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The Crocuta crocuta spelaea (Goldfuss 1823) population from the early Late Pleistocene hyena open air prey deposit site Biedensteg (Bad Wildungen, Hess, NW Germany), a contribution to their phylogenetic position, coprolites and prey

Cajus G. Diedrich

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Summary

Four skulls, three lower jaws, a few incomplete postcranial bones and many coprolites of the early Late Pleistocene (Early Weichselian, 90,000 - 65,000 BP) ice age spotted hyena open air prey deposit site Biedensteg at Bad Wildungen (Hessia, NW-Germany) all show crack-, bite- and nibbling-marks as a result of cannibalism. Originally, the bones belong to three young adult to adult individuals. For the first time in Europe, a skull and postcranial bones belonging to a young animal of *C. c. spelaea* (Goldfuss 1823) of only a few days or weeks old are described and figured. The animal was possibly killed and for sure eaten by members of the same species. The material has been compared to remains from a younger Late Weichselian hyena population of Perick Caves (Sauerland, NW Germany). The hyenas from Biedensteg possess an upper first molar, in contrast to those from Perick Caves in which these are often lacking. At the Bad Wildungen-Biedensteg open air prey deposit site, the hyenas represent 6% of the mammoth steppe fauna bones. The site indicates a mixed diet consisting of all larger ice age mammals. The very high percentage (47%) of *Coelodonta* prey remains results of one disarticulated female and one young animal carcass, on which the hyenas fed strongly. Additionally, woolly rhinoceros bones indicate a specialization of the hyenas to large rhinoceros prey. This can be observed at other places, too, such as the hyena Perick Cave den. The abundant coprolites of the Biedensteg hyena population show different shapes, although most are droplet shaped or partly connected pellets which seemed to be of dry origin. Other coprolites, up to ten cm large, must have resulted from more soft dung. Many coprolites contain up to 1,5 cm small and well rounded bone *compacta* fragments, but also quite often bone *spongiosa*. The latter corresponds with the hyenas feeding on long bones of the woolly rhinoceros and steppe bison, which constitutes therefore another proof, next to the many chewing and gnawing marks at all prey bones. During the early Late Pleistocene, Biedensteg was a well frequented hyena open air den and prey deposit site close to the margin of a large sinkhole, filled with a shallow lake or muddy area, close to the small Wilde river. Also owls left many pellets at Biedensteg with thousands remains of micromammals, frogs and fishes.

Samenvatting

Vier schedels, drie onderkaken, een paar incomplete botten en vele coprolieten van de vroeg Laat-Pleistocene (Vroeg Weichselien, 65.000-90.000 voor heden) grottenhyena, gevonden in de site Biedensteg bij Bad Wildungen (Hessen, NW-Duitsland) tonen allemaal knaag-, bijt- en kauwsporen, veroorzaakt door kannibalisme. Oorspronkelijk behoorden de botten toe aan drie jong volwassen tot volwassen individuen. Voor het eerst in Europa worden de schedel en de postcraniale botten van een jong dier van slechts een paar dagen of weken oud beschreven en afgebeeld als grottenhyena, *Crocuta crocuta spelaea* (Goldfuss 1823). Het dier is mogelijk gedood en in ieder geval opgegeten door leden van zijn eigen soort. Een vergelijking met de groep Laat-Weichselien hyena's gevonden in de Perick grotten (Sauerland, NW Duitsland), laat zien dat de hyena's uit Biedensteg een bovenste eerste kies bezitten, in tegenstelling tot die van de Perick grotten, waar ze vaak ontbreken. In Bad Wildungen-Biedensteg maken de hyenas 6% uit van de mammoetsteppe-dieren. De site wijst op een gemengd dieet dat bestond uit alle grotere ijstijddieren. Het zeer hoge percentage (47%) van *Coelodonta*-prooiresten wordt veroorzaakt door een uiteengevallen skelet van een volwassen vrouwtje en een karkas van een jong dier, die beiden sterk door de hyena's zijn aangevreten. De botten van de wolharige neushoorn wijzen op een aanpassing van de hyenas aan een grote neushoorn als prooi. Dit wordt ook gezien op andere plaatsen, zoals de hyenaplek in de Perick grotten. De overvloedig aanwezige coprolieten van de Biedensteg hyena-populatie laten verschillende vormen zien, hoewel de meeste druppelvormig zijn of bestaan uit gedeeltelijk aaneengeschakelde keutels die van een droge oorsprong lijken te zijn. Andere coprolieten, tot tien cm lang, moeten ontstaan zijn uit een zachtere ontlasting. Veel coprolieten bevatten tot 1,5 cm grote mooi afgeronde fragmenten van hard bot (*compacta*), maar ook vrij vaak trabeculair bot (*spongiosa*). Dat laatste stemt overeen met hyenas die zich tegoed hebben gedaan aan de lange beenderen van de wolharige neushoorn en de wisent. Dit vormt daarmee weer een bewijs, naast de vele knaag- en kauwsporen op alle prooibotten. Gedurende het vroege Laat

Pleistoceen was Biedensteg een goed bezochte hyena plek in de open lucht en verzamelplaats voor prooibotten niet ver van de rand van een verdwijngat, gevuld met een ondiep meer of een moerasachtig gebied, dichtbij de kleine Wilde rivier. Ook uilen lieten veel braakballen achter in Biedensteg met duizenden overblijfselen van kleine zoogdieren, kikkers en vissen.

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 large mammals. In 1952, E. Jacobshagen and R. Lorenz found snow owl pellets in a "pellet horizon", but the latter also found two hyena skulls. Jacobshagen described this fauna, mainly the micromammals, in 1963, and Huckriede & Jacobshagen (1963) published the first section in the same volume. New results were later added by Semmel (1968) and Kulick (1973). Storch (1969) did the last palaeontological research on the snow owl pellet material. Ever since, the poorly determined macrofauna was forgotten. Thus, a very important ice age hyena prey deposit open air site in Europe was not understood, despite the mentioning of hyena gnawing and bone deposits by Jacobshagen (1963).

With the "European Ice Age Spotted hyena Project" the macromammalian material of Biedensteg became important again. Before the rediscovery and reunification of different collections (Stadtmuseum Bad Wildungen, coll. Pusch and coll. Lorenz in the Lorenz-Stiftung, coll. Jacobshagen at the University of Marburg) of this old material in 2005, only hyena den sites in the cave rich region of Sauerland (north-western Germany) were studied (Diedrich, 2005d).

With Biedensteg, a open air bone deposit site that allows a comparison of cave sites can be presented for the first time. With this, it is possible to get 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 hyena prey and bone taphonomy for caves and open air sites becomes more clear. Finally, the influence of hyenas on bone destruction is of importance for the interpretation of archaeological sites, where these animals were certainly collecting bones (Diedrich, 2005d) or fed on bone rubbish left by the Middle Palaeolithic Neanderthals or modern human groups of the early Late Palaeolithic (Von Koenigswald, 2002).

The macromammal bone collection was prepared for study by the company PaleoLogic. Many broken bones were fixed and only the

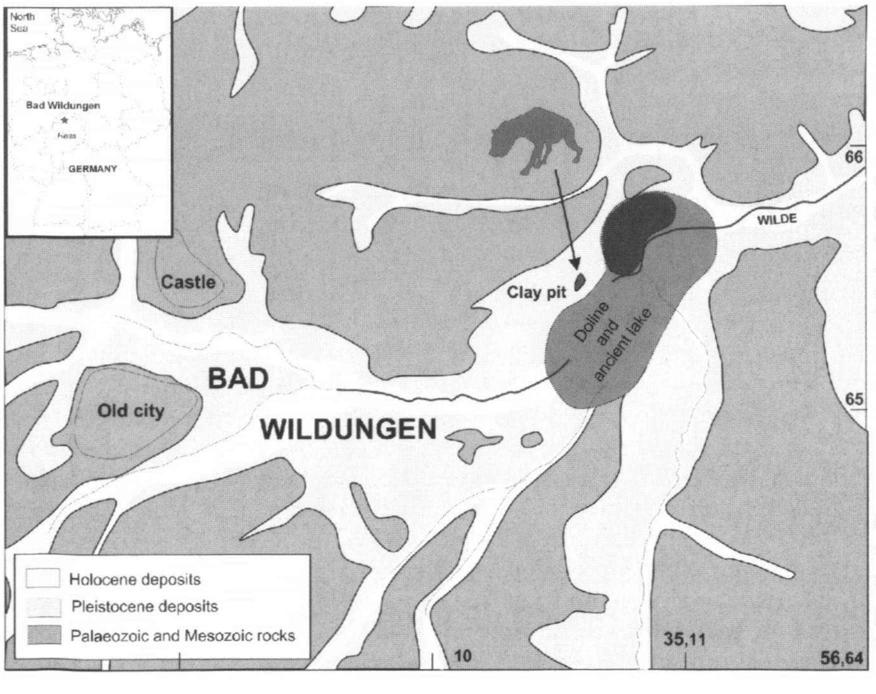

Fig 1 Topographical position of the Ice Age Spotted Hyena *Crocuta crocuta spelaea* (Goldfuss 1823) prey deposit site Biedensteg near Bad Wildungen (Hessia, NW-Germany). The bones were deposited at the margin of an ancient small lake created by the old Wilde river that filled up a doline depression during the early Weichselian ice age period. © Paleologic.

