RHK 1970 4/9.820), cranial. 3. Left humerus shaft from Bottrop (MFUOB No. RHK 1970 4/2.596), cranial. 4. Right complete radius from Selm-Ternsche (GPIM without No.). cranial. 5. Left radius from Bottrop (MFUOB No. RHK 1970 4/2.430), cranial. 6. Right radius from Bottrop (MFUOB No. RHK 1970 4/2.434), cranial. 7. Right radius from Bottrop (MFUOB No. RHK 1970 4/2.433), cranial. 8. Left radius of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/2.445), cranial. 9. Right radius of a grown up animal from Bottrop (MFUOB No. RHK 1970 4/2.464), cranial. 10. Right radius of a grown up animal from Bottrop (MFUOB No. RHK 1975 4/2.462), cranial.

tooth scratch marks on the shaft (Fig. 5.3). The tibiae, in particular those from Bottrop, again provide evidence of systematic damage, that started at the femora opposite on the proximal joint (Fig. 18.2, Stage I). The distal parts of tibiae are repeatedly chewed in the same places, anterior-laterally on both sides (Fig. 18.3–7, Stage II). In the final stage of bone damage (Stage III) the shaft again remained unbreakable and many central portions of tibia shafts also document the eventual complete consumption of the distal joint

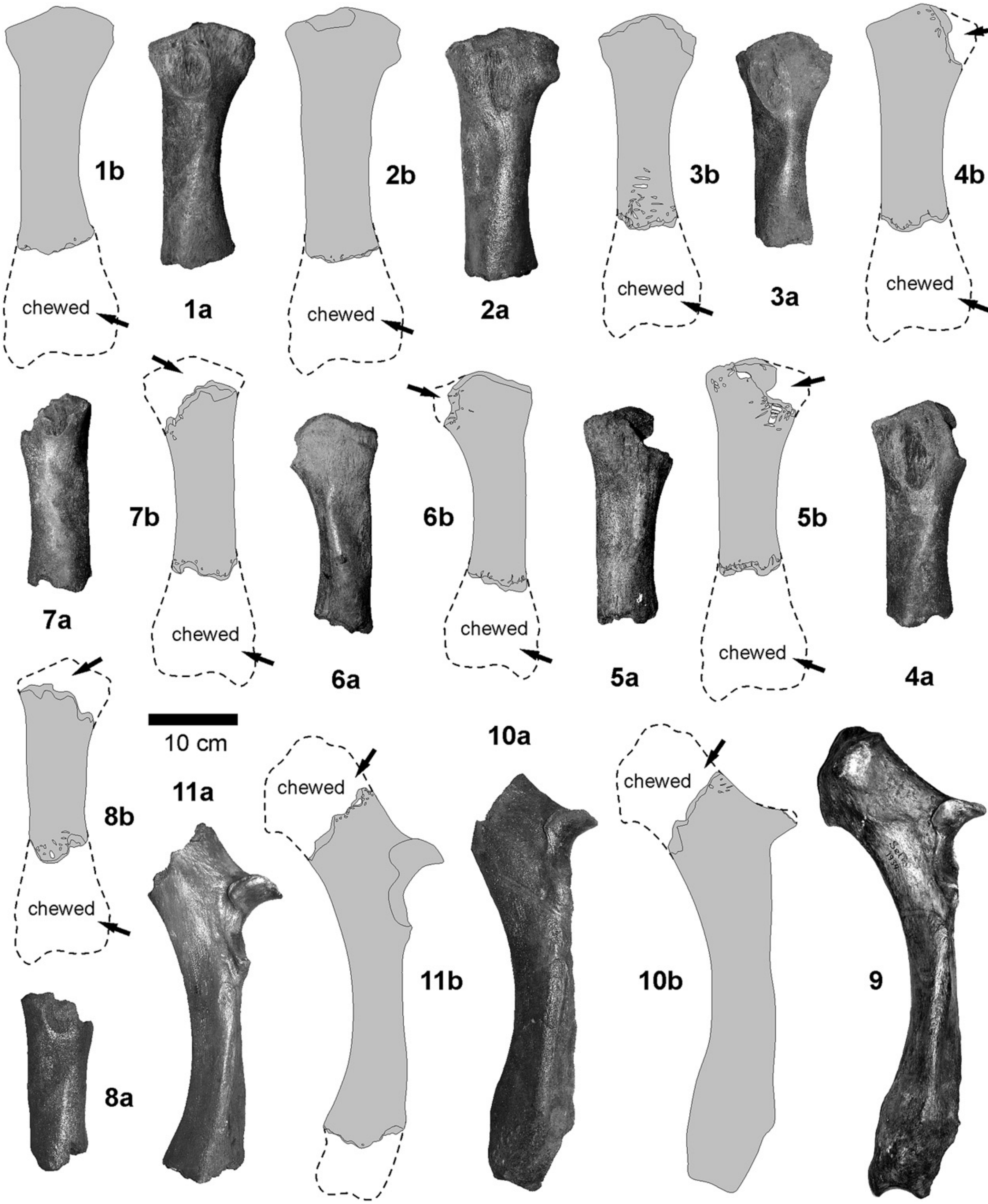

Fig. 11. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb radii and ulna bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right radius from Bottrop (MFUOB No. RHK 1975 4/2.471), cranial. 2. Right radius from Bottrop (MFUOB No. RHK 1975 4/2.458), cranial. 3. Right radius from Bottrop (MFUOB No. RHK 1970 4/2.445), cranial. 4. Right radius from Bottrop (MFUOB No. RHK 1975 4/2.479), cranial. 5. Right radius from Bottrop (MFUOB No. RHK 1970 4/9.817), cranial. 6. Left radius from Bottrop (MFUOB No. RHK 1970 4/2.439), cranial. 7. Left radius from Bottrop (MFUOB No. RHK 1975 4/2.489), cranial. 8. Right radius from Bottrop (MFUOB No. RHK 1976 4/2.489), cranial. 9. Right ulna from Selm-Ternsche (GPIM without No.), lateral. 10. Right ulna from Bottrop (MFUOB No. RHK 1970 4/2.475), lateral. 11. Right ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.086), lateral.

(Figs. 18.8–11, 19.1–3). Tooth scratch marks on astragals (Fig. 19.5) and bite marks on the distal joints of calcanei (Fig. 19.4) are also common, and can be found amongst the Bottrop woolly rhinoceros material. The distal halves of some of the metatarsi have also been chewed (Fig. 19.6,7).

4.3. Types of bone damage and bite marks

Particular types of bite mark sometimes enable the identification of the carnivore that made them, but only hyena or lion bite marks (not those of their cubs) can be distinguished from those of smaller

