Mietje Germonpré
Royal Belgian Institute for Natural Sciences, Brussels

Mammoth taphonomy of two fluvial sites from the Flemish Valley, Belgium

Germonpré, M., 2003 - Mammoth taphonomy of two fluvial sites from the Flemish Valley, Belgium - in: Reumer, J.W.F., De Vos, J. & Mol, D. (eds.) - ADVANCES IN MAMMOTH RESEARCH (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999) - DEINSEA 9: 171-183 [ISSN 0923-9308] Published 24 May 2003

In Belgium, more specific in the Flemish Valley, large quantities of mammalian remains are found in several localities. The Flemish Valley is a palaeovalley dating from the Middle Pleistocene; it was filled up during the Weichselian. The richest assemblages of the Flemish Valley are Zemst IIB, dating from the very beginning of the Weichselian and Hofstade I, dating from the Middle Weichselian. The fossils accumulated mainly through gradual, long-term processes as indicated by the scattered and dispersed spatial distribution of the bones in the fluvial deposits, the abundance of scavenged and weathered bones and the low numbers of carnivores. The bones are from mammals that died within the confines of the river valleys, due to predation, disease, accident or old age. Remains of large grazing mammals (woolly mammoth, woolly rhinoceros, steppe bison, and horse) dominate the faunal assemblages. Woolly mammoth is the best-represented species. At Zemst IIB, mammoth is represented with 747 numbers of identified specimens (NISP) and 26 minimum number of individuals (MNI) and at Hofstade I with 508 NISP and 30 MNI. The age profiles of woolly mammoth from Zemst IIB and Hofstade I differ from a catastrophic profile and resemble more an attritional profile.

Correspondence: Mietje Germonpré, Department of Palaeontology, Royal Belgian Institute for Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium; e-mail: mietje.germonpre@naturalsciences.be

Key words: Late Pleistocene, mammoths, Belgium, taphonomy, palaeoecology

INTRODUCTION

Mammoth assemblages with a clear taphonomic origin can be used as reference material for the study of presumed humanly induced accumulations of mammoth remains. This study reports on two assemblages discovered in braided river deposits from the Weichselian in Belgium. This material is housed in the collections of the Royal Belgian Institute for Natural Sciences (K.B.I.N.), several other museums, universities and private collectors (Germonpré 1989, 1993a). At the two studied localities (Zemst and Hofstade) woolly mammoth is the dominant species. These sites are located in the Flemish Valley, Belgium (Fig. 1). The Flemish Valley is a palaeovalley dating from the Cromerian. During consecutive stages, it was formed by phases of fluvial and, to a lesser extent, of estuarine erosional activities, which alternated with periods of sediment accumulation. The valley was filled up during the Weichselian (Bogemans 1993; De Moor & Heyse 1976; Paepe 1967; Paepe *et al.* 1981).

SITE DESCRIPTIONS

Bos van Aa, Zemst

Since the beginning of the 1980s fossil bones were collected in large sand exploitations at Bos van Aa, Zemst. A number of them were found in situ in the sediments. Others were gathered at the sand sieve of the exploitations. The concentration of bones, estimated on the remains recovered *in situ*, is generally below 0.1 bone/m^2. Bogemans (1988, 1993) studied in detail the geology of these sandpits.

In the sandpits three fossil bearing deposits were discovered. The lowest deposit, only locally present, has been described as the Grimbergen Member by Bogemans (1988, 1993). Sedimentary structures and palaeobotanical evidence indicate that a meandering river in a tree-rich environment during the Eemian formed the deposit. The bones discovered in this bed are grouped into faunal assemblage Zemst A. Species such as straight-tusked elephant, roe deer, wild boar and beaver indicate a wooded or parkland environment in a temperate climate.

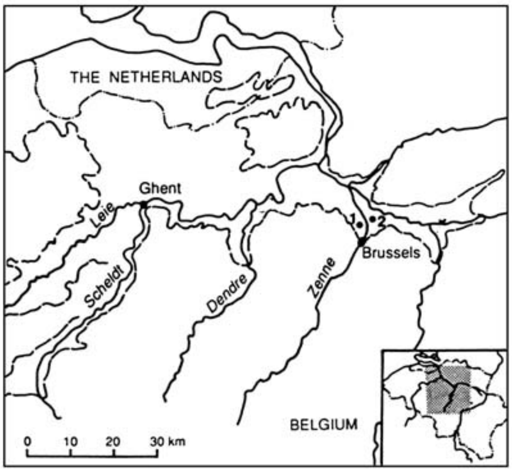


Figure 1 The Flemish Valley with the sites of Zemst (**1**), Hofstade (**2**). Dashed line indicates the boundary of the Flemish Valley.

The second and richest layer yielding mammalian remains erodes the top of the Grimbergen Member or of the Tertiary. The sediments consist of blue grey coarse sands that were deposited by a braided river system with few major channels and several topographic levels. Trees such as *Populus*, *Alnus*, *Prunus*, *Fraxinus*, *Quercus* and *Pinus* protected the higher levels. A lot of trees growing on the higher levels were probably "left overs" from the Eemian. Higher in the sequence they are replaced by *Pinus* (Bogemans pers. com.).The river system had limited mobility with small variations in the hydrological regime. Probably the channels contained water the year round. The environment can be described as cold and humid (Bogemans 1988, 1993). The bones are grouped in assemblage Zemst IIB. They are mainly from woolly mammoth, woolly rhinoceros, steppe bison and horse indicating a grassland environment. The few

