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THE EARLY PLEISTOCENE (EPIVILLAFRANCHIAN) FAUNAL SITE OF UNTERMASSFELD (THURINGIA, CENTRAL GERMANY) SYNTHESIS OF NEW RESULTS

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Summary

The Pleistocene fauna of Untermassfeld (Southern Thuringia, Central Germany) comprises some 99 taxa, among them 43 mammalian species. The faunal remains were accumulated by repeated high flood events on the lee-side of a clastic fan of interfingering fluviatile sediments. Approximately 50% of larger mammal individuals (total MNI=310) indicated from the site fell victim to floods. The survival pattern of members of the recovered species was primarily determined by their respective specific behavior and motor abilities. Most animals died between October and the end of March/early April.

A Pleistocene landscape consisting of a more or less damp river valley with thicket-like bank vegetation, low growing to higher mixed forests, limestone slopes with dry meadows and poor shrub to tree vegetation, as well as park-like to open landscapes out of the valley is deduced. The fossil assemblage mainly consists of moderate and thermophile elements, which illustrate a prevailing warm and humid climate balanced by atlanto-mediterranean influence. The summers with more than 60 days of air temperature above 25˚ C were warmer than recorded in the area today. Mainly during autumn and winter, extensive rainfalls led to repeated flood events. The mild winters were characterized by minimum temperatures of only a few degrees below 0˚ C.

Combined lithostratigraphic, paleomagnetic and paleozoologic data make it more likely that the deposition of the fossiliferous sands of Untermassfeld can be assigned to the onset of the Jaramillo event (late Early Pleistocene), rather than to the Matuyama/Brunhes boundary.

Introduction

In 1978, the fossil site of Untermassfeld was discovered on the right slope of the River Werra, 2 km south of the town of Meiningen in Southern Thuringia (Central Germany). Until 1997, an area of about 600m^2 had been excavated annually in four to five month field seasons (R-D. Kahlke, 1997a, in press a). Some 9500 determinable remains of larger mammals, as well as approximately 3000 finds of smaller vertebrates have been recovered. The bio-diversity, quality and quantity of the fossil material, as well as the rarity of such complete vertebrate assemblages of Early Pleistocene age in Eurasia, and especially in Central Europe, required a multidisciplinary approach to the site and its fossil contents. It soon became obvious that the Untermassfeld fossil assemblage illustrates an important step in the transition from Latest Villafranchian to Early Middle Pleistocene faunas in Europe.

Geology and Paleomagnetism

Near Untermassfeld, the eastern slope of the Werra Valley cuts through Lower and Middle Triassic sediments. In the subsoil of the excavated area, at 69m relative height above the present day river floodplain (359m above sea level), the Pleistocene sequence (fig. 1) starts with a 7-8m thick bed of coarse gravels, the Younger "*Zersatzgrobschotter*", which, according to the terrace sequence of the Werra Valley (Ellenberg and R-D. Kahlke, 1997:31f; Ellenberg *et al*., 1997:38) were deposited during the Eburonian (Early Pleistocene). The "*Zersatzgrobschotter*" is covered by up to 21m of floodplain deposits (*Auesediment*).

In a normal stratigraphic sequence, fine and medium grained sands, called the Lower Fluviatile Sands (*Untere Fluviatile Sande*) follow. According to their lithologic characteristics these sands, which have produced well preserved bone material in recent years, represent high flood deposits of the Early Pleistocene Werra River. The Upper Fluviatile Sands (*Obere Fluviatile Sande*) form an up to 4m thick bed preserved as the infill of a channel which had cut through the Lower Fluviatile Sands. An up to 3m thick basal part forms the main fossiliferous horizon of the site (fig. 1, right).

