The Upper Pleistocene mammalian fauna from the Große Grotte near Blaubeuren (southwestern Germany)

By Jaco Weinstock, Stuttgart

With 13 figs., 32 tabs.

Abstract

The fauna from the Große Grotte, a cave site in the Blau valley (southwestern Germany) is presented. Quantitatively, *Ursus spelaeus* is by far the main component. Its remains represent individuals – mostly juveniles – which died in the cave during hibernation. The cave was also used by other carnivores as well as by neanderthals. A relatively large proportion of the bones shows gnawing marks, whereas not a single butchering mark was recorded. Thus, the relative contribution of hominids to the accumulation of the carnivores and herbivore remains seems to have been limited at best. In any event, this fauna cannot be used to explore the subsistence practices of Middle Palaeolithic hominids. According to the micro- and macrofaunal remains, at least the upper layers (IV–II) were deposited under a cold spell within the first half of the Wuermian Glacial.

Zusammenfassung

Die Fauna von der Großen Grotte im Blautal (Baden-Württemberg, Südwestdeutschland) wird vorgestellt. Sie besteht hauptsächlich aus Resten von *Ursus spelaeus*. Die Individuen dieser Art – meistens Jungtiere – sind während des Winterschlafs gestorben. Die Höhle wurde auch von anderen Carnivoren und von Menschen genutzt. Ein relativ großer Anteil der Knochenfragmente zeigt Fraßspuren; Schnitt- bzw. Schlagspuren wurden dagegen nicht beobachtet. Der Beitrag des Menschen bei der Akkumulation der Faunenreste scheint also zumindest sehr gering gewesen zu sein. Die Fauna aus der Großen Grotte darf nicht in Betracht gezogen werden bei Untersuchungen der Ökonomie mittelpaläolithischer Hominiden. Nach der Säugerfauna stammen mindestens die oberen Schichten der Höhle (II–IV) aus einer Kaltphase in der ersten Hälfte des Würm-Glazials.

Contents

1. Introduction

The site. – The Große Grotte*) is a cave site situated on the east side of the Blau valley, at 580 m above sea level, i.e. 76 m above the valley floor. At the beginning of the Würm glaciation, however, the valley floor was a further 25–30 m below the present level (Wagner 1983: 14). The cave entrance faces westwards; it is 25 m wide and 18 m high. As one moves inwards, the cave becomes much narrower and lower, at its rear end it reaches only 3 m in height (Wagner 1983: 15). However, during the Palaeolithic, the Große Grotte must have had a narrower entrance than nowadays, permitting the formation of a microclimate inside the cave. This is suggested by the investigation of the phosphate contents of the sediments (Wagner 1983: 17).

Previous work. – Excavations at the Große Grotte were carried out by G. Riek in three seasons between August 1960 and April 1964. Riek himself published only a short note on preliminary results of the dig (1962: 199 ff.). The results were finally published in a monograph by E. Wagner (Wagner 1983: 11 ff.). Riek distinguished twelve Palaeolithic layers (II–XIII). Based on sedimentological and typological grounds, layers XIII–XII – and perhaps also XI – were referred to the Eemian interglacial, whereas layers IX–II were assigned to the first half of the last glacial. The uppermost layer (I) contained numerous fragments of wood charcoal which are obviously a product of much more recent (postmedieval) fires (Wagner 1983: 21).

Technotypologically, Wagner assigns the lithic material of layer XI to a late Acheulean with Levallois technique and the quantitatively poor industry of layer IX to the late Micoquian; the lithic material from layers III–VIII was classified as Mousterian with Levallois-technique, and layer II – the richest in lithic material (ca. 450 tools + 600 débitage) – to a younger Mousterian with bifacial points (Blattspitzen).

Aim of the present paper. – Wagner devoted a chapter of his monograph to the study of the fauna (1983: 69 ff.). There are, however, a number of reasons which in the present author's opinion make a revaluation of the material desirable. To be-

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*) To be read: Grosse Grotte.

gin with, WAGNER's report was certainly not intended to be more than a preliminary study. During an inventory of the material stored at the Staatliches Museum für Naturkunde in Stuttgart (SMNS), it became apparent that, in his report, WAGNER only considered part of the faunal material. He lists 588 identified bones (excluding microfauna), whereas during the new analysis more than 1100 fragments were identified to the species or genus level (Tab.1). It is significant that some of the newly identified fragments established the presence of some species not mentioned by WAGNER. Other fragments contribute important taphonomical information which leads to a different interpretation of the fauna than that proposed by him (WAGNER 1983: 77ff.). Since the faunal report in the original publication has been used to support certain models of the economic behaviour of neanderthals (e.g., WEBB 1988: 90), a complete and accurate description of the fauna is important.

Additionally, the original study did not include osteometrical data; this type of information, however, is very valuable since, in some cases, it allows the separation of bones from morphologically similar taxa – such as the arctic fox (*Alopex lagopus*) and the red fox (*Vulpes vulpes*) – and can contribute to the gender determination of dimorphic species.

With the exception of layer X, animal bones were recovered from all of the Palaeolithic layers. Most of the faunal material comes from layers II, III and V – the most substantial, with maximal depths of 1.70 m, 0.50 m, and 1.40 m respectively – whereas in layers XIII, XII only a handful of bones were present. According to WAGNER (1983: 69) the only bone fragments recovered from layers XIII and XII were two cave bear teeth and two fox (*Vulpes* vel *Alopex*) metapodials respectively. Regrettably, these fragments are not found anymore in the collection stored at the SMNS. Also missing from the material stored at the Museum are the mandibles of *Bos/Bison* (layer II) and an M_1 of *Crocuta* (layer XI) (see below) listed by WAGNER (1983: 69ff.). The reason for the absence of these fragments is unknown. A mandible of *Cervus* from layer II was not available for study since it was sent to Oxford for AMS-dating (J. WAIBLINGER, pers. comm.; see below).

It is important to mention that, in addition to the mammalian remains, over 100 bones of birds were recovered during the excavations. These specimens were examined and identified by H. PIEPER (Kiel) in 1985–86 (Tab. 32), but no report has yet been prepared.

M e t h o d . – This study is mainly concerned with the large mammal fauna. Remains of small rodents are scarce and were not systematically collected. Thus, they will be dealt with only briefly in a separate section discussing the biostratigraphical position of the site and the palaeoecology of its surroundings.

While the deposits in the Große Grotte may span a large fraction of the Middle Palaeolithic, the number of faunal specimens is relatively small, and for most practical purposes they do not warrant a meaningful separate analysis of each layer. Moreover, there are some indications that faunal material from different layers was mixed during the excavations or immediately afterwards. For example, the left half of an *Ursus* mandible (SMNS 34078.58, new break in diastema area) was assigned to layer II, while the right half (SMNS 34110.141) was marked as coming from layer V. More difficult to interpret is the fact that a left paw of a bear found in layer III seems to belong to the same individual as a right-side paw determined as coming from layer XI (see description below). Thus, under these circumstances, it is justified to regard the material as a single complex.

Each identified fragment was individually weighted. This information enables the comparison of the relative representation of the remains of the different species within a site or between sites regardless of their degree of fragmentation (Uerp-mann 1972: 13). Unidentified fragments were separated into size categories; all fragments in each category were then weighted together.

Bones and teeth were measured to the nearest 0.1 mm following the definitions of von den Driesch (1976).

Tab. 1.   Large mammal remains recovered from the Große Grotte; number of identified specimens (NISP) and weight (g).

Species	NISP	NISP (%)	weight (g)	weight (%)
Lepus cf. *timidus*	35	2,0	50.2	0.2
Canis lupus	9	0,8	27.8	0.1
Alopex lagopus	2	0,2	7.3	0.0
Vulpes vulpes	8	0,7	31.8	0.2
Vulpes vel *Alopex*	6	0,5	9.2	0.0
Mustela putorius vel *eversmanni*	1	0,1	0.8	0.0
Martes martes	1	0,1	2.7	0.0
Crocuta crocuta spelaea	1	0,1	12.0	0.1
Felis silvestris	1	0,1	1.0	0.0
Panthera leo spelaea	3	0,3	38.7	0.2
Ursus spelaeus	857	73,2	16705.1	80.6
Mammuthus primigenius	2	0,2	196.0	0.9
Equus germanicus	9	0,8	215.3	1.0
Coelodonta antiquitatis	1	0,1	67.0	0.3
Cervus elaphus	3	0,3	428.0	2.1
Rangifer tarandus	50	4,3	467.2	2.3
Cervidae indet.	2	0,2	4.0	0.0
Rupicapra rupicapra	5	0,4	22.0	0.1
Capra ibex	114	9,7	2065.2	10.0
Caprinae indet.	1	0,1	2.9	0.0
Artiodactyla indet.	54	4,6	304.2	1.5
TOTAL	1165	100	20729	100

2. Description of the material

Family Leporidae Gray 1821

Genus *Lepus* Linnaeus 1758

Lepus cf. *timidus* Linnaeus 1758

Material: SMNS 34077.1–9, 34083.1–9, 34097.1–5, 34104.1–6, 34116.1–4, 34121.1, 34126.1–2

Two species of hare are known from Upper Pleistocene deposits in Central Europe: the arctic hare (*Lepus timidus*) and the brown hare (*L. europaeus*). While morphological differences in their skull, mandible, and teeth exist (KOBY 1959: 39ff.), no reliable differences have been reported for the postcranial skeleton. However, since *L. europaeus* is generally larger than *L. timidus*, body size can serve as a useful criterion.

A total of 35 hare bones were recovered, all from the upper layers (II–VII); *Lepus* was absent from other layers in which faunal remains were present (VIII, IX, and XI).

All specimens come from the postcranial skeleton (Tab. 2). The osteometrical data indicates that the specimens belong to *Lepus timidus* (Tab. 3).

Tab. 2.   *Lepus* cf. *timidus*; skeletal distribution.

skeletal element	NISP
scapula	7
humerus	5
ulna	2
metacarpal II	2
pelvis	5
femur	1
calcaneus	2
astragalus	1
metatarsal II	1
metatarsal III	1
metatarsal V	1
lumbar vertebra	5
ribs	2
total	35

Tab. 3.   *Lepus* cf. *timidus*; measurements of postcranial bones (in mm)

scapula

layer	SLC	GLP	LG	BG
II	8.2	(14.5)	13.5	12.5
II	7.7	14.4	12.8	12.5
III	–	12.8	–	11.4
V	7.9	12.8	–	11.6
V	(7.3)	13.1	12.4	–

humerus

layer	Bd	Dp
II	–	20.5
V	13.1	–

ulna

layer	BPC	DPA	SDO
II	8.6	12.1	11.0

pelvis

layer	LA
II	12.1
VI	(11.5)

calcaneus

layer	GL	GB
II	31.0	12.8

astragalus

layer	GL
II	16.8

metatarsal V

layer	SD	Bd	Dd	GL
VII	3.4	5.3	4.5	50.8
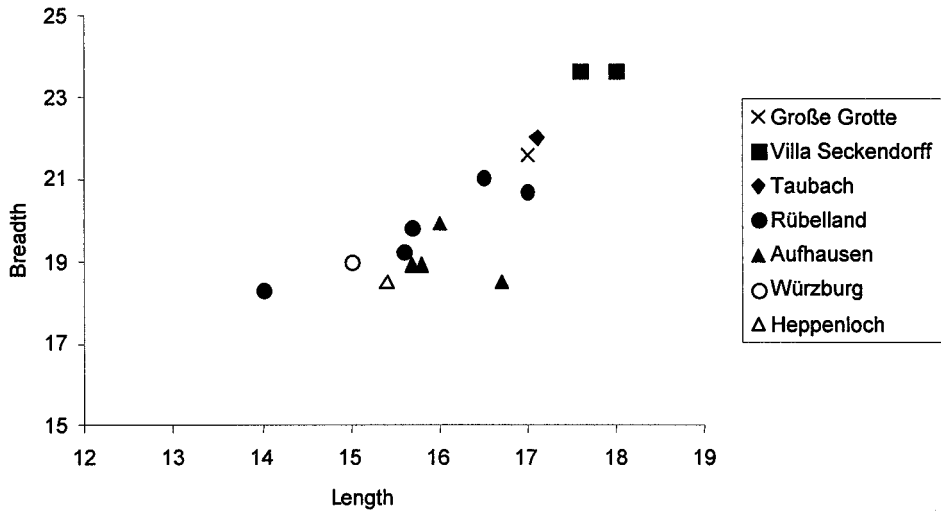
Fig. 1.   Pleistocene wolves; M^1 length/breadth. Black symbols = Upper Pleistocene (*Canis lupus* L.); white symbols = Middle Pleistocene (*C. l. mosbachensis*). (Data from: ADAM 1975; HEMMER 1977; SCHÜTT 1969; SCHÜTT 1974; ZIEGLER 1996).

Family Canidae GRAY 1821

Genus *Canis* LINNAEUS 1758

Canis lupus LINNAEUS 1758

Material: SMNS 34103.1–3, 34118.1–2, 34129.1, 34138.1, 34143.1, 34147.1

A total of nine fragments from the wolf, *Canis lupus*, were recorded from the site. They are distributed over six different layers (Tab. 4). Only two of the fragments could be measured: a M^1 and a 1st phalanx (Tab. 5). The measurements of the M^1 fall in the mid-upper range of Late Pleistocene wolves, and are comparable to those from the travertine of Taubach near Weimar. It is, however, much larger than those of the Middle Pleistocene wolves from southern Germany, which are assigned to a different subspecies, *Canis lupus mosbachensis* (Fig. 1). The size of the 1st phalanx is more difficult to evaluate since, as is very often the case, it is impossible to identify

Tab. 4.   *Canis lupus*; distribution of the fragments among the different layers.

skeletal element	Layer
sternum	II
phalanx III	II
phalanx I	IV
phalanx III	IV
M^1, dext.	IV
cervical vertebra	V
os tarsale quartum, dext.	VII
caudal vertebra	IX
ulna, sin.	XI

the digit to which it belongs (Boessneck & von den Driesch 1973: 15). The remaining fragments, while not measurable, reinforce the impression of a medium to large size for the wolves of the Große Grotte.

Tab. 5. *Canis lupus*; measurements of skeletal elements.

skeletal element / layer	measurement (mm)
M¹, dext / IV	L: 17.0 B: 21.6
phalanx I / IV	Bp: 11.5 SD: 6.6 Bd: (9.5) GL: 35.0 Dp: 10.7 Dd: 4.8

Genus *Vulpes* Frisch 1775

Vulpes vulpes (Linnaeus 1758)
and
Genus *Alopex* Kaup 1829

Alopex lagopus (Linnaeus 1758)

Material: SMNS 34078.1–2, 34079.1–6, 34080.1, 34105.1, 34115.1, 34117.1–2, 34127.1, 34136.1, 34141.1

The present geographic distributions of the arctic fox (*Alopex lagopus*) and the red fox (*Vulpes vulpes*) overlap only slightly. Nevertheless both species occur together in several Pleistocene assemblages of central Europe (see e.g., Boessneck & von den Driesch 1973: 15 ff.; Lehmann 1954: 49 ff.; Musil 1965: 28 ff.). Lehmann explains this fact (1954: 49) with the notion that during these times the ecological preferences of both species were more similar than they are at present, i.e., that *Alopex* was not an exclusive inhabitant of the tundra/steppe. In the opinion of the present author, a

Tab. 6. *Vulpes vulpes* (V) and *Alopex lagopus* (A); measurements of postcranial bones.

humerus

layer	Bd	BT	
V	22.8	15.1	*V*

ulna

layer	BPC	TPA	SDO	GL	
XI	8.9	15.0	12.4	131.0	*V*

radius

layer	Bp	SD	Bd	GL	
VII	11.1	7.6	14.4	111.7	*V*
II		8.0	15.8		*V*

metacarpal II

layer	SD	Bd	Dd	GL	
II	3.6	5.2	4.8	44.7	*V*

metacarpal III

layer	SD	Bd	Dd	GL	
II	3.2	5.0	5.1	50.3	*V*

metacarpal V

layer	SD	Bd	Dd	GL	
IV	5.1	–	–	44.0	*V*

tibia

layer	SD	Bd	Dd	GL	
II	9.5	17.4	12.1	–	*V*
II	7.0	12.9	9.1	(114.2)	*A*

metatarsal IV

layer	Bp	SD	Bd	Dd	GL	
II	4.5	3.4	5.2	4.9	39.3	*A*

more probable explanation for the occurrence of both species is simply, that biotopes which permitted the sympatry of *Vulpes* and *Alopex* during the Pleistocene are non-existent today.

Although very different in their external appearance, the identification of the bone remains of *Alopex* and *Vulpes* can be problematic, especially when dealing with young individuals and/or with fragmentary material (BOESSNECK & VON DEN DRIESCH 1973: 16). Morphological differences between the teeth of both taxa have been described by HAGMANN (1899: 29). Elements of the postcranial skeleton, however, can only be separated by the relative slenderness and smaller size of *Alopex* bones (BOESSNECK & VON DEN DRIESCH 1973: 16). For the present study the measurements of fox bones are compared to those of early Wuermian sites of Villa Seckendorff near Stuttgart (ZIEGLER 1996), the Aurignacian-Magdalenian foxes from the Brillenhöhle near Blaubeuren (BOESSNECK & VON DEN DRIESCH 1973: 16ff.), and three recent skeletons of *Alopex lagopus* from Banks Island, Canada (Comparative collection of the Institute of Prehistory and Early History, Tübingen University, No. CN78, CN79, and CN41).

A total of 16 bones of foxes were identified; they come from layers II (n=9), V (n=3), IV, VII, IX and XI (n=1 each). Osteometrical data were recorded from ten of the bones (Tab. 6). According to these measurements, eight fragments belong to *Vulpes* and two, both from layer II, are those of *Alopex*. The remaining pieces – ribs, vertebrae and a humerus with the epiphyses not yet fused – could not be unambiguously assigned to any of both species.