Topografische positie van de site Biedensteg bij Bad Wildungen (Hessen, NW-Duitsland) met een leger van de grottenhyena, *Crocuta crocuta spelaea* (Goldfuss 1823). De botten zijn afgezet aan de rand van een oud meertje, ontstaan doordat de oude Wilde rivier een doline depressie met water vulde gedurende het vroege Weichselien van de ijstijd. © Paleologic.

excavation-caused hit marks were refilled. The bones were finally conserved with a nitrogen based lacquer, CLOU L1. Samples for radiocarbon isotope analysis were not taken, because the material had already been dated to be from the Early Weichselian period. A few bone fragments, marked as such, are not conserved for possible geochemical studies in the future.

The main collection (including coll. Pusch, coll. Lorenz) is owned by the Rudolf-Lorenz-Stiftung and was partly presented in the Stadtmuseum of Bad Wildungen or was stored by Jacobshagen in the collection of the University of Marburg. Additionally a few macromammal bones and many micromammal bones from the collection at the University of Marburg were integrated. In the Stadtmuseum Bad Wildungen, all bones from at least three collections are reunited now. In this museum a new presentation of the hyena prey deposit site and the Weichselian fauna and climate will open in 2007.

Comparitive hyena material of different collections was used. The most important bones belong to an articulated incomplete skeleton from the Biggetal Cave (Sauerland, NW Germany) in the collection of the Geologisch-Paläontologische Museum der Westfälischen Wilhelms-Universität Münster. Material from the Srbsko-Chlum-Komin vertical cave and hyena prey deposit site (Czech Republic) was studied as well. Among this material, stored at the National Museum of Prague, there is one of the few *C. c. spelaea* skeletons with excellent preserved postcranial bones. Skull and postcranial material was additionally compared with the large collection of the Perick Caves, which has recently been published (Diedrich, 2005a).

Geology and Datation

The geological situation at the hyena deposit site "Lehmgrube Biedensteg" was published by Huckriede & Jacobshagen (1963), Semmel (1968) and Kulick (1973). An overview of the redrawn sketch of the outcrop section in combination with all published results and new own interpretations about the hyena deposits is presented in fig. 2.

The Wilde river gravels at the base of the section were deposited during the Eemian interglacial period. They consist of red Bunter sandstone- and claystone-, lydit-, quartz-, and diabas-pebbles. These deposits are overlaid by a palaeosoil, caused by solifluctation. In this "Eemian-Soil", the river pebbles are resedimented with reddish-brown loess. The Lower Loess is from the early to middle Early Weichselian and a product of the first maximum glaciation (fig. 2), during which loess was deposited in this mountainous region in a mammoth steppe environment. Some snails were found in the Lower Loess by Jacobshagen (1963), among others, the loess soil snail *Pupilla muscornum* (Müller), which fits to the climatical and environmental interpretation.

In the middle and at the end of the Early Weichselian, a climatic stasis resulted in a palaeosoil along the Wilde river gravels which were on the shore of a small lake at that time. This lake was positioned in a doline, caused by subsurface salt dissolution. The lake was filled up by the Wilde river, which can be proved by the presence of many aquatic species such as frogs (*Rana agiloides* Brunner 1951), but mainly by salmonid fish (Jacobshagen 1963) that needed flowing water. The lake shore was used by the ice age spotted hyenas as mud pit prey deposit sites. Carcass remains from animals of the mammoth steppe macrofauna were deposited here, whereas "bone nests" were mentioned 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 of bioturbational origin and were possibly caused by the hyenas, which burried prey remains in the soft soil. Most of the bones are from the woolly rhinoceros (*Coelodonta antiquitatis*). Other animals, such as the woolly mammoth (*Mammuthus primigenius*), the giant elk (*Megaloceros giganteus*), the reindeer (*Rangifer tarandus*), the Przewalski horse (*Equus ferus przewalskii*), the steppe bison (*Bison priscus*), the cave bear (*Ursus spelaeus*), the snow hare and the European hare (*Lepus timidus, L. europaeus*), the arctic fox (*Alopex lagopus*), the red fox (*Vulpes vulpes*), the steppe iltis (*Putorius eversmanni*) and the badger (*Meles meles*) are present in this fauna. Additionally, there are many rodents such as the lemming (*Lemmus lemmus*), and others, such as *Dicrostonyx henseli, Microtus gregalis* and, finally, *Alactaga saliens*, being typical for steppe environments. Birds such as *Lagopus lagopus* were listed with many other species by Jacobshagen (1963). Also the spotted hyena (*Crocuta crocuta*

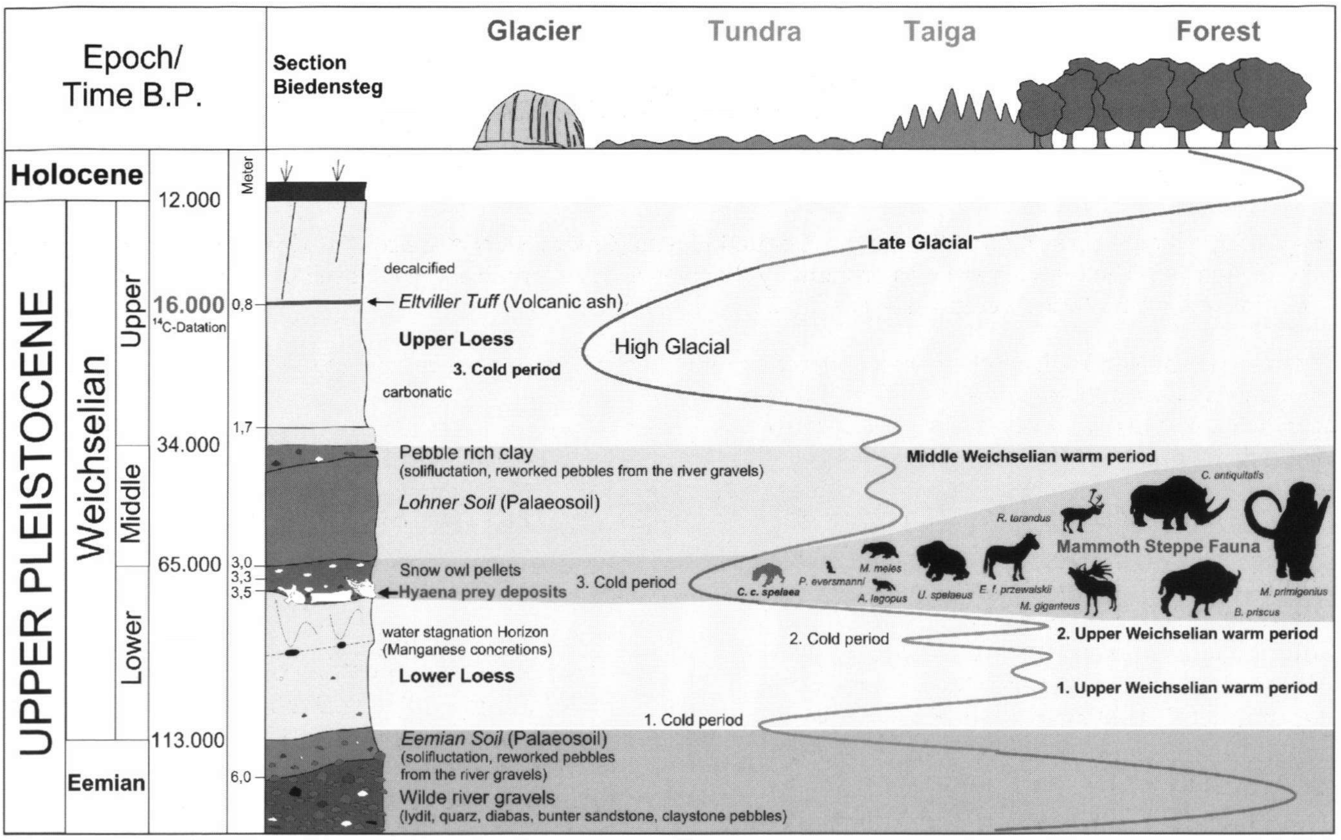

Fig 2 Generalized section at the Ice Age Spotted Hyena *Crocuta crocuta spelaea* (Goldfuss 1823) prey deposit site Biedensteg. The macrofauna deposited by the hyenas during the Early Weichselian is dominated by woolly rhinoceros bones, while the rest of the prey fauna is a typical mammoth steppe fauna consisting of *M. primigenius, C. antiquitatis, B. priscus, M. giganteus, R. tarandus, E. ferus przewalskii, U. spelaeus, A. lagopus, M. meles, P. eversmanni* and *C. c. spelaea.*