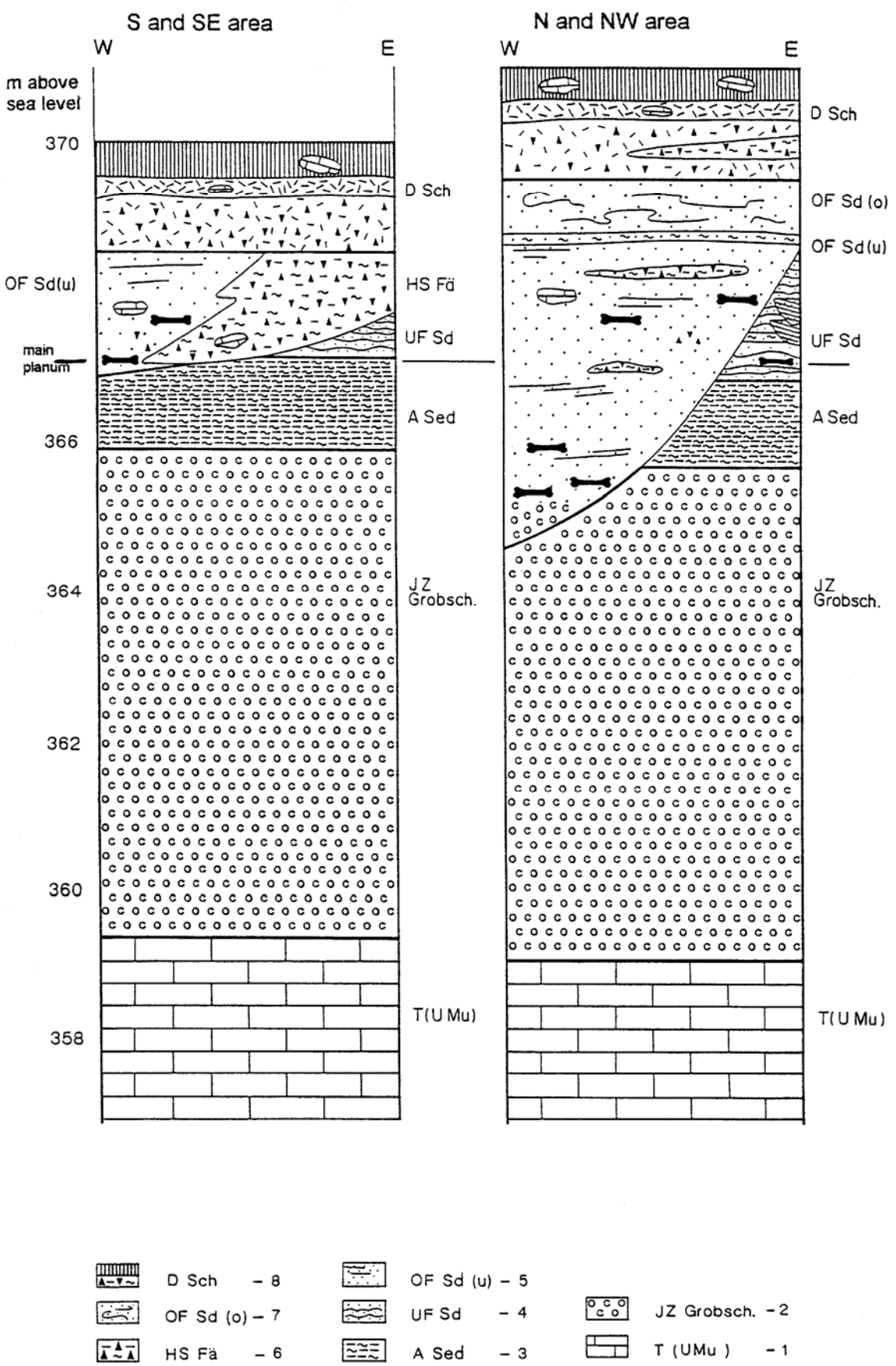

Figure 1. Untermassfeld, diagrammatic sections of the excavated area (neotectonic movements eliminated). 1. T (U Mu): Triassic (Lower Muschelkalk limestones); 2. JZ Grobsch.: Younger Coarse Gravels; 3. A Sed: flood plain deposits; 4. UF Sd: Lower Fluviatile Sands; 5. OF Sd (u): Upper Fluviatile Sands (lower part); 6. HS Fä: coarse elastic mudflow fan; 7. OF Sd (o): Upper Fluviatile Sands (upper part); 8. D Sch: cover sediments (final drawing: N. Fiebig).

In the southern to south-eastern area of the excavated site, i.e. upstream, the fossiliferous lower part of the Upper Fluviatile Sand interfingers with an up to 1m thick coarse clastic mudflow fan (*Hangschuttfächer*) (fig. 1, left). Within the excavated area it may be observed that the fluviatile and accumulative processes had been significantly influenced by this situation (fig. 5; see also below). Lee-side (north) of the clastic fan, skeletal remains of several hundred vertebrate individuals (see below) have accumulated. A predominantly silty-clayish complex of cover sediments (*Deckschichten*) some 1-2m thick overlay the fluviatile sequence.

According to Wiegank (1997), the Younger Zersatzgrobschotter, as well as the basal and middle part of the Lower Fluviatile Sands, are primarily magnetically reversed. However, the uppermost part of the Lower Fluviatile Sands, along with the find level, shows normal polarization.

Fauna

To date (1st November 1998), the faunal spectrum from Untermassfeld comprises some 99 taxa (species/forms) from the following classes: Gastropoda (36), Osteichtyes (3), Amphibia (7), Reptilia (3), Mammalia (43) (preliminary faunal list in R-D. Kahlke, 1997c:387–390; emended in R-D. Kahlke, in press d).

Amongst the moderately abundant gastropod remains from Untermassfeld (Krolopp, 1997) terrestrial forms dominate, with 95.1% of the total number of individuals. The scarce fish remains (Esocidae, Cyprinidae) (Rutte, 1997) represent only a minor part of the assumed ichthyofauna. Evidence of amphibians is comprised of caudates (*Triturus* cf. *cristatus, Triturus* cf. *vulgaris*) and anurans (*Bufo* cf. *bufo*), *Bufo* cf. *viridis, Hyla* cf. *arborea, Rana* cf. *arvalis, Rana* cf. *dalmatina*) (Böhme, 1997). Isolated finds of reptiles belong to squamates (*Chalcides* sp., *Eublepharis* sp.) as well as to a pond tortoise (Emydini, gen. et sp. indet. - Maul, 1997). The avian fauna consists of waterfowl (*Cygnus* sp. (cf. *olor*), *Anser* sp. (aff. *subanser*), birds of prey (*Haliaëtus* sp. (aff. *brevipes*)), gallinaceous birds (*Francolinus (Lambrechtia) capeki*) and perching birds (*Turdus* sp. (aff. *philomelos*), *Corvus* sp. (aff. *janossyi*), *Garrulus* aff. *glandarius*) (Jánossy, 1997).

Special attention was paid to the mammal remains of the site. More than 1000 finds belong to a large and long legged, but not heavily built form of true bison, established as a new species *Bison menneri* by Sher (1997) (fig. 2c). The many cervid remains include at least four species in differing proportions (H-D. Kahlke, 1997, in press a). One antler beam as well as a few fragments of dentition and postcranial elements illustrate the occurrence of a form of roe deer (fig. 2b), more primitive than *Capreolus suessenbornensis.* Another rare faunal element is a large sized, delicately constructed moose (*Alces carnutorum*) (fig. 2a) which links the Villafranchian *A. gallicus* of Europe and Middle Asia with the holarctically dispersed *A. latifrons* of the early Middle Pleistocene (H-D. Kahlke, 1995). More abundant at Untermassfeld are remains of a moderately small cervid preliminarily named *Cervus* s. 1. *nestii vallonnetensis* by H-D. Kahlke (1997) (fig. 2e, f). These forms derived from a Villafranchian stock of Mediterranean origin (genus *Pseudodama* in the terminology of Azzaroli, 1992). Recently, Pfeiffer (in press) includes fallow deer-like cervids of Early to early Middle Pleistocene age without any antler palmation in the genus *Dama* (subgenus *Pseudodama*). A trend of relative shortening of the premolar rows in the Late Villafranchian *nestii* - "populations" is continued by the slightly younger small deer from Untermassfeld. The most common cervid from Untermassfeld, recorded by more than 1000 pieces and primarily characterized by its antler morphology, is an advanced member of the genus *Eucladoceros* (fig. 2d). For this long-legged and very large form, the new species *E. giulii* was established (H-D. Kahlke, 1997).

The remains of hippopotamus (*Hippopotamus amphibius antiquus*) (fig. 3a-d) form the most complete assemblage of material from this species known so far in mainland Europe and, for the first time, allowed a description and osteometric analysis of almost all skeletal parts of the population (R-D. Kahlke, 1997b). Bone configurations within the facial part of the skull as well as the complete reduction of the incisor dentition to tetraprotodonty place the fossil population of Untermassfeld into the *amphibius* branch of the African-European *Hippopotamus* stock. Advanced morphological features of a newly found adult skull (R-D. Kahlke, in press b) indicate a more evolved condition in comparison with the Upper Villafranchian lectotype from Figline (Upper Valdarno, Italy).