The small number of measurements do not give much information on the size of either red or arctic fox in southern Germany during the Middle Palaeolithic. Nevertheless, concerning the red fox it is clear that both large as well as small individuals are present at the Große Grotte (Figs. 2–4). This variability could be due to the presence of both males and females in the assemblage.
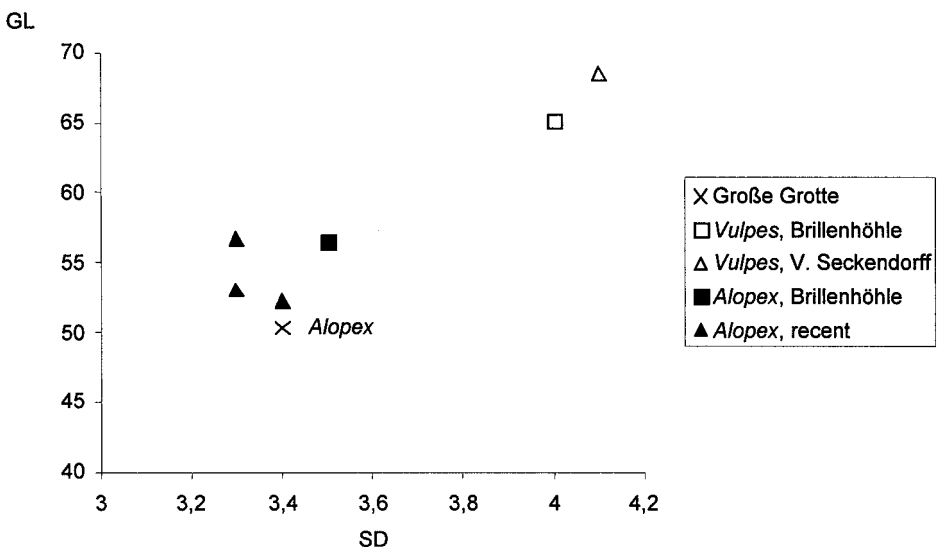
Fig. 2. *Vulpes vulpes* and *Alopex lagopus*; metatarsal IV, smallest breadth of diaphysis/greatest length. (Data from: BOESSNECK & VON DEN DRIESCH 1973; ZIEGLER 1996).

Fig. 3. *Vulpes vulpes* and *Alopex lagopus*; tibia, smallest breadth of diaphysis/distal breadth. (Brillenhöhle: BOESSNECK & VON DEN DRIESCH 1973).
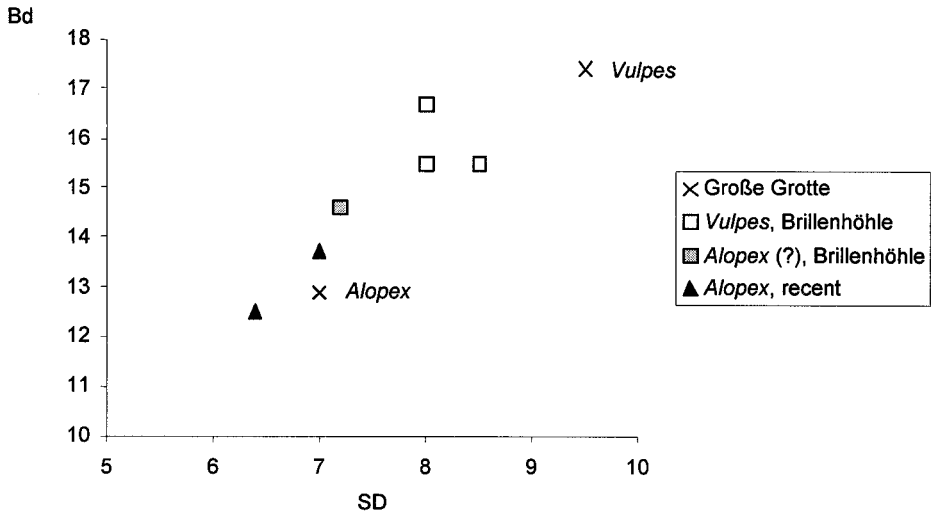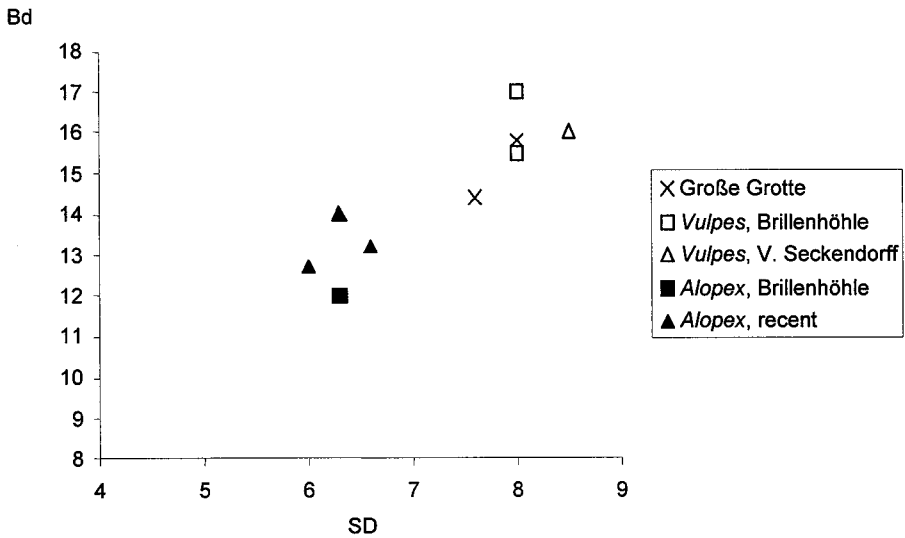

Fig. 4. *Vulpes vulpes* and *Alopex lagopus*; radius, smallest breadth of diaphysis / greatest distal breadth. (Brillenhöhle: BOESSNECK & VON DEN DRIESCH 1973; Villa Seckendorff: ZIEGLER 1996).

Family Ursidae GRAY 1825

Genus *Ursus* LINNAEUS 1758

Ursus spelaeus ROSENMÜLLER & HEINROTH 1793

Material: SMNS 34070.1–281, 34090.1–109, 34100.1–23, 34110.1–233, 34119.1–11, 34123.1–119, 34131.1–8, 34139.1–19.

Both the cave bear *Ursus spelaeus* and the brown bear *Ursus arctos* occur, sometimes together, in Upper Pleistocene deposits in central Europe, e.g. in Villa Seckendorff (ZIEGLER 1996: 10 ff.) and Brillenhöhle (BOESSNECK & VON DEN DRIESCH 1973: 18). In most instances, it is possible to identify the bear remains to the species level. The skull, mandible, and teeth of both species show size as well as morphological differences (see e.g., EHRENBERG 1931: 537 ff.; KURTÉN 1959: 89; 1976: 19 ff.; RODE 1935: 114 ff.). The morphology of the upper and lower teeth found at the site show spelaeoid characteristics: For example, the M^1 are angular and relatively narrow, with an anterior lobe broader than the posterior one. The M_2 are also relatively narrow and show a marked constriction between the anterior and the posterior lobes, which KURTÉN (1959: 89) sees as diagnostic characters of *U. spelaeus*. A single M_2, still in a mandible (SMNS 34070.1), shows a rather arctoid form. The specimen is moderately worn, so the exact architecture of its occlusal surface cannot be seen anymore. The mandible, nevertheless, with its relatively long diastema and an articular process placed well above the occlusal plane, is clearly spelaeoid. Thus, one must conclude that while there is certainly a typical form for the teeth of *spelaeus*, atypical forms occur as well. The same is true for *U. arctos*. For example, a mandible from the Upper Pleistocene site of Hohlefels (without inv.-nr.) belongs clearly to a brown bear; the M_2, however, shows the typical "spelaeoid" proportions (Fig. 5).

Five mandibles, all from layer II, show no sign of an alveolus for P_3 – which is commonly found in *U. arctos* but almost never in *U. spelaeus* (RODE 1935: 40; BISHOP 1982: 43). It is worth mentioning that from these five mandibles three do show an
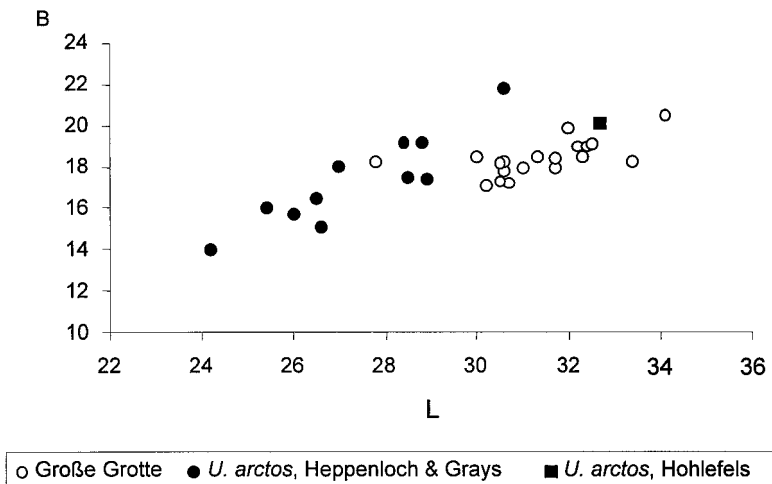
Fig. 5. *Ursus arctos* and *U. spelaeus*; M_2, length/breadth of posterior lobe. (Heppenloch & Grays: KURTÉN 1959).

alveolus for P_1. Interesting is also the fact that one right mandible has a P_1-alveolus while the left one, belonging to the same individual, does not (Inv. nos. 34070.58 and 34110.141; Pl. 1, fig. 4). According to RODE (1935: 40), only about 2.5 % of the mandibles of *spelaeus* show an P_1-alveolus, whereas in *arctos* (e.g. from Taubach) it occurs in more than 63 %. MUSIL (1965: 67), however, states that in Pod hradem ca. 20 % of the mandibles showed an alveolus anterior to P_4. Concerning the postcranial material, limb and foot bones of the cave bear are relatively heavier and more stout than those of brown bear (see e.g. KURTÉN 1976: 23 ff.). While the bones of *U. spelaeus* are generally larger than those of *U. arctos*, there was a marked sexual dimorphism in both species. Thus, since there is an overlap in the size of female *spelaeus* and male *arctos*, absolute measurements do not always provide a good criterion for the distinction between both taxa (see e.g., EHRENBERG 1935: 66; KOBY & FRITZ 1950: 289).

The examination of the bear remains indicates that only *Ursus spelaeus* is present in the Große Grotte. In fact, this species comprises the great majority of bone finds from the site. More than 850 specimens from this taxon were recovered. They represent a minimum of 21 individuals (MNI calculated from isolated I^3). Taking into account the problems and limitations of the MNI method (see e.g. UERPMANN 1972), the actual number of bears represented in the material is certainly much higher. Since there is no evidence for the presence of *U. arctos* in the well preserved material, the small fragments of skull and postcranial elements were assigned to *U. spelaeus*. The
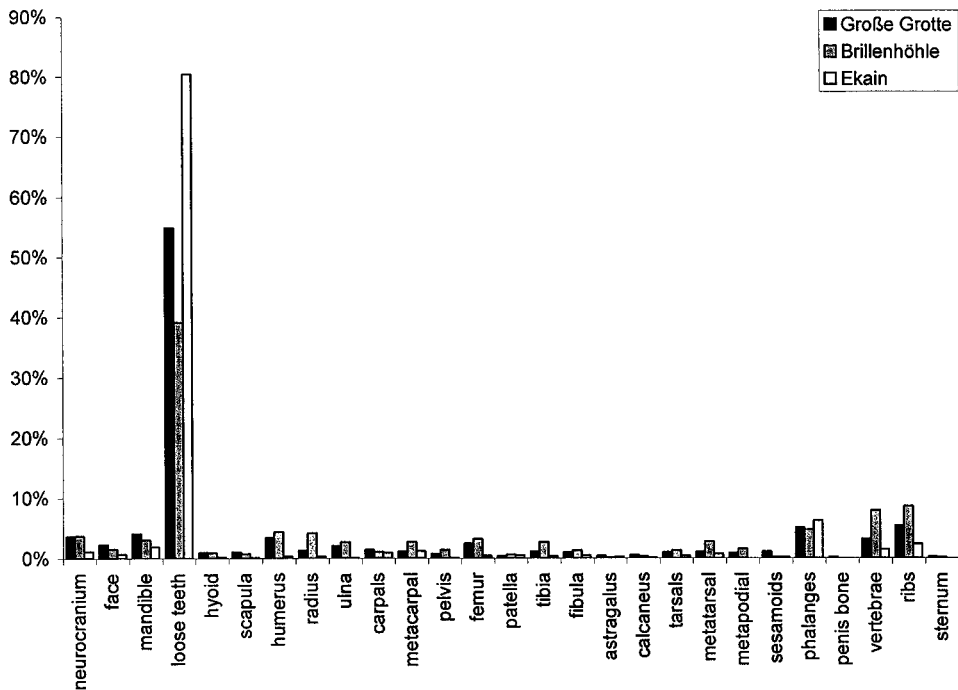
Fig. 6. *Ursus spelaeus*; skeletal representation in the Große Grotte and Brillenhöhle, SW-Germany (BOESSNECK & VON DEN DRIESCH 1973) and Ekain, N-Spain (TORRES PÉREZ-HIDALGO 1984).
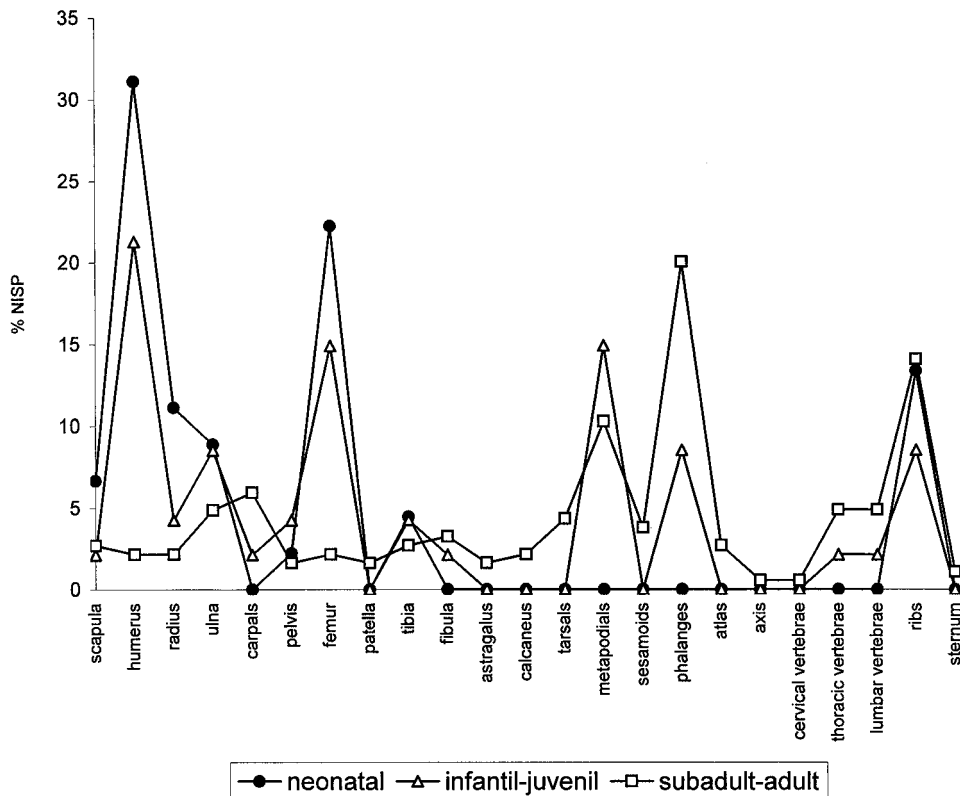
Fig. 7. *Ursus spelaeus*; skeletal representation of the different age categories.

possibility cannot be ruled out, however, that among these fragments some belong to the brown bear.

Most of the material is very fragmented. More than half of the bear remains are isolated teeth. From the remaining finds, ribs and phalanges are somewhat more common than other postcranial elements (Tab. 7–8). Only some short, compact bones – metapodials, carpals, tarsals, and phalanges – were found whole. This pattern of skeletal representation is known from many other cave bear assemblages in central and western Europe, e.g. Brillenhöhle (BOESSNECK & VON DEN DRIESCH 1973: 78), Trou de Sureau (EHRENBERG 1935: 75 ff.), Ekain (TORRES PEREZ-HIDALGO 1984: 39), Pod Hradem (MUSIL 1965: 30 ff.), Cotencher (DUBOIS & STEHLIN 1933: 39), and Westbury-Sub-Mendip (ANDREWS & TURNER 1992: 140; see Fig. 6). The significance of this skeletal representation for understanding the taphonomic history of the bone assemblage of the Große Grotte will be discussed in a later section (see page 37).

No information is available on whether some of the bear bones were found still in anatomical articulation. However, during the present study, some metapodials, carpals, tarsals, and phalanges were recognised as coming from three different bear paws belonging to two or three individuals. They are described below.