Gegeneralizeerde doorsnede van de site Biedensteg van een leger van de grottenhyena *Crocuta crocuta spelaea* (Goldfuss 1823). De macrofauna die gedeponeerd is door de hyenas gedurende het Vroeg Weichselien wordt gedomineerd door botten van de wolharige neushoorn, terwijl de rest van de prooidieren typisch is voor de mammoetsteppe-fauna, bestaande uit *M. primigenius, C. antiquitatis, B. priscus, M. giganteus, R. tarandus, E. ferus przewalskii, U. spelaeus, A. lagopus, M. meles, P. eversmanni* and *C. c. spelaea.*

spelaea) itself is represented by skulls, postcranial material and many coprolites being described here. The idea of bioturbation would fit a "hyena prey deposit site", but cannot be studied or proven anymore. In the section (fig. 2) such depressions are figured here as hyena bone deposits. It may be that a later cryoturbation, which fits to the environment and climatic situation of that time, was responsible for a secondary overprint of the primary sedimentary structures.

The "pellet horizon" is figured differently in the publications (Jacobshagen *et al.*, 1963; Kulick 1973). Surely, the pellets do not originate from snow owls alone, because these birds do not feed on frogs and fishes. Especially the high amount of frog bones must have resulted from some other owl species, large water birds or other predators, e.g. the pole-cat *Putorius eversmanni.* The section of Kulick (1973) indicates that the pellets and the mammal bones are mixed in a single horizon. This is proven by caliche concretions around hyena coprolites, in which many bones and teeth of micromammals and frogs are cemented in. The "hyena prey deposit site" and the "pellet horizon" are from the same period and are dated relatively into the late middle Early Weichselian (90,000 - 65,000 BP, see fig. 2). Therefore the complete micro- and macrofauna and its taphonomy has to be studied again to understand the site, its surroundings and the climatic situation of a mammoth steppe environment more in detail.

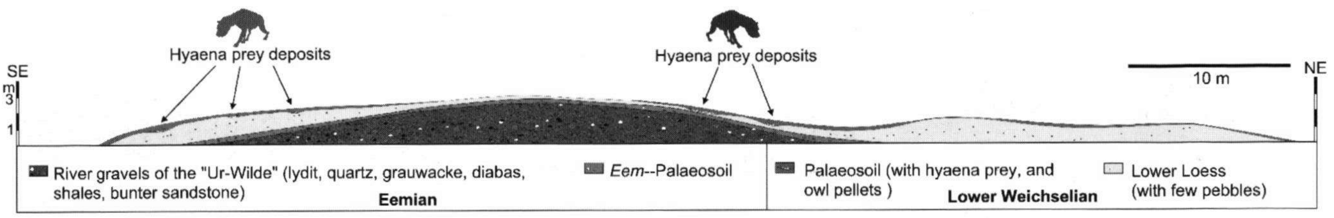

Fig 3 Clay pit outcrop section at the Ice Age Spotted Hyena (*Crocuta crocuta spelaea* (Goldfuss 1823)) prey deposit site Biedensteg. The macrofauna was brought by the hyenas during the Early Weichselian to loess mud pits at the margins of the Ur-Wilde river gravels (see fig. 2). © PaleoLogic.

Doorsnede van een kleilaag van het leger van de grottenhyena (*Crocuta crocuta spelaea* (Goldfuss 1823)) van de site Biedensteg. De macrofauna werd door de hyenas gedurende het Vroeg Weichselien naar modderpoelen van löss gebracht aan de randen van de Oer-Wilde riviergrindgronden (zie fig. 2). © PaleoLogic.

The bone rich horizon is overlain by another palaeosoil, the "Lohner Soil", which can be found in the region at different sections (Semmel, 1968; Kulick, 1973). According to their interpretations, a solifluctation of loess and Wilde river gravel material took place in the warmer Middle Weichselian (fig. 3). It seems that some mammal species, which are also described from the "bone rich horizon" are also from that time. The red fox (*Vulpes vulpes*) and the badger (*Meles meles*) are the dominating faunal elements, besides the European hare (*Lepus europaeus*) and the red deer (*Cervus elaphus*). The fauna from this warm period fits to badger/red fox den sites in loess soils, in front of which they often left some prey bones. The large cave systems are often burrowed deeply, up to some meters, and would therefore have reached the "bone rich horizon" of the hyena prey deposits. It seems obvious, that such badger/red fox cave systems caused a mixture of the arctic fauna with that of a warmer period.

Finally, the Upper Loess was sedimented, the upper part of which was decalcified during the Holocene period. The "Eltviller Tuff" is a thin layer of one to two centimetres thick in the Upper Loess and the only absolutely dated horizon (age around 20.000 BP; Semmel, 1968), so its sedimentation took place during the maximal glaciation (fig. 3).

Palaeontology

Family Hyaenidae Gray 1821

Genus *Crocuta* Kaup 1828

Species *Crocuta crocuta* Erxleben 1777

Crocuta crocuta spelaea (Goldfuss 1823)

Material: Four skulls, three mandibulae, one radius and a femur are skeletal remains of at least four individuals, including a few remains of one of the smallest hyena individuals of Europe (fig. 4). Additionally, sixteen coprolites were recovered and could be conserved. About fifty coprolites were collected, from which, in most cases, only the caliche incrustations are left. The excrements are described and shown here, especially because of lacking detailed descriptions in the literature. From these droppings some bone fragments of the compacta and spongiosa were isolated.

The cranial material consists of four skulls, of which one could not be rediscovered in any collection, but it was mentioned by Jacobshagen

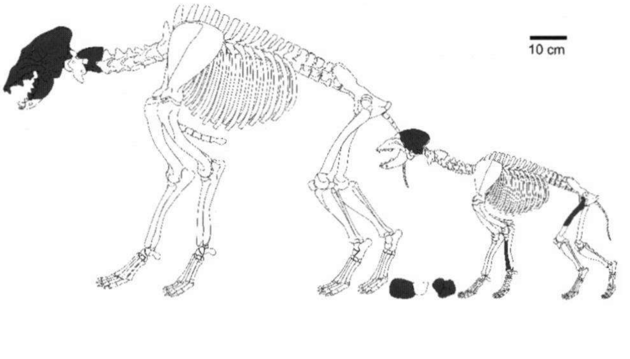

Fig 4 Bone remains (dark grey) from an adult female, her coprolites and a juvenile of a few weeks old from Biedensteg. © PaleoLogic.

Botresten (in donkergrijs) van een volwassen vrouwtje, haar coprolieten en van een jong van een paar weken van Biedensteg. © PaleoLogic.