Further, a few suid remains have been recovered at

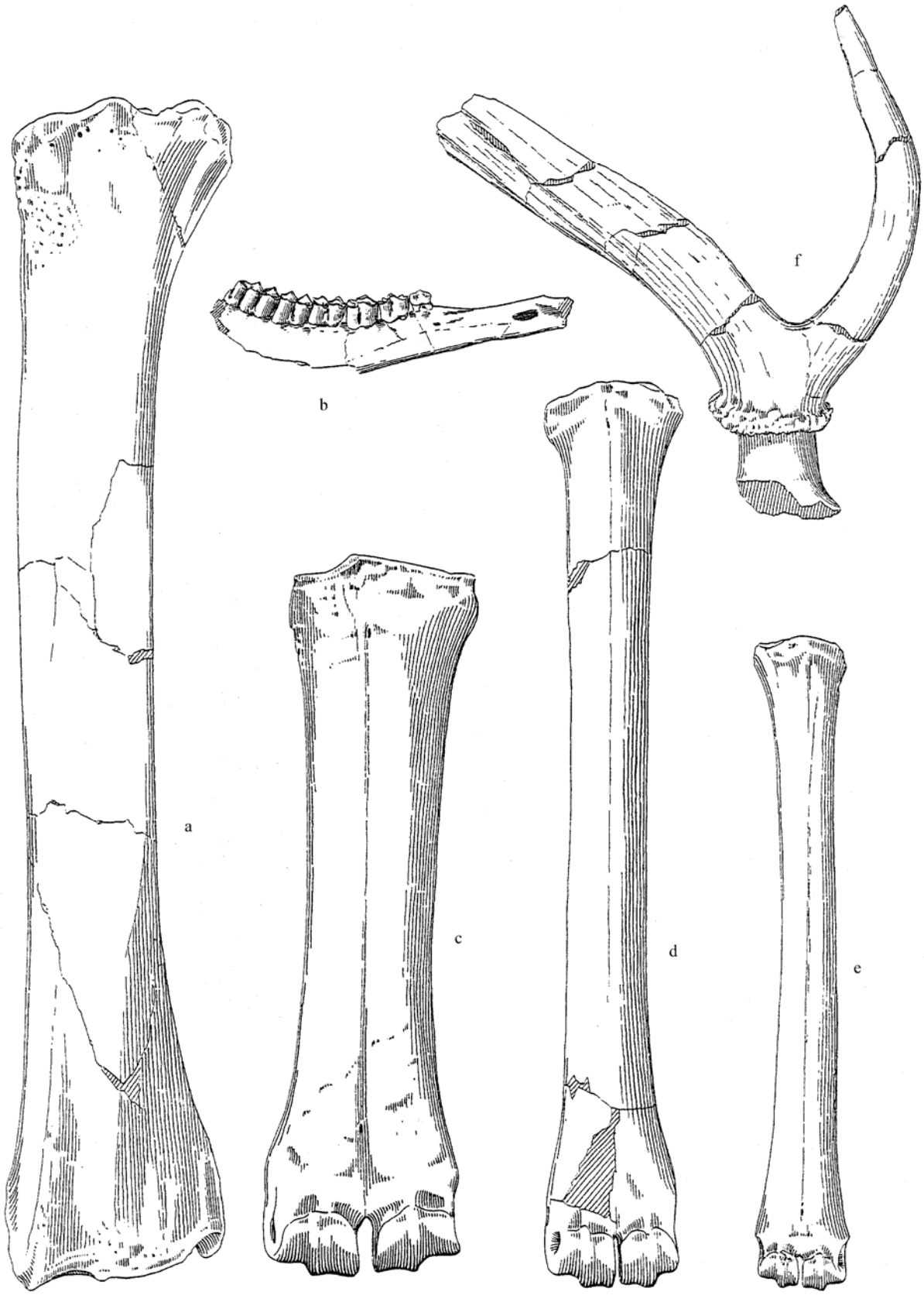

Figure 2. Untermassfeld. a. *Alces carnutorum* (Laugel), radius sin. [IQW 1981/17 632 (Mei. 17 154)]; b. *Capreolus* sp., mandibula dex. with P_2–M_3 [IQW 1982/18 586 (Mei. 18 106) + IQW 1983/18 900 (Mei. 18 420)]; c. *Bison menneri* Sher, metacarpal III + IV dex. (holotype) [IQW 1982/17 948 (Mei. 17 468)]; d. *Eucladoceros giulii* Kahlke, metacarpal III + IV dex. [IQW 1980/17 138 (Mei. 16 659)]; e. *Cervus s.1. nestii vallonnetensis* de Lumley, Kahlke, Moigne et Moullé, metacarpal III + IV sin. [IQW 1982/18 266 (Mei. 17 786)]; f - *Cervus s.1. nestii vallonnetensis* de Lumley, Kahlke, Moigne et Moullé, left antler frontlet [IQW 1983/19 031 (Mei. 18 551)]. ca. 1:2 nat. size (drawing: H. Wöllner).

Untermassfeld (Guérin and Faure, 1997). The material belongs to a large-sized wild boar, *Sus scrofa priscus.* Some 700 finds of *Stephanorhinus etruscus* (fig. 3f-h) characterize the Untermassfeld rhino population as morphometrically intermediate between the Upper Villafranchian type material of the Upper Valdarno and forms from stratigraphically younger sites such as Voigtstedt and Süssenborn (H-D. Kahlke, in press b). Some 180 horse remains can be referred to one medium-sized stenonid form only (Musil, in press a) (fig. 3e), whereas most Villafranchian to earliest Middle Pleistocene localities of Eurasia indicate two sympatric species (Forstén, 1988:24-25).

Compared to other groups of animal, elephant finds remain scanty. Based on the morphology of the only complete tooth (D^4) from the site, as well as the aserial configuration of a reconstructed carpus, Dubrovo (in press) refers the material to large-sized individuals of *Mammuthus trogontherii trogontherii.*

Remarkable and comparatively rich Carnivore material has been found as part of the Untermassfeld fossil assemblage. At present, remains of eleven medium to large-sized species have been recorded. Smaller forms are, however, more or less lacking so far. Felids are represented by the relatively abundant *Panthera onca gombaszoegensis,* by a large individual of *Acinonyx pardinensis pleistocaenicus* (fig. 4e, f), and by *Puma pardoides* (Syn. *Viretailurus schaubi*), *Lynx issiodorensis* ssp. ex aff. *spelaeus, Megantereon cultridens adroveri* and *Homotherium crenatidens* (Hemmer, this volume, in press).

Among the around 100 finds of *Pachycrocuta brevirostris* (fig. 4g-h) of different individual age stages, cubs predominate (table 1) (Turner, in press). Crushing and gnawing marks on the bones of nearly all recorded larger vertebrate species (see for instance R-D. Kahlke, 1997b; table 2, 3), as well as the presence of some 160 coprolites (Keiler, in press), document the activities of this powerful hyena in the area of the site. *Meles* is attested to by only two fragments (Wolsan, in press).

Bear remains from Untermassfeld are as common as are those of hyenas. The “arctoid” character of the dentition, as well as the slender metapodials place the fossil population in the ancestry of brown bears (Musil, in press, additional finds in R-D. Kahlke and Kierdorf, 1997).

The faunal communities of several Early to early Middle Pleistocene sites of the Palearctic contain two sympatric canids of different body size. At Untermassfeld, the large and rarer *Canis (Xenocyon) lycaonoides* (fig. 4c-d) is associated with the more common *Canis mosbachensis* (fig. 4a-b). More than 300 pieces of the latter have been studied. Dental features and limb bone proportions indicate an early, i.e., late Early Pleistocene member of the *mosbachensis*-line (Sotnikova, in press).