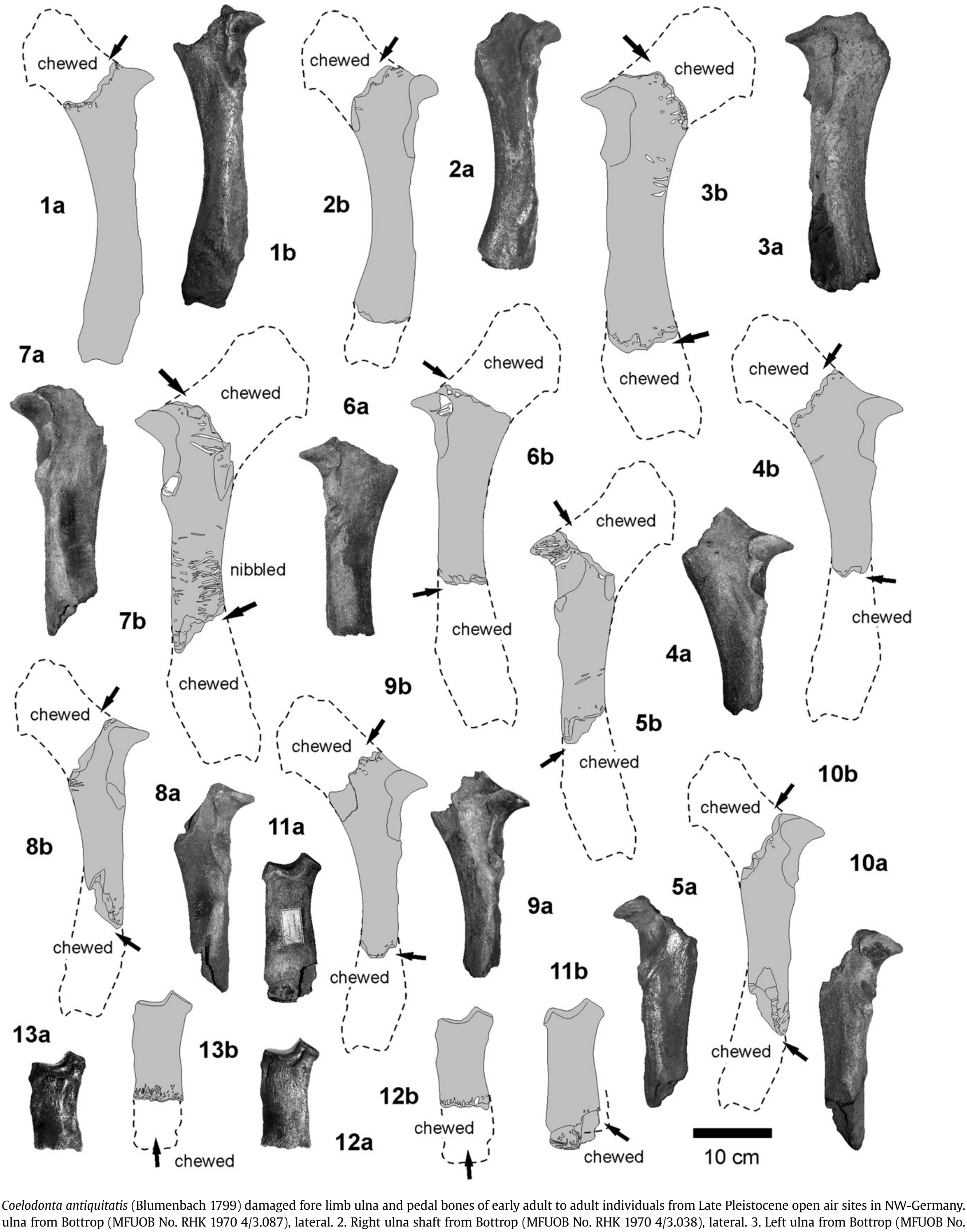

Fig. 12. *Coelodonta antiquitatis* (Blumenbach 1799) damaged fore limb ulna and pedal bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right ulna from Bottrop (MFUOB No. RHK 1970 4/3.087), lateral. 2. Right ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.038), lateral. 3. Left ulna from Bottrop (MFUOB No. RHK 1958 without No.), lateral. 4. Right ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.104), lateral. 5. Left ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.032), lateral. 6. Left ulna shaft from Bottrop (MFUOB No. RHK 1973 4/3.043), lateral. 7. Left ulna shaft of an ?adult animal from Bottrop (MFUOB No. RHK 1970 4/3.045), lateral. 8. Right ulna shaft from Bottrop (MFUOB No. RHK 1963 4/3.106), lateral. 9. Right ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.101), lateral. 10. Right ulna shaft from Bottrop (MFUOB No. RHK 1970 4/3.092), lateral. 11. Left mc III from Speldorf (GPIM No. A5H723), cranial. 12. Left half mc III from Bottrop (MFUOB No. RHK 1970 4/2.841), dorsal. 13. Left half mc III from Bottrop (MFUOB No. RHK 1975 4/2.849), dorsal.

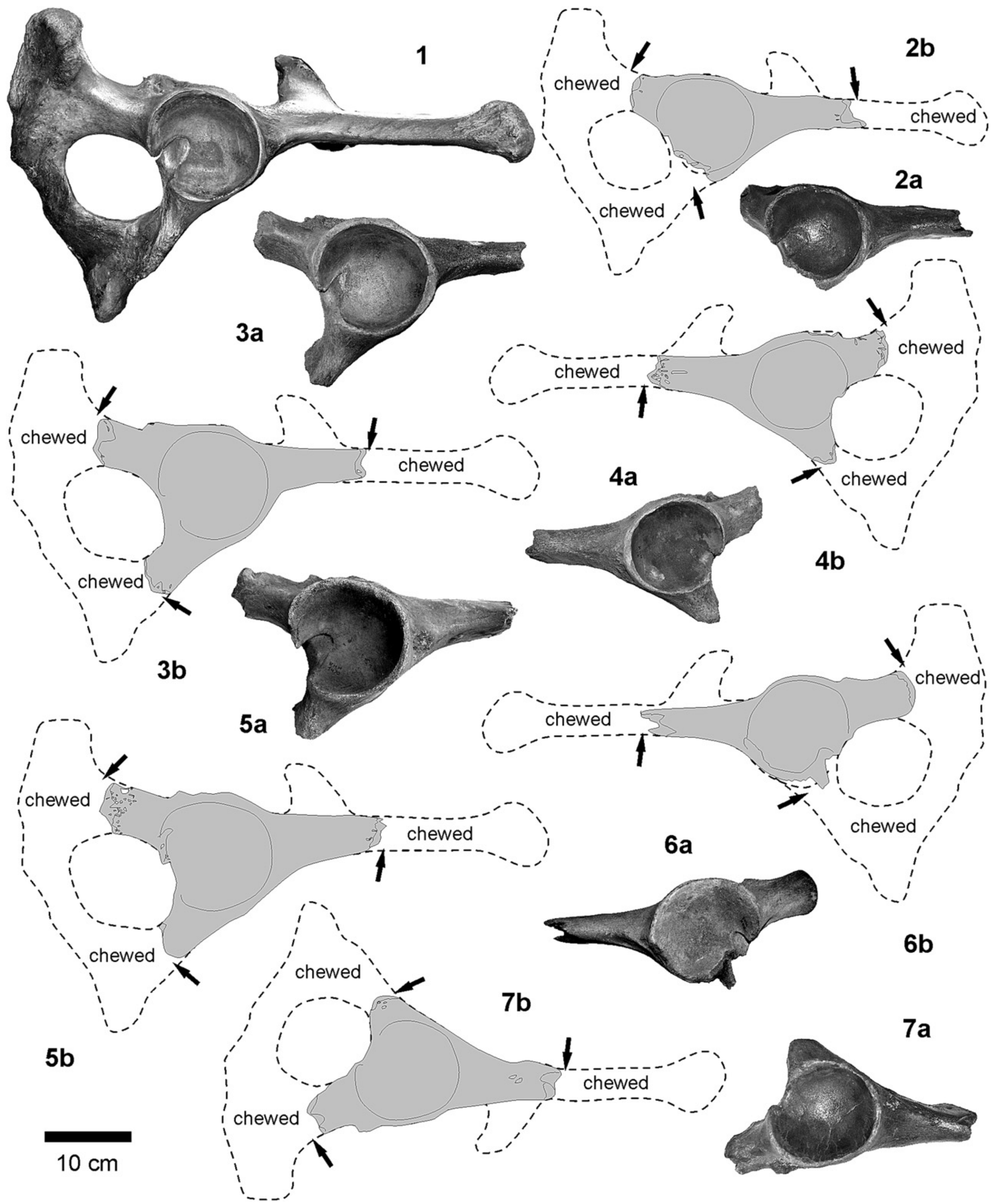

Fig. 13. *Coelodonta antiquitatis* (Blumenbach 1799) damaged pelvic bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right coxa from the skeleton of Petershagen (MNUB No. 1978/2-37), cranial. 2. Right acetabulum from Bottrop (MFUOB No. RHK 1976 4/3.631), cranial. 3. Right acetabulum from Bottrop (MFUOB No. RHK 1976 4/3.627), cranial. 4. Left acetabulum from Bottrop (MFUOB No. RHK 1976 4/3.575), cranial. 5. Right acetabulum from Bottrop (MFUOB No. RHK 1976 4/3.624), cranial. 6. Right acetabulum from Bottrop (MFUOB No. RHK 1976 4/3.572), cranial. 7. Left acetabulum from Bottrop (MFUOB No. RHK 1975 4/3.578), cranial.

carnivores. Broad scratches are herein mainly attributed to typical hyena activities, and are illustrated for the woolly rhinoceros bones of Bottrop (Fig. 20A). Typical damage on scapulae and pelvic bones is in the form of jagged margins, similar to those found on long bones, best to seen on humeri (Fig. 20A1,2). These irregular margins can be explained as having been caused by the premolar and molar teeth, as illustrated for modern hyenas (Fig. 20.7–9). Deep bite marks and tooth scratch marks with widths of 3–6 mm are best preserved in the spongiosa of joints such as those of femora or radii (Fig. 20A3,4), whereas elongated tooth scratch marks occur on the bone compacta