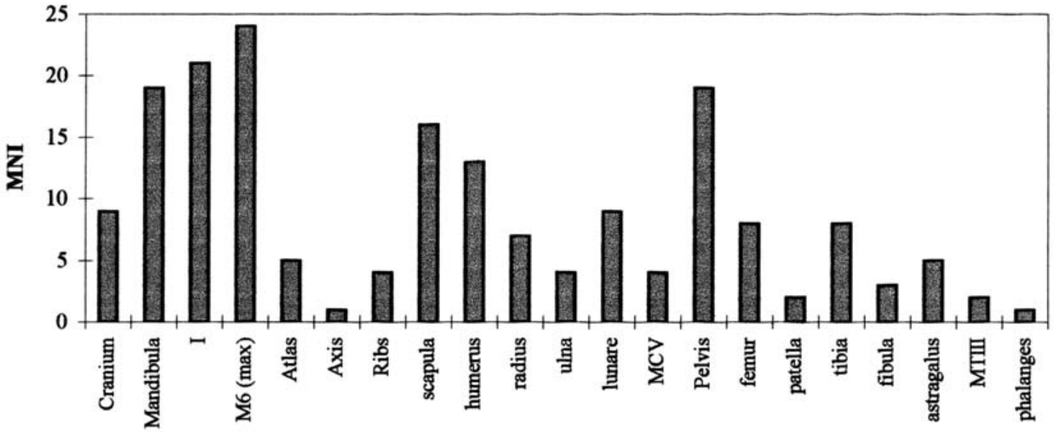


Figure 2 Distribution of the skeletal elements of the mammoths from assemblage Zemst IIB.

bones from aurochs, roe deer, red deer, wild boar and beaver point to the presence of wooded areas and parkland. An ESR date on a mammoth molar gave a mean early U-accumulation age of 126,200 y BP +/- 9,300 indicating that the sediments were deposited at the very beginning of the Weichselian (Germonpré *et al*. 1993).

Rusty coarse gravelly sand, containing mammalian bones, occur on top of the blue grey sand. These sediments were deposited by a braided river system in which a variety of shallow channels and longitudinal bars prevailed. This mobile system was characterised by strong fluctuating hydraulic conditions with sudden and abrupt releases of water as a result of thawing. Permafrost however did not develop. Bad drainage and dry conditions prevailed. Remains of woolly mammoth, woolly rhino, horse and bison dominate the assemblage (Zemst IIIC). Both the blue sands and the rusty sands are grouped in the Bos van Aa Member dating from the Early Weichselian (Bogemans 1988, 1993; Germonpré *et al*. 1993).

Hofstade

The fossil material of Hofstade was collected in the beginning of this century during works to extend the railway connection between Brussels and Mechelen. Rutot (1909a, b) and Mourlon (1909) described some sections of the site. Locally at the base of the Quaternary sediments a peaty deposit occurs. Above the Tertiary substrate or on top of the peaty sediments, a channel lag outcrops covered by stratified sand. According to Bogemans (1993), a river characterized by channels with flat bars and strongly reduced topographic levels deposited these sediments. The braided river was probably active during ephemeral peak discharges with huge sediment transport and consequently reduced erosional activity. These features point to a continental palaeoclimate with extreme temperatures and little precipitation. These sandy braided river deposits are incorporated in the Lembeke Member, dating from the Middle Weichselian (Bogemans *ibid*.; Germonpré *et al.* 1993).

The bone material of Hofstade can on the basis of colour and fossilisation be subdivided into three mammal assemblages. It is supposed that bones of assemblage Hofstade I, which is the richest, were recovered by

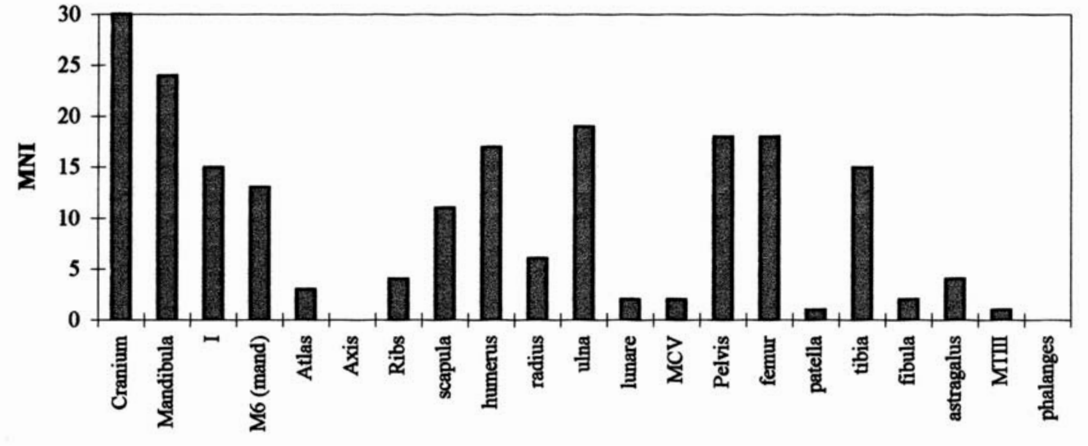


Figure 3 Distribution of the skeletal elements of the mammoths from assemblage Hofstade I.

Rutot (1909 a,b) and Mourlon (1909) in situ at the base of the Lembeke Member. The assemblages Hofstade II and Hofstade III are thought to be younger than assemblage Hofstade I (Germonpré *et al.*1993).

TAPHONOMY

Composition of the fossil assemblages

The mammalian species composition, the number of identified specimens, the minimum number of individuals and non-identifiable fragments for the assemblages are shown in Tables 1 and 2. The collections are biassed toward larger mammals. Bones of large mammals are not only more resistant to weathering and scavenging but also stand fluvial transport better than smaller ones, and are more easily spotted during collection.

The Eemian assemblage Zemst A is characterized by temperate species such as straight-tusked elephant, roe deer, wild boar, red deer and beaver, indicating a wooded environment (Table 1). All Weichselian assemblages are mainly composed of cold-adapted species (Table 2). Large herbivores such as woolly mammoth, woolly rhinoceros, steppe bison and horse dominate, indicating an open steppe-like environment, the so-called Mammoth Steppe (Guthrie 1982, 1990) or steppe-tundra (Giterman *et al.* 1982; Hibbert 1982). According to Putshkov (1997) and Kozhevnikov and Ukraintseva (1999) these terms should be avoided since they are ill-defined and since the mammoths not only lived in treeless landscapes over permafrost but mainly in parklands with stands of boreal trees and a rich herbaceous cover.