Rodents form the major part of the micromammals. Maul (1990, in press a) identified 12 taxa. A few finds attest to squirrels (*Sciurus* cf. *whitei*), characterized by significantly smaller molars compared to those of the recent *S. vulgaris*. Most abundant are the remains of ground squirrel (*Spermophilus (Urocitellus)* ex gr. *primigenius*/*polonicus*). The rarity of beaver finds can be explained by the model of the site assemblage (see below). A few teeth and mandibles show the occurrence of *Castor fiber* and of *Trogontherium cuvieri*. Gnawing marks on several bones of larger mammals led Maul (in press b) to conclude the occurrence of *Hystrix* sp. in the Untermassfeld fauna. Corresponding dental or skeletal remains of porcupine have not been found so far.

Some dormouse teeth fit the size range of *Glis sackdillingensis*. According to the tooth dimensions, the remains of large hamster have to be assigned to *Cricetus* cf. *runtonensis*. A few finds indicate bank vole (*Clethrionomys* cf. *hintonianus*). More numerous are the voles *Pliomys episcopalis*, *Mimomys savini* and *Mimomys* (*Cseria*) *pusillus*. *Microtus thenii* is very common in the Untermassfeld find layers. Some fragments of dentition also indicate *Apodemus* cf. *sylvaticus.* Minor differences to the recent form are visible in the formation of accessory cusps in the M_1.

Leporids belong to the rarest finds of the Untermassfeld fauna. So far, one upper premolar as well as two fragments of humeri have been identified. The latter could fit with *Lepus* as well as with *Hypolagus*. The premolar is that of a hare (cf. *Lepus* sp.).

The Untermassfeld assemblage contains six species of insectivores (Maul, 1990, in press a).

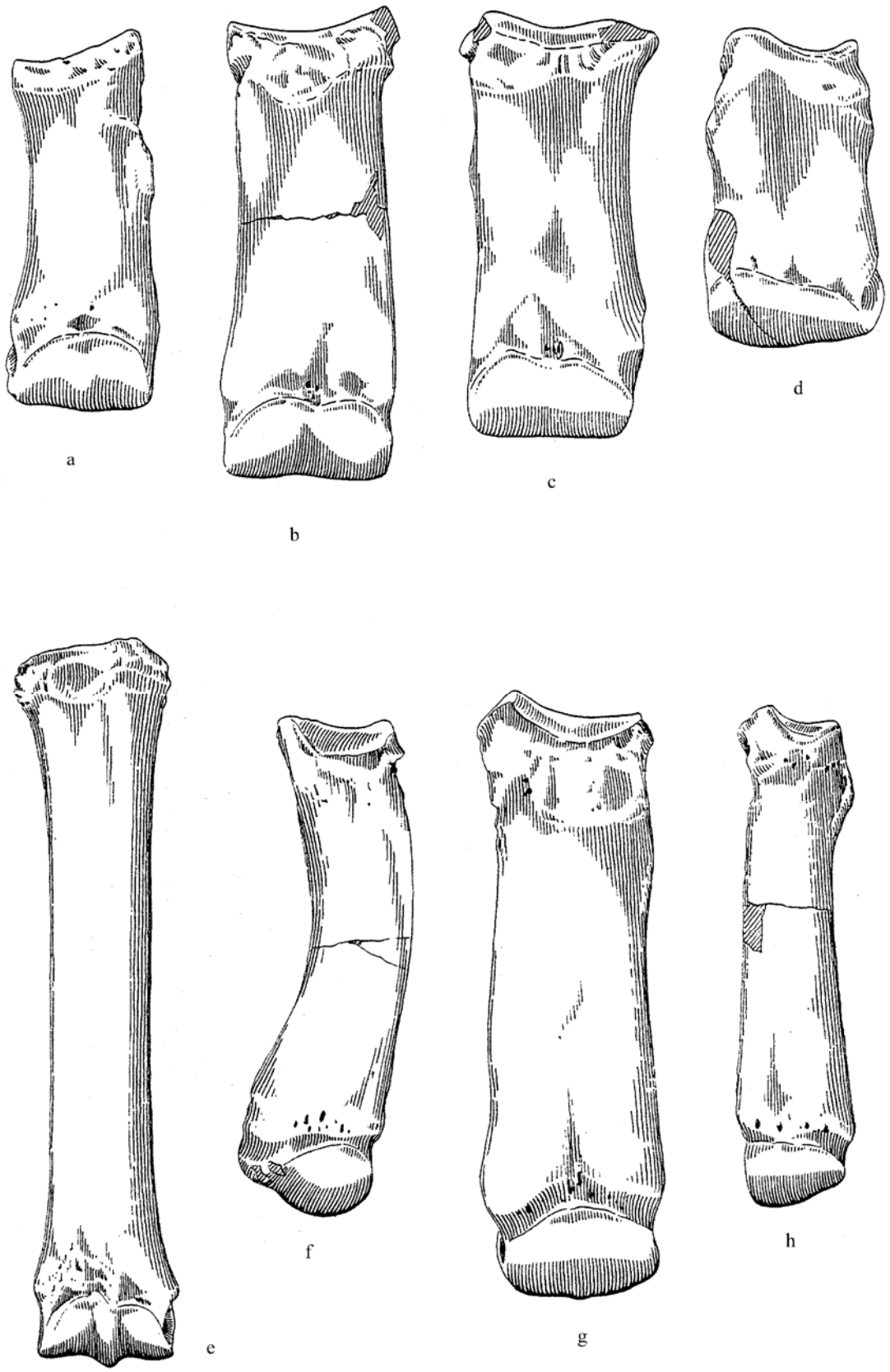

Figure 3. Untermassfeld. a–d. *Hippopotamus amphibius antiquus* Desmarest, a. metacarpal II sin. [IQW 1982/18 216 (Mei. 17 736)], b. metacarpal III sin. [IQW 1982/18 215 (Mei. 17 735)], c. metacarpal IV sin. [IQW 1982/18 217 (Mei. 17 737)], d. metacarpal V sin. [IQW 1982/18 214 (Mei. 17 734)]; e. *Equus* sp., metacarpal III sin. [IQW 1980/15 438 (Mei. 14 950)]; f–h. *Stephanorhinus etruscus* (Falconer), f. metacarpal IV dex. [IQW 1983/19 030 (Mei. 18 550)], g. metacarpal III dex. [IQW 1980/16 503 (Mei. 16 024)], h. metacarpal II dex. [IQW 1980/15 882 (Mei. 15 393)]. ca. 1:2 nat. size (drawing: H. Wöllner).