<u>SMNS 34131.1–10, 23 (Pl. 2), posterior right paw, layer VIII</u>: astragalus, calcaneus, os tarsi centrale, os tarsale I-IV, metatarsals II–V. Judging from its size (Tab. 14),

Tab. 7. *Ursus spelaeus*; skeletal distribution;
number of identified specimens (NISP) and weight (g).

skeletal element	NISP (n)	NISP (%)	weight (g)	weight (%)
neurocranium	31	3.6%	220.2	1.3%
face	19	2.2%	151.5	0.9%
mandible	35	4.1%	3775.4	22.6%
loose teeth	470	54.8%	1865.8	11.2%
hyoid	8	0.9%	19.3	0.1%
scapula	9	1.1%	1237	7.4%
humerus	29	3.4%	673.1	4.0%
radius	11	1.3%	281	1.7%
ulna	17	2.0%	1080	6.5%
carpals	12	1.4%	232.6	1.4%
metacarpal	10	1.2%	321.1	1.9%
pelvis	6	0.7%	941.3	5.6%
femur	21	2.5%	1964.9	11.8%
patella	3	0.4%	139	0.8%
tibia	9	1.1%	461.4	2.8%
fibula	8	0.9%	103.1	0.6%
astragalus	3	0.4%	161	1.0%
calcaneus	4	0.5%	329	2.0%
tarsals	8	0.9%	67.5	0.4%
metatarsal	9	1.1%	170.7	1.0%
indet. metapodial	7	0.8%	21	0.1%
sesamoids	9	1.1%	15.3	0.1%
phalanges	43	5.0%	214.5	1.3%
penis bone	1	0.1%	9.9	0.1%
atlas	5	0.6%	601.7	3.6%
axis	1	0.1%	62	0.4%
cervical vertebrae	1	0.1%	36	0.2%
thoracal vertebrae	10	1.2%	377.5	2.3%
lumbar vertebrae	10	1.2%	420.8	2.5%
ribs	46	5.4%	722.7	4.3%
sternum	2	0.2%	28.8	0.2%
total	857	100.0%	16705.1	100.0%

this paw must have belonged to a male individual. The astragalus and calcaneus show light gnawing marks. From metatarsals II, IV, and V only the proximal end is present; the distal end probably having been gnawed off. The metatarsal III is more or less complete, but shows a puncture on the dorsal face of its distal end made by a carnivore tooth.

SMNS 34139.1–8, anterior right paw, layer XI: os carpi ulnare, os carpi intermedio-radiale, os carpale I, os carpale IV, metacarpals II–V; all complete. Gnawing marks were found on the intermedio-radiale only.

SMNS 34091.48–50, 53–54, 56, 59, 61–68, anterior left paw, layer III: os carpale II–IV, os carpi intermedio-radiale, os carpi ulnare, metacarpals II-V, 1st phalanges (n=3), 2nd phalanges (n=3), and a 3rd phalanx. Gnawing marks are present in the intermedio-radiale, ulnare, and a 2nd phalanx. The measurements of the bones are almost identical to those of the right paw from layer XI described above, and non-metrical traits such as muscle insertions are very similar as well. Thus they may have belonged to the same individual. The colour of the bones of both paws differs, and this suggests that they were indeed found in different layers. If the two paws did be-

Tab. 8.   *Ursus spelaeus*; Skeletal distribution (NISP) by layer

skeletal element/layer	II	III	IV	V	VI	VII	VIII	IX	XI	total
neurocranium	12	3	1	10	–	5	1	–	–	32
face	5	2	–	6	1	4	–	–	–	18
loose maxillary teeth	59	16	7	80	4	13	2	2		183
mandible	11	5	2	12		4	–	–	1	35
loose mandibular teeth	55	32	3	28	4	20	–	–	2	144
loose mand./max. teeth	67	10	6	32	1	25	1	1	–	143
hyoid	2	–	1	4	–	–	–	1	–	8
scapula	4	2	–	1	–	1	1	–	–	9
humerus	7	2	3	9	–	7	1	–	–	29
radius	3	2	–	2		2	1		1	11
ulna	7	1	–	3	–	5	–	1	–	17
carpals	2	6	–	–	–	–	–	–	4	12
metacarpal II	–	1	–	–	–	–	–	–	1	2
metacarpal III	1	1	–	–	–	–	–	–	1	3
metacarpal IV	–	2	–	–	–	–	–	–	1	3
metacarpal V	–	1	–	–	–	–	–	–	1	2
phalanx 1, anterior	–	3	–	–	–	–	–	–	–	3
phalanx 2, anterior	–	3	–	–	–	–	–	–	–	3
phalanx 3, anterior	–	1	–	–	–	–	–	–	–	1
pelvis	3	–	–	2	–	–	–	–	1	6
femur	6	3	–	5	–	7	–	–	–	21
patella	–	–	–	1	–	2	–	–	–	3
tibia	6	2	–	–	–	1	–	–	–	9
fibula	3	1	–	1	–	1	2	–	–	8
astragalus	–	–	–	1	–	1	1	–	–	3
calcaneus	–	1	–	2	–	–	1	–	–	4
smaller tarsals	2	–	–	–	–	1	5	–	–	8
metatarsal I	–	–	–	–	–	–	–	–	–	0
metatarsal II	–	–	–	–	–	–	1	–	–	1
metatarsal III	–	–	–	–	–	–	1	–	–	1
metatarsal IV	–	–	–	2	–	–	1	–	–	3
metatarsal V	–	1	–	2	–	–	1	–	–	4
indet. metapodial	4	1	–	4	–	–	–	–	–	9
sesamoid	2	1	–	2	–	1	–	2	1	9
phalanx 1 ant. o. post.	4	1	–	4	–	2	2	–	–	13
phalanx 2 ant. o. post.	1	–	–	2	–	–	1	–	–	4
phalanx 3 ant. o. post.	7	2	–	8	–	1	1	–	–	19
atlas	3	–	–	1	–	–	–	–	1	5
epistropheus	–	–	–	–	–	–	–	–	1	1
cervical vertebrae	–	–	–	–	–	–	1	–	–	1
thoracic vertebrae	5	–	–	1	–	1	3	–	–	10
lumbar vertebrae	8	–	–	–	–	–	1	1	1	11
ribs	13	2	–	9	1	18	–	–	2	45
sternum	2	–	–	–	–	–	–	–	–	2
penis bone	–	–	–	–	–	–	1	–	–	1
total	304	108	23	234	11	122	30	8	19	859

long to the same individual, their differing stratigraphical position is in urgent need of an explanation. Regretably, the fine stratigraphical data which would help to clarify this issue was not recorded during the excavations.

Age distribution. – Given the fragmented state of the material, the investigation of the age structure of the bear taphocoenose at the Große Grotte is based main-

ly on isolated teeth and, to a lesser degree, on postcranial elements. Tables 9–11 show the absolute abundance of the teeth in different wear stages. Due to the small number of specimens, the investigation of the bear mortality can be only attempted by "lumping" teeth from all layers. It is assumed that the mortality pattern of *Ursus spelaeus* remained unchanged throughout the time-span represented by the stratigraphical sequence of the cave. This, however, was not necessarily the case. In his investigation of the cave bears from Pod hradem, MUSIL (1965: 62 ff.) found out that the number of immature individuals tended to increase in the uppermost layers. However, it is not clear whether the mortality pattern of the bear population indeed changed, or whether – as KURTÉN suggested (1976: 144) – the differing mortality pattern seen in the upper strata is a result of less males and more females with their young spending the winter in the cave.

The permanent bear teeth from the Große Grotte were grouped into four age-categories (following ANDREWS & TURNER 1992: 145): neonates, yearlings, ca. 2-years, and adults. The results are presented in Table 11. It is readily apparent, that the great majority of the teeth are those of yearlings, while the remaining ones are distributed more or less uniformly in the other three categories.

In addition to the permanent teeth, 85 deciduous teeth were also recovered, from which 74 are canines (Dc). They are an important source of information about the mortality of the bears during their first months of life (KURTÉN 1958: 25 ff.). Each Dc was assigned to one of the six categories defined by KURTÉN (1958: 9 & 25 ff.; 1976:115 ff.) in his investigation of the cave bear from Odessa (Tab. 12). Teeth in the first three categories (A–C) represent individuals up to 5–6 months old, whereas those in categories D–F come from yearlings. Following KURTÉN's method, the mortality of the cave bear from the Große Grotte in their first winter (i.e. categories A–C) was about 17.5 %, not very different from the 19.1 % which KURTÉN (1958: 26) calculated for Odessa.

The great majority of the deciduous canines show a broken root with advanced resorption (Pl. 1, figs. 1–3). In brown bears – and presumably in cave bears as well – the permanent canines erupt at about 1 year of age; their eruption stimulates the resorption of the roots of the Dc's, which then often breaks (DITTRICH 1960: 49). The actual expulsion of the Dc usually occurs during the cub's second winter, between the 13th and the 15th month, i.e. 3–5 months after the eruption of the permanent canines (DITTRICH 1960: 47; KURTÉN 1976: 117). Thus, the milk canines with resorbed, broken roots can be either changed teeth or teeth that were about to be changed (KURTÉN 1958: 9). The distinction is important: if they are indeed expulsed teeth, then they do not have to represent individuals who died in the cave, although they would confirm the presence of yearlings during the winter. If, on the other hand, these teeth were about to be shed, but still in the jaw at the moment of death, then they would represent yearlings who actually died at the site. A third alternative is, of course, also possible; namely that the bears which changed their canines at the cave died somewhat later during the same winter while still hibernating inside the cave (KURTÉN 1976: 117) and are thus also represented by permanent teeth. Given the large proportions of permanent teeth of yearlings in the Große Grotte (see above), it seems probable that the deciduous canines also represent animals which died in the cave.

The bones of the postcranial skeleton also contribute some information about the age structure of the cave bear sample in the Große Grotte (Pl. 4, figs. 5–9). Approxi-

mately 18,5 % (n=45) of the fragments belong to neonates, 19,5 % to juveniles (n=47), and the remaining 62 % (n=185) to subadults and adults (35 specimens belonging to three paws of adults/subadults found in layers III, VIII, and XI respectively were excluded in the calculation). However, the age structure as reflected by the postcranial elements cannot be uncritically accepted, since it is clear that the taphonomic history of the young and older bears differ. This can be concluded from the different skeletal representation shown by neonates, infantil-juveniles, and subadult-adults (Fig. 7). This issue will be discussed further in a later section (see page 37).

In summary: according to the eruption and wear of the teeth of *U. spelaeus* from the Große Grotte, it is apparent that a significant proportion of newborn died; this happened during hibernation in winter (newborns themselves do not hibernate and are thus in need of constant feeding. If their mother has unsufficient stores of fat, and cannot sustain lactation, the cubs die [GARGETT 1996: 40]). The most significant peak in the mortality, however, is at about 1 year, i.e. during the bears' second winter. A high mortality of yearlings – though still somewhat lower than in the Große Grotte – was also recorded from many other sites in western, central, and eastern Europe (see e.g. BOESSNECK & VON DEN DRIESCH 1973: 78; ANDREWS & TURNER 1992: 145; EHRENBERG 1931: 702; GRANDAL-D'ANGALDE & VIDAL ROMANÍ 1997: 729 ff.; MUSIL 1965: 62 ff.; STINER 1998: 317 ff.; TORRES PEREZ-HIDALGO et al. 1991: 62 ff.; see e.g. Tab. 10). While the proportion of newborn in the Große Grotte as reflected by teeth on the one hand, and postcranial elements on the other is nearly identical, the relative abundance of juveniles ("yearlings") as calculated by both methods differs strongly. Given that the age structure of cave bear populations has been almost invariably based on dental evidence, it is still unknown whether this discrepancy is common.

The high incidence of neonatal and juvenil mortality of bears in the Große Grotte has probably multiple causes. In brown bears, cubs lactate for approximately half a year (JAKUBIEC 1993: 289). If the mother was to die within this period, the cubs will starve to death. This must also have been a not uncommon occurrence in *U. spelaeus*.

Probable causes for the elevated mortality of yearlings must have included: predation by carnivores such as wolves, hyenas, lions, and male bears; illness; and starvation (for a discussion of causes of bear mortality see STINER 1998 and references therein). In his study of the cave bears from Mixnitz, EHRENBERG (1931: 659 ff.) suggested that the high yearling mortality at the site could be related to the replacement of the milk dentition with the permanent set of teeth. For most teeth, this takes place after weaning, i.e. around the end of the summer. At this time, fat reserves to withstand the coming winter must be accumulated. EHRENBERG argues that this task must have been complicated during the period of replacement of the deciduous dentition, and many yearlings would have failed to store enough reserves to survive their second winter.

Finally, the very high proportions of yearlings in the Große Grotte must be related to the proportion of females overwintering in the cave (see below).

Sex-ratio. – The proportion of adult males and females seem to vary among different modern populations of brown bears *U. arctos* (see e.g., JAKUBIEC 1993: 279; KURTÉN 1976:76). Whether this was also the case in *U. spelaeus* is of course not known, but the relative proportions of the sexes among sites do vary considerably. Thus, in Mixnitz (Austria) males outnumber females; in Spanish caves, both a pre-

Tab. 9.   *Ursus spelaeus*; wear-stages of maxillary and mandibular teeth (totals).

tooth	not yet erupted	erupting	in line, not worn	slightly worn	moderately worn	heavily worn
P4	–	7	15	2	1	1
M1	3	1	19	12	2	1
M2	2	14	15	2	1	1
M3	5	–	4	3	1	–
total	10	22	53	19	5	3

The different shadings represent the different age-stages (see text)

Tab. 10.   *Ursus spelaeus*; age-distribution according to wear stages of the cheeck teeth.

age stage	abundance (%)		
	Große Grotte	Cova Eirós[1]	Westbury[2]
neonatal	8.9	13.7	9.9
yearlings	76.4	59.1	56.0
2-year-old	7.31	20.0	9.9
> 2 years	7.31	7.0	24.1

1 = GRANDAL-D'ANGLADE & VIDAL ROMANÍ 1997; 2 = ANDREWS & TURNER 1992

Tab. 11.   *Ursus spelaeus*; wear-stages of maxillar and mandibular teeth (by layer).

tooth / wear-stage	II	III	IV	V	layer VI	VII	VIII	IX	XI
					P^4 & P_4				
↑		2		5					
°	5	5		3		2			
+	2								
++	1								
+++							1		
					M^1 & M_1				
not yet erupted		1		1		1			
↑		1							
°	6	3	1	4		2	1	1	1
+	5	4		2		1			
++				2					
+++	1								
					M^2 & M_2				
not yet erupted	1			1					
↑	4	3		5	1	1			
°	9	3		1	1	1			
+	1	1							
++	1								
+++					1				
					M^3 & M_3				
not yet erupted	3	2							
°				1		3			
+		2		1					
++		1							

Symbols: ↑ erupting; ° in line, not worn; + slightly worn; ++ moderately worn; +++ heavily worn.

Tab. 12.   *Ursus spelaeus*; root development of deciduous canines.

wear-stage (after KURTÉN 1958)*	layer						
	II	III	IV	V	VI	VII	total
a) root not fully developed	1	1	1	1	–	1	5
c) root fully developed	2	3	–	2	1	–	8
d) root with resorption traces	2	–	–	3	–	–	5
e) root partially resorbed	–	–	–	2	–	–	2
f) tooth changed or about to be changed	16	2	2	24	–	10	54

* no Dc from the Große Grotte in Kurténs group "b"

ponderance of females – as in Ekaín and Troskaeta – and a clear dominance of males – e.g. Arrikrutz – have been observed (TORRES PEREZ-HIDALGO et al. 1991: 62); and a balanced sex-ratio exists for Odessa (Ukraine), Cotencher (Switzerland), and Dachstein (Austria).

The investigation of the sex distribution of *U. spelaeus* from the Große Grotte is hampered by the relative scarcity and the almost unvariably bad preservation of permanent canines – which are strongly dimorphic and thus useful in the separation of males and females (KOBY 1949: 675 ff.). Other teeth are better preserved but are not as dimorphic. Nevertheless, the distribution of the length of the M_1 is clearly bimodal (Fig. 8) and – assuming the bimodal distribution is caused by sexual dimorphism – points to the presence of both sexes with a possible preponderance of females.

Measurable postcranial specimens, which in bear show a large degree of sexual dimorphism and are thus helpful in the determination of sex ratios, are very rare (see Tab. 14) and do not provide further information here. In their size, the 3rd metacarpals of a right and a left paw from a single individual – found in layers XI and III respectively (see above) – fall into the uppermost range of the female cave bears at the Sibyllenhöhle, an Upper Pleistocene cave site near Kirchheim/Teck, southern Germany (Fig. 9). The partial paw recovered from layer VIII belonged in all probability to a rather small male bear (Fig. 10).
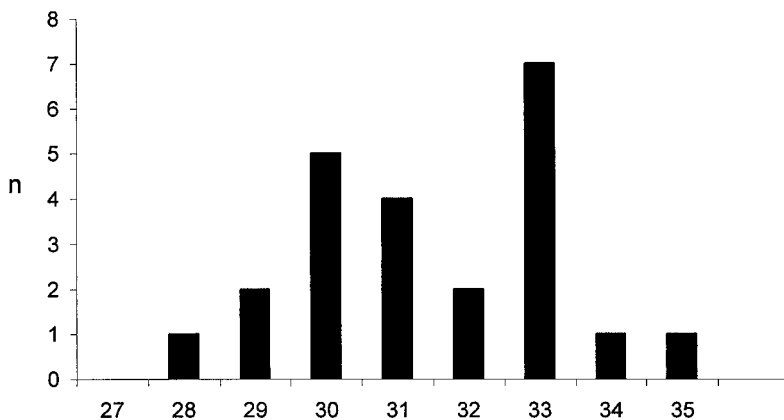
Fig. 8.   *Ursus spelaeus*; length of M_1.
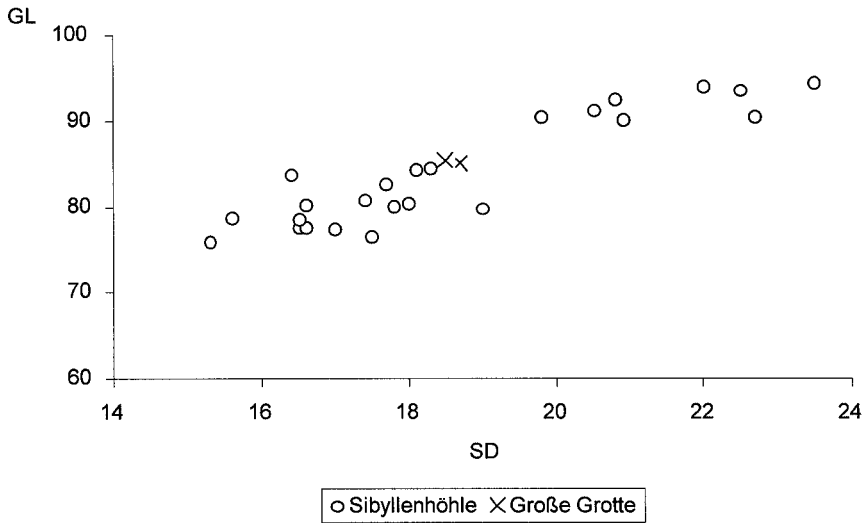
Fig. 9. *Ursus spelaeus*; metacarpal IV, smallest breadth of diaphysis/greatest length.
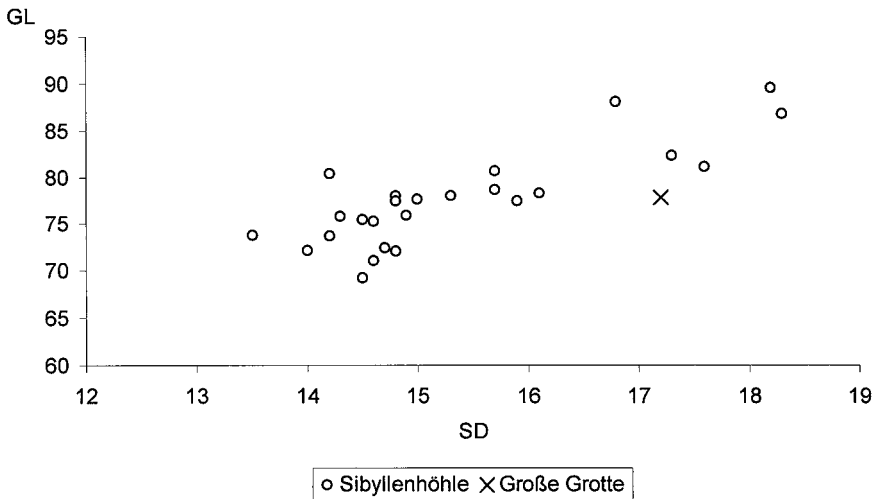
Fig. 10. *Ursus spelaeus*; metatarsal III, smallest breadth of diaphysis/greatest length.