The presence of some temperate species in the beginning of the Weichselian agrees with the fact that the Early Glacial was on the whole considerably warmer that the later phases of the Last Glacial (Stuart 1991). Declining climatic and environmental conditions can also be deduced from the shoulder heights of the horses. According to Forsten (1991) European horses underwent a size reduction during the Middle and Late Pleistocene. However, the size decrease was not continuous and size stasis occurred. The mean shoulder height of the horses from Zemst IIB is 149 cm and from Hofstade I 139 cm (Germonpré *et al.* 1993).

Disarticulation of the dead remains

Weathering Disarticulation of carcasses can happen through several processes such as weathering, scavenging, trampling, gravity. The rate of weathering of bones depends on several factors such as temperature and humidity. The relative time span between death and burial of bones can be deduced from the weathering stages. The assemblages from Zemst and Hofstade were checked for the subaerial weathering stages described by Behrensmeyer (1978).They can on basis of the weathering stages be subdivided in three groups (Germonpré 1993a):

Weathering group 1: at least 65% of the bones belong to Behrensmeyer Stage 0: Assemblage Hofstade II

Weathering group 2: the bones are evenly distributed among Behrensmeyer Stages 0 and 1: Assemblages Zemst IIB, Hofstade I

Table 1 Number of identified specimens (NISP) and minimum number of individuals (MNI) of the Eemian assemblage Zemst A (ZA).

	Zemst A	
	NISP	**MNI**
Proboscidea		
Elephas antiquus	5	1
Perissodactyla		
Equus sp.	7	1
Rhinocerotidae	9	1
Artiodactyla		
Sus scrofa	1	1
Cervus elaphus	1	1
Capreolus capreolus	6	1
Bos primigenius/Bison priscus	9	1
Rodentia		
Castor fiber	1	1
Total NISP / MNI	39	8

Table 2 Number of identified specimens (NISP) and minimum number of individuals (MNI) of theWeichselian assemblages Zemst IIB (ZIIB), Zemst IIIC (ZIIIC), Hofstade I (HSI), Hofstade II (HSII), Hofstade III (HSIII).

	Zemst IIB		**Zemst IIIC**		**Hofstade I**		**Hofstade II**		**Hofstade III**	
	NISP	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Lagomorpha										
Lepus timidus / L. capensis	1	1								
Carnivora										
Canis lupus	15	2	1	1						
Alopex/Vulpes	1	1			1	1				
Ursus arctos	7	2	2	1	3	2				
Mustela putorius	1	1								
Meles meles	2	1								
Crocuta crocuta spelaea	2	1			1	1	1	1		
Panthera leo spelaea	9	2	3	1					3	1
Proboscidea										
Mammuthus primigenius	746	26	101	4	508	30	44	3	33	2
Perissodactyla										
Equus sp.	399	22	31	3	93	12	25	4	13	2
Coelodonta antiquitatis	588	16	130	7	443	34	43	7	54	6
Artiodactyla										
Sus scrofa	5	1								
Cervus elaphus	79	8	3	2						
Rangifer tarandus	84	10	15	4	20	9			6	2
Capreolus capreolus	6	2								
Megaloceros giganteus	75	8	7	1	20	8	1	1	1	1
Bison priscus / Bos primigenius	209	11	40	2	52	7	3	1	10	2
Bos primigenius	1	1								
Rodentia										
Castor fiber	2	1								
Dicrostonyx torquatus			1	1						
Total NISP / MNI	2232	117	334	27	1141	104	117	17	120	16
Number unidentified specimens	1164		310		116		1		8	
TOTAL NISP+ NUSP	3396		644		1257		118		128	

Weathering group 3: bones belonging to Behrensmeyer Stage 1 are most numerous, Stage 2 and 3 contain together at least 12% of the bones: Assemblage Zemst IIIC, Hofstade III

The remains of weathering group 1 were buried more rapidly than those of weathering group 2, those of weathering group 3 were exposed the longest. Probably the activity of the fluvial system was different from one group to another. A more mobile river could collect bones from a more extensive surface, on which a larger range of weathering stages of the mammalian remains occurred. The weathering groups 1 to 3 may therefore correspond to an increase in lateral movements of the rivers. This is confirmed by the fact that the fluvial system that accumulated assemblage Zemst IIIC (weathering group 3) was more mobile than the system of assemblage Zemst IIB (weathering group 2).

Scavenging Predator or scavenger action on the mammals of the Flemish Valley is indicated by tooth and gnawing marks on the skeletal remains, especially on or near epiphyses of long bones. The characteristics of the damage compares very well with that due to spotted hyaena and wolf as observed by Haynes (1983). The assemblages can be subdivided into two groups:

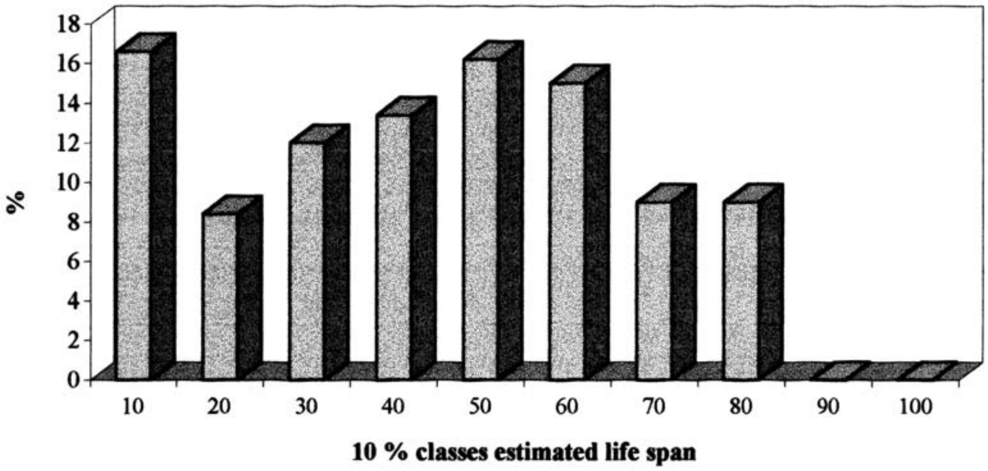


Figure 4 Age profile of the mammoths of assemblage Zemst IIB based on the mandibular dentition.