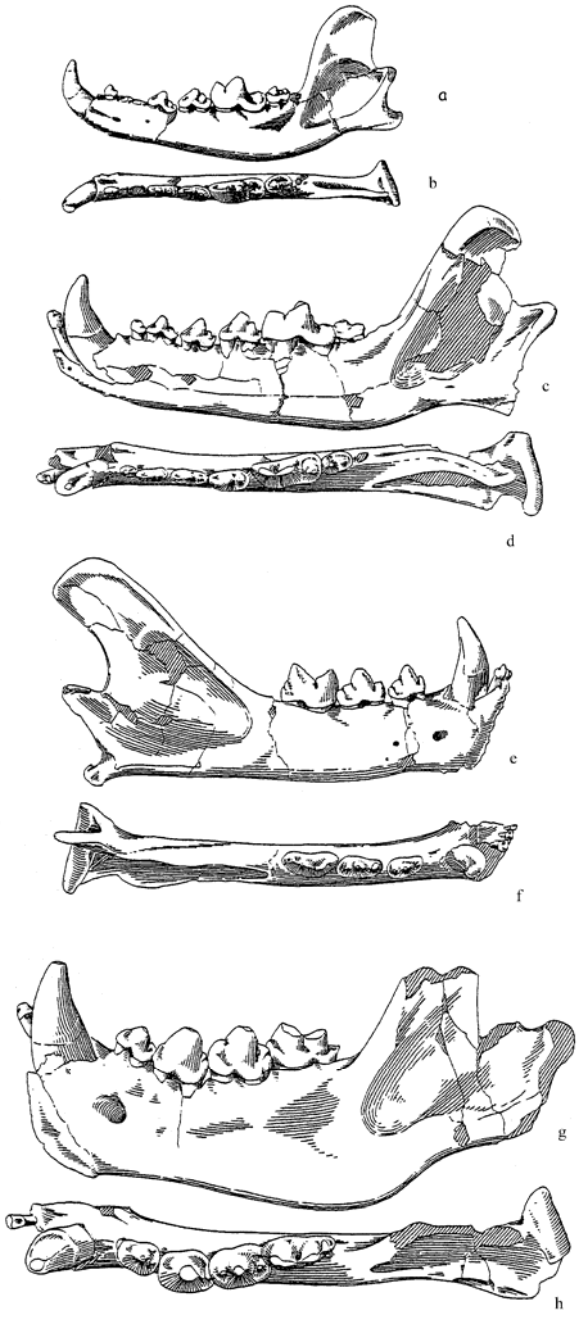

Figure 4. Untermassfeld. A-b. *Canis mosbachensis*, mandibula sin. with C, P_1, P_3 - M_2 [IQW 1980/15 309 (Mei. 14 821)]; c-d. *Canis (Xenocyon) lycaonoides*, mandibula sin. with I_3 - M_2 [IQW 1985/20 535 (Mei. 20 074)]; e-f. *Acinonyx pardinensis pleistocaenicus*, mandibula dex. with I_1 - M_1 [IQW 1980/15 503 (Mei. 15 015)]; g-h. *Pachycrocuta brevirostris*, mandibula sin. with I_3 - M_1 [IQW 1980/15 918 (Mei. 15 429)]. ca. 1:3 nat. size. (drawing: H. Wöllner).

Several finds can be referred to hedgehog (*Erinaceus* cf. *europaeus*) and to moles of different body sizes (*Talpa* cf. *europaea*, *T.* cf. *minor*). Further, some shrews (*Sorex runtonensis*, *Sorex (Drepanosorex)* ex gr. *margaritodon - savini* (transitional form), *Beremendia* cf. *fissidens*) are indicated.

Some isolated teeth of *Macaca sylvanus* can be referred to a male as well as to a female individual (Zapfe, in press). A subspecific determination is not so far possible.

Within the rich Untermassfeld collection, hominid remains have not been identified, nor have any traces of intentional activities of humans come to light. The overall taphonomic situation of the site shows no anthropogenic influence at all (see below).

Taphonomy

Due to a more or less constant carbonate impregnation of the fluviatile sand body (originating from Middle Triassic limestones slopeside of the locality), the bulk of recovered bones show good to excellent preservation. Most of the larger mammal remains, as well as the microvertebrate finds, show no traces of rolling or abrasion. Notable exceptions are a very few abraded pieces, which have undergone a longer phase of transportation as defleshed skeletal elements. The absence of stronger traces of weathering indicates that the bones had been covered by sediment quite rapidly.

The finds are heterogenously distributed within the channel infill (Upper Fluviatile Sands, see above, fig. 1) forming the main fossiliferous part of the site. Directly lee-side of the coarse clastic mudflow fan, smaller, lighter and in many cases badly fragmented skeletal elements dominate. The concentration of finds as well as their size/weight and degree of articulation increases toward the central part of the bone accumulation (detailed maps of the excavated area will be given in R-D. Kahlke, in press d). The northern and northeastern parts of the investigated area are characterized by a slight decrease in the average weight of the finds, as well as in the number of anatomically connected units. A modified situation was observed in the deepest levels of the channel infill. Here, unusually high concentrations (up to 100 finds per m^2) of mostly disarticulated and in part fragmented skeletal elements of medium size occurred.

The area excavated within the Lower Fluviatile Sands so far is smaller than the investigated area within the channel infill. It produced well preserved bones in lesser concentration (detailed plans and maps in R-D. Kahlke, in press d). A remarkable exception observed in the Lower Sands

was a bone concentration of some 800 pieces covering an area of less than $8m^2$, which is interpreted as a drift line formed in shallow water near to the river bank.

More detailed information to reconstruct the processes of disarticulation and accumulation of corpses and skeletal material within the area of the site can be taken from an analysis of the fine scale distribution pattern of the finds. The arrangement of bones is subdivided into anatomically connected units, isolated finds, polyspecific bone concentrations - i.e., accumulations of single bones from different species and individuals - and larger bone aggregations. Complete skeletons are lacking.

Anatomically connected finds are those elements recovered in normal anatomical association to each other or, notably, disarticulated elements whose close spatial juxtaposition indicates the original affiliation of the individual bones. These units consist mainly of complete or partially preserved extremities which have always been disconnected from the rest of the carcass at the shoulder or the pelvic girdle. An exemplary series of hippopotamus extremities, testifying to disarticulation sequences largely unmodified by carnivore activities, is given by R-D. Kahlke (1997c, Abb. 1-6). The more or less pronounced activities probably of all carnivore species (see above) represented in the thanatocoenosis of Untermassfeld could have modified the decomposition of the carcasses and skeletal units prior to and after deposition at the site.

The disarticulation of individual bones or the complete disintegration of skeletons produced a large number of isolated finds. There are only few indications of a patterned orientation of the bones deposited at the site. Remains of smaller vertebrates were found isolated in nearly all cases.

As a result of fluviatile processes within the area of the site, isolated finds became deposited as polyspecific bone concentrations. Large or bulky bones ("obstruction bones") probably acted as mechanical barriers on which other drifting skeletal elements became entangled in the shallow and gently flowing streams. In the deepest part of the channel infill a bone aggregation covering $11m^2$ has been recovered. Such an accumulation can be interpreted as a series of overlapping polyspecific bone concentrations.

Corresponding left and right counterparts of dental or skeletal elements have been identified from nearly all recorded larger mammal species. As well as the excellent preservation of the majority of bones, the relatively high number of 160 anatomically connected units, which were either found *in situ* or reconstructed (R-D. Kahlke, 1997c, in press d, e), indicates the influx of the skeletal material into the site as more or less intact cadavers. Analysis of sufficiently large bone samples (NISP=3399) of six species of different body weight (*Hippopotamus amphibius antiquus, Stephanorhinus etruscus, Bison menneri, Eucladoceros giulii, Equus sp., Cervus* s.1. *nestii vallonnetensis*) shows that robustly built animal species are represented by an evidently higher number of individually connected finds (R-D. Kahlke, 1997c). Smaller animal forms, with a more delicately built anatomy, more rapidly fell victim to biotic and abiotic processes of decomposition.

Complete axial skeletons are lacking for all cases studied. Even intact vertebrae and complete ribs are underrepresented, although fragments of both have commonly been found. Crania, too, are only recovered intact in exceptional cases. Bulky parts of skeletons such as shed antlers or antler frontlets, cranial fragments of adult bison with horncores, elephant tusks and intact hippopotamus mandibles with fully erupted canines, were also found in low numbers or were absent.

Based on the characteristics of dentitions and bones found at Untermassfeld up to 1995, a minimum number of 310 individuals (MNI) can be reckoned for the larger mammals so far (table 1).

The individual age structure shows for several of the more abundant species a high proportion of juvenile to subadult animals (*Bison menneri*, *Eucladoceros giulii*, *Hippopotamus amphibius antiquus*, *Sus scrofa priscus*, *Stephanorhinus etruscus*, *Equus* sp., *Mammuthus trogontherii trogontherii*, *Panthera onca gombaszoegensis*, *Pachycrocuta brevirostris*).

Synthesis of site assemblage[1]

From the geological data on the fossiliferous parts of Lower and Upper Fluviatile Sands the following processes are to be concluded: the accumulation of vertebrate remains in both of the sand bodies occurred in identical positions lee-site of a clastic mudflow fan interfingering with fluviatile sediments. Lithological data from the different layers of the Lower Fluviatile Sands establish repeated high flood events. Several of these more

[1] A more detailed discussion of the assemblage model of the site will be given in R.-D. Kahlke (in press c).

or less similar flood situations deposited animal remains. Just after the accumulation of the Lower Fluviatile Sands, a new flood event with unusually high erosive power cut a channel up to 4m deep into the sands and refilled it immediately (fig. 5). A high influx of necromass took place, mainly during the very beginning of channel filling.

The recent geomorphology of the middle and upper reach of the Werra River and minor tributaries, as well as the configuration of upstream-formed river terraces, has allowed the reconstruction of the potential flood area (R-D. Kahlke, in press d). Altogether, the finds concentrated in the site originated from approximately 94 km^2 of flood plain. The high floods eroded the larger areas upstream of the site. Any available necromass, including plant remains, isolated bones and cadaver fragments was washed away. The catastrophic impact of the high flood events on the animal life of the river valley was increased by a significant narrowing of the valley (the so-called "Nadelöhr" - eye of the needle) from >1.5 km to <1.0 km some 12 km upstream of the place of final deposition. During flood situations, the resulting bottleneck caused a rapid raising of water levels upstream of the narrowing. Around the narrowest pass of the valley, the rapidly swollen river water combined with an increase in the velocity of currents and turbulence, which would have proven fatal even for the good swimmers among the mammals, such as the cervids and perhaps even the adult hippos.

In keeping with the different biotope preferences and lifestyles of the recorded species, their causes of death could have been various. However, from the activities of the diverse guild of carnivores (see above), including many active hunters (Hemmer, this volume, in press), the permanent occurrence of cadavers in successive stages of decomposition within the flood plain of the Werra River has to be concluded. Further loss, for instance among cervid calves, probably happened during periods of high humidity. Other animals died of disease, exhaustion, or weakness due to old age.

The relatively high quantity of matching left and right skeletal elements, as well as the specific and individual composition of the thanatocoenosis indicate a large portion of fresh flood victims among the recovered animals. Taking into account the percentage of carnivore prey estimated by Hemmer (in press) and the much lower number of individuals dying from "minor" causes, approximately 50% of the whole quantity of larger mammal individuals from the site fell victim to flood events. Crucially important for determining the numbers, ages and sex of individual species preserved are the population densities of different species within their Lower Pleistocene biotope, the specific patterns of behavior and motor abilities - especially swimming and climbing capabilities - and the typical resting spots of these animals, as well as absolute weight and transportability of the carcasses.

First of all in flooded areas island complexes of different sizes form according to the geomorphological situation. Such islands are used by endangered animals to avoid the rising water. With further flooding, these refugia have to be given up. According to the numbers of individuals as well as the length of time of isolation, some of these animals would begin to suffer from food limitation.

The obviously high number of freshly dead victims within the Untermassfeld assemblage allows us to discuss the individual age structure of the more common species of larger mammals (see table 1). The pattern of vulnerability is in some ways similar between a carnivore-accumulated and catastrophic flood event assemblage. For the *Bison menneri* remains, Sher (1997:104) showed an age and sex ratio close to that of a natural population. It seems bison groups with herd-like structure met their death here. The analysis of *Eucladoceros giulii* mandibular tooth wear has permitted a detailed reconstruction of the age classes of this species in the fossil sample (H-D. Kahlke, 1997:243). Very young and old individuals predominate. Prime-aged adults are much rarer. However, analysis of the mandibles of *Cervus* s.1. *nestii vallonnetensis* indicate an age-class distribution clearly different to that of *Eucladoceros* (H-D. Kahlke, 1997:204). Remains of this "small cervid" include only a few calves, while the bulk of the material must be referred to prime-age adults. The lower physical capability of the fallow deer-sized, smaller cervid led to an endangering of all age stages during the flood, while the stronger prime-aged individuals of *Eucladoceros* were able to escape the water in higher numbers.