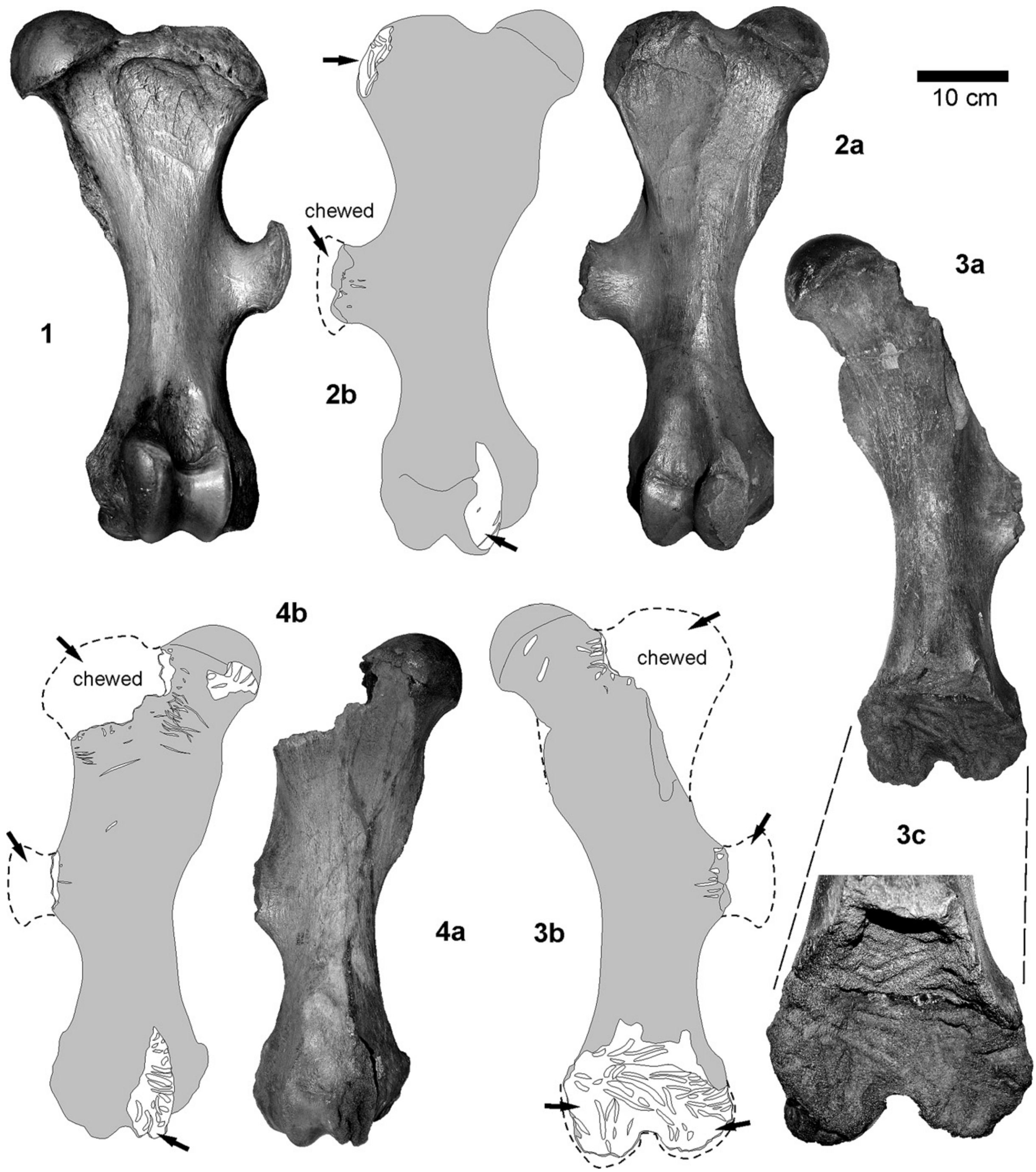

Fig. 14. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb femora bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Left femur from the skeleton of Petershagen (MNUB No. 1978/2-21), cranial. 2. Right femur from Herne, Rhine-Herne Canal (MB Ma.43223), cranial. 3. Right femur from Bottrop (MFUOB No. RHK 1970 4/2.733), a-b. cranial, c. detail of bite mark scratches. 4. Right femur from Bottrop (MFUOB No. RHK 1970 4/2.737), cranial.

of shafts and on joint surfaces (Fig. 20A5,6), probably resulting mainly from hyena C or P teeth. All bite mark types (elongated, oval to round, and triangular) can be attributed to the different teeth in the dentition of a hyena (Fig. 20.9), but analyses of individual bite marks are speculative as there is a probably a degree of overlap with bite marks of the second large carnivore, the steppe lion. The bite marks of hyena cubs, wolves, and foxes are also likely to be of similar shapes and sizes. Bite mark analyses are also problematic because so many bones have had additional modern damage or even been fragmented by machinery, and corrosion has sometimes affected bite mark depressions. However, the well-preserved bite marks on woolly rhinoceros bones, and also on mammoth bones, are in general large, 3–8 mm wide scratch marks, and the diameter of oval-round punctures is commonly between 5 and 10 mm, all of which indicates that these traces were made by large carnivores and predominantly by hyenas, which is further supported by additional analyses described below.

4.4. Body part bone analyses

In addition to the bite mark analyses, further analyses were carried out to detect repetitive types of bone damage, for which

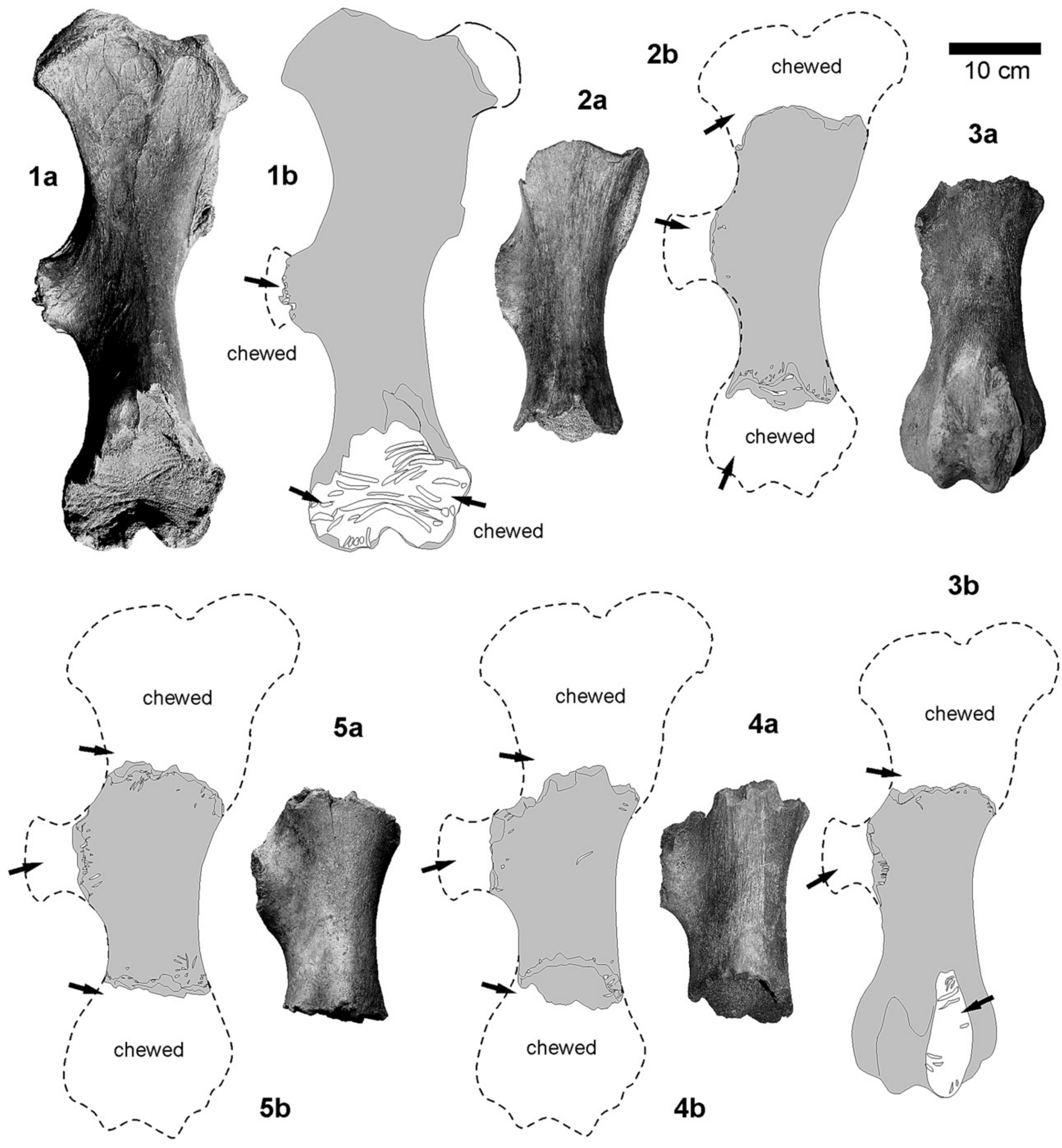

Fig. 15. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb femora bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Right femur from Bottrop (MFUOB No. RHK 1970 4/2.728), cranial. 2. Rigth femur shaft from Dankersen (GMB without No.), cranial. 3. Right femur from Bottrop (MFUOB No. RHK 1970 4/2.733), cranial. 4. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.785), cranial. 5. Right femur shaft from Petershagen (MNUB No. 1978/2-76), cranial

three stages of damage were distinguished (Fig. 20B). Many similarly preserved incomplete bones illustrate the possible dismembering and scavenging techniques employed, which support the identification of the main carnivores as being hyenas. The "body part bone analyses" provide important information about the dismembering of woolly rhinoceros carcasses in open air environments, the bone taphonomy, and even about which large carnivore is likely to have been responsible (Fig. 20C). This type of analysis is important for an understanding of the repeated patterns of woolly rhinoceros carcass destruction. Material from the bone accumulations in the Perick Caves hyena den (NISP = 103) and the Bottrop open air site (NISP = 1601) was compared against the normal number of postcranial woolly rhinoceros bones (NISP = 162; Fig. 20C). Both sites contain *C. antiquitatis* bone material from all parts of the body, and the excavation and collection activities appear to have been less selective than in other cases because the material from both sites contains bone fragments and many damaged bones, not only from the woolly rhinoceros but also from other animals. The presence or absence, or the dominance of particular bones and body parts are likely to reflect in the activities of carnivores. At both the Bottrop open air site and the Perick Caves site there is a marked overrepresentation of large leg bones, particularly in the material from the Perick Caves. The smaller fore and hind limb distal bones are, in contrast, underrepresented. The thoracic region is overrepresented by cervical vertebra at Bottrop, with a predominance of the atlas/axes vertebrae, whereas at Perick