scavenged group 1: percentage of gnawed bones < 7%: Assemblages Zemst IIB, Zemst IIIC

scavenged group 2: percentage of gnawed bones > 20%: Assemblages Hofstade I, Hofstade II, Hofstade III

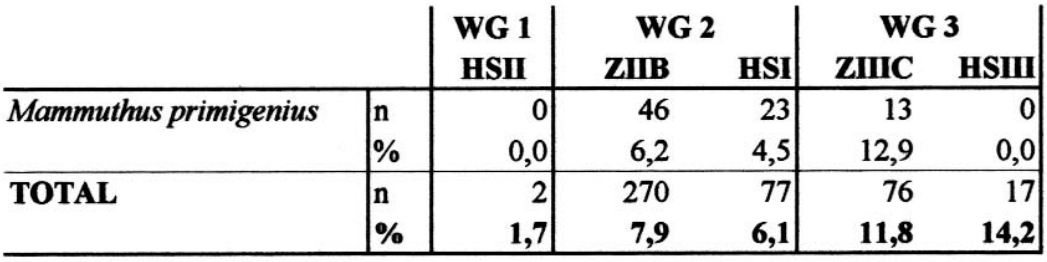
The difference in frequency of chewed bones in the Flemish Valley assemblages can be caused by several factors. Predators will turn to bone gnawing when there is a prolonged shortage of prey. However, many parameters play a role (abundance, vulnerability and concentration of prey; concentration, quality and location of carcasses etc.). All assemblages dating from the Pleniglacial contain relative high frequencies of gnawed bones. This could mean that the abundance of prey in the Flemish Valley was lower during the Middle Weichselian than during the Early Weichselian, so their remains were more extensively used by scavengers (Germonpré 1993a).

Transport of the bone material

Isolated finds The bones of the studied assemblages were recovered from braided-fluvial deposits. Skeletal remains can become incorporated into fluvial deposits directly by burial during floods, by trampling, by overland transport into the channel, by carcasses arriving directly in the channel or by reworking of older depositional features (Behrensmeyer 1982). Bones found *in situ* at Zemst were almost always isolated (Germonpré 1993a). At Hofstade, according to Rutot (1909a: 243) no associated skeletal elements were collected: "Les ossements ne se trouvent pas en connexion anatomique".

Modification by abrasion During the transition from thanatocoenosis to taphocoenosis, bone can be scoured and rounded by the impact of sediment grains. Also on the flood plain abrasion can occur via trampling. The percentages of abraded bones in each assemblage are low (Table 3). Furthermore, the higher the weathering, the more bones are abraded. Fresh bones, which could have entered the channel still protected by some soft tissue, resisted better the abrasion. Bones in weathering stages 1 and 2 have small cracks

Table 3 Abrasion and weathering groups from Zemst and Hofstade.



		WG 1	WG 2		WG 3	
		HSII	ZIIB	HSI	ZIIIC	HSIII
Mammuthus primigenius	n	0	46	23	13	0
	%	0,0	6,2	4,5	12,9	0,0
TOTAL	n	2	270	77	76	17
	%	**1,7**	**7,9**	**6,1**	**11,8**	**14,2**

and were probably more easily rounded. The correlation influences the assemblages as a whole: the most weathered assemblages (weathering group 3) are the most abraded (Table 3). Although longer transport of the carcasses can not be excluded, the bones were probably only carried over a relatively short distance and had a limited residence time in the active fluvial system before burial (Germonpré 1993a).

MAMMOTH TAPHONOMY

In what follows, only the woolly mammoths from assemblage Zemst IIB and Hofstade I are described. Complete biometric information on this species can be found in Germonpré (1993b).

Skeletal representation

Remains of woolly mammoths account for 33% and 45% of the NISP and 22% and 29% of the MNI for resp. the Zemst IIB and Hofstade I assemblage. The frequency of the skeletal elements is shown in Figures 2 and 3. Jugal teeth, carpals, tarsals, MC and MT are represented with their most frequent occurring element. The skeletal distribution of the mammoths corresponds to one expected in a channel and flood plain environment. For Zemst IIB the last lower molar is the best represented element, followed by tusks and lower jaws. For Hofstade I skulls, lower jaws and ulnae are the highest-ranking elements. Both assemblages are characterised by a low number of vertebrae, ribs, MC, MT and phalanges. Elements such as ribs and vertebrae are relatively easily removed by currents while skulls and jaws remain behind as lag deposits, long bones have an intermediate behaviour (Voorhies 1969; Behrensmeyer 1975; Shipman 1981). The low frequency of the carpals, tarsals, MC, MT and phalanges relates maybe to a biassed collection of these elements in the field.