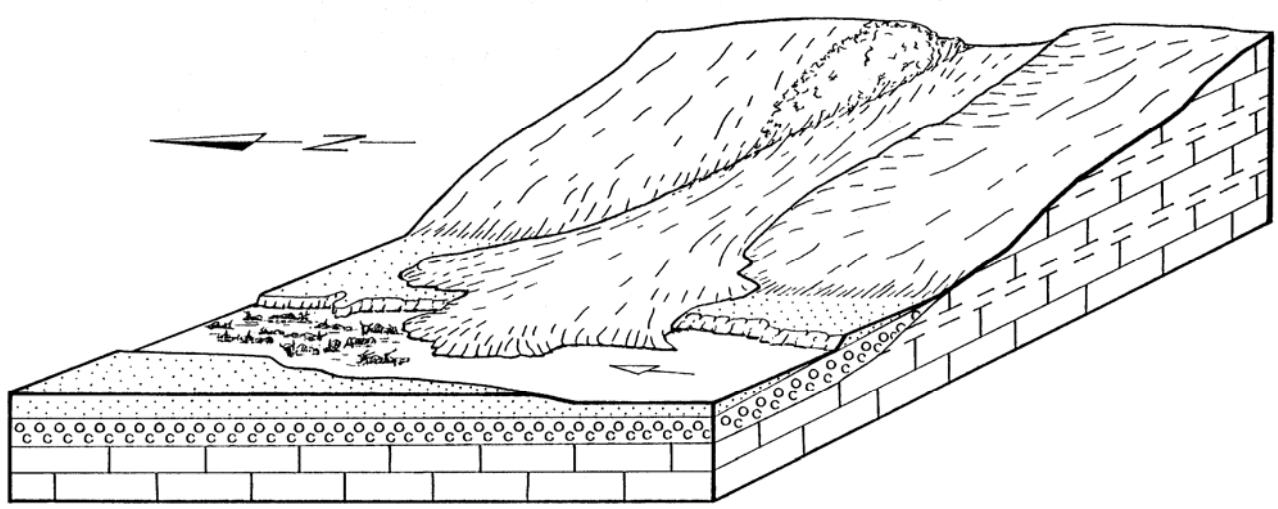

Fig. 5 Untermassfeld, reconstruction of the site during accumulation of the Upper Fluviatile Sands (channel refilling) (final drawing: N. Fiebig).

The proportion of calves with milk dentition among *Hippopotamus amphibius antiquus* is slightly higher than that observed in recent populations. Today the main cause of death among juvenile African hippos is separation from their mothers by flowing water. *Stephanorhinus etruscus* was not a powerful swimmer. Its abilities should be estimated as between those of the African black rhino (*Diceros bicornis*) and the Asian species. Generally, juvenile as well as adult individuals of the Untermassfeld population were endangered by rising waters levels. This is also true for the Untermassfeld horses (*Equus* sp.).

Elephants are good swimmers. Their trunk used as a snorkel, and the pneumatic construction of the upper skull region supports their ability to survive in water (Sondaar, 1986). At the site of Untermassfeld, remains of only six individuals have been found, half of them juvenile to sub-adult animals. Probably some of these elephants failed to reach a safe bank because of their poor climbing ability.

For the felid fauna, rich in species and poor in number of individuals, the question remains of whether the individual animals fell victim to the rising flood, or were lured by other flood victims and met their death while preying. Amongst the rather common finds of *Pachycrocuta brevirostris*, cubs predominate. Because of this, the occurrence of hyena dens containing highly vulnerable juveniles within the flooded area can be assumed. In contrast to hyenas, the material of the "small wolf' *Canis mosbachensis* mostly represents adults of both sexes. This case does not reflect a natural age distribution - obviously the packs' dens and the "rendez-vous" of the juveniles were distributed outside the flooded area. The brown bear (*Ursus* sp.) is attested to only by fully adult individuals, with the exception of one younger animal. These bears may have been accustomed to fishing in shallow river waters. Nevertheless, the huge flooded plains overextended their physical power. In addition, it is possible that some of the recorded individuals were taken by surprise by the rising river during hibernation.

Within the Untermassfeld thanatocoenosis, smaller sized species of body weight less than 10 kg are lacking. Juveniles of larger species, which extend this weight class only to a lesser degree are also under-represented. Whether as prey, or during fluviatile transportation, cadavers of this size are destroyed more completely and much faster than large-sized carcasses (see above). Furthermore, animal bodies of smaller dimensions can be filtered out more easily from the running water by bushes or tree branches than can larger and heavier cadavers.

Remains of microvertebrates were collected from the site in rather large quantities (160 tons of screen washed sediments). Maul (1990:88) calculates 23 small mammal remains per ton for the main collecting period (1983–1989). The dental and skeletal fragments originate from reworked bird pellets as well as from the droppings of mammalian hunters. The number and specific representation of the finds, as well as the osteological spectra result from various ecologic and taphonomic selection processes (Maul, in press a).

The more or less complete cadavers washed from upstream areas of the flooded valley underwent successive destructive processes during transportation and after deposition at the fossil site. The sequence of disintegration and redeposition of skeletal material at the site includes the following steps: partial skeleton (anatomically connected unit) - individual skeletal element (isolated find) - and local accumulation of bones (polyspecific bone concentration) (see above).

The disintegration of the skeletal material was supported and modified by the activities of scavengers. An individual rhino skeleton reconstructed from isolated and mostly gnawed bones (H-D. Kahlke, in press b) illustrates the destructive activities of carnivores at the site. Most of the crushing and gnaw marks observed on the bones originate from *Pachycrocuta brevirostris* - fewer pieces have been chewed by other species. Obviously, the cadaver fragments were easily available to scavengers in the area of the site. This supports the conclusion of bone deposition in mainly shallow waters after the climax of the floods.

It seems the accumulation surfaces of the site may have dried out from time to time. Signs marking the occasional drying of at least parts of the fluviatile sands include the excellent state of preservation of the recovered coprolites, with undamaged surfaces, as well as the occurrence of grouped, fossil droppings representing remains of latrines (Keiler, in press). Gnaw marks by rodents (primarily by *Hystrix* sp.) observed on bone surfaces also indicate a periodic lack of water cover at the site (Maul, in press b). The good state of preservation of such marks and the concentration of the finds within very few of the excavated squares (m^2) make transportation of rodent gnawed-specimens from upstream flood-plain areas into the site not a very likely scenario. In contrast, one isolated find showing traces of herbivorous osteophagy was certainly redeposited (R-D. Kahlke, in press c).

Data on the seasonality of the bone accumulations at Untermassfeld are first of all available from antler finds (H-D. Kahlke, in press a). The majority are not shed. Therefore most of the animals met their death between October and the end of March/early April. To obtain more detailed information on seasonal processes, root cementum of a series of isolated cervid teeth has been analyzed (H. Kierdorf, Köln). Unfortunately, diagenetic recrystallization within the samples prevents further results.

During sedimentation of the upper part of the Upper Fluviatile Sands (see above) the clastic mudflow fan lost its accumulating effect within the running water. The deposition of vertebrate remains in the area of the site came to an end.

The Untermassfeld fossil assemblage in its stratigraphic context documents the accumulation and modification of a paleontological site which formed in a geologically short period, i.e., over a biostratigraphically insignificant length of time.

Paleoecology[2]

By using all geological, paleontological and taphonomical data available for the site of Untermassfeld, a rather detailed ecological picture can be painted. During times of normal water levels, the flat and mostly broad Lower Pleistocene Werra Valley was traversed by a dynamic river. Its bed and banks were formed by colored gravels, reddish sands and darker, fine-grained floodplain deposits. On parts of the river bottom, rich plant cover was developed. At more protected positions of the river, clear and open waters with a gentle current existed. Besides the main stream and its more or less active side channels and tributaries, in wetter parts of the flood plain there were stagnating waters and regions filled with sediment. A rapid swelling of the river caused by particular meteorologic and hydrologic combinations could lead to powerful flowing water and, at a bottleneck-like narrowing of the valley, to a dangerously turbulent stream. Large areas of the valley were regularly (probably seasonally) flooded.

As a result of the high floods within the Early Pleistocene Werra Valley, temporary ponds and pools persisted due to the unstable relief of the valley bottom. Depending on their depth and the intensity of insolation, these water bodies attained different temperatures. Damp floodplain meadows included swamp areas. In moist places, for instance on the riverbanks, thicket-like lightwoods grew in larger quantities. In areas badly endangered by flooding, the remaining forest was low-growing and affected by the duration and sequence of water cover. In dryer, more stable parts of the valley, higher and clearer mixed forest was dispersed with

[2] A detailed compilation and discussion of the ecological parameters of the faunal elements from Untermassfeld will be given in R.-D. Kahlke (in press d).

little undergrowth. On soft soils, rich herbaceous vegetation developed.

The limestone slopes near the site included biotopes with poor tree to shrub vegetation, as well as open areas. Dry slope meadows and debris fields expanded mainly on the right slope of the valley (locality side). Downslope, rocky-clayish fans formed. The sandstone subsoil of areas outside the river valley was covered by sandy to loamy sediments. Loamy-clayish soils rich in stone debris developed in limestone areas, and tended to dry up quickly. Depending on soil quality and the availability of water, park-like landscapes, and, over larger areas, biotopes poor in trees expanded outside the Werra valley.

The composition of the Untermassfeld faunal spectrum and the resulting sketch of the landscape indicate undoubtedly warm climatic conditions. The fossil assemblage mainly consists of moderate to thermophile elements linked to differing biotopes in varying manners and degrees. Animals of cool to cold environmental conditions are completely lacking.

Summer temperatures higher than recorded today in southern Thuringia are signaled by a find of pond tortoise. The embryos of Emydini can be incubated only with more than 60 summer days of air temperatures above 25˚C (Maul, 1997:92-93). Winter temperatures can be estimated from the frequent occurrence of *Hippopotamus amphibius antiquus.* Because the survival of hippos is impossible when ice covers their water habitats, mild winters with minimum temperatures of a few degrees below 0˚ C have to be concluded. Regular and permanent snow cover during the winter seems unlikely, at least in the close vicinity of the site. For the valley bottom as well as the slopes and the park-like plains outside the river valley, several local climates are concluded, according to differing degrees of moisture and insolation. There was enough precipitation to allow standing water and damp floodplains within the valley around the year. Mainly during the autumn and winter, extensive rainfalls led to repeated floods. Because of drainage, the adjacent area was generally dryer than the river valley itself, but had more or less similar air temperatures. The limestone slopes were not capable of storing much water. Especially in southern exposed positions, the dryness of the summers was combined with a higher than average warming of soil and air.

Generally, a warm humid climate without extreme daily and yearly variation of temperature prevailed, balanced by an atlanto-mediterranean influence.

Stratigraphy

Based on lithostratigraphic data on the evolutionary history of the Werra Valley, a timespan of latest Waalian to earliest Cromerian s.1. was established for the deposition of the fossiliferous sands of Untermassfeld (Ellenberg and R-D. Kahlke, 1997). A combination of available paleomagnetic data (see above) together with the paleontological record, seems to indicate a more precise date for the age of the site. The composition of the faunal community, as well as the evolutionary level of corresponding taxa, make it most likely that the interpretation of the change in polarity from reverse to normal just below the bone bearing part of the fluviatile sands equates to the base of the Jaramillo event rather than to the Matuyama/Brunhes boundary. For the Jaramillo onset, Shackleton (1995:243) gives an absolute date of 1.07 myr B.P. (recent radiometric calibration 1.05±0.11 myr B.P., 1.01 myr B.P.; for references see Shackleton, 1995, tab. 17.2).

The mammalian faunal community of Untermassfeld primarily includes survivors from the Villafranchian, as well as more evolved forms characteristic to the early Middle Pleistocene. Due to the lack of a term commonly used for larger mammal associations of the Late Villafranchian/early Middle Pleistocene transitional zone in Eurasia, the name Epivillafranchian, first introduced by Bourdier (1961:745-249), is available (see also Lumley *et al.*, 1988:420). The Epivillafranchian, with the fossiliferous sands of Untermassfeld as European reference horizon, fits into the MNQ zone 20 of Guérin (1982:596f).

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	Juvenile/ Subadult	Adult	Total	Established by

Bison menneri	10+3[3]	27+6[3]	46	A. V. Sher
Capreolus sp.	0	5	5	H-D. Kahlke
Alces carnutorum	1	3	4	H-D. Kahlke
Cervus s.l. *nestii vallonnetensis*	7	40	47	H-D. Kahlke
Eucladoceros giulii	28	32	60	H-D. Kahlke
Hippopotamus amphibius antiquus	11	9	20	R-D. Kahlke
Sus scrofa priscus	3	3	6	R-D. Kahlke
Stephanorhinus etruscus	13	16	29	H-D. Kahlke
Equus sp.	5	8	13	R-D. Kahlke
Mammuthus trogontherii trogontherii	4	2	6	I. Dubrovo R-D. Kahlke
Panthera onca gombaszoegensis	2	3	5	H. Hemmer
Acinonyx pardinensis pleistocaenicus	0	1	1	H. Hemmer
Puma pardoides	0	1	1	H. Hemmer
Lynx issiodorensis ssp. ex aff. *spelaeus*	0	2	2	H. Hemmer
Megantereon cultridens adroveri	1	1	2	H. Hemmer
Homotherium crenatidens	0	3	3	H. Hemmer
Pachycrocuta brevirostris	17	5	22	A. Turner R-D. Kahlke
Meles sp.	0	1	1	M. Wolsan
Ursus sp.	1	8	9	R-D. Kahlke
Canis (Xenocyon) lycaonoides	0	5	5	R-D. Kahlke
Canis mosbachensis	2	16	18	R-D. Kahlke
Castor fiber	0	2	2	L. Maul
Trogontherium cuvieri	0	1	1	L. Maul
Macaca sylvanus	0	2	2	H. Zapfe
Total MNI	**108**	**202**	**310**	

Table 1 Untermassfeld, minimum number of individuals (MNI) of larger mammals according to dental and skeletal remains, based on the material excavated up to 1995.

[3] Estimated MNI of additional finds recovered from the site after Sher's studies, material not yet prepared completely.