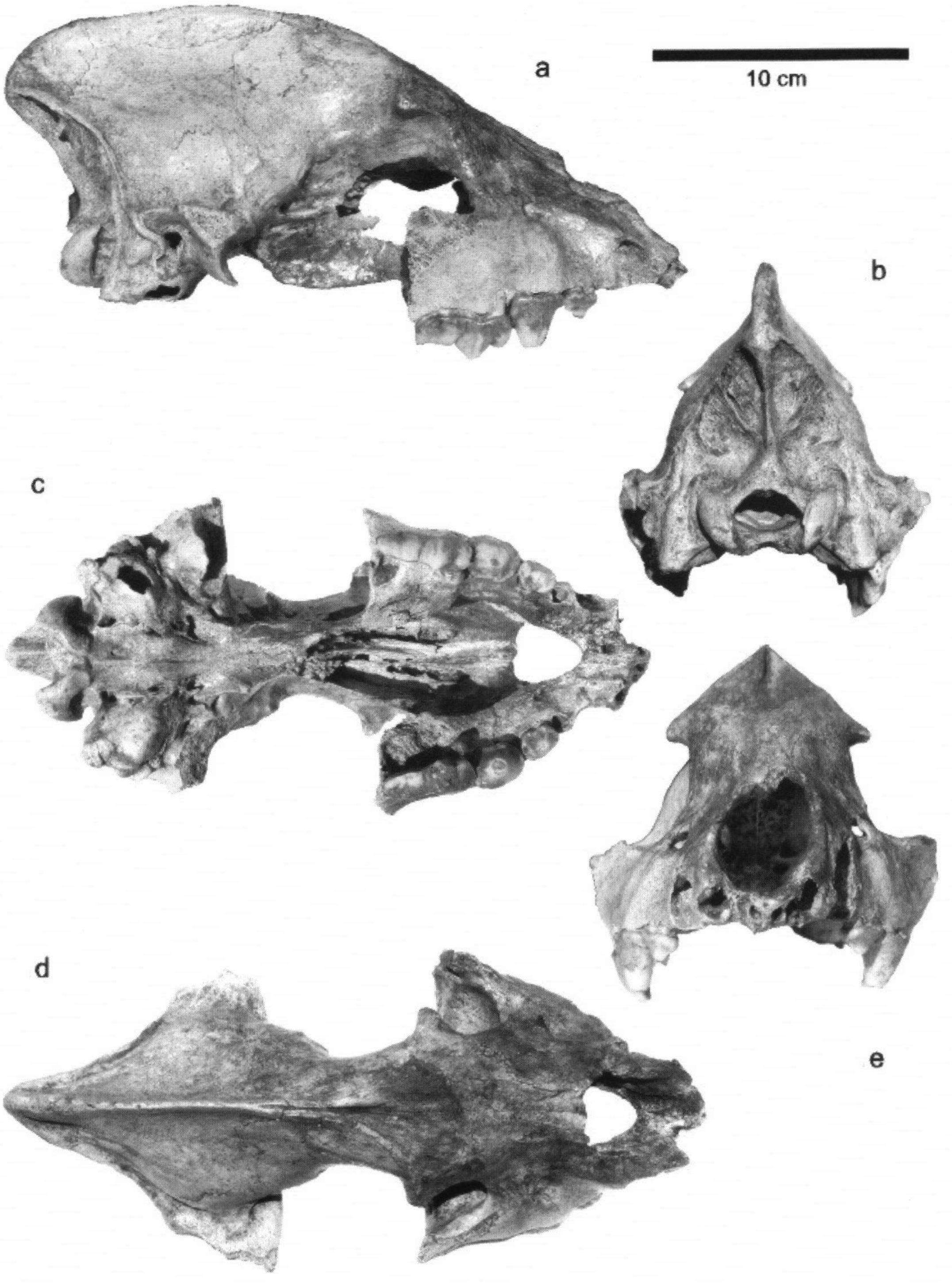

Fig 5 Adult female skull of a *Crocuta crocuta spelaea* (Goldfuss 1823) of advanced age (no. Bi-10at) from Biedensteg. Seen from a) right side, b) caudal, c) ventral, d) dorsal, and e) cranial. The cannibalistic hyenas typically broke off the lower jaws and thus damaged the jugals. The skull is slightly deformed due to sediment pressure. Remarkable is also the presence of double and eight shaped alveoles of the upper jaw M1. © PaleoLogic.

Schedel van een oud volwassen vrouwtje van de grottenhyena *Crocuta crocuta spelaea* (Goldfuss 1823) (no. Bi-10at) van Biedensteg. Gezien van a) rechts, b) achteren, c) onder, d) boven, en e) voren. De kannibalistische hyenas braken de onderkaken op karakteristieke wijze af en beschadigden zo de jukbeenderen. De schedel is enigszins vervormd door de druk van het sediment. Opmerkelijk is ook de aanwezigheid van dubbele en achtvormige tandkassen van de bovenkaaks M1. © PaleoLogic.

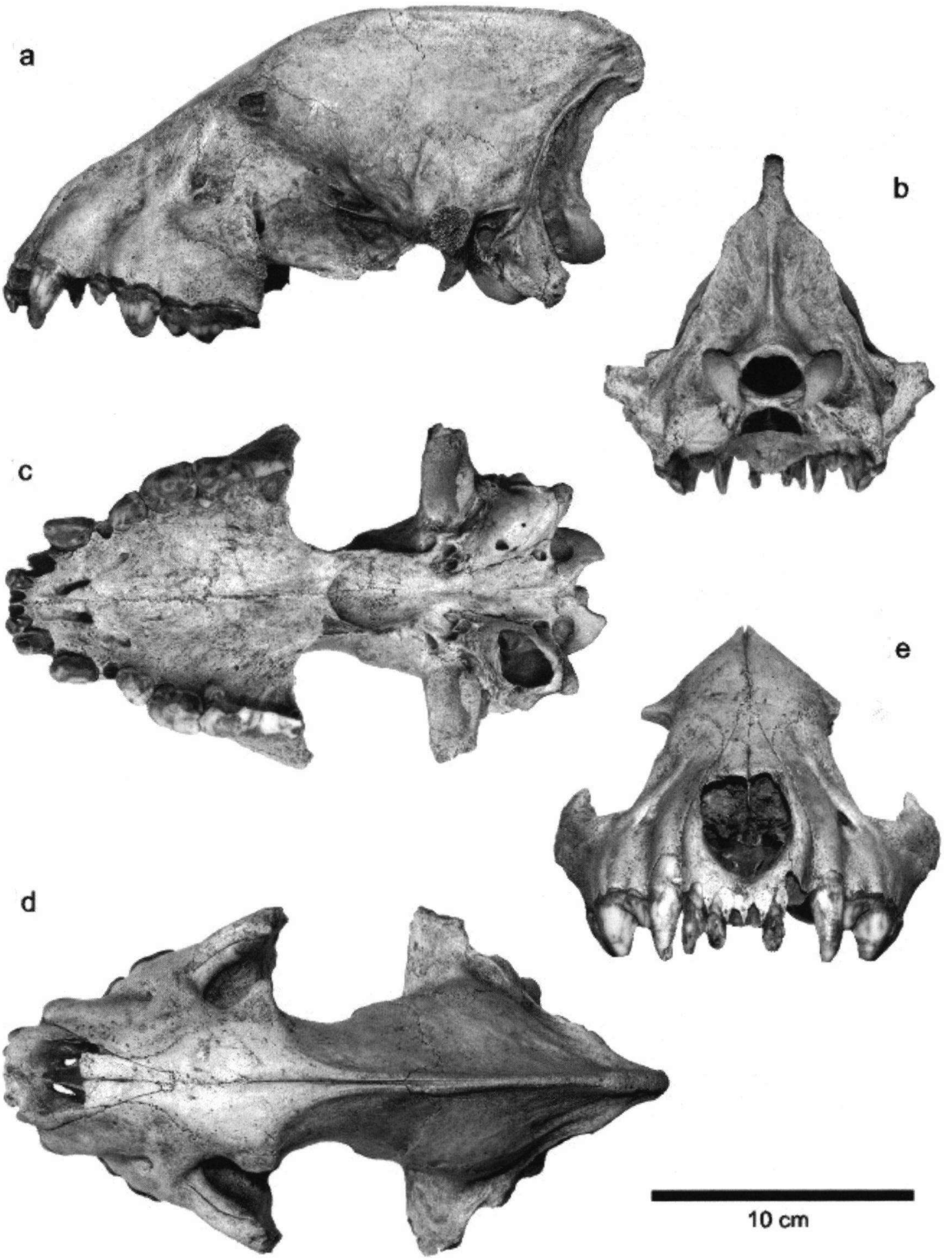

Fig 6 Adult female skull of *Crocuta crocuta spelaea* (Goldfuss 1823) (no. Bi-52/45) from Biedensteg. Seen from a) left, b) caudal, c) ventral, d) dorsal, and e) cranial. The cannibalistic hyenas typically broke off the lower jaws and thus damaged the jugals (see also fig. 5). Remarkable is also the presence of single alveoles of the upper jaw M1 (see also fig. 7). © PaleoLogic.