Skeletal height

Garutt (1964) gives for certain mounted mammoth skeletons the height of the skeleton with the length of the shoulder blade and long bones. With these data we calculated the best fitting regression line and obtained the following formulas (Germonpré 1989):

scapula: $y = 3.19x + 30.8$ $r = 0.96$
humerus: $y = 2.55x + 43.2$ $r = 0.90$
ulna: $y = 2.74x + 65.0$ $r = 0.70$
femur: $y = 2.32x + 25.1$ $r = 0.82$
tibia: $y = 4.35x + 12.7$ $r = 0.94$
fibula: $y = 4.31x + 25.0$ $r = 0.90$

With these formulas we calculated the skeletal height for mammoths of Zemst IIB and Hofstade I for those long bones that were complete. The range in height for the mammoths of Zemst IIB and Hofstade I is more or less 80 cm. The mean height for Zemst IIB is 277 cm and 300 cm for Hofstade I with a minimum of resp. 246 cm and 248 cm and a maximum of resp. 318 cm and 333 cm. According to Coope & Lister (1987) the shoulder height is obtained by adding 30 cm to the skeletal height. The mean shoulder height for the mammoths from Zemst IIB and Hofstade I would then be 307 cm and 330 cm.

Molar morphology

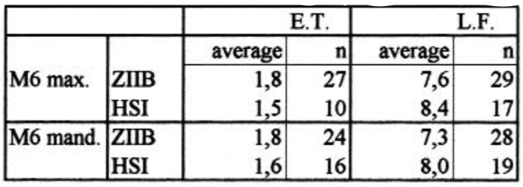
Lamellar frequency and enamel thickness is considered to be major features in the evolution of mammoths (Foronova & Zudin 1999). Table 4 mentions the mean values of these features for the mammoths from Zemst IIB and Hofstade I. Mammoths from Zemst IIB have a thicker enamel and a lower lamellar frequency than those of Hofstade I. According to Foromova & Zudin (*ibid.*) thick enamel forms are adapted for soft vegetation while thin enamel forms, having an increased cutting ability, are adapted for abrasive food from more arid environments. They correlate the thick enamel mammoths to interglacial and transitional landscapes and the thin enamel ones to periglacial habitats. This agrees well with the environments in which the mammoths of Zemst IIB and Hofstade I lived.

Age distribution

Several authors reconstruct the age distribution of fossil proboscideans based on the eruption sequence and wear of their jugal teeth compared with those of recent elephants (Saunders 1977, 1980; Haynes 1985, 1991). The two modern elephant species are very similar in the major aspects of their biology and behaviour. The closely related mammoths probably behaved in a similar way (Saunders 1980; Olivier 1982; Haynes 1988, 1991).

Laws (1966) establishes 30 age groups for the African elephant, based on the progress of eruption and wear of the jugal teeth and assigns real ages to these groups. Laws' technique is used here in an adapted form (Germonpré, 1993a: table 10). This age attribution facilitates calculations and comparisons without implying real absolute ages for the mammoths. Furthermore, by regrouping the classes, the error in age attribution is reduced. Finally the mean distribution per African elephant year (A.e.y.) is calculated and these data are grouped in 10% classes of the estimated life span.

Table 4 Enamel thickness and lamellar frequency of the mammoths from assemblage Zemst IIB and Hofstade I.



		E.T.		L.F.	
		average	n	average	n
M6 max.	ZIIB	1,8	27	7,6	29
	HSI	1,5	10	8,4	17
M6 mand.	ZIIB	1,8	24	7,3	28
	HSI	1,6	16	8,0	19

The age distribution of the fossil remains from woolly mammoth of the fluvial assemblages Zemst IIB and Hofstade I is given in Fig. 4 and 5. At Zemst IIB remains from very young animals (< 6 A.e.y.) dominate. The second peak in the profile corresponds to an age group between 24 and 30 A.e.y. At Hofstade I juvenile mammoth remains are very scanty. Maybe scavenger activity is responsible for the low frequency of very young animals (cf. high percentage of gnawing traces). Also, the collecting of the fossil bones of assemblage Hofstade I could be more biassed. The profile Hofstade I is notable for its relatively high frequency of prime-age individuals between 36 and 48 A.e.y. The age distributions of Zemst IIB and Hofstade I do not correspond completely with a typical attritional mortality distribution characterised by a high number of very young and old individuals (Voorhies 1969; Shipman 1981). Juvenile weakness, disease, predation and old age (Koster 1987, Behrensmeyer 1991) cause attritional mortality.

The profiles are very different from the classical catastrophic age profile where representation diminishes with age. Mass mortality follows sudden changes in ecological conditions such as floods, droughts or epidemics (Koster *ibid.*; Behrensmeyer *ibid.*). Examples of these latter types are the mass mortality of African elephant populations that occurred in Tsavo National Park (Kenya) during the dry years 1970 and 1971 (Corfield 1973: table 5). Mortality was clearly concentrated along watercourses and permanent water bodies,

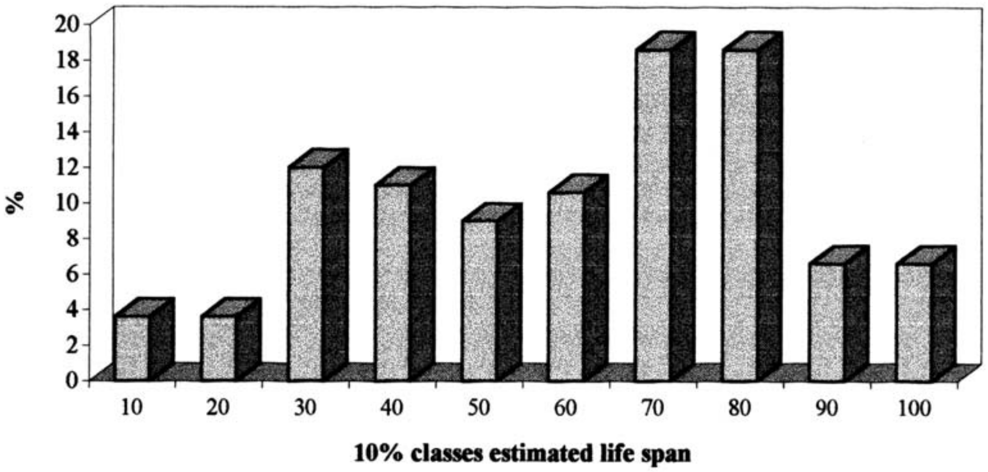


Figure 5 Age profile of the mammoths of assemblage Hofstade I based on the mandibular dentition.

and was age and sex-specific (Corfield *ibid.*). The profiles of Zemst IIB and Hofstade I differ also from those from cull sites of African elephants in Zimbabwe as described by Haynes (1985) and from the hunted mammoths from Lehner Ranch, Arizona (Saunders 1977, 1980). These latter profiles have a high number of young animals and a sharply decreasing quantity of older individuals.