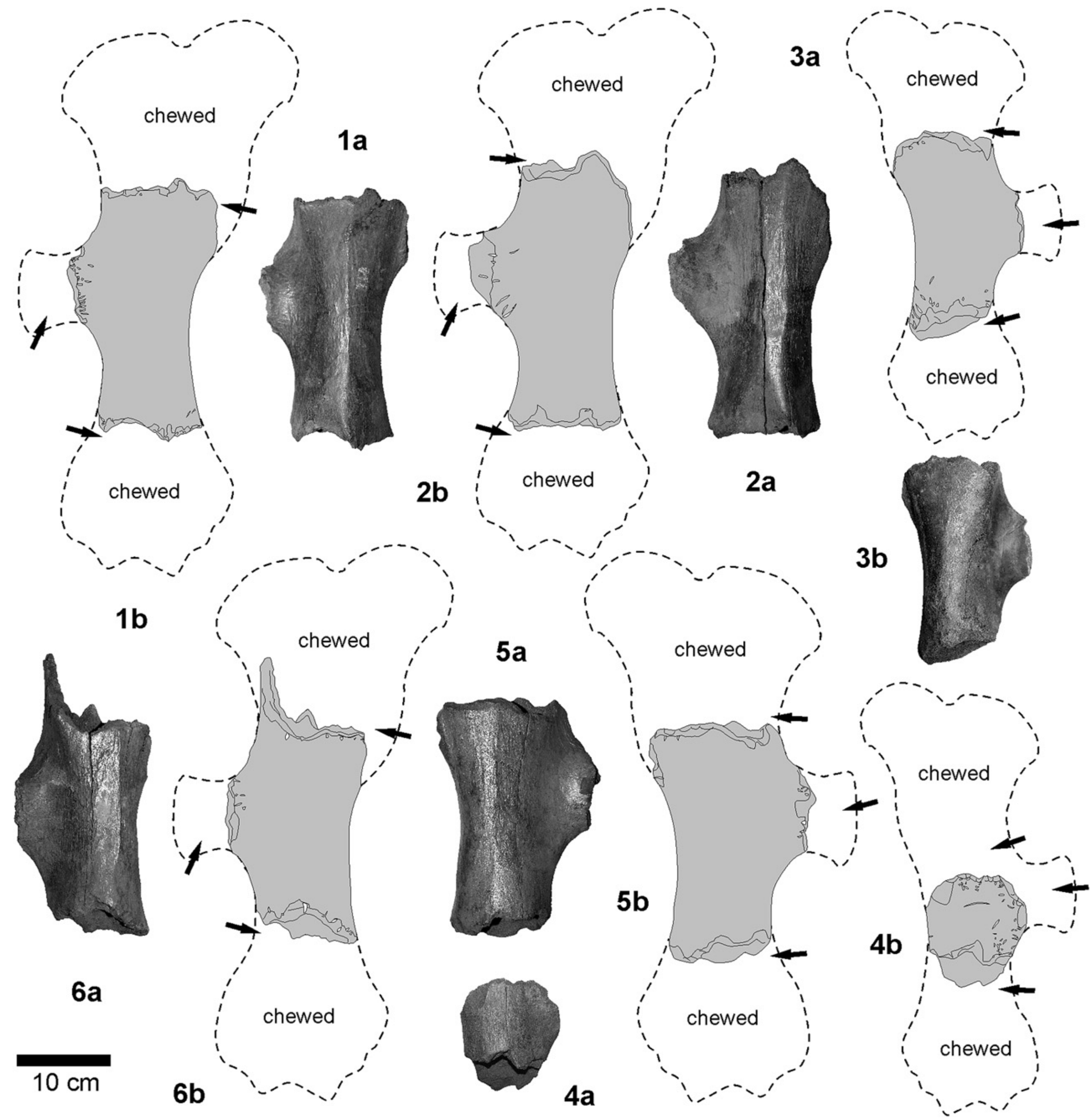

Fig. 16. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb femora bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.782), cranial. 2. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.729), cranial. 3. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.806), cranial. 4. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.816), cranial. 5. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.769), cranial. 6. Rigth femur shaft from Bottrop (MFUOB No. RHK 1975 4/2.789), cranial

Caves the vertebral column is underrepresented. The number of ribs is low at both sites.

5. Discussion

5.1. Hyena populations of Bottrop and NW Germany

Overviews of hyena den caves and hyena clan populations in the Sauerland Karst Mountains of NW Germany have been published previously (Diedrich, 2011f). This information, together with that published herein from the Münsterland Bay Lowlands, is important for an understanding of the palaeobiology of these hyenas, of the differences between the types of hyena dens and bone accumulations in mountain areas and lowland areas and of their palaeoecological adaptations due to the presence or absence of particular types of prey in the different landscapes.

The large number of *C. c. spelaea* crania and bones at the Bottrop site make it the most bone-rich open air hyena river terrace locality in Germany. However, these carnivores are represented by less then 1% of the total number of megafauna bones at Bottrop (NISP = 3280). Other open air sites have yielded mainly skulls and long bones of hyenas from river terraces in northern and southern Germany (Diedrich, 2004a, 2008b). The hyena bones from Bottrop are predominantly from adult to senile animals with very few from cubs, which is typical of communal den localities (Diedrich, 2011f; Fig. 21B) rather than cub-raising dens, as has been described for the

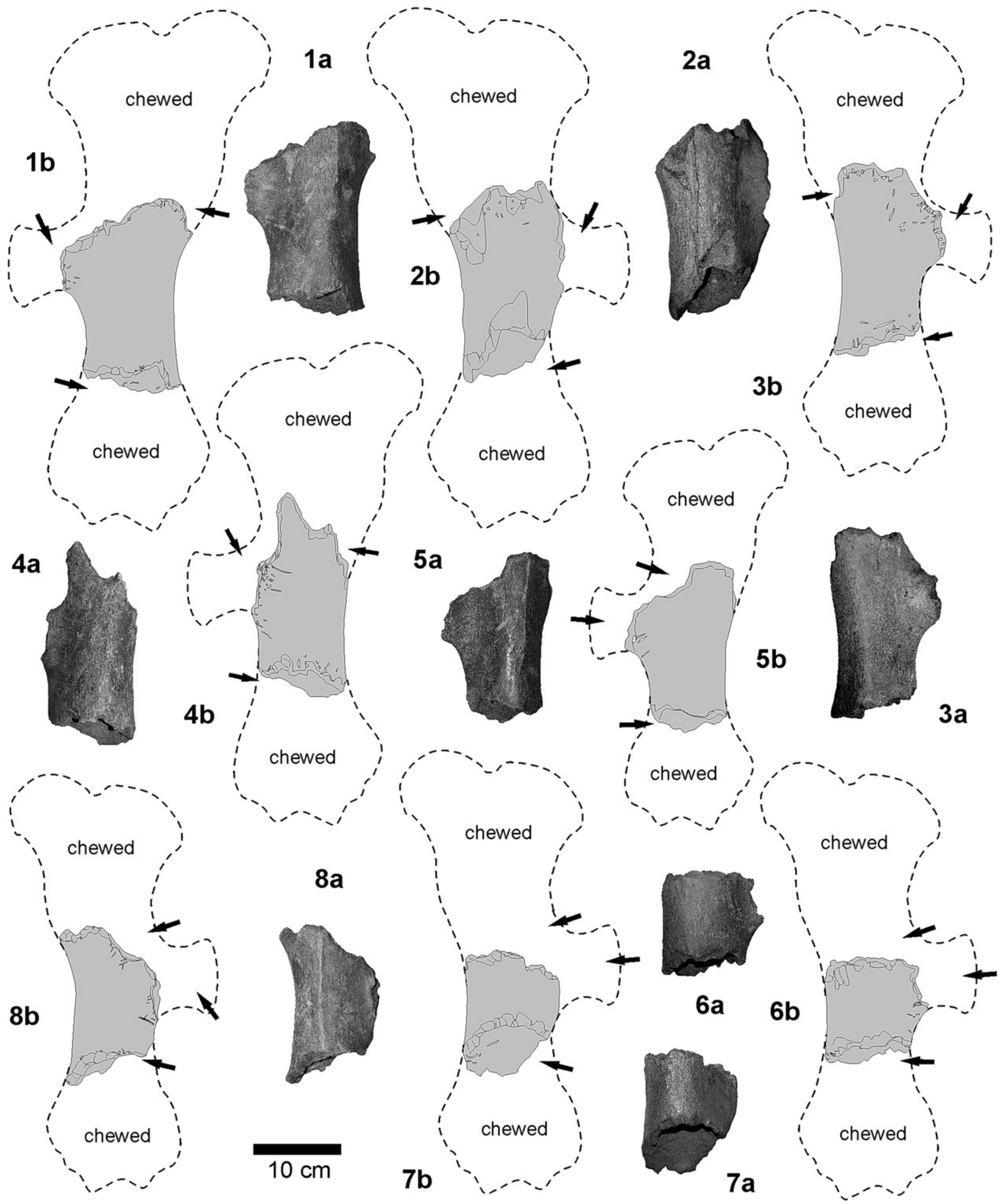

Fig. 17. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb femora bones of early adult to adult individuals from Late Pleistocene open air sites in NW-Germany. 1. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.762), cranial. 2. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.767), cranial. 3. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.777), cranial. 4. Left femur shaft mal from Bottrop (MFUOB No. RHK 1970 4/2.803), cranial. 5. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.765), cranial. 6. Rigth femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.761), cranial. 7. Left femur shaft from Bottrop (MFUOB No. RHK 1975 4/2.757), cranial. 8. Left femur shaft from Bottrop (MFUOB No. RHK 1970 4/2.801), cranial.

open air hyena den site in loess at Bad Wildungen (Diedrich, 2006a). The few complete hyena bones from Bottrop fall within the variability of male/female sex proportions for glacial Upper Pleistocene spotted hyenas of central Europe (see Diedrich, 2011f), but do not allow further analysis or comparisons to interglacial species (cf. Klein and Scott, 1989; Baryshnikov, 1999) because of the fragmented and damaged condition of most of the *C. c. spelaea* bone material. Hyenas seem to have been present at a number of open air sites in the Münsterland Bay Lowlands, with possible den sites at Herten-Stuckenbusch and Bad Wildungen, as well as at the main site near Bottrop, as discussed herein. The problem of identifying hyena dens on river terraces has also been discussed for the Upper

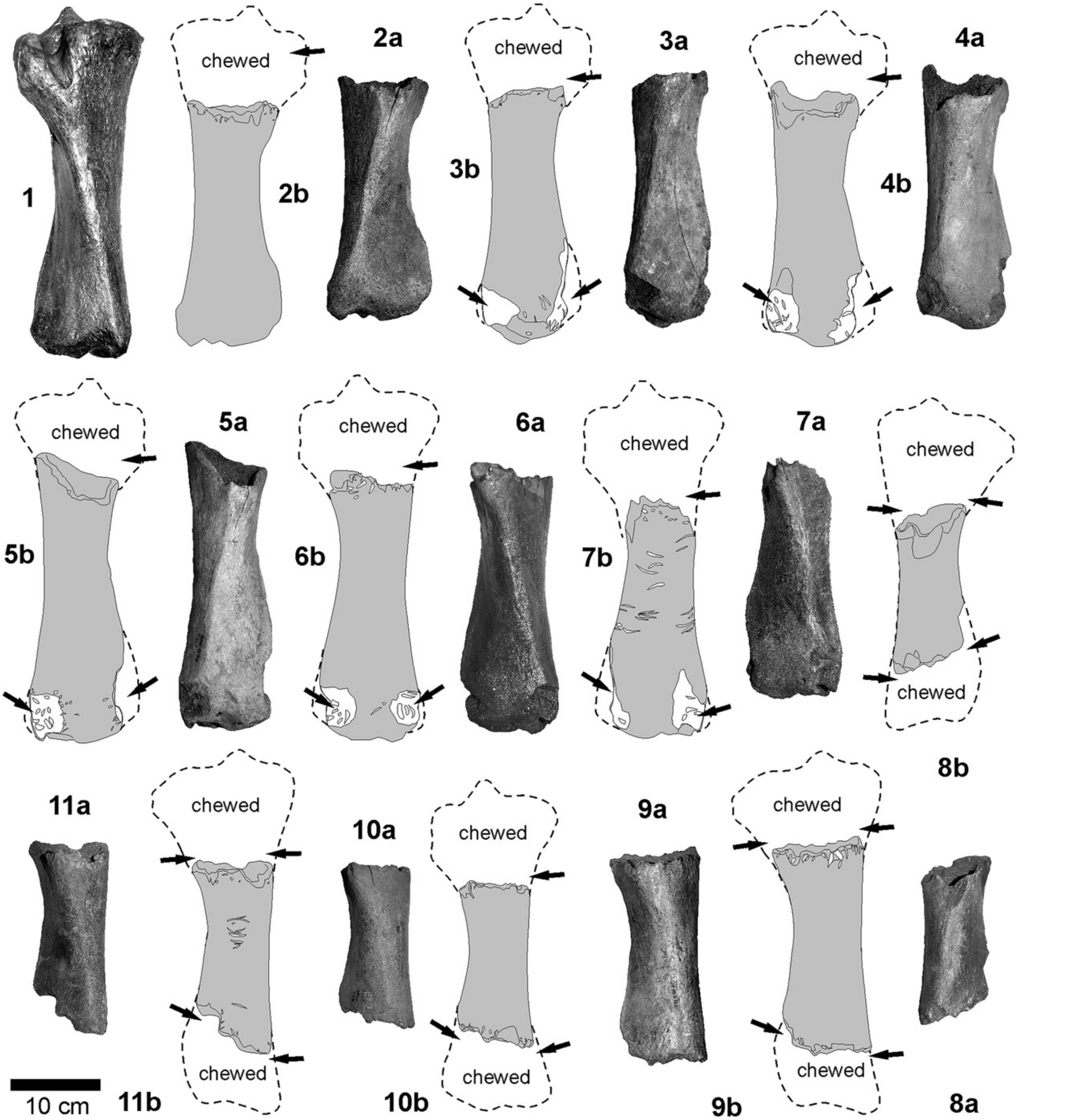

Fig. 18. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb tibia bones of grown up individuals from Late Pleistocene open air sites in NW-Germany. 1. Right tibia from Herten-Stuckenbusch (GPIM without No.), cranial. 2. Left tibia of from Bottrop (MFUOB No. RHK 1970 4/2.668), cranial. 3. Left tibia from Bottrop (MFUOB No. RHK 1970 4/2.667), cranial. 4. Left tibia from Bottrop (MFUOB No. RHK 1970 4/2.663), cranial. 5. Left tibia from Bottrop (MFUOB No. RHK 1970 4/2.665), cranial. 6. Right tibia from Bottrop (MFUOB No. RHK 1970 4/2.687), cranial. 7. Right tibia from Bottrop (MFUOB No. RHK 1970 4/2.103), cranial. 8. Left tibia shaft from Bottrop (MFUOB No. RHK 1962 4/2.712), cranial. 9. Right tibia shaft from Speldorf (GPIM No. A5H721), cranial. 10. Right tibia shaft from Bottrop (MFUOB No. RHK 1962 4/2.700), cranial. 11. Right tibia shaft from Bottrop (MFUOB No. RHK 1970 4/2.689), cranial.

Rhine Valley (SW Germany), where hyena skulls are one important indicator for such sites (Diedrich, 2008b).

The hyena material of "only" 50 pieces (which is high for open air sites) from the late Pleistocene open air site at Bottrop was compared to material from the closest hyena den cave sites in the Sauerland Karst, such as that from the large hyena populations of the Perick Caves (NISP = 142; Diedrich, 2005), Balve Cave (NISP = 34; Diedrich, 2011e), Rösenbeck Cave (NISP = 83; Diedrich, 2011f), Teufelskammer Cave (NISP = 78; Diedrich, 2007c, 2010c), unpublished material from Martins Cave (NISP = 147), Wilhelms Cave (NISP = 174), and a small amount of material from the Grürmanns, Hohle Stein, and Johannes Caves. A composite skeleton assembled in former times from the remains of different animals found in three different caves (but mainly the Wilhelms Cave = "Biggethal Cave") has been mounted in the GPIM (Humpohl et al., 1997, cf. Fig. 1). Nine incomplete skulls and about 615 additional hyena bones, teeth, and jaws in total are known from the hyena den caves in the Sauerland Karst mountain region of NW Germany, demonstrating a well established presence of Ice Age spotted hyena clans during the early to

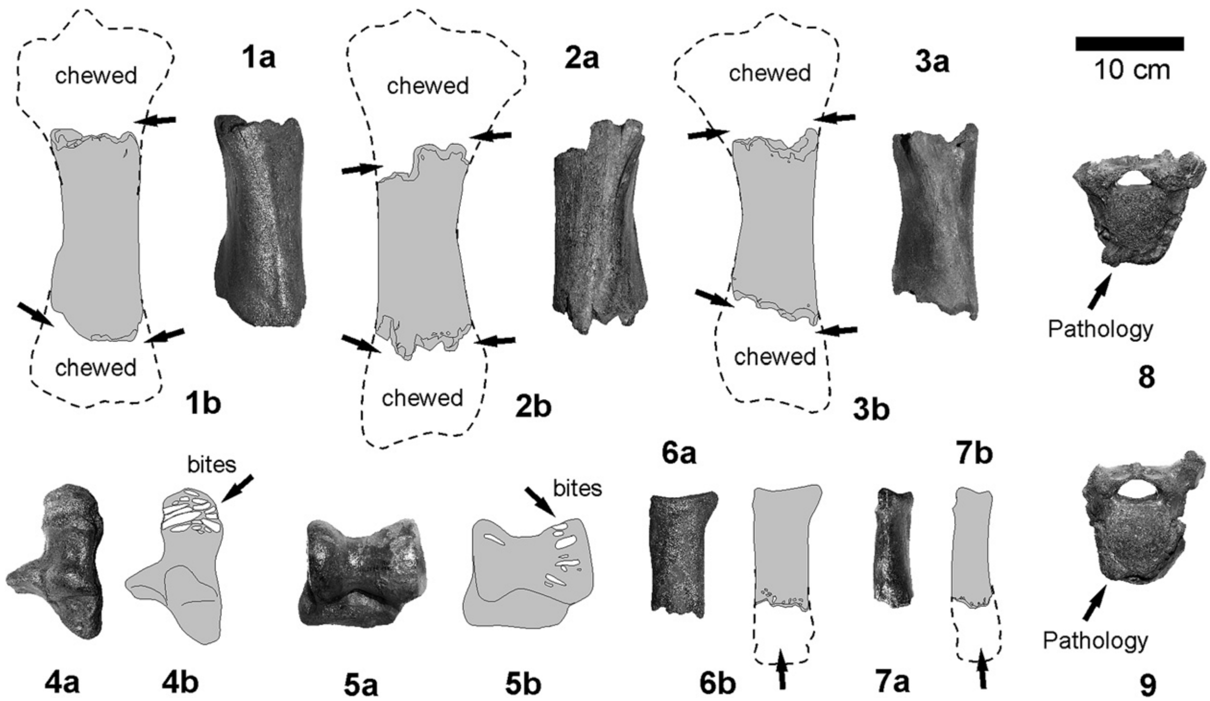

Fig. 19. *Coelodonta antiquitatis* (Blumenbach 1799) damaged hind limb tibia, pedal bones and pathological vertebrae of grown up individuals from Late Pleistocene open air sites in NW-Germany. 1. Right tibia shaft from Bottrop (MFUOB No. RHK 1975 4/2.684), cranial. 2. Left tibia shaft from Bottrop (MFUOB No. RHK 1970 4/2.651), cranial. 3. Right tibia shaft from Bottrop (MFUOB No. RHK 1962 4/2.686), cranial. 4. Left calcaneus from Bottrop (MFUOB No. RHK 1970 4/2.876), dorsal. 5. Left astragal from Bottrop (MFUOB No. RHK 1970 4/2.896), dorsal. 6. Right mt II imal from Bottrop (MFUOB No. RHK 1970 4/3.383), dorsal. 7. Left mt III from Bottrop (MFUOB No. RHK 1970 4/2.875), dorsal. 8. Middle thoracic vertebra with bite marks and pathology (MFUOB without No.), cranial. 9. Middle thoracic vertebra with bite marks and pathology (MFUOB without No.), cranial.

middle Upper Pleistocene. The NISP-percentages of hyena remains between 10 and 42% (Diedrich, 2005, 2010c, 2011e) in the bone assemblages from the Sauerland Karst hyena dens indicates similar high proportions of hyena remains in other Late Pleistocene hyena dens (e.g. Fosse et al., 1998; Tournepiche and Couture, 1999; Diedrich and Žák, 2006), but those percentages seem to be highly variable between the different den types (communal den, prey depot, and cub-raising den), which has not yet been well investigated in these Upper Pleistocene sites. In present-day African spotted hyena dens the quantity of hyena remains at cub raising den sites (cf. definition for modern spotted hyenas: East et al., 1989; Hofer, 1998; Boydston et al., 2006) sometimes reaches only 1% of the NISP (Mills and Mills, 1977; Pokines et al., 2007), which is similar to the percentage of hyena remains at the Bottrop open air site. Large quantities of hyena remains are not always firm proof of a bone assemblage accumulated by hyenas or of a hyena den site. Such large quantities of hyena remains seem to be typical of cave sites, whereas too few open air sites have been investigated to allow any firm conclusions to be drawn. The comparable open air loess site at Bad Wildungen (Fig. 1) has similarly low quantities of hyena bones (7%) in a cub-raising type of den (Diedrich, 2006a).

5.2. Hyenas versus lions as destroyers of big game carcasses

Lions are known to consume mainly the intestines and inner organs of their largest prey, such as elephant or rhinoceros, often eating very little of the flesh (Diedrich, 2010e), and are not known to dismember the carcasses and destroy the bones of these large megafauna in the way that both extant (cf. Sutcliffe, 1970; Kruuk, 1972; Frank, 1986) and extinct spotted hyenas do. In Neumark-Nord (central Germany), Eemian interglacial spotted hyenas may have possibly left some bite marks on elephant carcasses, but it is uncertain whether these were from hyenas or from lions feeding first on the intestines and inner organs (Diedrich, 2010b, e). The destruction of big game (elephant) carcasses and damage to massive bones have been demonstrated to be the main result of the carcass dismembering technique of hyenas (Diedrich, 2010e). Only hyenas dismember the carcasses of their largest prey in order to avoid antagonistic conflicts with prides of lions, and only the spotted hyenas remove these body parts from their prey to their den sites in the way that extant spotted hyenas do (e.g. Henschel et al., 1979; Behrensmeyer and Boaz, 1980; Brain, 1980; Avery et al., 1984; Skinner et al., 1986; Cooper, 1993; Di Silvestre et al., 2000) and extinct Ice Age spotted hyenas also used to do (e.g. Fosse et al., 1998; Diedrich and Žák, 2006).

5.3. Hyena clans as woolly rhinoceros hunters or scavengers

Woolly rhinoceros calf remains are known from some of the German Sauerland Karst and the Czech Republic's Bohemian Karst hyena den caves (Diedrich and Žák, 2006; Diedrich, 2006b, 2008d, 2011f), which suggests that hyena clans may have actively hunted the calves of *C. antiquitatis*. The material from Bottrop includes about 5% calf remains; some calf long bones with bite and chewing damage are illustrated herein (skull: Fig. 5.1, humerus: Fig. 5.2,3, femur: Fig. 5.4, tibia: Fig. 5.5). Hyena clans may have not only scavenged on carcasses of dead rhinoceros calves, but also actively hunted young animals, although this remains pure speculation. Selective preying on herbivorous and migratory big game is well known for both extant and extinct lions and hyenas (Kruuk, 1972; Cooper, 2008), as is preying on smaller juvenile animals.

5.4. Hyena clans as woolly rhinoceros carcass scavengers and bone destroyers/accumulators

One of the best examples of a woolly rhinoceros carcass that has not been either scavenged or transported by a fluvial system is the

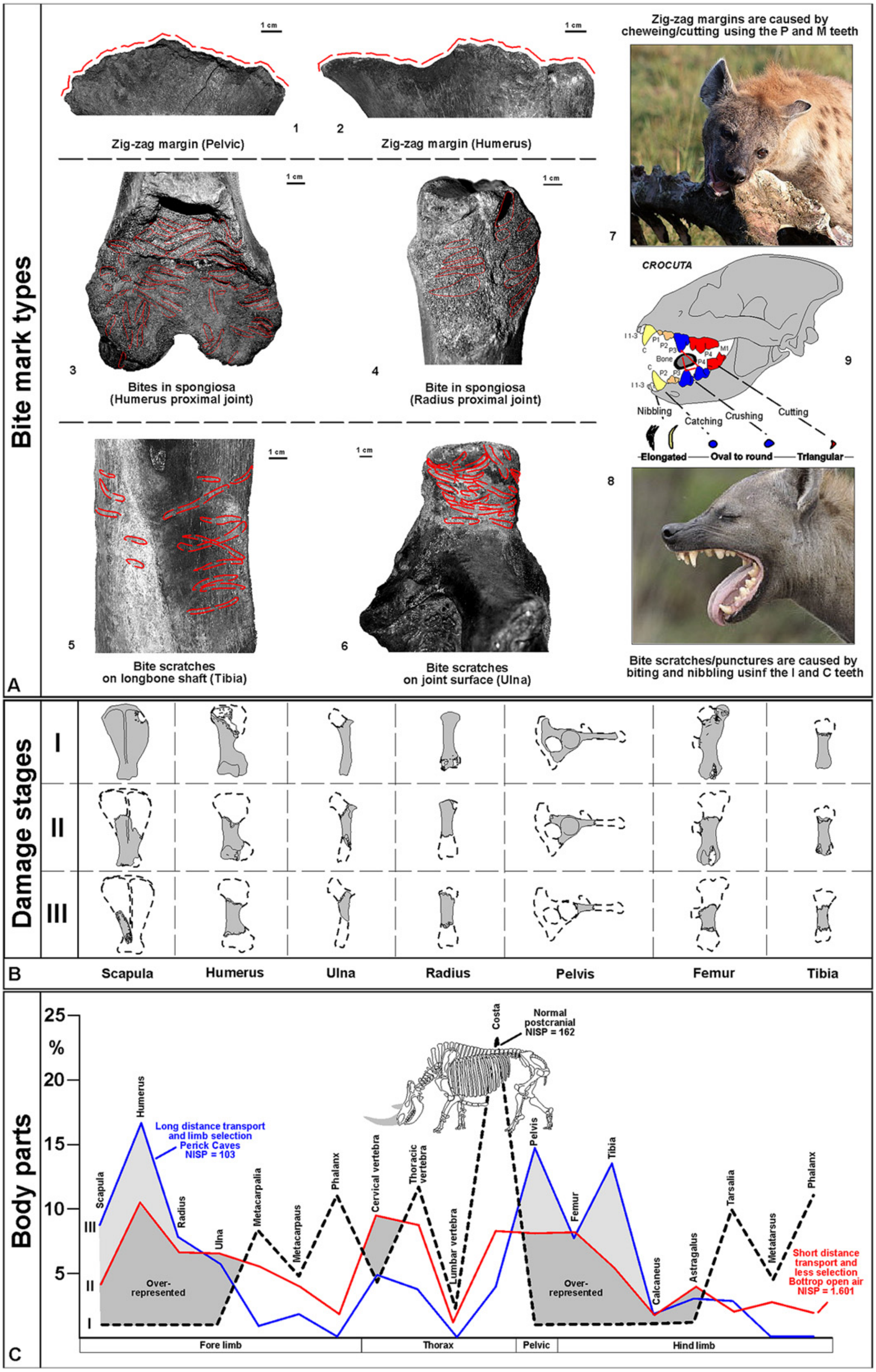

Fig. 20. A. Bite mark types at the bone material from the Bottrop open air site. 1. Zig-zag-margin on a pelvic bone from Bottrop caused by P/M teeth due to cutting. 2. Zig-zag-margin on the proximal half of a humerus (cf. Fig. 4.7) as result of chewing the proximal joint with the P/M teeth. 3. Deep 3-6 mm in width bite scratch mark impressions in the distal femur joint (cf. Fig.) resulting from the I and C teeth. 4. Deep bite impacts laterally on a proximal radius joint made by the anterior dentition. 5. Bite scratches on the bone compacta of an ulna shaft (cf. Fig. 5.26) produced be the I/C or the P teeth. 6. Bite scratch marks in with of 3-5 mm on the inner ulna proximal joint (cf. Fig. 5.32) caused by the I/C or the P teeth. 7. Modern spotted hyena chewing on a megamammal pelvic margin. 8. Modern spotted hyena dentition. 9. Spotted hyena dentition function and resulting bite mark types. B. *Coelodonta antiquitatis* represented bones and body parts at the site Bottrop. B. Woolly rhinoceros bone damage types which can be divided in three stages for large bones. C. Woolly rhinoceros carcass body part removements analyses on the woolly rhinoceros bones of the NW German open air site Bottrop open air site in comparison to the Perick Caves and normal present amount of postcranial bones in percentages.

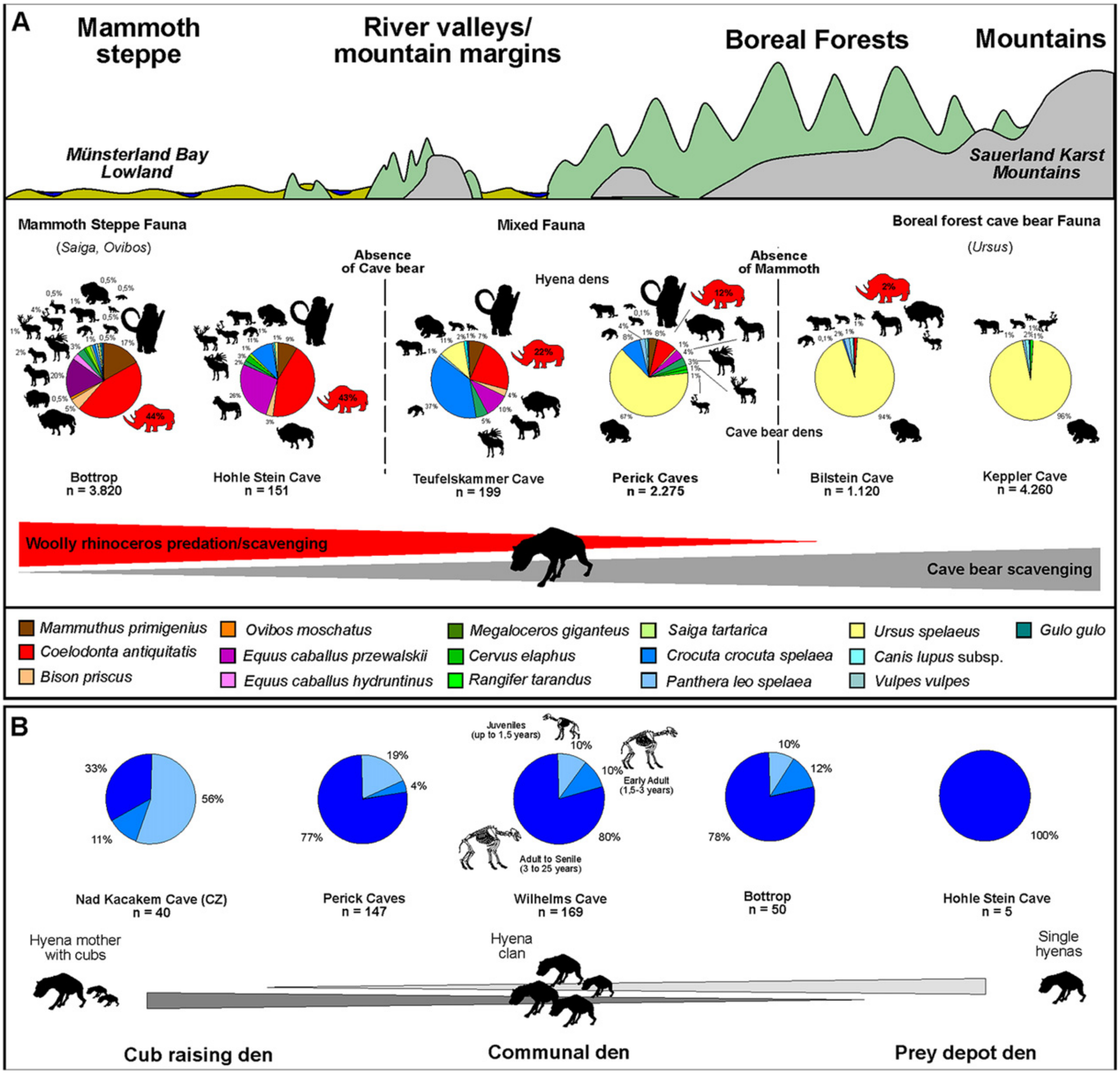

Fig. 21. A. Faunal hyena den compositions (mainly hyena prey fauna) with overlapping cave bear dens in a cross-section from the Münsterland Bay Lowlands and the Sauerland Karst Mountains. The woolly rhinoceros prey in hyena den bone accumulations decreases from the mammoth steppe lowlands to the mountain regions, where hyenas specialized instead on the cave bear scavenging. B. The hyena population of Bottrop seem to have been a communal den with prey storage and at one place also a cub raising den site along the Emscher River.

articulated skeleton from Petershagen (Diedrich, 2008c, Fig. 1), which was found on the banks of the Elbe River. The bone preservation and the general lack of rounding on bones from sites around Bottrop, Herne-Herne-Stuckenbusch, and Selm-Tersche, indicate that these have undergone little or no fluvial transport. Woolly rhinoceros remains and other megafauna bones in the Münsterland Bay Lowlands have previously always been described as natural bone accumulations resulting from floods, especially the "bone gravels" along the Emscher, Lippe and Ruhr Rivers of NW Germany (Siegfried, 1983; Heinrich, 1987). These bone accumulations had, however, never been analysed taphonomically, not even the mammoth skeleton from Ahlen (Siegfried, 1959). This second megamammal skeleton to have been found in loess deposits was analysed recently, together with all other mammoth remains from Bottrop and the Münsterland Bay Lowland (Diedrich, 2010a–b) and these have also found to have not been affected by fluvial transport. The many bone accumulations, especially along the Emscher and Lippe Rivers, must therefore have mostly had a different origin, and can best be explained as the result of the activities of hyenas.

Evidence for a hyena origin for these Pleistocene bone accumulations lies in the modern bone accumulations that are due to hyenas, which contain large mammal bones exhibiting similar patterns of damage and hyena chew marks (e.g. Hill, 1989; Arribas and Palmqvist, 1998; Kahlke, 2006; Diedrich and Žák, 2006; Pokines et al., 2007). Open air bone accumulations due to hyenas have been known since the Miocene, whereas in the Lower Pleistocene these are limited to a few sites recorded in Spain (Arribas and Palmqvist, 1998) and Germany (Kahlke, 2006). The higher density of hyena dens in Europe during the Upper Pleistocene has provided a much better basis for research, but previous studies have focussed mainly on the identification of cave sites.

Most of the Upper Pleistocene open air sites in the Münsterland Bay Lowlands of NW Germany seem, by comparisons with the above-mentioned studies and others, to be related to

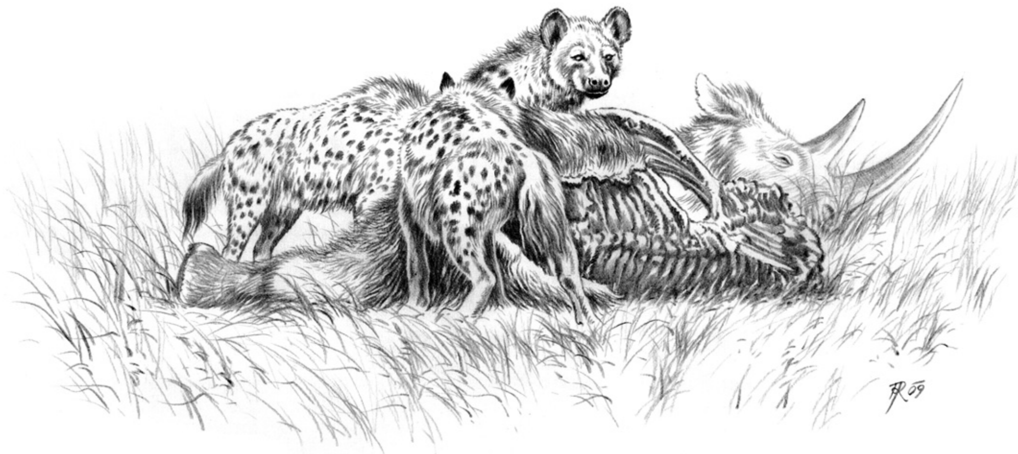

Fig. 22. Upper Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) clan feeding and decomposing a woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach 1799) carcass nearby the Emscher River terrace open air hyena den site Bottrop in the Münsterland Bay Lowland mammoth steppe (Illustration G. Rinaldino" Teichmann 2010; after a photo from Modern spotted hyenas scavenging a black rhino in Africa modified to the Ice Age hyenas and woolly rhinoceros).

hyena activities (Fig. 1), especially using the similarly damaged woolly rhinoceros bones as indicators for hyena den sites, or at least for hyena activity (Fig. 20A–C, 21). A number of different types of late Pleistocene hyena sites have been recognized in these lowlands including (1) scavenging sites such as at the Ahlen mammoth carcass site, (2) prey depot sites in which large quantities of megafauna remains were accumulated, especially along Upper Pleistocene rivers and streams, such as those found in Bottrop, Herten-Stuckenbusch and Selm-Ternsche, and (3) open air hyena dens in the form of communal den or cub raising den sites, which are similar to the sites in the caves of the Sauerland Karst mountains (cf. Diedrich, 2005, 2007c, 2010c, 2011e).

Bones damaged by carnivores have been found in Bottrop, especially the massive bones of mammoths and those of the woolly rhinoceros *C. antiquitatis* presented herein. Very large numbers of such incomplete woolly rhinoceros bones have been recovered from the Bottrop area (Figs. 5–20), indicating that they originated mainly from open air hyena activity and feeding sites. The open air material from the Münsterland Bay Lowlands demonstrates repetitions of similar stages of bone destruction. Similarly damaged rhinoceros humerus bones from a few different open air sites in Austria and Germany have already been illustrated as examples of hyena damaged bones (Zapfe, 1939; Thenius, 1961; Wernert, 1968), together with bones from hyena cave dens in the Czech Republic and open air loess sites around Prague (Diedrich and Žák, 2006). These have been illustrated together with some examples from the open air site at Bottrop discussed herein (Koenigswald and Walders, 1995), whose bone damage patterns are now known to relate to the activities of hyenas (Fig. 20A) on the basis of comparisons with modern bone damage and bite mark types (e.g. Hill, 1989; Faith, 2007; Pokines et al., 2007), and with different destruction stages from hyena cave dens such as those at Perick Caves (Diedrich, 2008d), Teufelskammer Cave (Diedrich, 2010c), Balve Cave (Diedrich, 2011f), and the open air loess site at Bad Wildungen (Diedrich, 2006b) in NW Germany. These sites were mainly used for the woolly rhinoceros bone damage comparisons, a review of which has allowed the classification of the damage into three main stages (Fig. 20B). In Stage 1 there is minor damage on the proximal or distal parts of the bone, in Stage 2 one joint is completely chewed off, and in Stage 3 only a shaft remains, with characteristically jagged ends (cf. Fig. 20A).

An analysis of the presence or absence of different woolly rhinoceros body parts in the Bottrop material has supported the identification of this bone assemblage as having been accumulated by hyenas, and also the identification of open air den sites because of the marked overrepresentation of leg bone material (Fig. 20C). Similar overrepresentations of leg remains are well known in bone accumulations at other Pleistocene hyena den sites (e.g. Arribas and Palmqvist, 1998; Tournepiche and Couture, 1999; Kahlke, 2006) as well as in modern African hyena dens (Hill, 1980a, 1989, 1998; Scott and Klein, 1981; Avery et al., 1984; Arribas and Palmquist, 1998; Pickering, 2002; Lansing et al., 2007; Pokines et al., 2007). Hyenas remove mainly the legs from megafauna carcasses (cf. for zebras/horses: Pokines et al., 2007; Diedrich, 2010d), which explains the dominance of woolly rhinoceros fore and hind leg bones at the Bottrop site (62.5% limb bones; Fig. 20C). Thorax bones such as vertebral columns, ribs and even the pelvic bones are also typically documented damaged from modern hyena scavenging sites (Behrensmeyer and Boaz, 1980; Avery et al., 1984; Di Silvestre et al., 2000). The overrepresentation is even greater in the Perick Caves hyena den, which may reflect a greater preference for legs or possibly a longer transport distance into the cave dens of the Sauerland Karst. However, the comparisons indicate a bone assemblage at the Bottrop open air site that has been predominantly accumulated by hyenas, and shorter transport distances for the body parts. Hyena dens in the mammoth steppe appear to have been closer to the carcass sources than in the mountains, which may also explain the decrease in the quantity of woolly rhinoceros remains in the Sauerland Karst (Fig. 21).

6. Conclusions

Remains of the Upper Pleistocene spotted hyena *Crocuta crocuta spelaea* population from the open air Emscher River terrace site near Bottrop and other hyena remains from the Münsterland Bay Lowlands indicate a strong presence of these important carnivores during the early to middle Upper Pleistocene, which is also supported by larger quantities of hyena remains from several caves in the Sauerland Karst Mountains of NW Germany, at a time when big game was abundant on the mammoth steppe lowlands and in the mountainous boreal forest areas. Hyena had three different types of sites for their different activities, reflected in the bone records from these sites: (1) At carcass scavenging sites, such as the mammoth of Ahlen, the hyenas left in place damaged skeletons from which they deported body parts, not only from woolly rhinoceros but also from other megafauna (Fig. 22). (2) Along the rivers in the lowlands hyenas appear to have accumulated thousands of body parts and bones, as do extant African spotted hyenas and as is probably documented at Bottrop, Herten-Stuckenbusch, and Selm-Ternsche, as well as at other sites. The best evidence for such bone accumulations being due to hyena activities comes from the similar, repetitive patterns of damage to woolly rhinoceros bones, which were not as heavy as mammoth bones and therefore easier to move over longer distances, and even into cave dens. Few individual bones were removed from the *C. antiquitatis* carcasses, but rather complete legs or parts of legs appear to have been taken to the bone accumulation or den sites. (3) The den sites in open air lowlands can best be identified by the large quantities of hyena remains and the typical repeated damage patterns on the massive bones of woolly rhinoceros, which are indicative of food storage and communal dens of adult animals. Bottrop is probably the best example, but also possibly included in this type of den are the sites at Selm-Ternsche and Herten-Stuckenbusch. Finally, another den type, the cub raising den, may also have been present at Bottrop with its moderate to high quantities of cub remains within the population. These cub raising dens, communal dens, and prey depots, often overlap but can be distinguished through comparisons with the modern situation at African spotted hyena den sites. Such differences between the den types have been documented for hyena dens in the Sauerland Karst caves. The bone accumulation at Bottrop appears to be mainly a result of overlapping hyena prey depot, communal, and cub raising den sites. The abundant and repetitive types of damage on the bones of their largest prey, the woolly rhinoceros and the woolly mammoth, exclude the bulk of these bones from having accumulated as a result of hunting by Neanderthals or of natural flooding events.

Acknowledgments

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