The age structure described above can be used to gain some information, though indirectly, about the sex representation of the adult bears in the cave. Since, by analogy with *U. arctos*, the cubs usually spent the first two winters with their mother, the high relative abundance of neonates and yearlings indicates that female bears commonly hibernated in the Große Grotte. One could therefore suggest, that most of the grown-up bears represented at the site are females. Indeed, Kurtén (1976: 119) has pointed out to the positive correlation between the proportional representation of females and the number of yearlings in cave sites.

Tab. 13.   *Ursus spelaeus*; measurements of bones of neonates and juveniles.

skeletal element	layer	GL	side	age-stage
femur	II	31.2	dext.	
scapula	III	(23.6)	sin.	
radius	III	(24.5)	dext.	
ulna	III	27.7	sin.	
tibia	III	23.6	sin.	
humerus	V	(28.7)	sin.	
humerus	V	(32.0)	sin.	
humerus	V	29.5	sin.	neonate
radius	V	(24.5)	sin.	
humerus	VII	35.0	dext.	
radius	VII	26.9	dext.	
ulna	VII	30.7	dext.	
ulna	VII	30.2	sin.	
femur	VII	33.6	dext.	
femur	VII	(30.0)	sin.	
femur	VII	(29.0)	dext.	
humerus	VII	(85.5)	dext.	juvenile
femur	VII	(66.0)	dext.	

Tab. 14.   *Ursus spelaeus*; measurements of cranial and postcranial skeleton.

maxilla

layer	length of molar row
III	73.5

isolated maxillar teeth

layer	LM^1	BM^1		layer	LM^2	BM^2
II	29.0	18.8		II	45.6	23.1
II	28.2	18.8		II	45.9	–
II	28.6	19.6		II	46.4	23.4
III	28.1	19.1		II	45.8	22.4
III	29.8	19.2		III	47.8	24.1
V	27.2	19.0		III	45.2	24.5
VIII	26.6	18.8		V	47.7	25.1
IX	31.0	20.9		VI	(50.0)	24.5
				VII	41.4	22.8
mean	28.5	19.2		mean	46.2	23.7
s. d.	1.39	0.71		s. d.	2.34	0.95
n	8	8		n	9	8

mandible

layer	LCR	LMR	LPR	LDi	L C-M3	smallest height of diast.	height in front of M1	
II	89.7	76.5	13.3	53.1	142.5	50.8	–	Indiv. A
II	101.1	85.9	12.8	36.5	136.4	51.8	–	P1 present
II	108.1	90.9	14.3	60.5	167.5	–	–	Indiv. C
II	108.0	92.5	14.0	58.0	170.0	71.0	–	Indiv. C
II	105.5	88.0	13.5	65.5	169.5	62.0	–	Indiv. D
V	105.1	87.1	14.5	–	–	–	70.8	Indiv. A

isolated mandibular teeth

layer	LM$_1$	BM$_1$
II	32.1	14.8
II	32.4	15.7
II	30.0	14.1
II	31.4	14.7
II	31.4	14.4
II	30.0	13.9
III	30.0	13.5
III	32.1	15.0
III	32.6	15.4
III	32.7	16.8
III	29.0	14.3
IV	29.8	14.1
V	30.8	14.8
V	33.4	15.4
V	30.2	14.0
V	27.9	13.4
V	34.1	17.2
V	29.9	–
V	29.0	13.8
VI	30.9	14.9
VII	32.6	15.0
VII	32.1	15.7
XI	30.8	14.5
mean	31.1	14.8
s.d.	1.55	0.97
n	23	22

layer	LM$_2$	BM$_2$
II	33.4	18.5
II	30.3	18.1
II	31.3	18.8
II	30.6	17.4
II	31.0	18.1
II	31.7	18.5
II	(30.0)	18.9
III	30.5	17.8
III	31.7	17.9
III	32.1	18.1
III	34.0	20.5
III	30.7	18.1
V	32.3	19.8
V	31.7	20.0
V	32.1	19.1
V	32.4	20.0
V	30.5	18.1
VI	29.9	19.0
VII	32.3	18.6
mean	31.5	18.7
s.d.	1.12	0.86
n	19	19

layer	LM$_3$	BM$_3$
III	25.7	–
V	28.6	–
VI	26.2	19.0
VII	28.5	20.7
VII	27.0	19.9
mean	27.2	19.8
s.d.	1.32	0.85
n	5	3

scapula

layer	BG
VIII	52.7

ulna

layer	BPC
IX	71.0

humerus

layer	Bd
II	134.7

os carpi intermedio-radiale

layer	B	D
XI*	61.0	59.7

* same individual as
metacarpal from layer XI

metacarpal

layer	Bp	Dp	SD	Bd	Dd	GL	DD	digit
II	19.1	32.9	20.1	29.0	23.7	83.8	17.6	III
III*	19.3	29.3	17.0	21.5	21.5	76.6	–	II
III*	21.3	30.5	18.0	22.3	22.3	80.8	–	III
III*	25.2	31.8	18.7	23.8	23.0	85.1	–	IV
III*	32.3	36.3	19.2	29.0	23.2	87.5	–	V
XI**	19.4	29.2	18.1	21.6	21.7	75.8	–	II
XI**	21.0	30.4	17.6	22.1	23.1	80.8	–	III
XI**	24.2	31.5	18.5	23.8	22.9	85.4	–	IV
XI**	30.7	35.8	19.1	30.0	23.8	87.8	–	V

 * same individual
** same individual

pelvis

Layer	LA	LAR
II	–	69.4
V	69.5	–

patella

Layer	L	B
V	–	53.0
VII	67.7	47.6

astragalus

layer	GL	GB	BC
V	57.1	–	61.3
VII	59.1	63.7	–
VIII	60.7	–	64.9

femur

Layer	SD	Bd
II	46.7	–
II	(53.7)	117.1
VII	45.8	–

tibia

layer	SD	Bd	Dd
VII	34.4	82.7	46.9

calcaneus

layer	GB
III	65.0
V	69.7
VIII	75.0

metatarsal

Layer	Bp	Dp	SD	Bd	Dd	GL	digit
V	21.6	26.2	13.2	17.9	16.7	59.0	I
V	20.6	21.3	14.2	19.5	19.0	63.6	I
VIII	16.7	26.4	–	–	–	–	II
VIII	21.0	32.0	17.2	–	–	77.8	III
V	21.3	34.4	18.9	25.4	–	98.0	IV
VIII	25.0	31.0	–	–	–	–	IV
III	33.6	31.2	14.0	–	–	–	V

atlas

layer	BFcr	BFcd
II	97.9	86.0
II	99.1	83.4

axis

layer	BFcr
XI	84.0

The material from the Große Grotte cannot contribute much information about the body size of *U. spelaeus* during the Middle Palaeolithic in our region. Most of the measurable bear specimens are isolated teeth (Tab. 14). While tooth size is very often used in palaeontological and archaeozoological studies, it does not seem to be a very reliable indicator of body size (DAYAN et al. 1991, 117; VAN VALKENBURG 1990, 181 ff.; WEINSTOCK 1998, 1999). Bone size correlates much closer with body size (i.e. body weight); however, as mentioned above, measurable cranial and postcranial material in the Große Grotte is scarce, and consists mostly of metapodials, carpals and tarsals belonging probably to just 2–3 individuals (Tab. 14).

Family Mustelidae SWAINSON 1835

Genus *Mustela* LINNAEUS 1758

Mustela putorius LINNAEUS 1758 vel *eversmanni* LESSON 1827

Material: SMNS 34143.1

A complete ulna from *Mustela* was recovered from layer VIII (SMNS 34143.1). Its metrical characters fall in the uppermost range of recent European *putorius*

(Tab. 15). While the identification of this specimen cannot be carried out beyond the generic level, it is certain that it belonged to a male individual.

During the Upper Pleistocene, two species of polecat lived in central Europe: the common polecat *Mustela putorius* and the steppe polecat *Mustela eversmanni*. Modern members of these species are regarded as having different preferred habitats. *Mustela putorius*, in contrast to *M. eversmanni*, can be found usually in the edge of temperate forests, while the latter inhabits steppic environments (WOLSAN 1993: 748, 801).

The identification of postcranial remains of polecats to the species level is highly problematic, since no clear morphological differences in their skeletons have been described. Absolute size cannot be used as an infallible criterion: in most of its geographical range, the steppe polecat tends to be larger than the common polecat; in Europe, however, both species seem to be of similar size (WOLSAN 1993: 770).

Tab. 15. *Mustela*; measurements of the ulna from the Große Grotte and from recent *M. putorius*
MU: osteological comparative collection of the Institute of Prehistory, Univ. of Tübingen
Europe: after WOLSAN 1993: 705.

	GL	BPC	DPA	SDO
Große Grotte (34143.1)	50.6	5.8	8.3	7.4
MU 6 ♀	42.1	4.8	6.3	5.4
MU 21 ♀	38.8	4.7	6.2	5.4
Europe ♀	32–43.8	–	–	–
MU 20 ♂	49.6	6.1	7.8	6.5
MU 25 ♂	51.3	6.8	8.6	7.3
Europe ♂	38–54	–	–	–

Genus *Martes* PINEL 1792

Martes martes LINNAEUS 1758

Material: SMNS 34142.1

The corpus of a right mandible of a marten was found in layer III. The identification of the specimen to the pine marten, *Martes martes*, rather than to the stone marten, *Martes foina*, is based mainly on the distance between the foramina mentalia, which is longer in *M. martes* than in *M. foina* (STUBBE 1993: 370 ff.). The measurements taken on the mandible are given in Tab. 16.

Recent populations of pine marten usually inhabit forested areas; they occurr in the taiga, in both dense and relative open coniferous forests, and in mixed as well as in deciduous oak or beech forests (STUBBE 1993: 402 ff.).

Tab. 16. *Martes martes*; measurements of mandible.

length of cheektooth row (alveoli)	31.6
length of premolar row (alveoli)	18.0
length of molar row (alveoli)	14.5
length of M_1 (alveolus)	10.5
height between P_2 and P_3	9.8
height behind M_1	11.5

Family Hyaenidae GRAY 1869

Genus *Crocuta* KAUP 1828

Crocuta crocuta spelaea (GOLDFUSS 1823)

Material: SMNS 34114.1

In the material investigated, only one specimen of the cave hyena was identified. It is a well preserved metatarsal II from layer V, showing light gnawing marks on its distal end (Pl. 3, fig. 3). This piece is not mentioned in the previous study of the material from the Große Grotte (WAGNER 1983: 69 ff.). WAGNER does mention a hyena specimen, namely an upper M1 from layer XI. Such a specimen is not in the collection of the SMNS today. In fact, the M^1 was almost always absent in Upper Pleistocene hyenas (ZIEGLER 1996: 13), and when present it is only in a very reduced form (EHRENBERG 1938: 34; 1939: 112). Either there was a mistake in the determination, or the specimen was lost after WAGNER's study.

In the morphology of its extremities, the cave hyena is characterised by shorter but broader bones than modern hyena, *Crocuta crocuta* (KERNERKNECHT 1940: 247; MUSIL 1965: 26). Nevertheless, the metatarsal II from the Große Grotte is relatively long and gracile, without reaching, however, the typical proportions of *C. crocuta* (Fig. 11; Tab. 17). It is similar to the more slender specimens from the Upper Pleistocene site of Teufelslucken in Austria, from which an abundant *C. spelaea* assemblage was recovered (EHRENBERG & KERNERKNECHT 1940: 131 ff.; KERNERKNECHT 1940: 192 ff.).
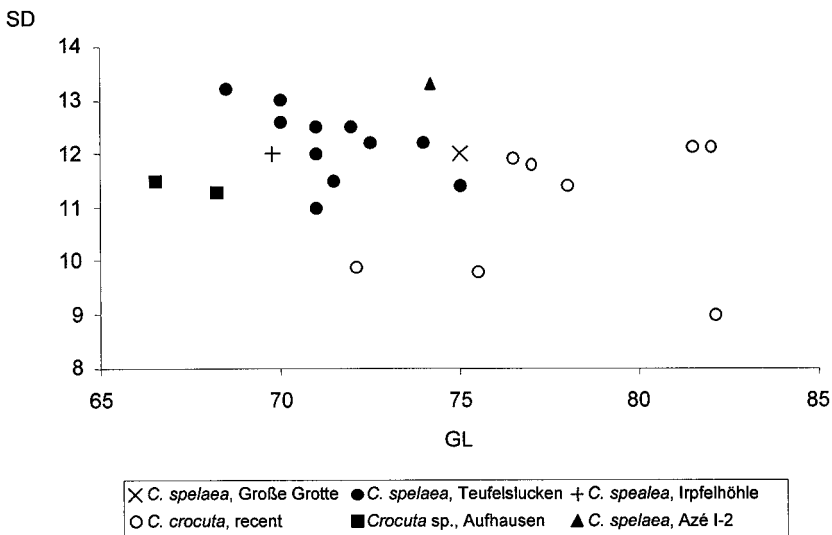

Fig. 11. *Crocuta*; metatarsal II, greatest length/smallest breadth of diaphysis. (Teufelslucken and recent: KERNERKNECHT 1940; Azé 1–2: ARGANT 1991).

Tab. 17. *Crocuta crocuta spelaea*; measurements of metatarsus II
from Große Grotte and other sites in southern Germany and Austria.

site	n	Bp	SD	GL	Bd	Bd art.
Große Grotte	1	13.6	12	74.6	15.8	13.6
Aufhausen	2	13.8 / 13.4	11.3 / 11.5	68.2 / 66.5	15.2 / 14.6	13.5 /13.6
Irpfelhöhle	1	13.3	12	69.8	15.3	13.6
Teufelslucken[1]	12		11–13.2	68.5–75		
Hermannshöhle[2]				70.0		

1= KERNERKNECHT 1940; 2=SCHÜTT 1969

Family Felidae GRAY 1821

Genus *Panthera* OWEN 1816

Panthera leo spelaea (GOLDFUSS 1810)

Material: SMNS 34073.1–2, 34099.1

Given the close morphological similarity between the bones of the lion (*Panthera leo*) and the tiger (*Panthera tigris*), the question to which taxon did the big cats of the European Pleistocene belong has been under discussion since a long time (see GROSS 1992: 94 ff.; GROISS 1996: 399–414 and references therein). Nevertheless, a concensus seems to have been reached, with the majority of the scholars advocating for the inclusion of the "cave lion" within *Panthera leo* (ZIEGLER 1994: 47).

The lion in the Große Grotte is represented by three finds: a proximal fragment of a right metatarsal IV (Bp 19.7, SD 16.5) and a fragment of a fibula – both from layer II – and the proximal end of a left metacarpal V (Bp 23.6, Dp (25.0); Pl. 3, figs. 1–2) from layer III. These fragments were not mentioned by WAGNER (1983) in his study of the fauna from the Große Grotte and thus *Panthera* is absent from his species list.
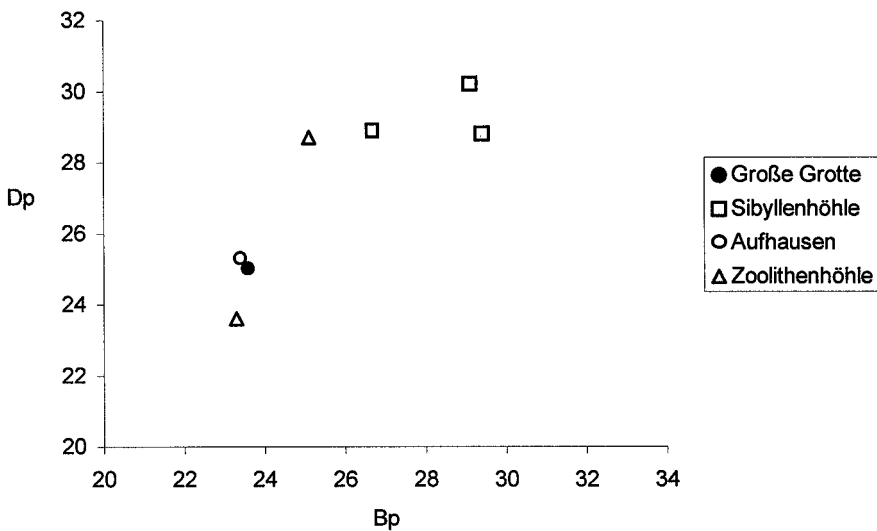

Fig. 12. *Panthera leo spelaea*; metatarsal V, proximal breadth/proximal depth.