At Zemst a few stone artefacts were found. They were attributed to a "Moustérien typique". Their small number indicates that the occupations of middle Palaeolithic man were only of a limited duration (Van Peer & Smith 1990). No artefacts, associated with assemblage Hofstade I, are known. The foregoing indicates that hunting did not cause the death of the mammoths from the Flemish Valley.

The age distributions of mammoths in the fluvial deposits of the Flemish Valley are clearly not in the range of die-off sites or culled sites. They represent attritional mortality over an extended period of time.

At Hofstade I important quantities were recovered from another pachyderm: the woolly rhinoceros. The age distribution of its well-preserved remains is compared to the one of woolly mammoth. The age distribution of the woolly rhinoceros material is based on the stage of dental eruption and wear pattern of the mandibular dentition as proposed by Goddard (1970). This author grouped mandibular material of black rhinoceros from Tsavo National Park, Kenya, in 20 age classes, assigning approximate mean ages to each class. The pattern in woolly rhino is similar to the one of the black rhino (Guérin 1980; Germonpré 1993a). Goddard's classes are regrouped into 8 groups (Germonpré 1993a: tables 12, 13). The woolly rhino classes are attributed a "black rhino year" age (b.r.y.), which does not imply an absolute age but enables a better visualisation of the age structure of the rhino assemblage. Then, just as with the mammoths the data are grouped in 10% age classes of the estimated life span of the rhinos.

The age profile is characterised by a peak of subadult and prime adult animals (4-12 b.r.y.) and the low frequency of older rhinoceroses, as in a catastrophic profile (Fig. 6). The under representation of material of very young rhinos is attributed to the greater susceptibility of juvenile remains to weathering and scavenging (cf. the high percentage of gnawing traces). The Hofstade I profile is comparable to the one described by Hunt (1990: fig. 27) for rhinoceros remains found

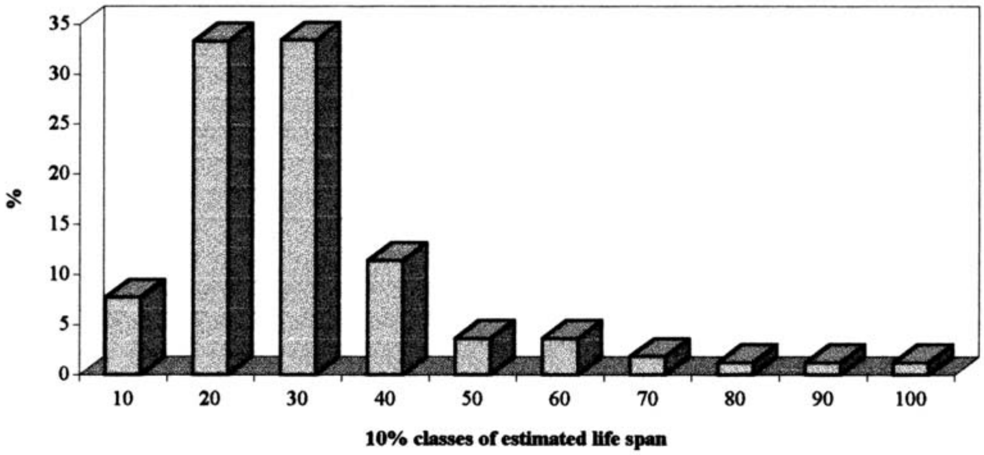


Figure 6 Age profile of the woolly rhinos of assemblage Hofstade I based on the mandibular dentition.

in Miocene waterhole deposits from Nebraska, with a good representation of subadults and prime adults and few aged individuals. According to Hunt (*ibid.*) the death of the rhinos was caused by severe drought.

The profile of the rhinos from assemblage Hofstade I suggest that the animals died as a result of a single or regularly recurring catastrophic events. Maybe a combination of harsh winter conditions preceded or followed by a prolonged drought period, as can be expected in the continental palaeoclimate during which the Lembeke Member was formed, was fatal to many rhinos of Hofstade. But why is the event, causing mass mortality in the rhinos, not reflected in the mammoth profile (Fig. 5)?

According to Kingdon (1979: 66) rhinoceroses are in periods of drought more vulnerable than elephants: "Elephant feeding and trampling favours some species but in times of shortage competition can be serious for large species like the rhino, which also have bulk needs. In Tsavo rhinoceroses have been particularly affected during drought years with both species (=elephant and rhino, M.G.) finishing all edible vegetation near the river, and the rhinos having a shorter range, dying first."

From the foregoing it can be concluded that the rhinos of Hofstade may have perished in mass due to harsh winter conditions, possibly combined with severe drought. The mammoths, just like the recent elephants, had the ability to feed at every vegetation storey from below the surface (roots, bulbs) to the top of the trees and to dig drinking wells in dried-up rivers; during extreme droughts periods they even could have chased other animals (Laws 1970; Haynes 1991; Putshkov 1997). In the assemblage some broken tip fragments of mammoth tusks were recovered (Germonpré 1993a). Maybe mammoths damaged their tusks while breaking the ice from ice veins and ice wedges, which they ate to relieve their thirst. Furthermore, the mammoths could also have escaped the catastrophe at Hofstade thanks to their larger range.