Schedel van een volwassen vrouwtje van de grottenhyena *Crocuta crocuta spelaea* (Goldfuss 1823) (no. Bi-52/45) van Biedensteg. Gezien van a) links, b) achteren, c) onder, d) boven, en e) voren. De kannibalistische hyenas braken de onderkaken op karakteristieke wijze af en beschadigden zo de jukbeenderen (zie ook fig. 5). Opmerkelijk is ook de aanwezigheid van enkele tandkassen van de bovenkaaks M1 (zie ook fig. 7). © PaleoLogic.

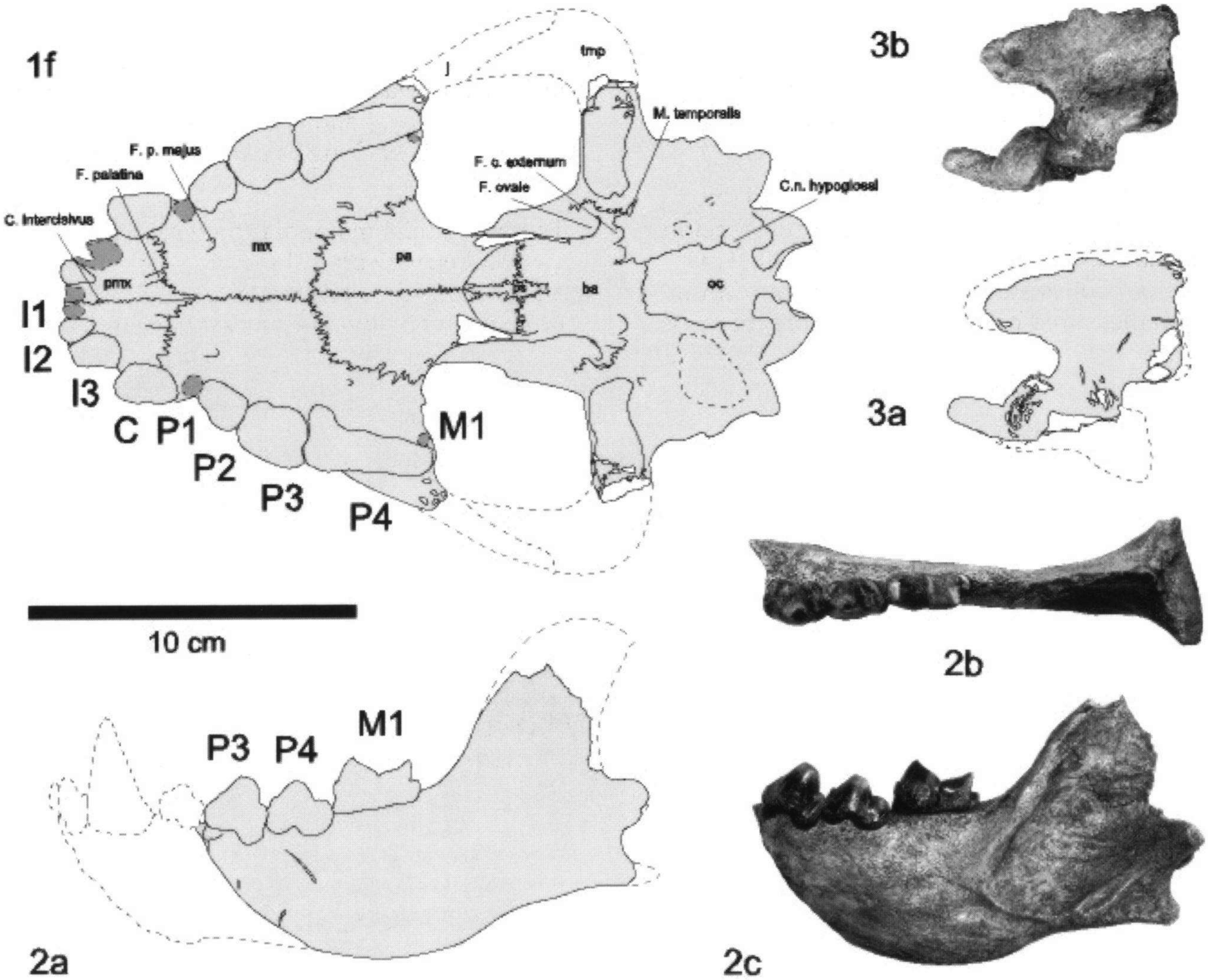

Fig 7 Skull, jaw and axis of *Crocuta crocuta spelaea* (Goldfuss 1823) from Biedensteg. 1f) Redrawing of the young adult female skull of fig. 6 (no. Bi-52/45), in which pmx = premaxillar, mx = maxillar, pa = palatinar, ba = basisoccipital, oc = occipital, j = jugal, tmp = temporal). 2) Left lower jaw of an adult female (no. Bi-52/51), seen from a) lateral (labial), in drawing, b) same, in photograph, and c) in occlusal view. This jaw was cracked by the hyenas in front of the p3, whereas fractures at the ramus are a result of the excavation. 3) Strongly chewn axis of an adult animal (no. Bi-52/234), seen from lateral. © PaleoLogic.

Schedel, kaak en draaier van *Crocuta crocuta spelaea* (Goldfuss 1823) van Biedensteg. 1f) Tekening van de schedel van het jong volwassen vrouwtje van fig. 6 (no. Bi-52/45), waarbij pmx = premaxillare, mx = maxillare, pa = palatinale, ba = basi-occipitale, oc = occipitale, j = jugale, tmp = temporale). 2) Linker onderkaak van een volwassen vrouwtje (no. Bi-52/51), gezien van a) zijkant (wangzijde), in tekening, b) zelfde, in foto, en c) van boven (kauwvlakte). Deze kaak is door de hyenas gebroken net voor de p3, maar de breuken bij de ramus zijn het gevolg van de opgraving. 3) Ernstig aangevreten draaier van een volwassen dier (no. Bi-52/234), gezien van de zijkant. © PaleoLogic.

(1963). Two skulls are differently preserved. One of them is deformed and incomplete (fig. 5), the other one is one of the most complete skulls in Europe, and lacks only the jugal bones and some parts of the temporal bones (figs. 6, 7). Finally, there is a very unique skull of a cub of only a few days or weeks old (fig. 8.1a-e).

The first skull (No. Bi-10at, fig. 5) is difficult to measure due to the deformation. Therefore, exact data can not be given here. The second skull (No. Bi-52/45, figs. 6, 7) has a total length of 29 cm and measures 26.5 cm between the incisors and occipital condyl. The largest height is measured just behind the frontal processus

(11.4 cm). The distance between the anterior part of the canine and the posterior part of P4 is about 6.8 cm. The width of the frontal bones between the zygomatic processes measures 9 cm. Finally, the outer distance between the canines is 5.8 cm. The largest diameter of the canine at the middle of the tooth is 1.8 cm.

The skull symphyses of the third animal (No. Bi-10ev, fig. 8.1) are slightly fused and therefore articulated. The parietal, frontal, palatinal and temporal bones are incomplete. The maximum width measured between the temporal bones is 7.3 cm, whereas it has a preserved length of 7.6 cm.

Three lower jaws were mentioned by Jacobshagen (1963), of which only one could be traced and shown here (fig. 7.2). It is the left lower jaw of a young adult animal, as indicated by the minimal wear of the teeth. It could therefore belong to the skull of figure 6, which show similar enamel wear. The anterior part is lacking and was cracked by hyenas between p2 and p3. The p3-4 and m1 are present. Parts of the ramus are lacking as a result of excavation damage.

The postcranial material is only represented by an axis (second cervical vertebra) of an adult animal with clear chewing marks (fig. 7.3). From one very juvenile or new born individual two bones were found, a left radius and a left femur, both incomplete due to scavenging by carnivores (fig. 8.2-3).

Hyena coprolites from Bad Wildungen-Biedensteg are generally white

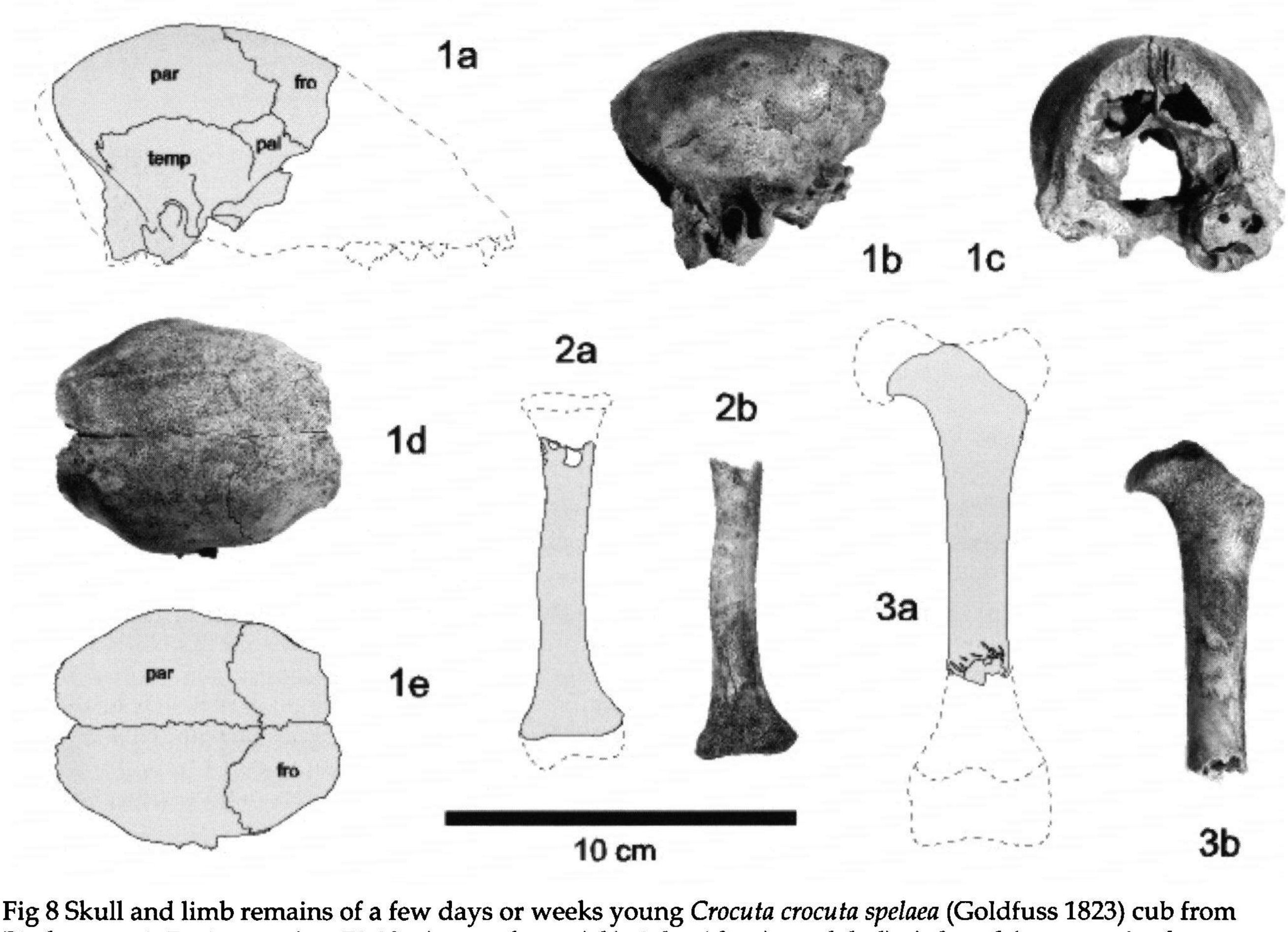

Fig 8 Skull and limb remains of a few days or weeks young *Crocuta crocuta spelaea* (Goldfuss 1823) cub from Biedensteg. 1. Brain case (no. Bi-10ev), seen from a)-b) right side, c) caudal, d)-e) dorsal (par = parietal, temp = temporal, pal = palatinal, fr = frontal). 2. Left radial (no. Bi-10ew), seen from craniolateral. 3. Left femur (no. Bi-10em), seen from cranial. © PaleoLogic.

Schedel en pootresten van een paar dagen of weken oude pup van *Crocuta crocuta spelaea* (Goldfuss 1823) van Biedensteg. 1. Hersenschedel (no. Bi-10ev), gezien van a)-b) de rechterkant, c) achteren, d)-e) boven (par = parietale, temp = temporale, pal = palatinale, fr = frontale). 2. Linkerspaakbeen (no. Bi-10ew), gezien scheef van voren (craniolateraal). 3. Linker dijbeen (no. Bi-10em), gezien van voren. © PaleoLogic.

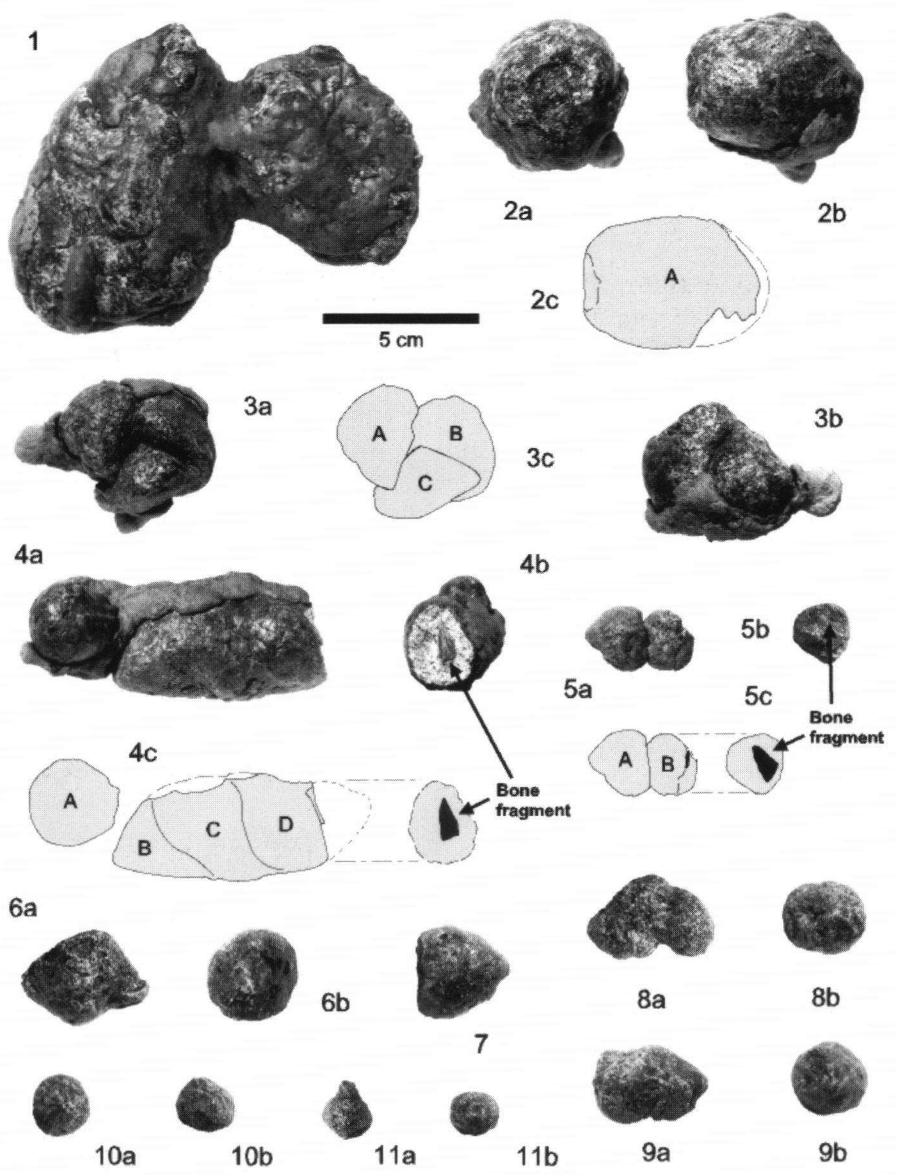

Fig 9 Hyena coprolites from Biedensteg. 1) Two large pellets, partly encrusted by caliche (no. Bi-52/221). 2) Large oval pellet, partly encrusted by caliche at which originally another pellet was attached (no. Bi-52/213). 3) Three articulated pellets of different shape, partly encrusted by caliche (no. Bi-52/214). 4) Four partly articulated pellets, encrusted by caliche. Pellet D is broken; the end exposes a small prey bone fragment (no. Bi-52/210). 5) Two articulated pellets. In pellet B a bone fragment is present (no. Bi-52/219). 6) Sigmoidal drop shaped and pointed single pellet (no. Bi-52/209). 7) Cone shaped and basal flat single pellet, originally attached to another pellet (no. Bi-52/220). 8) Irregular U-shaped pellet, originally attached to other pellets (no. Bi-52/207). The same type is present at the pellet of Fig. 3c. 9) Irregular shaped pellet, originally attached to other pellets (no. Bi-52/212). 10) Small flat drop shaped pellet (no. Bi-52/218). 11) Small drop shaped single pellet (no. Bi-52/211). © PaleoLogic.

Hyena-coprolieten van Biedensteg. 1) Twee grote keutels, ten dele met een kalkkorst (no. Bi-52/221). 2) Grote ovale keutel, ten dele met een kalkkorst waar oorspronkelijk een andere keutel aan vastzat (no. Bi-52/213). 3) Drie aaneengeschakelde keutels van verschillende vorm, ten dele met een kalkkorst (no. Bi-52/214). 4) Vier gedeeltelijk aaneengeschakelde keutels met kalkkorst. Keutel D is gebroken, en het eind laat een klein prooibotfragment zien (no. Bi-52/210). 5) Twee aaneengeschakelde keutels. In keutel B is een botfragment aanwezig (no. Bi-52/219). 6) S-vormige en spits toelopende enkele keutel (no. Bi-52/209). 7) Kegelvormige en aan de basis afgeplatte enkele keutel, oorspronkelijk vastzittend aan een andere keutel (no. Bi-52/220). 8) Onregelmatige U-vormige keutel, oorspronkelijk vastzittend aan andere keutels (no. Bi-52/207). Hetzelfde type is te zien in de keutel van figuur 3c. 9) Onregelmatige gevormde keutel, oorspronkelijk vastzittend aan andere keutels (no. Bi-52/212). 10) Kleine afgeplatte druppelvormige keutel (no. Bi-52/218). 11) Kleine druppelvormige enkele keutel (no. Bi-52/211). © PaleoLogic.

inside and the pores are filled with reddish iron and black-brownish manganese minerals. Such coprolites have a very porous internal structure. This makes them fragile, so they fall into many small pieces if they are not well cemented, fossilized or at least conserved.

The coprolites can be viewed in figure 10, showing their variability and contents. The largest one (fig. 9.1) is a double pellet connected by caliche incrustations; no separate single pellets can be observed. It seems to be the result of more soft and humid fecal material. In most cases the pellets have typical shapes and three to five smaller pellets are attached to each other (figs. 10.2-5). These more typical and abundant shapes could have resulted from more dry dung.

They can be spindle-like (fig. 9.4), or consist of irregularly accumulated aggregations (fig. 9.3). In the single pellets, some different shapes can be distinguished. The most typical one is the "drop- shaped pellet" (figs. 10.6-7, 10-11). They may have protuberances at both sides or they can be round to flat on one side as a result of attachment to another pellet. Other pellets are more or less "unshaped" and irregular (figs. 10.8-9). The latter were often found in the non-spindle-like pellet aggregations (fig. 9.3).

Prey bone fragments, very typical and nearly unique for hyena excrements, are quite abundant in these pellets. In the material from Biedensteg, each coprolite contains several bone fragments. These bone fragments can be small pieces of compact bone, in most cases well rounded (fig. 10). Some of the, partly broken, coprolites expose such bone fragments (fig. 9.4-5). The bone fragments can also consist of pieces of bone *spongiosa*. *Spongiosa* is very fragile and one would expect it to be completely dissolved. However, the large pores of some bigger *spongiosa* pieces (fig. 10) look a lot like the bones of the woolly rhinoceros. Unfortunately such bone pieces are impossible to determine on genus or species level without genetic analysis; this could be an interesting future project.

Discussion

The hyena material from Biedensteg plays an important role in understanding the ontogeny, phylogeny and the palaeoecology of the Ice Age spotted hyenas in the Late Pleistocene of Europe.

The identification of the bones of the cub (fig. 8) was difficult at first. Jacobshagen (1963) believed that the skull belonged to an adult brown bear, and identified the femur as from a wolf. The radius was not determined at all. However, the fused skull bones are typical for a very young but non-neonate carnivore. The skull from Biedensteg originally looked similar to those of cave bears to which it was compared first. Later, a subadult hyena skull turned out to

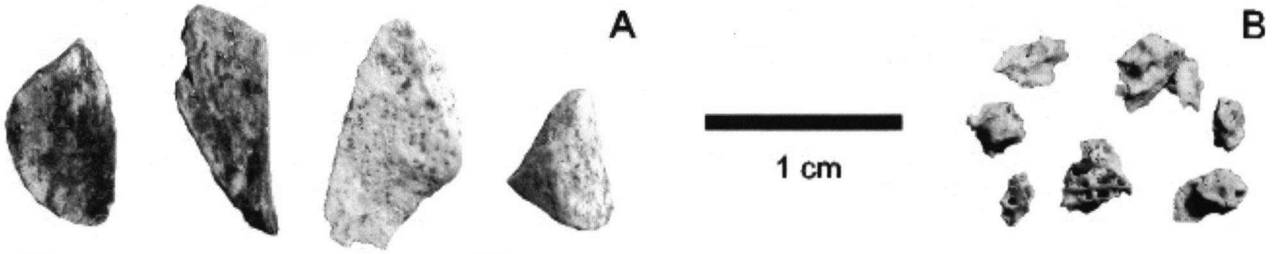

Fig 10 A) Prey bone *compacta* fragments (no. Bi-52/233). All are well rounded on the edges as a result of acid dissolution in the hyena stomach. The fragments are from destroyed and processed pellets and not larger than 2 cm. B) Prey bone *spongiosa*, maybe mainly from the woolly rhinoceros, but possibly also from long bones of the steppe bison. © PaleoLogic.

A) Fragmenten van hard bot (*compacta*) van prooidieren (no. Bi-52/233). Ze hebben allemaal mooi afgeronde hoeken als gevolg van oplossing door zuur in de maag van de hyena. De fragmenten zijn afkomstig van vernietigde en verwerkte keutels en zijn niet groter dan 2 cm. B) Trabeculair bot (*spongiosa*) van prooidieren, misschien hoofdzakelijk van de wolharige neushoorn, maar mogelijk ook van lange beenderen van de wisent. © PaleoLogic.

be crucial for the correct identification of the skull as that of a *C. c. spelaea.*

The skull bones of Late Pleistocene *U. spelaeus* are fused and are larger than those of the much smaller hyenas. The smallest skull of a cave bear in a complete bone collection of a population with neonate, juvenile, adult up to senile cave bears measured 9 cm. The skull bones are not fused in neonate animals; the fusion starts after birth. Therefore, the smaller skull of Biedensteg, which measures only 7.3 cm in width, can be referred to a few days to weeks old animal. The lacking maxillas and dentition could give a more clear individual age. A problem is the lack of comparative neonate and young juvenile hyena material from other European sites. Therefore, the skull was originally compared to those of cave bears, which are more abundant and very similar in shape, but they differ clearly in two main features. In skulls of *U. spelaeus* cubs, the palatines are smaller than in skulls of hyenas. An important difference between skulls of cubs of the two carnivore species can be found in the symphysis between the parietal and the frontal bone. As shown here for the hyena cub (fig. 8.1d-e) the symphysis is strongly convex to the anterior side. In cave bears this is at most hardly convex to nearly straight. This difference is helpful to distinguish hyena from cave bear cubs. Finally, hyena cub skulls are smaller than those of cave bears of the same individual age.

The postcranial bones of the Biedensteg hyena cub were also compared to cave bears of the same individual age and to bones of juvenile hyena animals from the Perick Caves. The latter material contains animals which were at least a few months old (Diedrich, 2005a), but the features are similar in both the Biedensteg hyena and Perick Caves cubs.

The proportions of the skull and the two postcranial bones fit to one individual very well. Also, the cracking and chewing marks, which indicate a cannibalistic killing or at least scavenging of that cub by older hyenas, is similar. Such cub kills in hyena populations occur quite frequently in recent African spotted hyena *Crocuta crocuta* (e.g. Sutcliffe, 1970; Frank, 1986a, b) and is proven here for the spotted hyena *C. c. spelaea* from the Ice Age. Postcranial material of the juvenile is hardly represented in the material of Biedensteg, which fits to scavenging activities. Two incomplete limb bones, a left radius (fig. 8.2) and a left femur (fig. 8.3) are lacking their joints. They also show bite marks and must have been cracked by the carnivores.

Both skulls of adult female hyenas from Biedensteg are anatomically interesting in their dentition, but they fall within the variability of *C. c. spelaea* because of the presence of the alveolus for the upper M1 (figs. 6-8). The first skull has more or less eight-shaped root alveoli (fig. 5) which are a bit further away from the upper jaw P4 and more close to the centre. In the second skull (figs. 7-8) only one small round alveolar groove is present at both maxillas. Very small teeth must have been present with a nearly round to branched root in both female skulls.

The skulls from the Biedensteg population were compared to another hyena population from the Upper Weichselian hyena den site, the Perick Caves (Diedrich, 2004b, 2005a). From this site the five skulls of females, males and a juvenile animal all lack the upper jaw M1 alveoli. The problem with these skulls is the incompleteness of the posterior palatinal region. Definitely, one skull of a juvenile female did not posses an M1, the other (senile to fully adult) animals are not complete enough to confirm whether or not M1 was present. However, cave bear teeth from the Perick Caves have been dated to be of the Middle to Late Weichselian period, whereas the skulls from Biedensteg are from the Early Weichselian. The reduction of the upper jaw M1 could therefore be an evolutionary trend, which has already been described for the phylogeny of different hyena genera since the Tertiary (Werdelin & Solounias, 1991). The skulls of two Late Pleistocene skeletons from the cave locality Wooky Hole in southern England (Reynolds, 1902) are also comparable. In the description of these skulls, no alveoli or upper jaw M1 are mentioned. The figure of one skull in ventral view seems not to show M1 alveoli. However, the skull material of Biedensteg falls into the variability of *C. c. spelaea* (Klein Scott, 1989; Baryshnikov, 1999) from a few open air sites of northern Germany (Diedrich, 2004a) and from caves (Diedrich, 2005b).

Compared to recent *Crocuta crocuta*, the fossil *C. c. spelaea* possesses a very small upper jaw M1, which sometimes lacks altogether. The eight-shaped and larger alveoli of the Biedensteg hyena skulls are also comparable to

the recent brown hyena *Parahyena brunnaea*) (Werdelin & Solounias, 1991). The systematic close relationships between *Crocuta crocuta* and *Parahyena brunnaea* as possible sister groups are discussed in a parsimony analysis (Werdelin & Solounias, 1991). The Biedensteg material shows intermediate features, which can be found in both recent hyena species. To verify the variability or trend of M1 reduction at *C. c spelaea* in the Late Pleistocene of Europe, more complete and well dated skulls have to be studied.

All bones of the Biedensteg hyena population, including the skulls, show typical hyena nibbling, chewing and cracking marks. The lack of the jugals and temporal parts of the skulls are the result of cracking lower jaws at their joints. This can be observed at most *Crocuta* and other carnivore skulls from hyena den sites (Diedrich, 2005a). Even cave bears which were scavenged by hyenas have this incomplete skull preservation (Diedrich, 2005c). All other postcranial hyena bones lack joints or have bite marks, which is also a prove for cannibalism at the Biedensteg site. The scavenging of their own species mostly leaves behind cranial remains, such as the skulls, lower jaws and teeth, but also long bones. It seems that hyenas did not crack the skulls to get the brain marrow, as they did with other prey animals, like the cave bears in the Perick Caves (Diedrich, 2005c) or the woolly rhinoceros at the Biedensteg site (Diedrich, in press).

The dominance of cranial material in hyena den sites is comparable to the Perick Caves hyena den (Diedrich, 2005a), but also to other caves in the Sauerland region. Especially vertebrae and ribs are under-represented at hyena den sites, because they were easily eaten completely or they were not brought to the depot site.

Coprolites from the Ice Age spotted hyenas are not yet studied in detail. Sometimes they are mentioned for some European caves, if collected. At many hyena open air and cave sites such excrements were hardly ever collected, with the exception of the Hess open air site Morschen-Konnefeld, where they were exactly mapped (Keller & Försterling, 2002). A problem is the fragility of the material, which made it difficult to survive in collections or excavations. Only half of the coprolites from Biedensteg could be saved. When they dry too much, they disarticulate into small pieces. This happened to most of the coprolites from Biedensteg. Interesting is the preservation in many cases caused by the encrustation of caliche. Some pellets of the old finds could be rescued and were prepared; the ones figured here and additionally five other ones. Many other coprolites were broken in many tiny pieces which were processed chemically (H_2O_2) for the study of their bone fragment content.

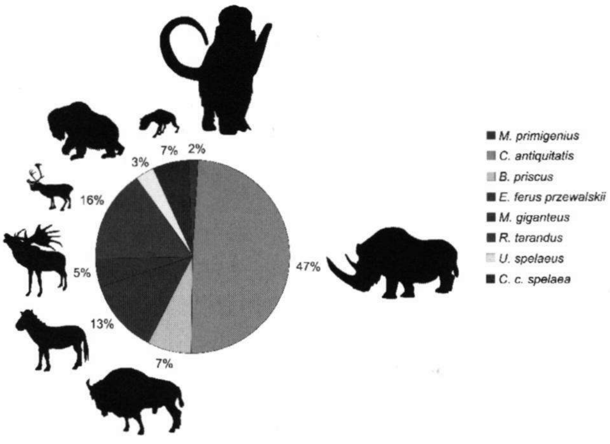

Fig 11 Percentages of bones (n = 152) of Biedensteg. Dominant are the bones of the woolly rhinoceros (*C. antiquitatis*), maybe the result of the remains of the skeleton of one female individual, but maybe also because of the more resistant bones of this species. The hyenas at Biedensteg mainly fed on a woolly rhinoceros carcass of one adult animal.
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Percentages van botten (n = 152) van Biedensteg. Dominant zijn de botten van de wolharige neushoorn (*C. antiquitatis*), wellicht veroorzaakt door de overblijfselen van het skelet van een enkel vrouwelijk individu, maar wellicht ook door de resistentere botten van deze soort. De hyenas van Biedensteg voedden zich voornamelijk met het karkas van volwassen wolharig neushoornvrouwtje.
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The hyena prey remain percentages of the bones (fig. 11) show a dominance of woolly rhinoceros as a main prey (47%), which is present with at least eight scavenged animals. These colossal animals formed the main nutrition source for the hyenas, but their massive bones could not be cracked or destroyed completely by them – the compacta is too

massive and is filled with spongiosa. Therefore, at many hyena den or prey deposit sites woolly rhinoceros bones and even articulated legs are quite abundant, typically with bite, chew and nibbling marks (Wernert, 1968; Keller & Försterling, 2002; Diedrich, 2006a), as was also found in Biedensteg (Diedrich, in press).

Despite the fact that mammoth bones are similar in structure as bones from the woolly rhinoceros, those from the mammoth (*M. primigenius*) are less common and constitute only 2% of the prey bone material. This may have been caused by heavy body parts that are more difficult to carry along or by the scarcity of the mammoth in the mountainous region during the early Late Pleistocene. The next dominant prey is the Przwalski horse (*Equus ferus przewalskii*) (13%), followed by the steppe bison (*Bison priscus*) (7%). Bones of the giant elk (*Megaloceros giganteus*) make up only 5%, those of reindeer (*Rangifer tarandus*) make up 16% of the prey bone material. Collected dropped antlers are typical for hyena den and prey deposit sites and in Biedensteg, three were found from reindeer. The percentage of 7% of the prey bones by the hyenas itself corresponds to the statistics in the hyena Perick Cave den (Diedrich, 2005a). Interesting are the cave bear bone remains from one animal (3% of the prey bones), being one of the few known non-cave finds in Germany (Diedrich, 2006b). They are preserved identically as the cave bear bones found in the Perick Cave hyena den site, where hyenas scavenged strongly on *U. spelaeus* carcasses (Diedrich, 2005c).

If other animals, such as the badger *Meles meles*, the arctic fox *Alopex lagopus* or the red fox *Vulpes vulpes* and smaller animals, were also eaten and scavenged upon by hyenas, this can not be proven. It seems more likely that badgers and red fox had their dens close to the hyena prey deposits and were responsible for the accumulation of hare *Lepus europaeus/timidus* and other small animal bones. Finally some owls must have been responsible for the pellets and accumulation of thousands of micromammals. Frog and fish remains are remains of different predators (birds, mustelids etc.).

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