The metacarpals represent rather small individuals, much smaller than those from the Upper Pleistocene Sibyllenhöhle, also in southwest Germany, and similar to that from Aufhausen, an Upper Pleistocene cave site in the same region (Fig. 12, Tab. 18). Given the considerable degree of sexual dimorphism in both fossil and recent lions, it can be safely assumed that the specimens from the Große Grotte and Aufhausen represent females, while in the Sibyllenhöhle only males are present. However, the possibility that the size difference of lions between the former and latter sites is due to changes in the body size of *Panthera leo spelaea* during the first half of the Wuermian glaciation cannot be ruled out; this subject is still in need of investigation.

Tab. 18.   *Panthera leo spelaea*; measurements of metatarsal IV
from the Große Grotte and other sites in southern Germany.

site	Bp	SD
Große Grotte	19.7	16.5
V. Seckendorff	19.4	17.8
Sibyllenhöhle	20.7, 22.00	18.5, 18.0

Genus *Felis* LINNAEUS 1758

Felis silvestris SCHREBER 1777

Material: SMNS 34084.1

The only find of wild cat in the Große Grotte is a fragment of a right metatarsal III. The proximal width is 6.7 mm and the smallest width of the diaphysis 4.8 mm. The distal end of the bone is missing.

Family Elephantidae GRAY 1821

Genus *Mammuthus* BURNETT 1830

Mammuthus primigenius (BLUMENBACH 1799)

Material: SMNS 34075.1–2

Two specimens were identified as belonging to the mammoth, both from layer II: a small fragment of an upper tooth – either a m³ or a M¹ – and a rib fragment. The latter shows the typical modifications usually seen in ribs which were used as artifacts, possibly for the preparation of animal skins ("Fellglätter"; HAHN 1993: 363 ff.).

Family Equidae GRAY 1821

Genus *Equus* LINNAEUS 1758

Equus germanicus NEHRING 1884

Material: SMNS 34071.1–5, 34098.1, 34113.1, 34124.1–2

During the first part of the last glacial, two forms of horses – a stenonid and a caballine – coexisted, at least at some points in time, in the area of what today is southern Germany (FORSTEN & ZIEGLER 1995; ZIEGLER 1996: 24). The stenonid form is

known as *Equus hydruntinus*. About the correct taxonomic designation for the caballine form, there is some disagreement. Since horses from the early Weichsel (=Würm) usually show a smaller size than Middle Pleistocene horses and larger size than Late Weichsel ones, they are often assigned to a different species, *Equus germanicus* (FORSTEN & ZIEGLER 1995: 12), and this name is used also in the present paper. It is known, however, that species in different families suffered dramatic and often quite rapid size changes in the course of the Pleistocene (see e.g. DELPECH 1983 and WEINSTOCK 1998 on *Rangifer tarandus*; LISTER 1989 on *Cervus elaphus*; VARTANYAN et al. 1993 on *Mammuthus primigenius*; McFARLANE et al. 1998 on the large North American rodent *Amblyrhiza inundata*). In spite of the size changes, it is generally accepted that in all cases a single species is involved. Following this logic, it could be suggested that no more than one species of caballine horse existed during the Pleistocene (for a discussion on this subject see FORSTEN 1993 and FORSTEN & ZIEGLER 1995).

In the Große Grotte, only the caballine form is represented. All nine specimens are either isolated teeth (n=3) or very fragmented remains of the postcranial skeleton (n=6; Tab. 19). Three finds represent young animals: a deciduous incisor, a deciduous $Dp^{3/4}$, and a second phalanx with its distal end gnawed away by a carnivore. Two other fragments – a distal end of a right femur and the distal end of a 1st phalanx – also show gnawing marks.

With the specimens at hand it is impossible to make an assessment of the size of *Equus* from the Große Grotte. The only measurable fragment is the proximal phalanx II (Bp 53.0; Dp 35.4). This piece, however, comes from a young individual (epiphysis fusing), and thus the measurements can be regarded as minimal values only.

Tab. 19. *Equus germanicus*; distribution of the fragments among the different layers.

skeletal element	side	layer
phalanx II	dext.	II
tibia (diaphysis)	sin.	II
incisor		II
deciduous incisor		II
cervical vertebra		II
femur dist.	dext.	III
phalanx I dist.		V
radius / ulna	sin.	VII
Dp^{3-4}	sin.	VII

Family Rhinocerotidae OWEN 1845

Genus *Coelodonta* BRONN 1831

Coelodonta antiquitatis (BLUMENBACH 1807)

Material: SMNS 34076.1

The only specimen of the wooly rhino in the Große Grotte – a slightly worn P_4 – was found in layer II. The tooth shows both the rough enamel and extensive cementum cover characteristic of this species. The length and width are 39.2 mm and 28.6 mm respectively (measured after DIETRICH 1945: 53).

Family Cervidae GRAY 1821

Genus *Cervus* LINNAEUS 1758

Cervus elaphus LINNAEUS 1758

Material: SMNS 34081.1–3

Three specimens of red deer were found in the assemblage: a mandible fragment, a metacarpus diaphysis fragment, and the distal end of a 1st phalanx, all from layer II. An AMS-date was obtained from the mandible. It falls within the early medieval period, which indicates the contamination of at least the uppermost part of the deposits by recent material (J. WAIBLINGER, Tübingen, pers. comm.). While the other two fragments must not be medieval, the date of the mandible nevertheless casts doubts about the presence of this taxon in the original palaeolithic thanatocoenose.

Genus *Rangifer* FRISCH 1775

Rangifer tarandus LINNAEUS 1758

Material: SMNS 34074.1–14, 34092.1–5, 34102.1–4, 34112.1–15, 34128.1–4, 34132.1–5, 34137.1, 34148.1

Finds of reindeer, fifty in total, were recovered from almost all layers (Tab. 20). The preservation of the material is poor. Some of the phalanges and carpals are complete but from the longer limb bones only small fragments are present. Whereas in the case of *Capra* isolated teeth comprised most of the assemblage, only three *Rangifer* loose teeth were represented in the material.

Some finds demonstrate the presence of young individuals: two shed antlers (basis with brow-tine), an unfused distal epiphysis of a metapodial, and a metatarsus shaft fragment. Adults are definitely represented by the proximal end of a tibia with a fused epiphysis, a proximal end of a femur (fused caput), and a moderately worn M_3. First and second phalanges with closed epiphyses (n=8) could come from either adults or subadults.

Six fragments show either gnawing marks or traces of having been in contact with the digestive juices of a carnivore (Tab. 22). In contrast, not a single cut/butchery mark was observed. However, an antler fragment (SMNS 34092.2) shows wear traces.

Family Bovidae GRAY 1821

Genus *Capra* LINNAEUS 1758

Capra ibex LINNAEUS 1758

Material: SMNS 34072.1–43, 34093.1–4, 34101.1–6, 34101.8, 34111.1–17, 34122.1, 34125.1–13, 34193.1–4, 34135.1–5,34140.1–3, 34101.7

The ibex is the second best represented species in the Große Grotte, with a total of 112 bone remains distributed among all the layers. While most skeletal elements are present, the great majority of the material consists of isolated maxillar and mandibular teeth and phalanges (Tab. 23). It must be pointed out, however, that most of

Tab. 20. *Rangifer tarandus*; skeletal representation in the different layers.

Skeletal element				layer					
	II	III	IV	V	VII	VIII	IX	XI	total
antler	–	3	1	–	–	3	–	–	7
mandible	–	–	–	–	1		–	–	1
loose tooth	1	–	–	2	–	–	–	–	3
humerus	–	–	–	1	–	–	–	–	1
radius / ulna	–	–	–	1	–	–	–	1	2
ulna	1	–	1	–	–	–	–	–	2
carpal II/III	–	–	–	1	–	–	–	–	1
intermediate carpal	3	–	–	–	–	–	–	–	3
metacarpal III/IV	–	–	–	1	–	–	–	–	1
metacarpal II or V	–	1	–	–	–	1	1	–	3
femur	1	–	–	2	–	1	–	–	4
tibia	1	–	1	–	–	–	–	–	2
metatarsal	1	–	–	1	1	–	–	–	3
indet. metapodial	1	–	–	–		–	–	–	1
phalanx I	1	–	1	1	1	–	–	–	4
phalanx II	1	–	1	3	–	–	–	–	5
phalanx III	–	1	–	1	–	–	–	–	2
sesamoid	–	–	–	–	1	–	–	–	1
atlas	1	–	–	–	–	–	–	–	1
lumbar vertebra	–	–	–	1	–	–	–	–	1
ribs	2	–	–	–	–	–	–	–	2
total	14	5	5	15	4	5	1	1	50

Tab. 21. *Rangifer tarandus*; measurements of skeletal elements.

M_3

layer	L	B
V	22.1	10.1

phalanx I

layer	Bp	SD	Bd	GL	Dp	DD	Dd	phys. L
V	19.3	13.4	16.0	44.6	19.8	9.6	12.1	42.7
V	19.4	12.8	15.8	44.3	19.8	9.2	11.8	42.9

tibia

layer	Bp
II	65.5

phalanx II

layer	Bp	SD	Bd	GL	Dp	DD	Dd
V	16.7	11.7	15.1	32.8	17.3	11.9	17.2
V	17.9	13.0	16.2	36.0	19.1	12.7	–
V	17.9	13.2	–	36.4	18.6	12.2	18.0

Tab. 22. *Rangifer tarandus*; gnawed and digested bones.

skeletal element (inv. number)	layer
gnawed:	
rib head (34074.12)	II
phalanx II (34102.2)	IV
femur, caput (34132.5)	VIII
digested:	
phalanx II (34074.10)	II
intermediate carpal (34074.8)	II
phalanx I (34128.1)	VII

the fragments of long bones which could only be identified as "medium-sized ungulate" most probably belonged to *Capra*. The same is true for ribs and vertebrae.

In some instances, several specimens could be assigned to the same individual. Thus, in layer II, two partial vertebral columns can be distinguished. Thirteen vertebrae come from a young individual – 3 cervicals and 10 thoracic. Three cervical vertebrae (2nd – 4th) and six lumbar vertebrae apparently belong to a single adult individual. Due to their large size (see Tab. 24 for measurements of axis), they must represent a male.

From the same layer come a left humerus and a left radius with their respective late-fusing epiphyses – proximal in humerus and distal in radius – still open, as well as an ulna with its proximal apophysis unfused. They belong undoubtedly to the same individual. These bones were ascribed by WAGNER to the (postulated) wild sheep species, *Ovis argaloides* (WAGNER 1983: 72, 74). However, the bones show characteristics typical of *Capra*. Thus the medial epicondyle of the humerus shows a smaller angle than the 90° characteristic of *Ovis* and the trochlea is relatively broad and low; the proximal radius has only a weekly developed lateral tuberosity (BOESSNECK, MÜLLER & TEICHERT 1964).

A second elbow joint (distal part of a humerus and proximal end of radius/ulna, left side) was recovered from layer VII. A complete left metacarpus, showing carnivore gnawing-marks on its distal end (Pl. 3, fig. 6), and a peripheral 1st phalanx most probably represent the same animal as the elbow joint. An axial 1st phalanx from this layer shows a different colour in it surface as the peripheral one, but it is almost identical in size. Thus it and a 2nd phalanx with which it articulates perfectly, may also form part of the same left forelimb. The large size of the bones and the thickness of their compacta suggest they come from a male (Tab. 24). The distal humerus and proximal radius/ulna show not only gnawing marks, but also pathological modifications (Pl. 3, fig. 4–5). The exostoses in the lateral aspects of radius and ulna show that this individual had some problems – and probably much pain – in its left elbow. In the cranial aspect of the humerus, a pseudoarthrose formed just above the medial part of the trochlea. A second pseudoarthrose is found in the dorsal aspect of the proximal radius in its medial side, just distal to the fovea capitis. These two "articular areas" could only develop if the elbow was being constantly flexed to its full extent. This flexion occurs normally only when an animal is resting on the ground. A pseudoarthrose can develop comparatively fast, in a matter of a few weeks (H.-P. UERPMANN, Tübingen, pers. comm.). Thus it seems that this buck was forced to spend a large part of the last weeks of its life laying, unable to move much around. It is impossible to tell whether it was finally killed by carnivores and then transported into the cave, or whether it succumbed to illness or starvation and was then scavenged upon.

The strong sexual dimorphism which exists in *Capra* allows, in most cases, a sex-determination of the better preserved remains (see Tab. 24). Besides the bones of the elbow joint from layer VII described above, six or seven fragments represent males, one belongs to a female, and three (including humerus and radius of a subadult) could be of either sex.

Tab. 23. *Capra ibex*; skeletal representation in the different layers.

skeletal element/layer	II	III	IV	IX	V	VI	VII	VIII	XI	total
horn cores	–	–	–	–	–	–	2	–	–	2
frontal with horn core	1	–	–	–	–	–	–	–	–	1
maxillary	1	1	–	–	–	–	–	–	–	2
isolated maxillar teeth	4	1	2	2	3	–	–	–	–	12
mandibula	2	1	–	1	–	–	1	1	–	6
loose mandibular teeth	6	–	3	1	2	–	–	–	–	12
loose max. or mand. teeth	–	–	1	–	–	–	–	–	–	1
scapula	2	–	1	–	1	–	–	–	1	5
humerus	2	2	–	–	–	1	1	–	1	7
radius	3	–	–	–	–	–	–	–	–	3
radius/ulna	–	–	–	–	–	–	1	1	–	2
ulna	1	–	–	–	–	–	–	–	–	1
carpal II/III	–	–	–	–	–	–	1	–	–	1
metacarpal	2	–	1	–	–	–	1	1	–	5
femur	1	1	–	–	1	–	–	–	–	3
patella	–	–	–	–	2	–	–	1	–	3
tibia	–	–	–	–	2	–	–	–	–	2
astragalus	–	–	–	–	1	–	–	–	–	1
centrotarsal	–	–	–	1	–	–	–	–	–	1
metatarsal	2	–	–	–	–	–	–	–	–	2
phalanx I	–	–	–	–	4	–	2	–	1	7
phalanx II	1	–	–	–	1	–	1	–	–	3
phalanx III	2	–	–	–	–	–	1	–	–	3
axis	1	–	–	–	–	–	–	–	–	1
cervical vertebrae *	5	–	–	–	–	–	–	–	–	5
lumbar vertebrae	6	–	–	–	–	–	–	–	–	6
thoracic vertebrae +	13	–	–	–	–	–	–	–	–	13
ribs	–	–	–	–	–	–	2	–	–	2
total	55	6	8	5	17	1	13	4	3	112

* 3 of them belong to same individual (SMNS 34072.1)
+ 10 of them belong to same individual (SMNS 34072.1)

Tab. 24. *Capra ibex*; measurements of cranial and postcranial skeleton.

maxillary

Layer	LCR
III	57.2

mandible

layer	LCR	LMR	LPR	small. height diastema	height in front M_1
II	–	–	22.5	–	26.6
VII	81.0	57.0	22.5	17.5	31.1

isolated M_3

layer	L	B
II	25.6	8.9
II	25.2	8.9
IX	27.1	9.7

scapula

layer	SLC	GLP	LG	BG	sex
II	33.1	48.6	41.4	34.0	♂
V	24.5	–	–	–	♀

humerus

layer	Bd	BT		sex
II*	39.8	38.1	subad.	?
VII**	–	(41.0)		♂

  * same indiv. as rad. in layer II
** same indiv. as rad. & probably metac.
   in same layer

radius

layer	Bp	BFp		sex
II *	40.7	–	subadult	?
VII**	45.6	43.0		♂

  * same indiv. as hum. from layer II
** same indiv. as hum. & metac.
   in same layer

metacarpal

layer	Bp	Dp	SD	Bd	Dd	GL	sex
II	–	–	–	36.3	–	–	?
VII**	38.1	25.3	26.1	43.3	(22.5)	(145.0)	♂

** probably same indiv. as humerus and radius in same layer

femur

layer	DC	sex
III	(29.5)	♂?

astragalus

layer	Ll	Lm	Dl	BC	sex
V	39.7	36.0	22.5	26.8	♂

tibia

layer	Bd	Dd	sex
V	36.5	29.5	♂

os centrotarsale

layer	B	D	sex
IX	31.8	26.3	♂

phalanx I

layer	Bp	SD	Bd	GL	Dp	DD	Dd	phys. L
V	18.4	15.7	17.3	46.1	20.9	12.7	16.1	44.5
V	17.9	14.2	16.7	46.1	20.1	12.3	15.5	44.2
VII	17.8	14.8	17.4	45.8	21.0	12.3	15.4	43.8
VII	17.9	15.5	17.4	44.8	20.6	12.7	15.6	–
XI	16.5	13.8	15.1	45.1	19.5	11.4	13.6	43.3

phalanx II

layer	Bp	SD	Bd	GL	Dp	DD	Dd
II	18.1	14.0	–	–	17.9	12.6	–
V	15.5	(9.8)	–	29.2	16.5	10.9	–
VII	17.1	12.8	14.0	27.7	16.8	13.2	16.6

axis

layer	BFcr	SBv	LCDe	sex
II	69.3	42.5	77.7	♂

Tab. 25. *Capra ibex* and *Capra pyrenaica*; distal breadth of the tibia from
the Große Grotte and other prehistoric and recent assemblages.

Site	Bd	n
Große Grotte	36.5	1
Brillenhöhle[1]	34	1
Pod hradem[2]	32.9	1
subfossil[3]	33.0 – 35.0	5
recent[3]	31.0 – 34.5	3
C. pyrenaica, Ekaín[4]	30.5, 31.0, 35.0	3
C. pyrenaica, La Vache	31.0 – 38.0	7

1 = BOESSNECK & VON DEN DRIESCH 1973; 2 = MUSIL 1965;
3 = KOBY 1958; 4 = ALTUNA & MARIEZKURRENA 1984.

Genus *Rupicapra* BLAINVILLE 1816

Rupicapra rupicapra (LINNAEUS 1758)

Material: SMNS 34082.1–3, 34142.1, 34144.1, 34145.1

During the Pleistocene, the chamois had a broader geographic distribution than at present. Remains of this species are often found at Palaeolithic sites, although always in relative small numbers (see e.g. ALTUNA & MARIEZKURRENA 1984: 266; BOESSNECK & VON DEN DRIESCH 1973: 33 ff.; LEHMANN 1954: 102 ff.; MUSIL 1965: 81; ZIEGLER 1996: 45 ff.).

Six specimens were assigned to the chamois: a deciduous fourth premolar (Dp$_4$, length 15.7 mm), a proximal metatarsus, a femur shaft fragment, and three fragments of 1st phalanges.

The femur fragment is too small for *Capra* but, in principle, it could also belong to the saiga antelope. In recent skeletons of *Rupicapra* (SMNS 7915) and *Saiga tatarica* (SMNS 7596) at the Museum of Natural History (Stuttgart) the fossa supracondylaris in the former is shallower than in the latter; in this respect, the fragment from the Große Grotte is more similar to *Rupicapra*. Though not complete, the 1st phalanx distal fragments show the relative long and slender proportions which characterise both *Rupicapra* and *Saiga*. However, the more rounded condyles and deeper sulcus between them allow the identification of the phalanges from the Große Grotte as *Rupicapra*. In one of the phalanges (SMNS 34082.3), the form of the condyles is more difficult to determine, since the piece was obviously modified by the action of gastric juices of a carnivore. Nevertheless, this piece probably belongs to the chamois as well.

The small number of finds of this species and their poor preservation do not allow an evaluation of the size of *Rupicapra*. Only two fragments, both 1st phalanges, could be measured:

SMNS 34082.1   Bd 12.8   Dd 11.2
SMNS 34142.1   Bd (12.5)   Dd (11.0)

3. Small mammals remains, biostratigraphy and palaeoecology

Many species of owls tend to roost in caves and rock shelters. While at the site, they regurgitate – once or twice a day – pellets containing mostly matted fur, hair, bones, and teeth from ingested prey. Given enough time, this may result in major accumulations of small mammal remains (Lyman 1994: 198 ff.), which can be of great value in biostratigraphical and palaeoenvironmental analyses. However, in contrast to the remains of larger mammals, the collection of the much smaller bones and teeth of rodents, insectivores and bats requires systematical sampling and screening. Regrettably, this was apparently not the case during the excavations at the Große Grotte. The resulting assemblage is small, and thus the biostratigraphical and palaeoenvironmental information derived from it should be regarded with caution.

Remains of small mammals are present in small quantities, and only in layers II–IV (see Tab. 26). Taxonomical determinations were usually based on mandibles showing a M_1 or on isolated M_1. At least six species of small rodents, belonging to four different genera within the family Arvicolidae, are represented in the assemblage: collared lemming (*Dicrostonyx gulielmi*), Norway lemming (*Lemmus lemmus*), vole rat (*Arvicola terrestris*), *Microtus gregalis*, snow vole (*Microtus nivalis*), and common vole/field vole (*Microtus arvalis/agrestis*).

Tab. 26.   Identified small-mammal remains from the Große Grotte.

Species	number of specimens		
	layer II	layer III	layer IV
Arvicola terrestris	6	2	–
Dicrostonyx gulielmi	5	2	3
Lemmus lemmus	5	4	4
Microtus arvalis/agrestis	4	3	1
Microtus gregalis	2	–	1
Microtus nivalis	2	–	–
Microtus sp.	7	–	–

Relevant to the biostratigraphical position of the fauna of the Große Grotte is the identification of the *Arvicola* remains. Molars of *Arvicola* from most of the Middle Pleistocene are characterised by a relatively thicker enamel band in the convex side and they are usually assigned to *A. cantiana*. During the late Middle Pleistocene and the Eem Interglacial, the thickness of the enamel in the concave and convex sides is more or less the same. In contrast, the molars from the Große Grotte show a thicker enamel band in the concave side than in the convex one, and are thus indicative of the Late Pleistocene form *A. terrestris* (Koenigswald 1985: 16). Within this Late Pleistocene taxon, two forms can be differentiated: a smaller one, *A. terrestris*, and a larger, chronologically younger, *A. t. antiquus* (Koenigswald 1985: 17); the larger form has also been regarded as a separate species, *A. antiquus* (e.g. Storch 1973: 117 ff., Ziegler, in prep.). The measurements from the two M_1 (4.24 mm and 4.26 mm) fall within the upper range of the Late Pleistocene *Arvicola* from southern Germany, but given the overlap in the dimensions of *A. terrestris* and *A. antiquus* (Ziegler, in prep.), they cannot be assigned unambiguously to one of the two forms.

The remains of the collared lemming *Dicrostonyx gulielmi* from the last glacial are usually separated into two forms: the chronologically older *D. g. rotundus*, which

occurs during the first half of the Würm (i.e. before the glacial maximum), and a later form, *D. g. henseli* (KOENIGSWALD 1985: 14). These subspecies can only be separated by their M^1 and M^2. Since these teeth are not present in the material from the Große Grotte, a subspecific determination of this taxon is not possible. The mean size of the M$_1$ from the Große Grotte is above that of most *Dicrostonyx* assemblages from the last glacial (Tab. 27). It must remain unclear whether this large size is only a "statistical artifact" due to the small number of specimens, or whether it has some chronological meaning; unambiguous chronological size gradients during the last glacial in southern Germany have not been observed for this species (ZIEGLER, in prep.).

The size of the seven M$_1$ from *Lemmus* in the Große Grotte leaves no doubt that they belong to the larger *Lemmus lemmus* and not to the smaller forest lemming, *Myopus schisticolor (=Lemmus schisticolor)*. In fact, the mean value for the teeth from Große Grotte is well above that of other south German sites from both the first and the second halves of the Würm glaciation (Tab. 28). However, since only eight teeth were measured, not much significance should be attached to this fact.

Tab. 27.   *Dicrostonyx gulielmi*, length of M$_1$.

Site	n	variability	mean
Gönnersdorf	35	3.28–4.03	3.61
Weinberghöhle C-E	73	2.90–3.90	3.43
Brillenhöhle V	23	3.20–3.90	3.56
Brillenhöhle VI	13	3–3.90	3.58
Brillenhöhle VII	15	3–4.10	3.56
Kogelstein	16	3.28–3.80	3.48
Große Grotte	**7**	**3.30–4.08**	**3.63**
Villa Seckendorff	11	3.20–3.60	3.40

Tab. 28.   *Lemmus lemmus*, length of M$_1$.

Site	n	variability	mean
Weinberghöhle C-E	54	2.70–3.60	3.13
Brillenhöhle V	10	3–3.80	3.32
Brillenhöhle VI	6	2.90–3.50	3.16
Brillenhöhle VII	55	3–4.10	3.36
Kogelstein	7	3.07–3.54	3.33
Große Grotte	**8**	**3.27–3.86**	**3.52**
Villa Seckendorff	17	2.60–3.48	3.14

Tab. 29.   *Microtus gregalis*, length of M$_1$.

site	n	variability	mean
Gönnersdorf	154	2.26–3.24	2.82
Weinberghöhle C-E	123	2.40–3.10	2.80
Brillenhöhle VI	9	2.50–2.90	2.73
Brillenhöhle VII	10	2.40–3	2.75
Kogelstein	83	2.42–3.15	2.77
Große Grotte	**3**	**2.68–2.89**	**2.79**
Villa Seckendorff	82	2.24–3	2.65
Burgtonna-SK	61	2.25–2.88	2.53

KOENIGSWALD (1985: 19 ff.) has suggested that the size of *Microtus gregalis* increased from the early to the late Glacial. The length of the three M_1 recovered from the Große Grotte show a mean size close to that from sites belonging in the later Anaglacial and late Glacial (e.g. Kogelstein, ZIEGLER, in prep.) and they are larger than the mean from the early glacial sites Villa Seckendorff and Burgtonna-SK (Tab. 29). However, the three values still fall within the variation of these early glacial sites.

Among the rodent taxa found in the cave, three are characteristic of the tundra: *Microtus gregalis*, *Dicrostonyx gulielmi* and *Lemmus lemmus*. Together, they comprise almost 60 % (n=26) of the small-mammal remains. *A. terrestris*, represented in the Große Grotte by eight specimens, is nowadays commonly found in banks of streams or lake margins with abundant vegetation. In southern Germany, however, it also inhabits dry areas such as meadows or forests with abundant subterranean food-supply. Therefore, this species must not be indicative of humid habitats (KOENIGSWALD 1985: 17; ZIEGLER, in prep.). *Mustela nivalis* inhabits nowadays "Felsfluren", and its presence in the assemblage from the Große Grotte is therefore no surprise. Individuals from the group *Microtus arvalis/agrestis* were present in Central Europe in glacial as well as in interglacial periods and thus no palaeoclimatic information can be derived from their presence.

Thus, while the number of remains of small mammals is scant, it does seem to indicate the existence of a largely open landscape. This view is reinforced by the presence of *Mammuthus*, *Coelodonta, Equus* and *Rangifer* among the large mammals. An AMS-date casts doubts on the presence of *Cervus elaphus*, a species often regarded as being suggestive of a more closed, forested landscape, in the Upper Pleistocene thanatocoenose of the Große Grotte (see above). Even if the remaining finds of this taxon do date to the Upper Pleistocene, their presence in such small numbers must not be seen as an indicator of the presence of forest; some red deer populations inhabit nowadays treeless landscapes, such as the Scottish highlands.

In summary, the fauna from the Große Grotte – at least from its upper layers – belongs to a cold episode during the first half of the last Glacial. The large size of *A. terrestris* and *Microtus gregalis* – if indeed real and not only apparent due the reduced number of finds – may suggest a rather late phase within the first half of the Weichsel.

4. Taphonomical considerations

While stone artifacts demonstrate the occupation of the Große Grotte by neanderthals during the Middle Palaeolithic, the extent – if any – to which they must be held responsible for the accumulation of the faunal remains in the cave is far from clear. Many of the carnivore taxa living in Central Europe and elsewhere during the Upper Pleistocene, such as wolves, bears, hyenas, lions, and foxes, are known to have used caves and rock shelters and – to different extents – to accumulate and damage bones (see e.g. BRAIN 1981; BINFORD 1981; D'ERRICO 1991; HAYNES 1980, 1983; LYMAN 1994; MAREAN 1991; SELVAGGIO 1994; SHIPMAN & ROSE 1983; STINER 1998).

Given that the vast majority of the bones from the Große Grotte belong to the cave bear *Ursus spelaeus*, it is important to clarify first how its bones came to be deposited in the cave. The overrepresentation of loose teeth relative to long bones,

skulls and axial skeleton, the strong fragmentation of bear bones, and the co-occur-rence of bear bones and stone tools – all three occurring in the Große Grotte – have been sometimes regarded as an indication of human hunting and/or ritual behaviour (see e.g. H. Bächler 1957: 131 ff.; Ehrenberg 1935: 76 ff.; 1955: 35 ff.; 1959: 17 ff.). Were the bears in the Große Grotte preyed upon by hominids?

In a series of publications, Koby argued (e.g. 1943: 59; 1953: 1 ff.) that the frag-mentation of bear bones in "bear caves" could be traced back to their exposure to different taphonomic factors, such as trampling and gnawing by bears themselves and other carnivores (on this topic see also Zapfe 1954: 1 ff.). Koby coined the term "charriage à sec" for the movement and breakage of the bones prior to their deposi-tion in the sediment.

In a more recent study, it was shown that bears scavenging for meat and/or mar-row are capable of fracturing and fragmenting the compact bones of large ungulates (Haynes 1980: 348) and certainly those of other bears.

The differential survivorship of the different skeletal elements – or parts of ele-ments – exposed to taphonomic factors such as trampling and gnawing depends in large measure on their structural density (Lyman 1994: 234 ff.). Thus teeth and small, compact bones such as metapodials, carpals, tarsals and phalanges tend to survive in relative higher quantities. It is not surprising that these elements are often the most common in many "bear caves", including the Große Grotte (see above), even those with no apparent sign of human occupation, such as Westbury (Andrews & Turn-er 1992: 139 ff.) and the "Pasillo" in Cova Eirós (Grandal-d'Anglade & Vidal Romaní 1997: 723 ff.). However, at least in the Große Grotte a distinction must be made between the skeletal representation of grown-up animals and that of younger age groups, i.e. juveniles and neonates. In the latter, the proportional representation of bones of the stylopodium and zeugopodium is consistently higher than in grown-ups, while the short bones of the hand and foot are rare. A possible explanation for this pattern is that, due to their smaller size, the long bones of younger animals were buried faster in the sediment and therefore not exposed to the constant trampling and gnawing experienced by the larger bones of adults and subadults. The absence of the very small carpals, tarsals and phalanges in younger age groups is probably due to recovery bias. Alternatively, these elements may be eaten whole by carnivores (Turk & Dirjec 1997: 108; see below). The scarcity of deciduous teeth other than canines could be also due to recovery bias.

Almost 20 % of the *Ursus* bones show clear gnawing marks, probably made both by bears – identified by the typical rounding of edges (Haynes 1983: 169) – and by large and small canids – probably wolves and foxes (Tab. 30). Finally, no cut marks were observed on any of the bear bones – or for that matter in any of the bones found at the cave.

Thus the skeletal representation, fragmentation, and mortality pattern (see above) observed in the *Ursus* assemblage from the Große Grotte indicates that the bears – mostly females and their young – used the cave as hibernation den, and perished in the cave in winter. Most individuals probably died of starvation or disease, and a few of old age. In isolated instances, bears – especially young – may have fell victims to predators such as hyenas or wolves. Their remains were scavenged, gnawed, and trampled by conspecifics and other carnivores using the cave.

More difficult is to decide whether the remains of herbivores in the Große Grotte represent the refuse of hominid or of carnivore consumption. Their relative scarcity
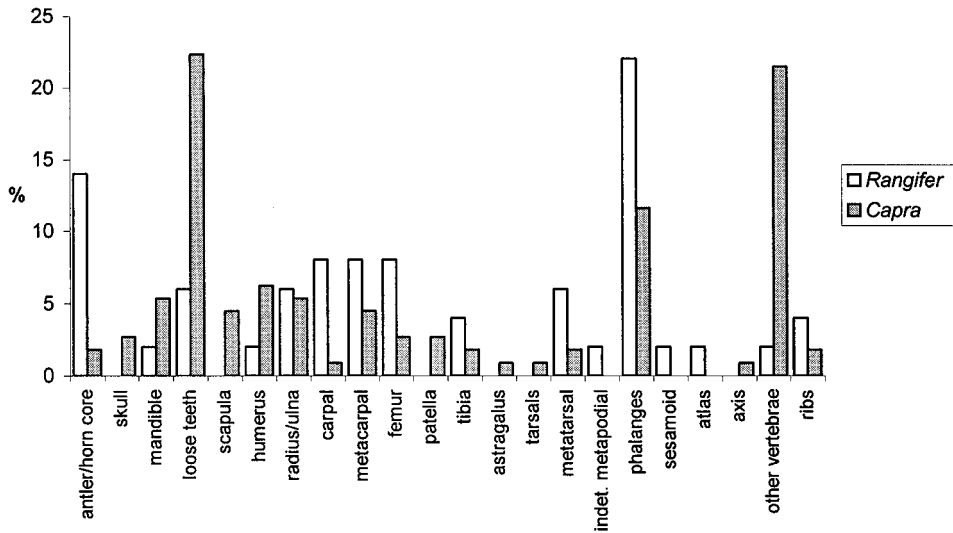
Fig. 13. *Rangifer tarandus* and *Capra ibex*; skeletal distribution.

prevents a reliable analysis of age structure and skeletal representation, which could give some clues about the taphonomic agents involved in their accumulation.

Most of these specimens are very fragmented. In *Capra*, loose teeth and phalanges show the higher frequencies (excluding the vertebrae, most of which belonged to two individuals), while phalanges and antler are the most abundant elements in *Rangifer* (Fig. 13). The presence of relative high frequencies of antlers – both shed and still attached to the skull – is not uncommon in carnivore dens, particularly those of hyaenids (STINER 1991: 112).

More than 30 % of *Capra* and *Rangifer* bones show gnawing marks, as do four out of six fragments of *Equus* (Tab. 30–31). At any given location, the proportion of bones showing gnawing-damage due to feeding by carnivores depends on several factors such as relative vulnerability of the prey and the size of the feeding group

Tab. 30.   Carnivore damage on bones, by species.

Species	gnawed bones (n)	NISP (excluding loose teeth)	gnawed bones (%)
Unidentified	191	2188	8.7
Lepus sp.	7	35	20
Canis lupus	1	8	
Vulpes vulpes & *Alopex*	2	16	
Martes martes	1	1	
Crocuta crocuta spelaea	1	1	
Ursus spelaeus	77	387	19.8
Equus germanicus	4	6	
Cervus elaphus	1	3	
Rangifer tarandus	15	47	31.9
Rupicapra rupicapra	3	5	
Capra ibex	28	89	31.4
Artiodactyla indet.	16	54	29.6

Tab. 31. Carnivore damage and burnt bones, by layer.

layer	gnawed/digested (n)	(%)	burnt (n)	(%)	total fragments in layer
II	77	6.1	75	6.0	1259
III	40	10.8	36	9.7	372
IV	29	20.3	3	2.1	143
V	109	11.0	81	8.2	990
VI	5	10.6	2	4.3	47
VII	46	11.5	34	8.5	401
VIII	19	18.1	3	2.9	105
IX	5	16.1	–	–	31
XI	17	23.3	–	–	73
TOTAL	347	10.1	234	6.8	3421

Tab. 32. Aves, number of specimens by layer
(Identifications by H. Pieper, Kiel, unpublished data).

| Species | | | | | layer | | | | |
	II	III	IV	V	VI	VII	VIII	IX	total
Podicipediformes									
Tachybaptus ruficollis, little grebe	1	–	–	–	–	–	–	–	1
Anseriformes									
Anatidae indet.	–	2	2	5	–	–	–	–	9
Anatinae indet.	–	–	–	–	–	–	–	1	1
Anas platyrhynchos, mallard	7	–	–	1	–	2	3	3	16
Bucephala clangula, goldeneye	–	–	–	–	–	–	–	1	1
Melanitta nigra, common scoter	1	–	–	–	–	–	–	–	–
Falconiformes									
Haliaeetus albicilla, sea eagle	1	–	–	–	–	–	–	–	1
Falco sp.	2	–	1	–	–	–	–	–	3
Falco peregrinus, peregrine	2	–	–	–	–	–	–	–	2
Galliformes									
Tetraonidae (Lagopus vel *Bonasa*)	2	2	1	2	–	–	–	–	7
Tetraonidae, small	–	–	–	1	–	–	–	–	1
Lyurus tetrix, black grouse	2	–	–	–	–	–	–	–	2
?Lyurus tetrix	2	–	–	–	–	–	–	–	2
Strigiformes									
Asio otus, long–eared owl	–	–	–	2	–	–	–	–	2
Bubo bubo, eagle owl	–	1	–	–	–	–	–	–	1
Strix aluco, tawny owl	1*	2	–	–	–	–	–	–	3
Passeriformes									
Corvus sp. (*corone*), carrion crow	1	–	–	–	–	–	–	–	1
Corvus monedula, jackdaw	4	–	–	6	–	–	–	2	12
Pica pica, magpie	–	–	3	–	–	–	–	–	3
Corvidae indet.	–	–	–	–	–	–	–	1	1
Passeriformes indet.	5	–	1	4	–	–	–	–	10
Aves indet.	8	1	6	9	–	1	–	–	24
Total	39	8	14	30	–	3	3	8	105

* *specimen identified by author*

(HAYNES 1983: 171). Under certain conditions, no identifiable gnaw damage may be found; in other circumstances, a large proportion of the assemblage may show gnawing marks (HAYNES 1983: 171). In any case, 30 % is certainly a high frequency. Wolves are probably to be held largely responsible for the gnawing damage on bones of these ungulates. *Crocuta* must have played an insignificant role – if any – since phalanges, carpals and tarsals of *Capra* and *Rangifer* are relatively abundant; these elements are rare in hyena-accumulated assemblages because they are usually swallowed and digestively destroyed (LYMAN 1994: 215).

As mentioned above, none of the specimens shows butchering marks. About 6 % of all specimens were carbonised (n=234). They are, without exception, small unidentified fragments: the weight of all burnt fragments comprises only 1.6 % of the total weight of the assemblage. In his short report about the excavations at the site, RIEK (1962: 200) mentions a couple of small hearths in "Planum 1" and "Planum 2". There is no information as to which layer these hearths belong; it is likewise unknown, whether the burnt bones were recovered from these structures. Even assuming that these burnt pieces are a product of hominid activities, they must not represent the bones of prey hunted by Middle Palaeolithic people. They may simply represent bones burnt as a source of heat for cooking or warmth. For this purpose, the abundant bones of bears laying on the cave floor were certainly good enough.

In summary: carnivore species present at the site can be regarded as being autochthonous. Bears used the Große Grotte repeatedly as an hibernation den, but also wolves, foxes, lions, and hyenas visited it, at least occasionally. This is reflected in the breakage and gnawing damage found on the bones. Most of the microfaunal assemblage has its origin in owl pellets, and the owls themselves can be regarded as being an autochthonous element as well. That neanderthals used the cave as well is indicated by the presence of stone and bone artifacts, hearths, and – perhaps – by burnt bone fragments. However, from the remains and information available, there is no way of telling whether the remains of herbivores – mostly ibex and reindeer – fell prey to human or/and non-human hunters.

5. Conclusions

The present analysis of the faunal material from the Große Grotte demonstrated the presence of some species not recorded in the investigation by WAGNER (1983), such as wolf (*Canis lupus*), cave lion (*Felis leo spelaea*), and chamoix (*Rupicapra rupicapra*). At the same time, the presence of *Ovis argaloides* (WAGNER 1983: 72, 74) can be discounted on morphological grounds.

Quantitatively, *Ursus spelaeus* is by far the main component of the fauna from the Große Grotte, and its remains represent mostly individuals which died in the cave during hibernation. The cave was also used by other carnivores, as their remains and gnawing marks show. While the presence of artifacts testifies to the use of the cave by neanderthals, their role in the accumulation of the faunal remains was probably very limited: a relatively large proportion of the bones shows gnawing marks, whereas not a single butchering mark was recorded. In any event, this fauna cannot be used to explore the subsistence practices of Middle Palaeolithic hominids.

According to the micro- and macrofaunal remains, at least the upper layers (IV–II) were deposited under a cold spell within the first half of the Wuermian Glacial.

6. References

ADAM, K. D. (1975): Die Mittelpleistozäne Säugetier-Fauna aus dem Heppenloch bei Gutenberg (Württemberg). – Stuttgarter Beitr. Naturk., B, **3**: 247 pp., 29 figs., 52 pls., 39 tabs.; Stuttgart.

ALTUNA, J. & MARRIEZKURRENA, K. (1984): Bases de subsistencia de origen animal en el yacimiento de Ekain. – *In*: ALTUNA, J. & MERINO, J. M. (eds.): El yacimiento prehistórico de la cueva de Ekain (Deba, Guipuzcoa), pp. 211–280, 11 figs., 53 tabs.; San Sebastián (Sociedad de Estudios Vascos).

ANDREWS, P. & TURNER, A. (1992): Life and death of the Westbury bears. – Ann. Zool. Fennici, **28**: 139–149, 6 figs., 5 tabs.; Helsinki.

ARGANT, A. (1991): Carnivores quaternaires de Bourgogne. – Doc. Lab. Géol. Lyon, **115**: 282 pp., 9 pls., 39 figs., 89 tabs.; Lyon.

BACHOFEN-ECHT, A. (1931): Fährten und andere Lebensspuren. – *In*: ABEL, O. & KYRLE, G. (eds.): Die Drachenhöhle bei Mixnitz, pp. 711–718; Wien (Österr. Staatsdruckerei).

BÄCHLER, H. (1957): Die Altersgliederung der Höhlenbärreste im Wildkirchli, Wildenmannlisloch und Drachenloch. – Quartär, **9**: 131–146, 1 pl.; Bonn.

BINFORD, L. R. (1981): Bones: ancient men and modern myths. – New York (Academic Press).

BISHOP, M. J. (1982). The Mammal Fauna of the Early Middle Pleistocene cavern infill site of Westbury-Sub-Mendip, Somerset. – Special Papers in Palaeontology, **28**: 1–108, 6 pls., 50 tabs., 47 figs.; London.

BOESSNECK, J. & VON DEN DRIESCH, A. (1973): Die jungpleistozänen Tierknochenfunde aus der Brillenhöhle. – *In*: RIEK, G.: Das Paläolithikum der Brillenhöhle bei Blaubeuren. – Forsch. u. Ber. Vor- Frühgesch. Baden-Württ., **4/2**: 1–105, 17 pls., 48 tabs.; Stuttgart.

BOESSNECK, J., MÜLLER, H. H. & TEICHERT, M. (1964): Osteologische Unterscheidungsmerkmale zwischen Schaf (*Ovis aries* LINNÉ) und Ziege (*Capra hircus* LINNÉ). – Kühn Archiv, **78**: 1–129, many figs.; Berlin.

BRAIN, C. K. (1981): The hunters or the hunted? An introduction to African cave taphonomy. – Chicago (Chicago University Press).

DAYAN, T., SIMBERLOFF, D., TCHERNOV, E. & YOM-TOV, Y. (1991): Calibrating the paleothermometer: climate, communities and the evolution of size. – Paleobiology, **17**: 189–199, 1 tab.; Chicago.

DELPECH, F. (1983): Les faunes du Paléolithique supérieur dans le sud-ouest de la France. – Cahiers du Quaternaire, **6**; Paris.

D'ERRICO, F. (1991): Comments on "The cultural significance of Grotta Guattari reconsidered". – Current Anthropology, **32**: 127–128; Chicago.

DIETRICH, W. O. (1945): Nashornreste aus dem Quartär Deutsch-Ostafrikas. – Palaeontographica, **96**: 45–90, 1 fig., pls. 13–19; Stuttgart.

DITTRICH, L. (1960): Milchgebißentwicklung und Zahnwechsel beim Braunbären (*Ursus arctos* L.) und anderen Ursiden. – Gegenbaurs morphologisches Jahrbuch, **101**: 1–141, 27 figs., many tables; Leipzig.

DRIESCH, A. VON DEN (1976): A guide to the measurement of animal bones from archaeological sites. – Peabody Museum Bulletin, **1**. 136 pp., 62 figs.; Cambridge/Mass.

DUBOIS, A. & STEHLIN, H.-G. (1933): La grotte de Cotencher, station Moustérienne. – Mém. Soc. paléont. Suisse, **52**: 1–178; Bâle.

EHRENBERG, K. (1931). Über die ontogenetische Entwicklung des Höhlenbären. – *In*: ABEL, O. & KYRLE, G. (eds.): Die Drachenhöhle bei Mixnitz. pp. 624–710; Wien (Österr. Staatsdruckerei).

– (1935): Die Pleistozaenen Baeren Belgiens II. Teil: Die Baeren vom „Trou du Sureau" (Montaigle). – Mém. Mus. roy. d'Hist. nat. d. Belg., **71**: 1–97, 6 pls.; Bruxelles.

– (1935): Über Höhlenbären und Bärenhöhlen. – Abh. zool.-bot. Ges. Wien, **95**: 19–41, 1 pl.; Wien.

– (1939): Untersuchungen über *Hyaena spelaea* Goldf. – Paläont. Z., **21**: 107–118; Berlin.

EHRENBERG, K. & KERNERKNECHT, S. (1940): Die Fuchs- oder Teufelslucken bei Eggenburg, part II: Die Höhlenhyäne, 2. Die Wirbelsäule. – Abh. zool.-bot. Ges. Wien, **17**: 131–191, pls. 19–21, 7 tabs.; Wien.

FORSTEN, A. (1993): Size decrease in Late Pleistocene-Holocene caballoid horses (Genus *Equus*), intra- or interspecific evolution? A discussion of the alternatives. – Quaternary International, **19**, 71–75, 2 figs.; London.

FORSTEN, A. & ZIEGLER, R. (1995): The horses (Mammalia, Equidae) from the early Wuermi-an of Villa Seckendorff, Stuttgart-Bad Cannstatt, Germany. – Stuttgarter Beitr. Naturk., B, **224**, 22 pp., 1 pl., 10 figs., 6 tabs.; Stuttgart.

GARGETT, R. (1996): Cave bears and modern human origins: the spatial taphonomy of Pod Hradem cave, Czech Republic; Lanham, New York & London (University Press of America).

GRANDAL-D'ANGLADE, A. & VIDAL ROMANÍ, J.-R. (1997): A population study on the cave bear (*Ursus spelaeus* Ros.-Hein.) from Cova Eirós (Triacastela, Galicia, Spain). – Geobios, **30**: 723–731, 7 figs., 3 tabs.; Lyon.

GROISS, J. TH. (1996): Der Höhlentiger *Panthera tigris spelaea* (GOLDFUSS). – N. Jb. Geol. Paläont., Mh., **7**: 399–414, 12 figs.; Stuttgart.

GROSS, C. (1992): Das Skelett des Höhlenlöwen (*Panthera leo spelaea* Goldfuss, 1810) aus Siegsdorf/Ldkr. Traunstein im Vergleich mit anderen Funden aus Deutschland und den Niederlanden. – Diss. Univ. München. 9 pls., 10 figs., 7 diags., 14 tabs.; München.

HAHN, J. (1993): Erkennen und Bestimmen von Stein- und Knochenartefakten: Einführung in die Artefaktmorphologie. 398 p., 113 figs.; Tübingen (Archaeologica Venatoria).

HAYNES, G. (1980): Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. – Paleobiology **6**: 341–351, 16 figs.; Chicago.

– (1983): A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. – Paleobiology, **9**: 164–172, 10 figs., 2 tabs.; Chicago.

HEMMER, H. (1977): Die Carnivorenreste (mit Ausnahme der Hyänen und Bären) aus den jungpleistozänen Travertinen von Taubach bei Weimar. – Quartärpaläontologie, **2**: 379–387, pls. 43–44, 3 figs., 4 tabs.; Berlin.

JAKUBIEC, Z. (1993): *Ursus arctos* Linnaeus 1758 – Braunbär. – *In*: STUBBE, M. & F. KRAPP (eds.): Handbuch der Säugetiere Europas, Band 5/I: 254–300; Wiesbaden (Aula).

KERNERKNECHT, S. (1940): Die Fuchs- oder Teufelslucken bei Eggenburg, II. Teil: Die Höhlenhyäne, 3. Das Gliedmaßenskelett. – Abh. zool.-bot. Ges. Wien, **17**: 192–301, 5 pls., 11 tabs.; Wien.

KOBY, F. (1949): Le dimorphisme sexuel des canines d'*Ursus arctos* et d'*U. spelaeus*. – Rev. Suisse de Zool., **56**: 675–687, 1 fig., 4 tabs.; Genève.

– (1953): Les paléolithiques ont-ils chassé l'ours des cavernes? – Actes Soc. Jurass. Emul., **57**: 1–48

– (1958): Ostéologie de la Chèvre Fossile des Pyrénées (*Capra pyrenaica* Schinz). – Ecl. geol. Helv., **51**: 475–480; Basel.

– (1959): Contribution au diagnostic osteologique différentiel de *Lepus timidus* LINNÉ et *L. europaeus* PALLAS. – Verh. naturforsch. Ges. Basel, **70**: 19–44; Basel.

KOBY, F. & FRITZ, E. (1950): Les proportions des métacarpiens et des phalanges de la main d'*Ursus spelaeus*. – Eclogae geol. Helv., **43**: 288–289; Basel.

KOENIGSWALD, W. v. (1985): Die Kleinsäuger aus der *Allactaga*-Fauna von der Villa Seckendorff in Stuttgart-Bad Cannnstatt aus dem frühen letzten Glazial. – Stuttgarter Beitr. Naturk., B, **110**: 40 pp., 2 pls., 39 figs.; Stuttgart.

KURTÉN, B. (1958): Life and death of the Pleistocene cave bear. – Acta zoologica Fennica, **95**: 1–59, 8 figs., 17 tabs.; Helsinki.

– (1959): On the bears of the Holsteinian interglacial. – Stockholm Contributions in Geology, **2**: 73–102, 1 pl., 9 figs., 8 tabs.; Stockholm.

– (1976): The cave bear story. 163 pp.; New York (Columbia University Press).

LEHMANN, U. (1954): Die Fauna des „Vogelherds" bei Stetten ob Lontal (Württemberg). – N. Jb. Geol. Paläont., Abh., **99**: 33–146, 4 pls., 7 figs., and many tables; Stuttgart.

LISTER, A. (1989): Rapid dwarfing of red deer on Jersey in the Last Interglacial. – Nature, **342**: 539–542; 3 figs., 1 tab.; London.

LYMAN, R. L. (1984): Vertebrate taphonomy. 524 pp., many figs. and tabs.; Cambridge (Cambridge University Press).

McFARLANE, D. A., MACPHEE, R. D. & FORD, D. C. (1998): Body size variability and a Sangamonian extinction model for *Amblyrhiza*, a West Indian megafaunal rodent. – Quaternary Research, **50**: 80–89, 5 figs., 2 tabs.; Washington.

MAREAN, C. W. (1991): Measuring the post-depositional destruction of bone in archaeological assemblages. – Journal of archaeological Science, **18**: 677–694.

MUSIL, R. (1965): Die Bärenhöhle Pod Hradem. Die Entwicklung der Höhlenbären im letzten Glazial. – Anthropos, **18**: 7–92, 12 pls., 38 figs., 21 tabs.; Brno.

RIEK, G. (1962): Fundbericht „Große Grotte". – Fundberichte aus Schwaben, **16**: 199–200; Stuttgart.

RODE, K. (1935): Untersuchungen über das Gebiß der Bären. – Monogr. Geol. u. Paläont., Ser. II, **7**, 162 pp., 8 pls., 24 figs., 59 tabs.; Leipzig.

SCHÜTT, G. (1969): Die Jungpleistozäne Fauna der Höhlen bei Rübeland im Harz. – Quartär, **20**: 79–125, pls. 3–5; Bonn.

SELVAGGIO, M. M. (1994): Carnivore tooth-marks and stone tool butchery marks on scavenged bones: archaeological implications. – Journal of human Evolution, **27**: 215–228, 4 figs., 4 tabs.; London.

SHIPMAN, P. & ROSE, J. (1983): Early hominid hunting, butchering, and carcass-processing behaviors: approaches to the fossil record. – Journal of anthropological Archaeology, **2**: 57–98; New York.

STINER, M. (1991): The faunal remains from Grotta Guattari: A taphonomic perspective. – Current Anthropology, **32**: 103–117, 10 figs., 7 tabs.; Chicago.

–   (1998): Mortality analysis of Pleistocene bears and its palaeoanthropological relevance. – Journal of human Evolution, **34**: 303–326, 7 figs., 3 tabs.; London.

STORCH, G. (1973): Jungpleistozäne Kleinsäugerfunde (Mammalia: Insectivora, Chiroptera, Rodentia) aus der Brillenhöhle. – *In*: RIEK, G.: Das Paläolithikum der Brillenhöhle bei Blaubeuren. – Forsch. u. Ber. Vor- Frühgesch. Baden-Württ., **4/2**: 106–120, 41 figs., many tabs.; Stuttgart.

STUBBE, M. (1993): Gattung *Martes* Pinel, 1792. – *In*: STUBBE, M. & F. KRAPP (eds.): Handbuch der Säugetiere Europas, Band 5/I. 370–373; Wiesbaden (Aula).

TORRES PEREZ-HIDALGO T. (1984): El oso de las cavernas (*Ursus spelaeus* Rosenmüller-Heinroth) de los niveles inferiores de Ekain. – *In*: ALTUNA, J. & J. M. MERINO: El yacimiento prehistorico de la cueva de Ekain (Deba, Guipuzcoa). 297–316, 1 pl. 36 figs., 45 tabs.; San Sebastián.

TORRES PEREZ-HIDALGO, T., COBO RAYAN, R., & SALAZAR RINCON, A. (1991): La población de oso de las cavernas (*Ursus spelaeus parvilatipedis* n. ssp.) de Troskaeta'ko-Kobea (Ataun-Guipuzkoa) (Campañas de excavación de 1987 y 1988). – Munibe, **43**: 3–85, 12 pls., 85 figs., 56 tabs.; San Sebastián.

TURK, I. & DIRJEC, J. (1997): Taxonomic and taphonomic survey of mammal macrofauna. – *In*: TURK, I. (ed.): Mousterian bone flute and other finds from Divje Babe I cave site in Slovenia. Pp. 99–113, 8 figs., 1 tab.; Lubljana.

UERPMANN, H.-P. (1972): Tierknochenfunde und Wirtschaftsarchäologie. Eine kritische Studie der Methoden der Osteo-Archäologie. – Arch. Informationen, **1**: 9–27; Bonn.

VALKENBURG, B. van (1990): Skeletal and dental predictors of body mass in carnivores. – *In*: DAMUTH, J. & MACFADDEN B. J. (eds.): Body size in mammalian paleobiology: estimation and biological implications. pp. 181–205, 7 figs., 4 tabs.; Cambridge (Cambridge University Press).

VARTANYAN, S. L., GARUTT, V. E. & SHER, A. V. (1993): Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. – Nature, **362**: 337–340, 3 figs., 1 tab.; London.

WAGNER, E. (1983): Das Mittelpaläolithikum der Großen Grotte bei Blaubeuren (Alb-Donau-Kreis). – Forsch. u. Ber. Vor-Frühgesch. Baden-Württ., **16**, 85 pp., 78 pls., 16 figs.; Stuttgart.

WEBB, E. (1988): Interpreting the faunal debris found in central European sites occupied by Neandertals. – *In*: WEBB, E. (ed.): Recent developments in environmental analysis in Old and New World Archaeology, pp. 79–104; Oxford (B.A.R.).

WEINSTOCK, J. (1998): Late Pleistocene reindeer populations in Central and Western Europe: an osteometrical study of *Rangifer tarandus*. – Diss. Univ. Tübingen.

–   (1999): Geographical variation of reindeer (*Rangifer tarandus*) in Europe during the Late Glacial (ca. 13–10 ky BP). – *In*: BENECKE, N. (ed.): The Holocene history of the European vertebrate fauna: modern aspects of research. pp. 283–294; Rahden/Westfalen (M Leidorf).

WOLSAN, M. (1993): *Mustela putorius* Linnaeus, 1758 – Waldiltis, Europäischer Iltis, Iltis. – *In*: STUBBE, M. & F. KRAPP (eds.): Handbuch der Säugetiere Europas, Band 5/I. 699–769; Wiesbaden (Aula).

ZAPFE, H. (1954): Beiträge zur Erklärung der Entstehung von Knochenlagerstätten in Karstspalten und Höhlen . – Geologie, Beih. **12**: 1–60, 1 pl., 12 figs.; Berlin.

ZIEGLER, R. (1994): Löwen aus dem Eiszeitalter Süddeutschlands. – *In*: Der Löwenmensch, Tier und Mensch in der Kunst der Eiszeit. pp. 46–51, 5 figs.; Sigmaringen (Thorbecke Verlag).

    –   (1996): Die Großsäuger aus der Frühwürm-zeitlichen Fauna von der Villa Seckendorff in Stuttgart-Bad-Cannstatt. – Stuttgarter Beitr. Naturk., B, **237**: 67 pp., 7 pls., 2 figs., 28 tabs.; Stuttgart.

Address of the author:

Dr. Jaco Weinstock, Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart.

Plate 1

Ursus spelaeus ROSENMÜLLER & HEINROTH

Fig. 1.   Deciduous canine with resorbed root; SMNS 34110.122. – Ca. x1.5.
Fig. 2.   Deciduous canine with resorbed root; SMNS 34110.121. – Ca. x1.5.
Fig. 3.   Deciduous canine with resorbed root; SMNS 34110.128. – Ca. x1.5.
Fig. 4.   Mandible with canines and P_4-M_3, pre-P_4 alveolus only in dext.; occlusal; SMNS 34070.58, 34110.141; left and right originally described as coming from different layers. – Ca. x0.25.
Fig. 5.   Humerus dext. juvenile; SMNS 34127.5; – Ca. x0.75.
Fig. 6.   Humerus dext. infantile/juvenile; SMNS 34110.164; – Ca. x0.75.
Fig. 7.   Humerus dext. newborn; SMNS 34123.7; – Ca. x0.75.
Fig. 8.   Humerus dext. newborn; SMNS 34123.11; – Ca. x0.75.
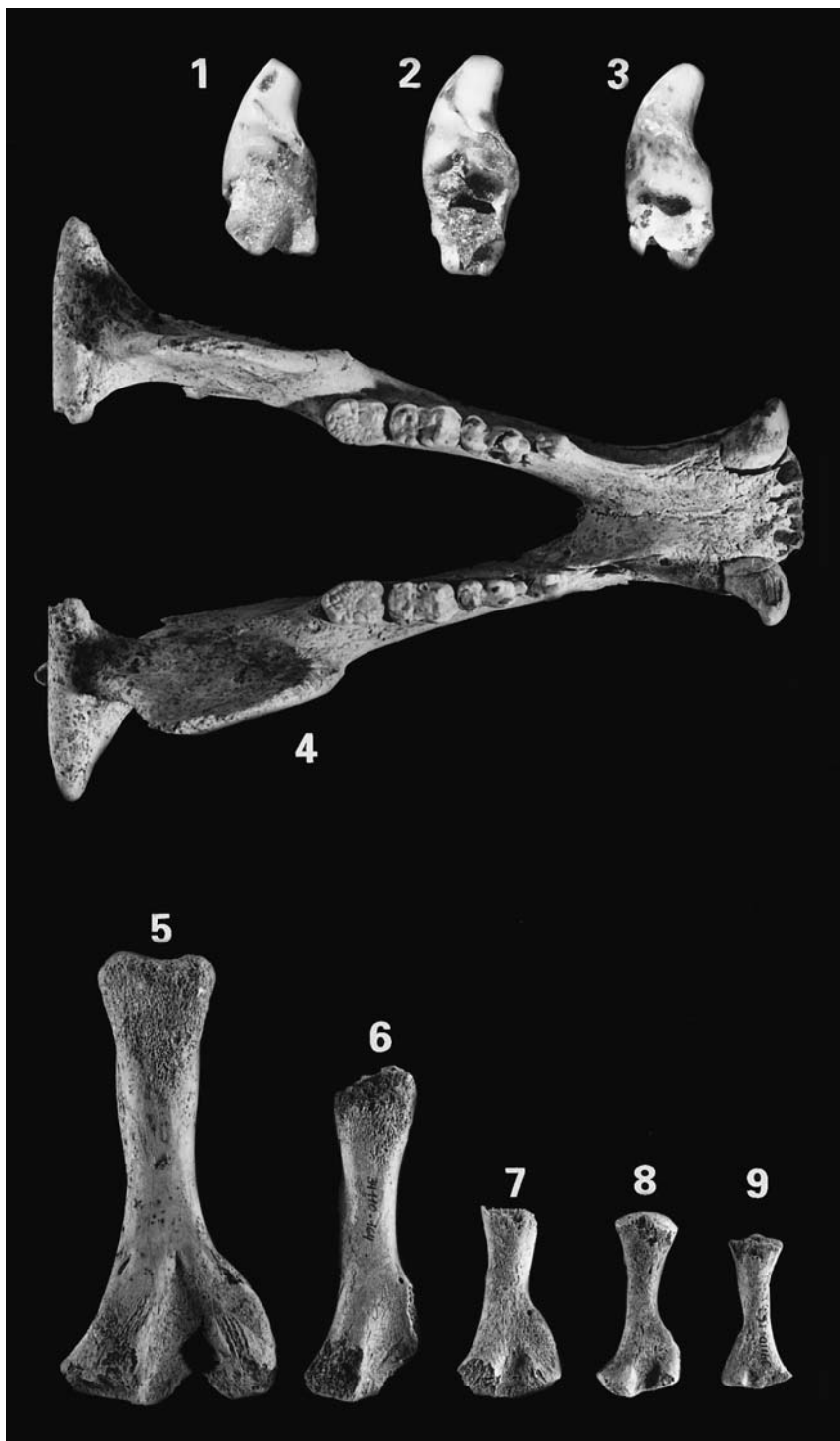Fig. 9.   Humerus dext. newborn; SMNS 34110.167; – Ca. x0.75.

Plate 2

Ursus spelaeus Rosenmüller & Heinroth

Fig. 1.   Calcaneus dext.; dorsal; SMNS 34131.9.
Fig. 2.   Astragalus dext.; dorsal; SMNS 34131.10.
Fig. 3.   Os tarsale quartum dext.; dorsal; SMNS 34131.6.
Fig. 4.   Os tarsi centrale dext.; dorsal; SMNS 34131.5.
Fig. 5.   Os tarsale tertium dext; dorsal; SMNS 34131.7.
Fig. 6.   Os tarsale secundum dext; dorsal; SMNS 34131.23.
Fig. 7.   Os tarsale primum dext; dorsal; SMNS 34131.8.
Fig. 8.   Metatarsus V proximal end and diaphysis dext.; dorsal; SMNS 34131.4.
Fig. 9.   Metatarsus IV proximal end and diaphysis dext.; dorsal; SMNS 34131.3.
Fig. 10. Metatarsus III dext.; dorsal; SMNS 34131.2.
Fig. 11. Metatarsus II proximal end and diaphysis dext.; dorsal; SMNS 34131.1.
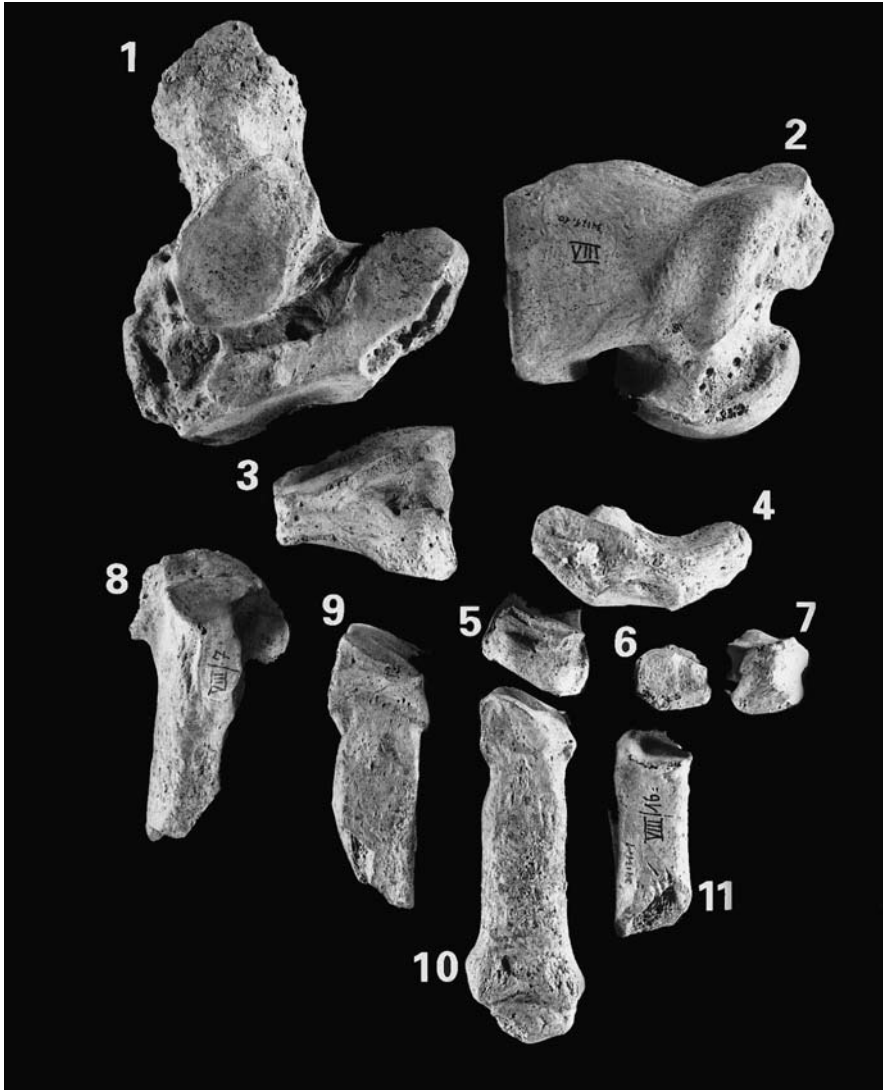
All figures ca. x0.75.
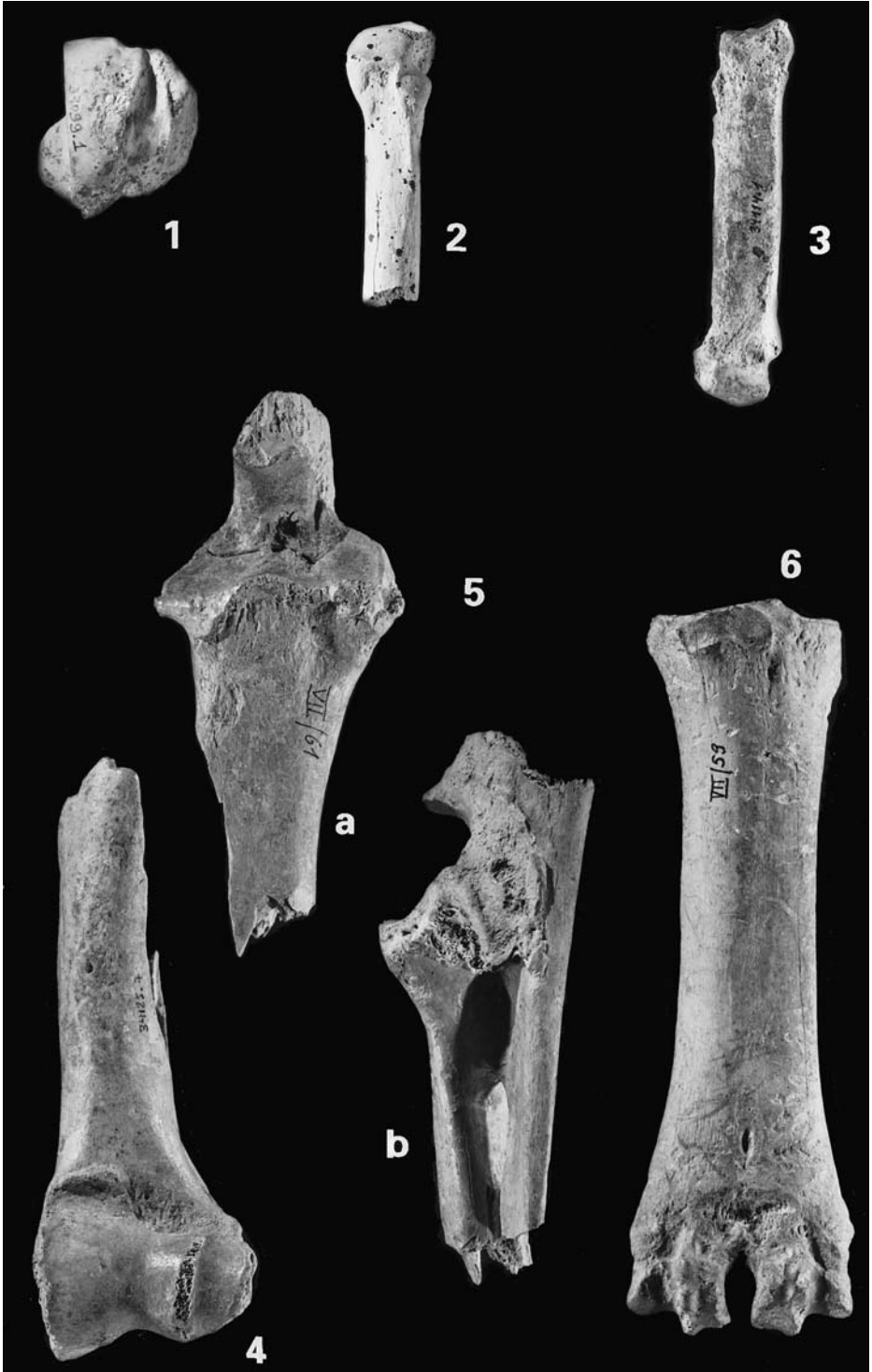
Plate 3

Panthera leo spelaea (GOLDFUSS)

Fig. 1.   Metacarpus V proximal end dext.; cranial; SMNS 34099.1. – Ca. x1.0.
Fig. 2.   Metatarsus IV proximal end and diaphysis sin.; dorsal; SMNS 34. – Ca. x0.5.

Crocuta crocuta spelaea (GOLDFUSS)

Fig. 3.   Metatarsus II sin.; SMNS 34114.1. – Ca. x0.75.

Capra ibex LINNAEUS

Fig. 4.   Humerus distal end and diaphysis sin.; SMNS 34125.7. – Ca. x0.75.
Fig. 5.   Radius/Ulna proximal end and diaphysis sin.; a. dorsal, b. lateral; SMNS 34125.8. – Ca. x0.75.
Fig. 6.   Metacarpus sin.; SMNS 34125.6. – Ca. x0.75.