CONCLUSION

Due to their large quantities of well preserved mammoth remains and the clear taphonomic processes involved in the accumulation thereof, Zemst and Hofstade can be used as reference sites for the study of mammoth ecology and taphonomy. Gautier (1974, 1985) developed a first taphonomic model for the Weichselian assemblages of the Flemish Valley. According to this author, herbivores concentrated during winter in the valleys for protection and food, where several died. Due to the low temperatures decay of the carrion was postponed. In spring, the blowfly *Protophormia terraenovae* contaminated carcasses of which fossil puparia were recovered in skulls and horn cores (Gautier 1974; Gautier & Schumann 1973). With the thawing of the ice, carcasses were collected by the floods and quickly covered with sediments.

This scenario can now be refined (see also Germonpré 1993a). The bones in the braided-fluvial deposits from Zemst and Hofstade are from mammals that died within the confines of the valleys. Probably most deaths occurred during winter when the mammals sought shelter, food and water. The mammoths bones that accumulated during the very beginning of the Early Weichselian at Zemst (assemblage Zemst IIB) are from animals that perished from attritional death causes. Their enamel is relatively thick, typical for mammoths living in a transitional landscape with a relatively rich vegetation in a grassland interspersed by wooded areas. The remains from beaver, roe deer, red deer, wild hog and aurochs further indicate the rather mild environmental conditions. Later during the Early Weichselian the climate deteriorated and the temperate species disappeared with the exception of a rare red deer.

During the Middle Weichselian temperate species are lacking completely (assemblage Hofstade I). Carnivores such as cave hyena and wolf scavenged a rather high frequency of bones. The predators may have turned to bone for food because prey animals were becoming scarce. The valley formed by the ephemeral braided river acted as an oasis amidst the arid interfluvia, where due to the little precipitation plant growth was surely limited. The mammals gathered along the watercourse searching for food and water. The mammoths have thin enamel adapted to the abrasive food of an arid habitat. At a certain moment or during several succeeding cold and extremely dry winters, the woolly rhinos succumbed massively. This event did not leave a signal in the age profile of the mammoths.

During the remainder of the Middle Weichselian enamel thickness of the mammoths continues to diminish just as the shoulder height of horses; both can be related to the declining ecological circumstances. Fossil remains of the Late Glacial have only been sparsely encountered in the Flemish Valley (Germonpré 1993a; Germonpré et al. 1993).

REFERENCES

Behrensmeyer, A. K., 1975 - The taphonomy and palaeoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya - Bulletin of the Museum of Comparative Zoology 146: 473-578

Behrensmeyer, A. K., 1978 - Taphonomic and ecologic information from bone weathering - Paleobiology 4: 150-162

Behrensmeyer, A. K., 1982 - Time resolution in fluvial vertebrate assemblages. Paleobiology 8: 211-217

Behrensmeyer, A.K., 1991 - Terrestrial vertebrate accumulations - in: Allison, P.A. & Briggs, D.E.G. (eds) - Taphonomy, releasing data locked in the fossil record. pp. 291-335, Plenum Press

Bogemans, F., 1988 - Thematische kwartairgeologische voorstellingen als toepassingsmodellen in de economische ontwikkeling - Doctoraal Proefschrift, Vrije Universiteit Brussel, Brussels (unpublished)

Bogemans, F., 1993 - Quaternary geological mapping on basis of sedimentary properties in the eastern branch of the Flemish Valley (sheets Boom-Mechelen and Vilvoorde-Zemst) - Mémoires pour servir à l'explication des cartes géologiques et minières de Belgique 33: 1-65

Coope, G.R. & Lister, A., 1987 - Late glacial mammoth skeletons from Condover, Shropshire, England -

Nature 330: 472-474

Corfield, T.F., 1973 - Elephant mortality in Tsavo National Park - East African Wildlife Journal 11: 339-368

De Moor, G. & Heyse, I., 1976 - Kwartairgeologie en geomorfologie in Noordwestelijk Vlaanderen - Werkstukken Nationaal Centrum Geomorfologisch Onderzoek 16: 1-71

Foronova, I.V. & Zudin, A.N., 1999 - The structure of the lineage *Archidiskodon-Mammuthus* in Eurasia and peculiarities of its evolution - in: Haynes, G.; Klimowicz, J. & Reumer, J.W.F. (Eds.) - Mammoths and the mammoth fauna: studies of an extinct ecosystem - Deinsea 6: 103-118

Forsten, A., 1991- Size decrease in Pleistocene-Holocene true or caballoid horses of Europe - Mammalia 55: 407-419

Gautier, A., 1974 - Fossiele vliegenmaden (Protophormia terraenovae Robineau-Desvoidy, 1830) in een schedel van de wolharige neushoorn (*Coelodonta antiquitatis*) uit het Onder-Wurmiaan te Dendermonde (Oost-Vlaanderen, België) - Natuurwetenschappelijk Tijdschrift, 56: 76-84

Gautier, A., 1985 - Pleistocene zoogdieren in België en waar ze gevonden worden - Lutra 28: 121-123

Gautier, A. & Schumann, H., 1973 - Puparia of the sub arctic or black blow fly (*Protophormia terraenovae* Robineau-Desvoidy, 1830) in a skull of a Late Eemian(?) bison at Zemst, Brabant (Belgium) - Natuurwetenschappelijk Tijdschrift 67: 119-125

Garutt, V.E., 1964 - Das Mammut *M. primigenius* (BLUMENBACH) - A. Ziemsen Verlag, Wittenberg Lutherstadt

Germonpré, M., 1989 - De boven-pleistocene zoogdieren uit de oostelijke uitloper van de Vlaamse Vallei (België) - Doctoraal proefschrift, Vrije Universiteit Brussel, Brussels (unpublished)

Germonpré, M., 1993a - Taphonomy of Pleistocene mammal assemblages of the Flemish Valley, Belgium - Bulletin Institut Royal Sciences Naturelles de Belgique 63: 271-309

Germonpré, M., 1993b - Osteometric data on Late Pleistocene mammals from the Flemish Valley, Belgium - Documents de Travail Institut Royal Sciences Naturelles de Belgique 72: 1-135

Germonpré, M., Bogemans, F., Van Neer, W. & Grün, R., 1993 - The dating of two Pleistocene mammal assemblages from the Flemish Valley, Belgium - Contributions Tertiary and Quaternary Geology 30: 147-153

Giterman, R.E., Sher, A.V. & Matthews, J.V. jr., 1982 - Comparison of the development of steppe-tundra environments in West and East Beringia: pollen and macrofossil evidence from key section - in: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds) - Palaeoecology of Beringia - pp. 43-73, Academic Press, New York

Goddard, J., 1970 - Age criteria and vital statistics of a black rhinoceros population - East African Wildlife Journal 8: 105-121

Guérin, C., 1980 - Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaisons avec les espèces actuelles -Documents des Laboratoires de Géologie 79: 1-1185

Guthrie, R.D., 1982 - Mammals of the mammoth steppes as paleoenvironmental indicators. - in: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds) - Palaeoecology of Beringia - pp. 307-326, Academic Press, New York

Guthrie, R.D., 1990 - Frozen fauna of the mammoth steppe. The story of Blue Babe - The University of Chicago Press, Chicago

Haynes, G., 1983 - A guide for differentiating mamma lian carnivore taxa responsible for gnaw damage to herbivore limb bones - Paleobiology 9: 164-172

Haynes, G., 1985 - Age profiles in elephant and mammoth bone assemblages - Quaternary Research 24: 333-345

Haynes, G., 1988 - Longitudinal studies of African elephant death and bone deposits - Journal Archaeological Sciences 15: 131-157

Haynes, G., 1991 - Mammoths, mastodonts, and elephants. Biology, behavior, and the fossil record - Cambridge University Press, Cambridge

Hibbert, D., 1982 - History of the steppe-tundra concept. - in: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds) - Palaeoecology of Beringia - pp. 153-156, Academic Press, New York

Hunt, R.M.Jr., 1990 - Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming; a paleobiota entomed in fine-grained volcaniclastic rocks - in: Lockley, M.G. & Rice, A. (eds.) - Volcanism and fossil biota - Geological Society of America, Special Paper 244: 69-111

Kingdon, J., 1979 - East African mammals. An atlas of evolution in Africa. Volume IIIB - Academic Press, New York

Koster, E.H., 1987 - Vertebrate taphonomy applied to the analysis of ancient fluvial systems - in: Ethridge, F.G., Flores, R.M. & Harvey, M.D. (eds) - Recent developments in fluvial sedimentology. Contributions from the third international Fluvial Sedimentology Conference. Society Economic Palaeontology & Mineralogy, Special Publication 39: 159-168

Kozhevnikov, J.P. & Ukraintseva, V.V., 1999 - Pleistocene tundra-steppe: arguments pro and con - in: Haynes, G.; Klimowicz, J. & Reumer, J.W.F. (Eds.) - Mammoths and the mammoth fauna: studies of an extinct ecosystem - Deinsea 6: 199-210

Laws, R.M., 1966 - Age criteria for the African elephant, *Loxodonta a. africana* - East African Wildlife Journal 4: 1-37

Laws, R.M, 1970 - Elephants as agents of habitat and landscape change in East Afrika - Oikos 21: 1-15

Mourlon, M., 1909 - Découverte d'un dépôt quaternaire campinien avec faune du mammouth et débris végétaux, dans les déblais profonds à Hofstade, à l'est de Sempst - Bulletin de l'Academie royal de Belgique, Classes des Sciences 2: 427-434

Olivier, R.C.D., 1982 - Ecology and behavior of living elephants: bases for assumptions concerning the extinct woolly mammoth. - in: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds) - Paleoecology of Beringia - pp. 267-279, Academic Press, New York

Paepe, R., 1967 - The rock sequences of the Late Pleistocene - in: Paepe, R. & Vanhoorne, R., (eds) - The stratigraphy and palaeobotany of the Late Pleistocene in Belgium - Mémoires pour servir à l' explication des Cartes géologiques et minières de la Belgique 8: 1-96

Paepe, R., Baeteman, C., Mortier, R., Vanhoorne, R. & C.Q.S., 1981 - The marine Pleistocene sediments in the Flandrian area - Geologie en Mijnbouw 60: 321-330

Putshkov, P.V., 1997 - Were the mammoths killed by the warming? (Testing of the climatic versions of Wurm extinctions) - Vestnik zoologii, supplement 4: 1-81

Rutot, A., 1909a - Note préliminaire sur la coupe des terrains quaternaires à Hofstade - Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 23: 235-245

Rutot, A., 1909b - Nouvelles observations dans les couches quaternaires à Hofstade - Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 23: 338-347

Saunders, J.J., 1977 - Lehner Ranch revisited - in: Johnson, E. (ed.) - Paleoindian lifeways - Museum Journal 17, Lubbock

Saunders, J.J., 1980 - A model for man-mammoth relationships in Late Pleistocene North America - Canadian Journal Anthropology 1: 87-98

Shipman, P., 1981 - Life history of a fossil. An introduction to taphonomy and paleoecology - Harvard University Press, Harvard

Stuart, A.J., 1991 - Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America - Biological Review 66: 453-562

Van Peer, P. & Smith, R., 1990 - Zemst "Bos van Aa": un site du paléolithique moyen de la partie orientale de la Vallée Flamande - Helinium 30: 157-171

Voorhies, M.R., 1969 - Taphonomy and population dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska - Contributions Geology, University Wyoming, Special Paper 1: 1-69

received 01 June 1999

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM
P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands