Taphonomy of Pleistocene mammal assemblages of the Flemish Valley, Belgium

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Abstract

Large quantities of fossil bones were recovered in the Flemish Valley at the sites of Zemst, Hofstade, Overmere and Dendermonde. Most of these Late Pleistocene assemblages date from the Weichselian and were recovered from fluvial deposits formed by braided river systems. Twenty-three mammalian taxa were collected. The fossils accumulated mainly through gradual, long-term processes as indicated by the scattered and dispersed spatial distribution of the bones, the abundance of scavenged and subaerially weathered bones, the low numbers of carnivores, the low CSI (corrected number of specimens per individual) values and the preponderance of Voorhies (1969) Group 3. Age profiles of mammoth support this interpretation. However, the age profile of rhinoceros of assemblage Hofstade I suggests episodic mass-mortality events affecting this large herbivore.

Key-words: Late Pleistocene, mammals, Belgium, Flemish Valley, taphonomy, paleoecology

Résumé

De grandes quantités d'ossements fossiles ont été trouvées dans la Vallée Flamande à Hofstade, Zemst, Dendermonde et Overmere. La plupart de ces assemblages pléistocènes supérieurs datent du Weichselien et proviennent de sédiments déposés par des réseaux fluviatiles anastomosés. Vingt-trois taxa mammaliens ont été récoltés. Les fossiles se sont accumulés sous l'action de phénomènes graduels de longue durée. Ceci est indiqué par la rareté et la dispersion des ossements, l'abondance d'os rongés et délités, la faible quantité de carnivores, la valeur peu élevée du CSI ("corrected number of specimen per individual") et la prédominance du groupe 3 de Voorhies (1969). Les distributions de fréquences d'âge du mammouth confirment cette interprétation. Dans l'assemblage Hofstade I, une seule répartition de fréquence d'âge du rhinocéros suggère d'épisodiques mortalités en masse de ces grands herbivores.

Mots-clefs: Pléistocène Supérieur, mammifères, Belgique, Vallée Flamande, taphonomie, paléoecologie

Introduction

The bulk of research on Belgian Pleistocene mammals has for a long time been focussed on material from cave deposits (GERMONPRE, 1982). In recent years however fossil remains from fluvial sites, especially in the Flemish Valley, have received more attention. The taphonomic origin, the paleoecology and biometric results of some assemblages have already been published (*eg.* GAUTIER, 1974, 1976; GAUTIER & SCHUMANN, 1973; GAUTIER *et al.* 1986; GERMONPRE 1984, 1985, 1986; VAN NEER 1981; VAN NEER & GERMONPRE, 1991). Thanks to an important outcrop of Upper Pleistocene sands in sandpits at Zemst, large quantities of fossil mammal remains were collected. Their stratigraphical research and environmental reconstruction were undertaken by BOGEMANS (1988 & 1993). This information helped to interpret the mammal assemblages of Zemst. Consequently, Zemst can be considered as a reference site for the region concerned. Comparison with previously excavated assemblages of Hofstade, Dendermonde and Overmere allows a rather detailed picture of the history of the mammalian fauna during the Early Weichselian and Pleniglacial to be drawn.

In the text, tables and figures following abbreviations are used:

A.e.y.	African elephant year
ab	abraded bones
b.r.y.	black rhinoceros year
ch	chewed bones
cm	bones with corrosion marks
CSI	corrected number of specimens per individual
d	depth
DI	assemblage Dendermonde I
DII	assemblage Dendermonde II
HSI	assemblage Hofstade I
HSII	assemblage Hofstade II
HSIII	assemblage Hofstade III
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen/Royal Belgian Institute for Natural Sciences
MNI	minimal number of individuals
NF	number of fragments
OVI	assemblage Overmere I
OVII	assemblage Overmere II
OVIII	assemblage Overmere III
rm	bones with root marks
s	shed antler
SG	scavenged group
sp	species

VG   Voorhies Group
w   width
WG   weathering group
ZA   assemblage Zemst A
ZIIB   assemblage Zemst IIB
ZIIIC   assemblage Zemst IIIC

Geological setting and regional stratigraphy

The fossil material described below was discovered at the fluvial sites of Overmere, Dendermonde, Hofstade and Zemst in the Flemish Valley. The limits of the Flemish Valley (Fig. 1) correspond with the 0 m contourline of the tertiary substratum as proposed by DE MOOR (1981).

The Flemish Valley consists of a buried polygenetic thalweg-complex. The main orientation is east-west. North of Ghent the complex has its greatest extension, with a width of more then 50 km. A southern branch along the Leie and Scheldt rivers and an eastern branch towards Vilvoorde completes the picture. To the west the boundaries are formed by the cuesta of Oedelem and to the south by the plateau-like interfluvia of the West Flemish Hills. Valleys coming from the south, like those of the Zenne, Dender and Dijle, debouch into the eastern branch. The northern side of the eastern branch is formed by a cuesta cut by the recent Scheldt Valley (DE MOOR, 1963, 1981; DE MOOR & HEYSE, 1978).

The Flemish Valley developed in consecutive stages starting in the Cromerian. Phases of erosion, each enlarging the complex, alternated with phases of accumulation. The valley was filled up during the Last Glacial, although even during the Weichselian, erosion occurred several times followed by accumulation (BOGEMANS, 1988; DE MOOR & HEYSE, 1976; PAEPE, 1967; PAEPE & VANHOORNE, 1976; PAEPE et al., 1981).

BOS VAN AA, ZEMST

Since the beginning of the 1980s fossil bones were collected in large sand exploitations at Bos van Aa, Zemst. The studied remains were found in two sandpits covering a large surface of approximately 365.000 m² (Fig. 2). The concentration of bones, estimated on the bones recovered in situ, is generally below 0.1 bone/m². For a detailed study of the geology of these sandpits the reader is referred to BOGEMANS (1983, 1986, 1988, 1989 & 1993); BOGEMANS & CASPAR (1984) and BOGEMANS & PAEPE (1982).

In the sandpits of the Bos van Aa three fossil bearing deposits were discovered, all located in the lower part of the outcropping sediments. The lowest, only locally present in the most southern sandpit and lying directly on the Tertiary substrate is typified by fine, to very fine, clastic material. This unit has been described as the Grimbergen Member by BOGEMANS (1988 & 1993). Sedimentary structures and paleobotanical evidence
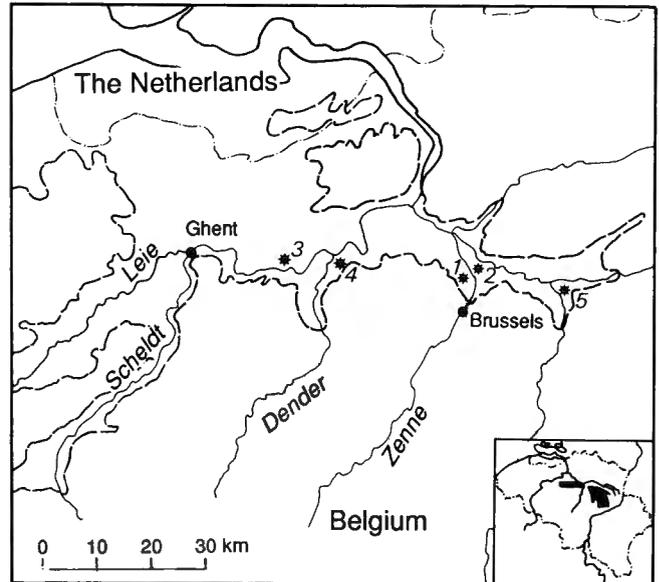

Figure 1 — The Flemish Valley with the sites of Zemst (1), Hofstade (2), Overmere (3), Dendermonde (4) and Rotselaar (5), dashed line indicates the boundary of the Flemish Valley

indicate that the deposit was formed by a meandering river in a tree-rich evironment during the Eemian (BOGEMANS, ibid.). Few bones were discovered in this bed. They are well preserved and have a mahogany brown colour. They are grouped into faunal assemblage Zemst A.

The second and richest layer yielding mammalian remains occurs either on top of the Grimbergen Member or lying directly on the Tertiary (Plate 1, Fig. A & B). The sediments consist of blue grey coarse sand; gravel is present as a channel lag deposit or concentrated along the foresets. Fine grained clastic top-facies also occur
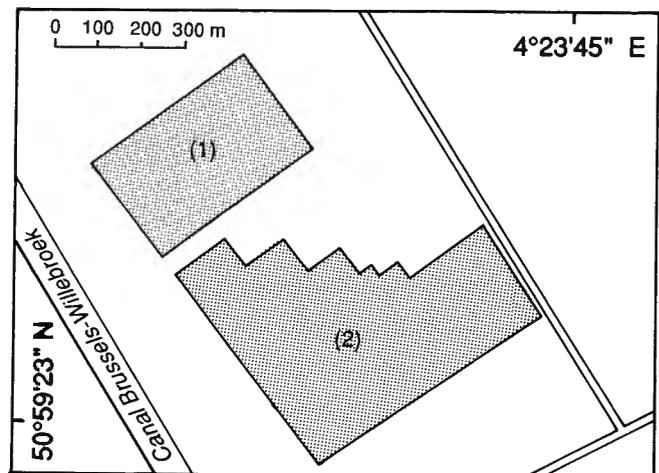

Figure 2 — Sandpits at Bos van Aa, Zemst (1: northern sandpit, 2: southern sandpit)

(BOGEMANS, 1993). According to BOGEMANS (*ibid.*) these sediments were deposited by a braided river and show facies accumulations corresponding to the Donjek type in the classification of MIALL (1978). Furthermore, she can construct the following model, named BWI, for the blue grey sands (BOGEMANS *ibid.*: 23): "These braided river deposits are situated in a sedimentary environment in which a few major channels and several topographic levels are present." The minor channels are scarce and weakly developed, the large bars have only small incisions. The higher topographic levels were only sporadically inundated and were covered with vegetation, which protected older depositional features. The mobility of the system was limited with small variations in the hydraulic regimes. The environment can be described as cold but humid (BOGEMANS, *ibid.*).

Bones found *in situ* in these sediments have a dark grey brown colour and are very well preserved. Teeth show a slightly different colour pattern: dentine and cement have a greybrown hue, enamel is grey or black. The fossils from the southern sandpit are united in mammal assemblage Zemst B, those from the northern sandpit in assemblage Zemst II. Since these sediments from the two sandpits can be correlated and the bones have the same degree of fossilization and colouring, the two assemblages are grouped into assemblage Zemst IIB. A lot of bones were collected from the spoil tip at the base of the screen in the sorting plant where the gravelly sands are processed to separate the coarse fraction. Even bones not discovered *in situ* can, on the basis of fossilization and colouring, be attributed to assemblage Zemst IIB.

A rusty coarse gravelly sand, containing mammalian bones occurs on top of the blue grey sand (Plate 1, Fig. C). For these sediments, also belonging to the Donjek type, BOGEMANS (1993: 25) introduced a second model (BWII): "The sedimentary features of this model illustrate a mobile fluvial system in which strong fluctuating hydraulic conditions dominate." Major channels are generally absent, minor channels, which cut the bars into separate features, are well developed. According to BOGEMANS (*ibid.*: 26) the environment was characterised by "sudden and abrupt releases of water as a result of thawing, possibly in correlation with precipitation. Bad drainage and dry conditions prevailed, permanent permafrost was nevertheless not present in the area."

The bones found in the rusty gravelly sands do not compare well with those of mammal assemblage Zemst IIB: they are somewhat more fragile and have a rusty beige colour. Dentine is pale brown, the enamel is yellow and transparent. Bones of these sands of the southern sandpit form assemblage Zemst C and those of the northern sandpit are grouped into assemblage Zemst III. Together they constitute assemblage Zemst IIIC. Bones gathered at the screen in the sorting plant can also be identified as belonging to this assemblage on basis of colour and fossilization.

The deposits described in both models belong to the Bos van Aa Member and were deposited during the Early Weichselian by a stream which ran approximately south-north and was most active in the southern part of the eastern branch of the Flemish Valley (BOGEMANS, 1993).

The Bos van Aa Member is locally eroded by a meandering river, although not at Zemst. This could be observed in borings made in the vicinity of Zemst (BOGEMANS, 1988). The palynological data investigated by C. Verbruggen and E. Van Overloop in BOGEMANS (*ibid.*) indicate that the meandering system was active during the Amersfoort and Brörup s.s. interstadials. According to BEHRE (1989) the Amersfoort interstadial represents the older part of the Brörup interstadial. Furthermore, he correlates the Brörup interstadial with the isotopic stage 5c of SHACKLETON (1969).

These deposits of the meandering river are attributed to the Hombeek Member (BOGEMANS, 1988) and prove the Early Weichselian age for the Bos van Aa Member, which could therefore correspond to the beginning of the Last Glacial.

Fossil bones were not recovered from the younger deposits which belong to the Lembeke Member, a sandy-braided river deposit, and the Zonnebeke Member, an eolian unit. The Quaternary section at the Bos van Aa, Zemst, reaches a total thickness of about 15 m. A schematic profile of the site of Bos van Aa, Zemst with the stratigraphic position of the assemblages is presented in Fig. 3.

Preliminary results of the mammal assemblages of Bos van Aa, Zemst were published by GERMONPRE (1985, 1986). Not only bones but also some Palaeolithic artefacts were recovered at Bos van Aa. Although most of these were collected from the spoil tip at the screen, they can be attributed to the Bos van Aa Member since only these gravelly sediments are being processed. A few artefacts were found in situ in the blue grey sands and one in the rusty gravelly sands (BOGEMANS & CASPAR, 1984). According to VAN PEER & SMITH (1990) the artefacts show a fresh aspect and fluvial transport was minimal. The quantity and concentration of the artefacts found in the outcropping area is quite low. Probably prehistoric man visited the area only during short periods. The artefacts are described as "Moustérien typique". A reindeer antler shows some traces which could be interpreted as cut marks (VAN PEER & SMITH, *ibid.*).

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 (Fig. 4). The excavated area covers a surface of approximately 465.000 m². Nowadays this area is an artificial lake. RUTOT (1909a, b) and MOURLON (1909) described some sections of the site.
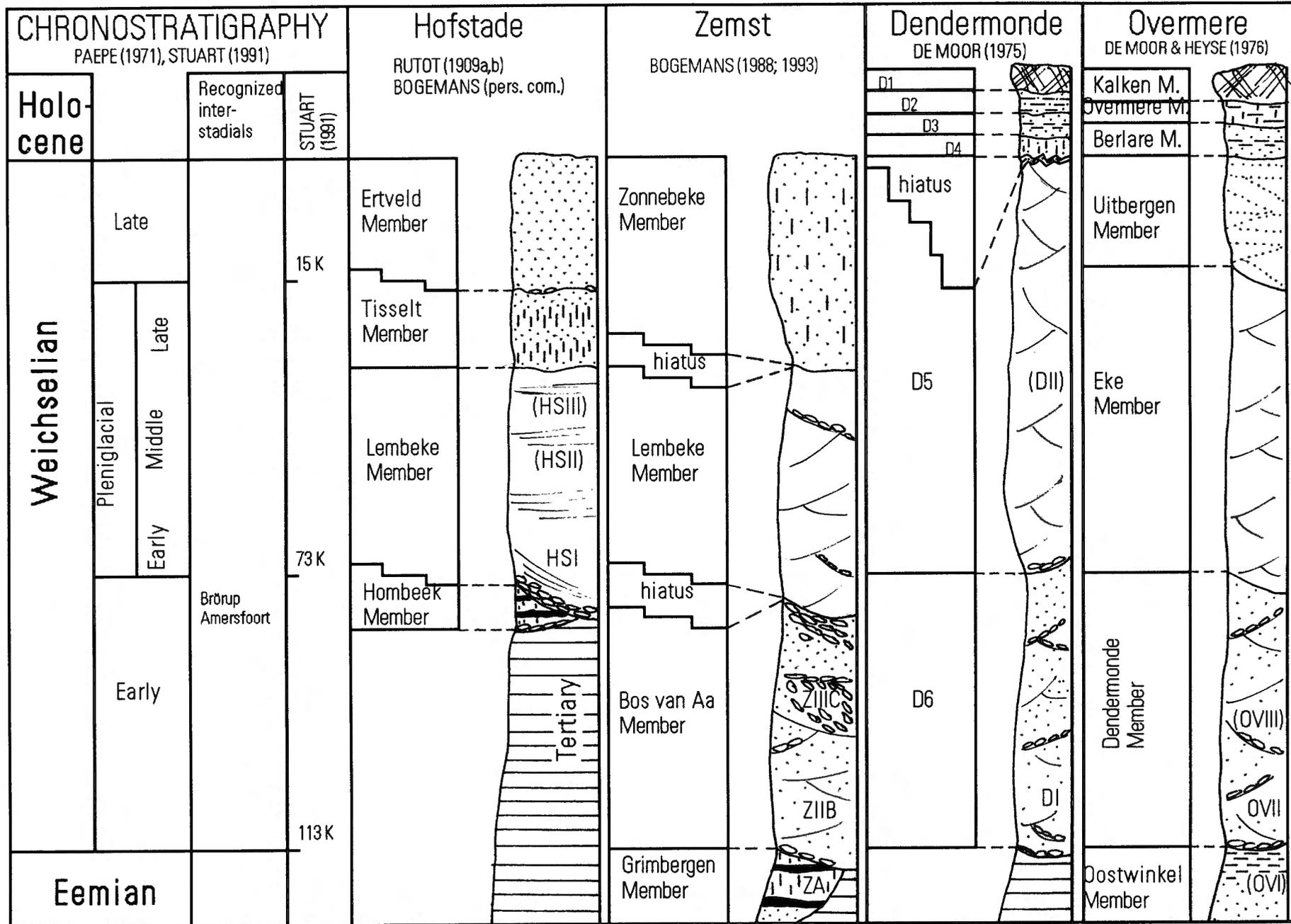
CHRONOSTRATIGRAPHY PAEPE (1971), STUART (1991)				Hofstade RUTOT (1909a,b) BOGEMANS (pers. com.)	Zemst BOGEMANS (1988; 1993)	Dendermonde DE MOOR (1975)	Overmere DE MOOR & HEYSE (1976)

CHRONOSTRATIGRAPHY (PAEPE 1971, STUART 1991):
- Holocene
- Weichselian
  - Late
  - Pleniglacial: Early / Middle / Late
  - Early
- Eemian

Recognized inter-stadials; Brörup Amersfoort

STUART (1991): 15 K, 73 K, 113 K

Hofstade (RUTOT 1909a,b; BOGEMANS pers. com.):
- Ertveld Member
- Tisselt Member
- Lembeke Member — (HSIII), (HSII), HSI
- Hombeek Member
- Tertiary

Zemst (BOGEMANS 1988; 1993):
- Zonnebeke Member
- hiatus
- Lembeke Member
- hiatus
- Bos van Aa Member — ZIIC, ZIIB
- Grimbergen Member — ZA

Dendermonde (DE MOOR 1975):
- D1, D2, D3, D4
- hiatus
- D5 — (DII)
- D6 — DI

Overmere (DE MOOR & HEYSE 1976):
- Kalken M.
- Overmere M.
- Berlare M.
- Uitbergen Member
- Eke Member
- Dendermonde Member — (OVIII), OVII
- Oostwinkel Member — (OVI)

Figure 3 — Chrono-and lithostratigraphic table with schematic lithostratigraphic profile of the sites of Hofstade, Zemst, Dendermonde, Overmere and the stratigraphic (or estimated) position of the assemblages Hofstade I (HSI), Hofstade II (HSII), Hofstade III (HSIII), Zemst A (ZA), Zemst IIB (ZIIB), Zemst IIIC (ZIIIC), Dendermonde I (DI), Dendermonde II (DII), Overmere I (OVI), Overmere II (OVII), Overmere III (OVIII) (not to scale)

←

Locally at the base of the Quaternary sediments a peaty deposit occurs in which a few unidentifiable bones were found: "une demi-douzaine de gros ossements sans caractères spécifiques tranchés" (RUTOT, 1909a: 242). Macrobotanical remains collected from this deposit were described by PASTIELS (1942). The remains indicate a rather temperate environment with growth of *eg. Pinus, Taxus, Corylus, Carpinus* and *Quercus* (PASTIELS, *ibid.*). According to BOGEMANS (pers. comm. 1992) the sediments belong to the Hombeek Member.

Above the Tertiary substrate or on top of the Hombeek Member, a channel lag outcrops followed by stratified sand. According to BOGEMANS (1993), these facies have an acyclic origin. The rivertype "is situated in a sedimentary palaeo-environment in which topographic levels are strongly reduced and where channels with flat bars are the main depositional features. This particular type of braided river was most probably active during ephemeral peak discharges, characterized by huge sediment transport and consequently a reduced erosional activity." (BOGEMANS, *ibid.*: 32). Furthermore, according to this author, these features indicate the existence of a continental palaeoclimate with extreme temperatures and little precipitation prevalent. This fluvial sequence corresponds to the Platte river type of MIALL (1978). These sandy braided river deposits are incorporated in the Lembeke Member.
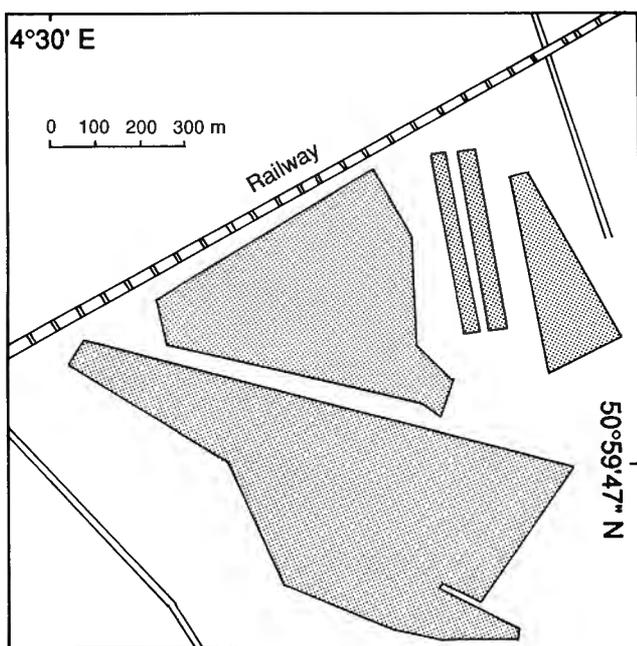
The braided river system of the Lembeke Member was active in almost the entire eastern branch of the Flemish Valley during the Early and Middle Pleniglacial; the source area was located in the northeastern and southeastern adjacent region. The environmental conditions changed gradually until fluvial processes became impossible. The deposits belonging to the Lembeke Member already show evidence of aridification (BOGEMANS, *ibid.*). No indication of permanent permafrost was found (BOGEMANS, 1988).

The two upper deposits (Tisselt and Ertvelde Member) have an eolian origin and date from the Late Pleniglacial and Late Glacial (BOGEMANS, 1988).

The material of Hofstade can on the basis of colour and fossilisation be subdivided into three mammal assemblages. Assemblage Hofstade I contains 3/4 of the bones. The colouring is dark grey brown, preservation is very good. The colour of the dentine is grey brown, while the enamel is grey to black. It is assumed that bones of this assemblage, which is the richest, were recovered by RUTOT (1909 a,b) and MOURLON (1909) *in situ* at the base of the Lembeke Member. These sediments do not correspond to the upper part of the Bos van Aa Member as was previously thought (GERMONPRE, 1989; VAN NEER & GERMONPRE, 1991).

Bones of assemblage Hofstade II are also well preserved. They have a redbrown hue. Dentine and enamel have the same colour. Bones of assemblage Hofstade III are characterized by their more fragile nature and light beige colour. These assemblages are certainly younger than assemblage Hofstade I and presumably originate from the fluvial Lembeke Member (see below).

The estimated position of the assemblages is shown on a schematic profile (Fig. 3).

FRIANT (1948, 1961) studied the cranial morphology of the woolly rhinos of Hofstade. A first general analysis of the fossil mammals was undertaken by BRAET (1973). The rhinoceros remains of Hofstade are included in the work of GUERIN (1980) on the Miocene to Pleistocene rhinoceroses of western Europe. According to GUERIN (*ibid.*) Hofstade yielded one of the richest collections of rhino material of western Europe. The material of Hofstade was reviewed for this study. Some results are already published (GERMONPRE 1984, 1985).

Figure 4 — Excavated surface at Hofstade

OVERMERE

Fossil bones of Overmere were collected at the Maes sandpit during the 1970s (Fig. 5). The outcropping surface approximates 190.000 m². The following litho-
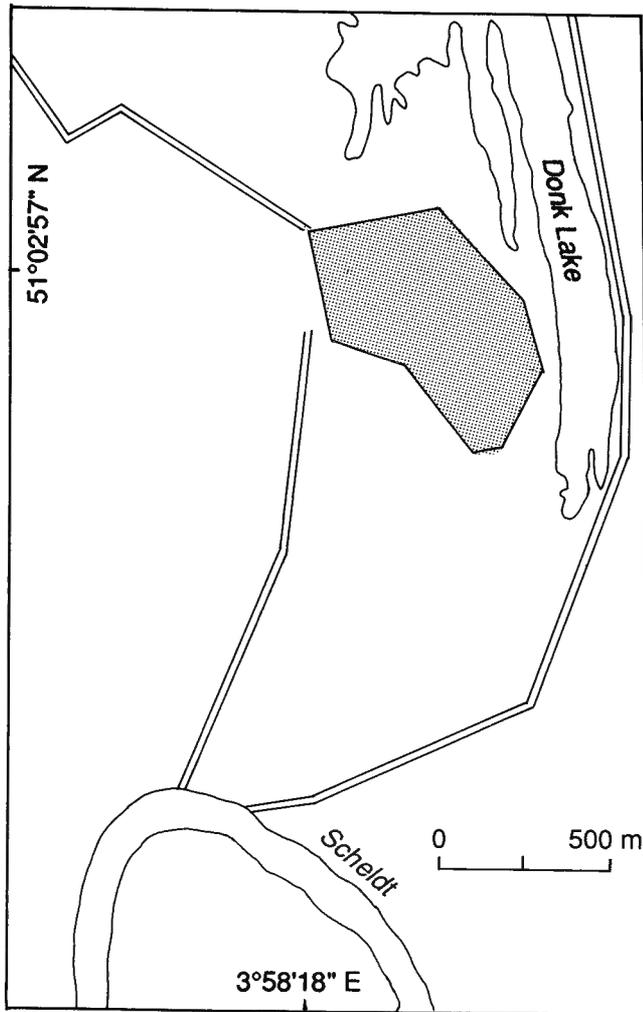
Figure 5 — Excavated surface at Overmere

deposited in the Late Glacial. Sedimentation continued in the Holocene (Berlare, Overmere and Kalken Member).

The bones found *in situ* in the Dendermonde Member are well preserved and have a grey brown colour. They are grouped into mammal assemblage Overmere II. Other assemblages can be distinguished. Assemblage Overmere III is composed of light brown bones, they are somewhat more fragile than those of Overmere II. Dark grey to black, very well preserved bones are grouped into assemblage Overmere I. The species composition of the assemblage Overmere III points to a Weichselian fauna, while the presence of straight-tusked elephant and aurochs in assemblage Overmere I indicates an Eemian age (Table 1). Although the state of fossilisation is not an absolute indicator of age, the age attribution can be supported by the fact that the bones of Overmere I are darker and better preserved than those of Overmere II which in turn are darker coloured and more fossilized than those of Overmere III. Two bones have a different aspect: they have a dark redbrown colour, are in a good state of preservation and are grouped as assemblage Overmere X. A schematic profile with the stratigraphic and estimated position of the assemblages is presented in Fig. 3. A summary of the mammal assemblages of Overmere is given in GERMONPRE & ERVYNCK (1988).
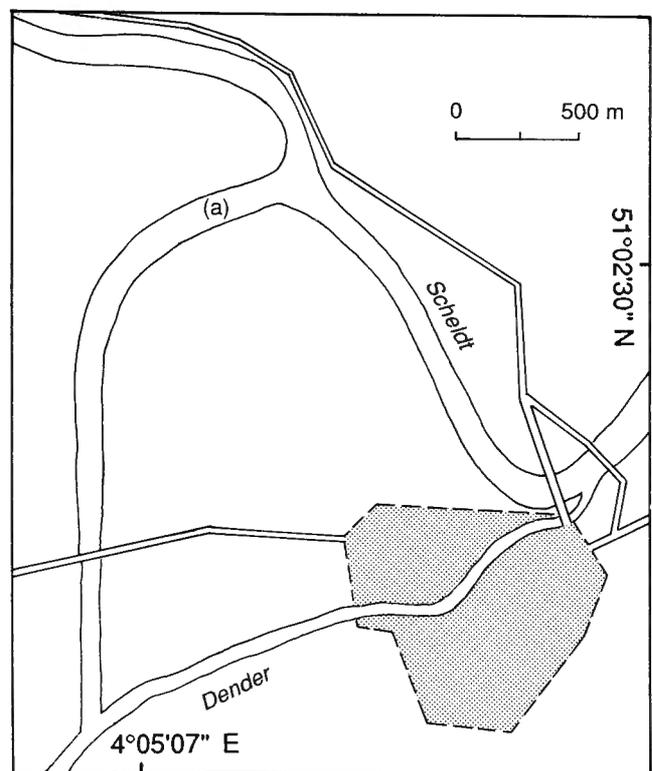
stratigraphic units were described by DE MOOR (1981); DE MOOR & HEYSE (1976, 1978) and HEYSE & DE MOOR (1979).

The lowest Quaternary deposit at the outcrop is the Oostwinkel Member which consists of two complexes each composed of a sandy and clayey facies. Palynological data allow an Eemian age to be attributed to this member (DE GROOTE, 1976). The Oostwinkel Member is incised by a coarse, gravelly sandy unit formed by a braided river. This deposit is the Dendermonde Member and dates from the Early Weichselian. A lot of bones were recovered *in situ* from this unit, although concentrations of fossil remains are not recorded. However, a fairly complete woolly mammoth skeleton was found *in situ* (TEMMERMAN, pers. com.) (Plate 2). On top of the Dendermonde Member occurs the Eke member, which consists of a sandy braided river deposit and dates from the Pleniglacial. Fine, subhorizontal stratified sands (Uitbergen Member) were

Figure 6 — Excavated surface at Dendermonde

	OVI		ZA	
	NF	%	NF	%
Proboscidea	3	8.3	5	12.5
Rhinocerotidae	1	2.8	9	22.5
Equus sp.	1	2.8	7	17.5
Bos/Bison	24	66.7	9	22.5
Cervus elaphus	2	5.6	1	2.5
Capreolus capreolus	1	2.8	6	15.0
Sus scrofa	*	*	1	2.5
Carnivora	3	8.3	1	2.5
Rodentia	1	2.8	1	2.5
Total identified	36	100.0	40	100.0
Unidentifiable	16		1	
TOTAL	52		41	

Table 1 — Number of fragments (NF) and relative frequency of assemblages Overmere I (OVI) and Zemst A (ZA)

DENDERMONDE

At the end of the 1960s and the beginning of the 1970s, Upper Pleistocene sediments were exposed at the St. Onolfspolder, Dendermonde during construction works for a new sluice between the Scheldt and Dender rivers (Fig. 6). A surface of about 400.000 m² was exposed. DE MOOR (1974) describes the following profile: on top of the Tertiary lies a gravelly sand unit (D6) which contains fossil bones. Unit D6 was formed by a braided river during the Early Glacial. The following unit (D5) was also deposited by a braided river. The sand is less coarse and does not contain so much gravel as unit D6. Unit D5 is covered by Holocene fluvial deposits (units D4, D3, D2 and D1).

The bones found *in situ* in the Early Glacial unit have a dark grey brown colour and are well preserved. They constitute assemblage Dendermonde I. On the basis of colour and fossilisation a second assemblage (Dendermonde II) can be distinguished. These bones have a beige colour and are somewhat more fragile. A C14 date of a mammoth tusk gave an age of 29 880 +/- 930 y (VANHOORNE et al. 1978). This age is not compatible with the Early Glacial origin of assemblage Dendermonde I. It is assumed that the mammoth tusk belongs to assemblage Dendermonde II. Three bones, including a bone of musk ox, belong to neither of the assemblages, they are in a good state of preservation, have a red brown colour and are grouped in assemblage Dendermonde x. Since they are so few, they are not treated in the taphonomic analysis.

The stratigraphic and estimated position of the assemblages is given in Fig. 3. Some fossil remains of Dendermonde were described by GAUTIER (1974, 1976) and VANLERBERGHE & GAUTIER (1980). GUERIN (1980) included the rhinos of Dendermonde in his study.

Taphonomy

COMPOSITION OF THE FOSSIL ASSEMBLAGES

The mammalian species composition, the number of fragments, identified and non-identifiable, and the relative frequencies for the assemblages are shown in Tables 1 and 2. Taxa collected include: wolf (*Canis lupus* LINNAEUS), fox (*Vulpes vulpes* (LINNAEUS) / *Alopex lagopus* (LINNAEUS)), bear (*Ursus arctos* LINNAEUS / *Ursus spelaeus* ROSENMULLER & HEINROTH), badger (*Meles meles* (LINNAEUS)), polecat (*Mustela putorius* LINNAEUS / *Mustela eversmanni* LESSON), spotted hyaena (*Crocuta crocuta* (ERXLEBEN)), lion (*Panthera leo* (LINNAEUS)), woolly mammoth (*Mammuthus primigenius* (BLUMENBACH)), straight-tusked elephant (*Elephas namadicus* FALCONER & CAUTLEY), horse (*Equus remagensis* SKORKOWSKI, *Equus ferus* BODDAERT), woolly rhino (*Coelodonta antiquitatis* (BLUMENBACH)), wild boar (*Sus scrofa* LINNAEUS), red deer (*Cervus elaphus* LINNAEUS), reindeer (*Rangifer tarandus* (LINNAEUS)), roe deer (*Capreolus capreolus* (LINNAEUS)), giant deer (*Megaloceros giganteus* (BLUMENBACH)), aurochs (*Bos primigenius* BOJANUS), steppe bison (*Bison priscus* (BOJANUS)), musk ox (*Ovibos moschatus* (ZIMMERMAN)), beaver (*Castor fiber* LINNAEUS), collared lemming (*Dicrostonyx torquatus* (PALLAS)) and hare (*Lepus sp.* LINNAEUS). Identification, description and measurements of the remains are given in GERMONPRE (1989). The collections are biased toward larger mammals. Mammals fall mainly in the very large - medium-sized range. Small species are clearly underrepresented as BEHRENSMEYER & DECHENT BOAZ (1980) also observed for a modern bone sample collected on the Amboseli Plain, Kenya. Furthermore, these authors discovered that carcasses of species with a weight of more than 100 kg are overrepresented. Remains of smaller species are more vulnerable to degradation prior to burial (BEHRENSMEYER et al., 1979). Bones of large species occur in the Flemish Valley assemblages in high frequencies; they are not only more resistant to weathering and scavenging but also stand fluvial transport better than smaller ones. Furthermore, larger specimens are more easily spotted during collection. Bones of similar size can undergo the taphonomic processes in a comparable way; so only species which have skeletal elements of similar size should be compared.

The number of species fluctuates between 8 (Overmere I) and 19 (Zemst IIB). The number of carnivore fragments relative to ungulate remains ranges between 0% (Dendermonde II) and 2.5% (Hofstade III) with assemblage Overmere I showing a larger value (9.1%) probably biased by the small size of the assemblage. According to CLARK & KIETZKE (1967) collections of under 100 specimens are of little value. Carnivores include mainly cave lion, bear, wolf and cave hyaena. Although extremely rare, some rodent remains were found: beaver in assemblages Overmere I,

Table 2 — Number of fragments (NF) and relative frequency of the Weichselian assemblages (DI: Dendermonde I; OVII: Overmere II; ZIIB: Zemst IIB; ZIIIC: Zemst IIIC; OVIII: Overmere III; HSI: Hofstade I; HSII: Hofstade II; HSIII: Hofstade III; DII: Dendermonde II)

	DI NF	%	OVII NF	%	ZIIB NF	%	ZIIIC NF	%	OVIII NF	%	HSI NF	%	HSII NF	%	HSIII NF	%	DII NF	%
Mammuthus primigenius	75	37.3	158	50.5	746	33.5	101	30.2	20	21.7	508	44.5	44	37.6	33	27.5	25	31.3
Coelodonta antiquitatis	70	34.8	57	18.2	588	26.4	130	38.9	31	33.7	444	38.9	43	36.8	54	45.0	39	48.8
Equus sp.	22	10.9	45	14.4	399	17.9	31	9.3	11	12.0	93	8.1	25	21.4	13	10.8	10	12.5
Bos/Bison	21	10.4	31	9.9	209	9.4	40	12.0	20	21.7	52	4.6	3	2.6	10	8.3	3	3.8
Megaloceros giganteus	4	2.0	4	1.3	75	3.4	7	2.1	6	6.5	20	1.8	1	0.9	1	0.8	1	1.3
Cervus elaphus	2	1.0	10	3.2	79	3.5	3	0.9	*	*	*	*	*	*	*	*	*	*
Rangifer tarandus	3	1.5	*	*	84	3.8	15	4.5	3	3.3	20	1.8	*	*	6	5.0	2	2.5
Capreolus capreolus	*	*	4	1.3	2	0.1	*	*	*	*	*	*	*	*	*	*	*	*
Sus scrofa			2	0.6	5	0.2												
Carnivora	4	2.0	2	0.6	36	1.6	6	1.8	1	1.1	5	0.4	1	0.9	3	2.5	*	*
Rodentia	*	*	*	*	3	0.1	1	0.3	*	*	*	*	*	*	*	*	*	*
Lagomorpha	*	*	*	*	1	0.0	*	*	*	*	*	*	*	*	*	*	*	*
Total identified	201	100.0	313	100.0	2227	100.0	334	100.0	92	100.0	1142	100.0	117	100.0	120	100.0	80	100.0
Unidentifiable	17		78		1164		310		27		116		1		8		11	
TOTAL	218		391		3391		644		119		1258		118		128		91	

Table 3 — Number (NF) and relative frequency of weathered bones of the Weichselian assemblages

	Weathering group 1				Weathering group 2						Weathering group 3							
	DI NF	%	HSII NF	%	OVII NF	%	ZIIB NF	%	HSI NF	%	ZIIIC NF	%	OVIII NF	%	HSIII NF	%	DII NF	%
Behrensmeyer Stage 0	145	66.5	81	68.6	140	35.8	1612	47.5	489	38.9	149	23.1	21	17.6	40	31.3	33	36.3
Behrensmeyer Stage 1	56	25.7	33	28.0	232	59.3	1666	49.1	639	50.8	414	64.3	74	62.2	62	48.4	44	48.4
Behrensmeyer Stage 2	15	6.9	2	1.7	14	3.6	109	3.2	112	8.9	78	12.1	22	18.5	24	18.8	14	15.4
Behrensmeyer Stage 3	2	0.9	2	1.7	5	1.3	4	0.1	18	1.4	3	0.5	2	1.7	2	1.6	0	0.0
Total	218	100.0	118	100.0	391	100.0	3391	100.0	1258	100.0	644	100.0	119	100.0	128	100.0	91	100.0

Zemst A and Zemst IIB, collared lemming in assemblage Zemst IIIC.

The percentage of non-identifiable bones is low for Hofstade and Dendermonde and is quite high for Zemst and Overmere (Table 2). At these latter two sites not only well preserved or spectacular specimens were collected. The assemblages of Zemst and Overmere resemble probably more the original taphocoenoses than those of Dendermonde and Hofstade for which no collecting data exist.

The bones of Hofstade are not heavily fragmented. Those of Zemst, Dendermonde and Overmere are more broken. The breakage is often of recent date and caused by the techniques used to process the sand in the sandpits.

The Eemian assemblage Zemst A is characterized by temperate species such as roe deer, wild boar, red deer and beaver, indicating a wooded environment. The same species together with aurochs and *Elephas namadicus* occur at Overmere I, which therefore, is supposed to date from the Eemian. Only a limited number of fossil remains was found, so these assemblages are excluded in the further study; their interpretation is of restricted value.

All Weichselian assemblages are mainly composed of cold-adapted species. Large herbivores such as woolly mammoth, woolly rhinoceros, steppe bison and horse constitute together at least 87% of the identified specimens. They indicate an open steppe-like environment, the so-called steppe-tundra (GITERMAN et al., 1982; HIBBERT, 1982) or Mammoth Steppe (GUTHRIE 1982, 1990). According to VERESHCHAGIN & BARYSHNIKOV (1991) the "mammoth fauna" existed in a continental dry climate having cold winters and short, hot summers in open steppe, meadow-steppe and tundra-steppe landscapes. Some tracts of leaf-bearing and coniferous forests could be found along river valleys.

Bones of large herbivores, such as the giant deer and red deer, are in general scarcer than bones from mammals with a comparable body size (bison, horse) or from smaller species (reindeer). One can assume that the skeletal elements of the mammals mentioned have equal chances to be preserved; therefore the rarity of deer could reflect real differences in representation of the animals on the hoof. The less common large ungulates may have ranged into the reach of the fluvial system only infrequently or they occurred there only in small populations.

Distinction between *Bison priscus* and *Bos primigenius* can confidently be made on the skull, horncores, canonbones and scapula (SCHERTZ, 1936; REYNOLDS, 1938; LEHMANN, 1949; STAMPFLI, 1963; BRUGAL, 1986). In the Eemian assemblage Overmere I, only *Bos primigenius* occurs: associated skeletal remains of especially the front legs have been found (GERMONPRE & ERVYNCK, 1988). In assemblage Zemst IIB cranial material points to the presence of the two species, although *Bison priscus* is much better represented.

The other Weichselian assemblages probably contain only *Bison priscus*.

Temperate species such as red deer, roe deer and wild boar occur in small quantities in the early-Weichselian assemblages of Zemst IIB and Overmere II. Red deer continues to persist in the Early Weichselian (Zemst IIIC, Overmere III) but is lacking in the Pleniglacial assemblages. It is however present (one shed antler) at Rotselaar, an assemblage which shows more affinities with assemblages Hofstade I and Hofstade II than with assemblage Zemst IIB (VAN NEER & GERMONPRE, 1991). The presence of temperate species agrees with the fact that the Early Glacial (ca 113 000 - 73 000 years BP) was on the whole considerably warmer than the later phases of the Last Glacial (STUART, 1991).

PRE-BURIAL MODIFICATIONS

Weathering

Disarticulation of carcasses can happen through several processes such as weathering, scavenging, trampling, gravity (HILL, 1979). 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. Six stages of subaerial weathering have been described for the bones of large mammals found in Amboseli National Park, Kenya. A bone without signs of decay is classified stage 0. A bone evolving from stage 1 through 4 will show more and deeper cracks as well as flaking of the outer layer. Patches of fibrous texture will appear until a completely fibrous surface is reached. At stage 5, the bone is falling apart *in situ* (BEHRENSMEYER, 1978). Subaerial weathering stops once a bone is completely buried. In a cold environment the weathering will proceed at a slower rate than in a warm environment where it takes more or less 15 years for a bone to desintegrate completely *in situ* (BEHRENSMEYER, *ibid.*). Many of the bones observed on the surface of the tundra are quite old, surviving mainly because they remain frozen for ten or more months a year (SUTCLIFFE, 1990).

Table 3 gives the distribution of the Behrensmeyer Stages of the fossils in the Flemish Valley. Most of the bones are fresh or belong to Behrensmeyer Stage 1. Behrensmeyer Stage 2 and 3 occur in lower quantities and later stages are completely absent. The lower frequency of bones in a late stage of weathering is maybe due to the fact that strongly weathered bones are more friable and do not survive transport. The wide range of weathering, from fresh till stage 3, indicates that the bones were exposed for varying periods of time on the surface before transport and/or burial.

The assemblages can on basis of the weathering stages be subdivided in three groups:

Weathering group 1:
   at least 65% of the bones belong to Behrensmeyer
   Stage 0:
      Assemblages Dendermonde I, Hofstade II
Weathering group 2:
   the bones are evenly distributed among Behrens-
   meyer Stages 0 and 1:
      Assemblages Zemst IIB, Overmere II,
      Hofstade I
Weathering group 3:
   bones belonging to Behrensmeyer Stage 1 are
   most numerous, Stage 2 and 3 contain together
   at least 12% of the bones:
      Assemblages Zemst IIIC, Overmere III,
      Hofstade III, Dendermonde II

It can be concluded that the death assemblages of weathering group 1 were more rapidly buried than those of weathering group 2. The assemblages of weathering group 3 would have been exposed longest. This could be related to the fact that the initial location of the death assemblages was further away from the active channels from group 1 to group 3 and/or to the activity of the fluvial system. A more mobile river could collect bones from a more extensive surface, on which a larger range of weathering stages of the mammalian remains occurs. The weathering groups 1 to 3 may therefore correspond to an increase in lateral movements of the rivers. The latter hypothesis is corroborated by the fact that the fluvial system in which assemblage Zemst IIB (weathering group 2) accumulated was less mobile than the system of assemblage Zemst IIIC (weathering group 3), which shows more strongly fluctuating hydraulic conditions. Moreover, limited reworking of the sediments could re-expose the bones and weathering could continue until the bones were once more buried. The more mobile the river system is, the more lateral erosion can occur resulting in increasing weathering of the assemblages.

Scavenging

According to BLUMENSHINE (1986, 1989) carcasses are consumed by predators and scavengers in a certain order and in two cycles. In the first cycle flesh-bearing parts are fed upon and in a second cycle the within-bone tissues are being consumed. The second cycle activities particularly will leave traces in the fossil record. Spotted hyaena and wolf but also bears and large felids damage bone (PEI 1938; SUTCLIFFE, 1970; RICHARDSON, 1980; HAYNES, 1983).

Predator or scavenger action on the mammals of the Flemish Valley is indictated by tooth and gnawing marks on the skeletal remains, especially on or near epiphyses of long bones. The gnawed bones were light to moderately damaged, showing scratches and tooth marks on the compact bone or furrows and gouging on the cancellous tissue (Plate 3, Figs. A and B). The characteristics of the damage compares very well with that due to spotted hyaena and wolf as observed by HAYNES (*ibid.*). In general, the more distally in the skeleton an element is located, the lesser its chances are of being gnawed (GERMONPRE, 1989). Few bones are damaged beyond recognition. Table 4 gives the total percentage of bones with gnawing traces for each assemblage. The assemblages can be subdivided into three groups:

scavenged group 1:
   percentage of gnawed bones <7%:
      Assemblages Zemst IIB, Zemst IIIC,
      Overmere II, Overmere III
scavenged group 2:
   percentage of gnawed bones ~15%:
      Assemblage Dendermonde I
scavenged group 3:
   percentage of gnawed bones between 20% and
   30%:
      Assemblages Hofstade I, Hofstade II,
      Hofstade III, Dendermonde II

For those species present with at least 25 identifiable fragments the percentage of chewed bones was calculated separately (Table 4). In scavenged group 1 no clear preference exists for a certain species. In group 2 and 3, scavengers left traces preferentially on rhinoceros bones, except at Dendermonde II, where mammoth was apparently more attractive.

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. In cases where overall carcass density is high, scavengers find an excess of available meat and do not need to turn to bones for food (BEHRENSMEYER & DECHENT BOAZ, 1980; HAYNES, 1985). COE (1978) ascertained that after the drought in 1970-71 in Eastern Tsavo National Park, Kenya, 30% of the elephant population (5900 individuals) died; the carcasses were only slightly affected by scavengers due to the abundance of carrion.

SHIPMAN (1981: 108) remarked that "the prevalence of chewing marks in an assemblage reflects both the length of time the bones were exposed prior to burial and the population density of bone-chewing species". However all depends on how long a bone stays interesting to a scavenger. RICHARDSON (1980) found that recent carcasses of bovids, equids and giraffes left in open sites in southern Africa were " after a certain period of time no longer disturbed by carnivores. This period was longer for large animals (~ 12 months) than small ones (~6 months) (*ibid.*: 119). According to HAYNES (1986) scavengers such as hyaenas can return to elephant skeletons several years after the animals died to chew the bones that still can be greasy 36 months after death, especially when they were relatively protected by vegetation or dried-on soft tissue. Furthermore, HAYNES (1982: 268) found that "if wolves encounter remains of bison or moose dead more than six

Table 4 — Number (N ch) and relative frequency of chewed bones of the Weichselian assemblages

	Scavenged group 1								SG 2		Scavenged group 3								
	OVII		ZIIB		ZIIIC		OVIII		DI		HSI		HSII		HSIII		DII	
	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp	N ch	% sp
Mammuthus primigenius	*	***	24	3.2	11	10.9	1	***	8	10.6	121	23.8	9	20.5	9	27.3	9	36.0
Coelodonta antiquitatis	2	3.5	31	5.3	9	6.9	2	7.4	15	21.4	167	37.8	12	27.9	15	27.8	8	20.5
Equus sp.	2	4.4	24	6.0	4	12.9	2	***	*	***	23	24.7	5	20.0	2	***	3	***
Bos/Bison	*	***	6	3.0	2	5.0	*	***	2	***	9	17.3	*	***	2	***	1	***
Megaloceros giganteus	*	***	8	10.7	*	***	1	***	1	***	5	***	*	***	*	***	*	***
Cervus elaphus	*	***	4	3.8	*	***	*	***	*	***	*	***	*	***	*	***	*	***
Rangifer tarandus	*	***	11	13.1	1	***	*	***	1	***	3	***	*	***	0	***	1	***
Unidentifiable	2	***	38	***	13	***	*	***	4	***	27	***	*	***	2	***	4	***
TOTAL chewed bones	6	TOT 1.5	146	TOT 4.3	40	TOT 6.2	6	TOT 5.0	31	TOT 14.2	355	TOT 28.3	26	TOT 21.7	30	TOT 23.4	26	TOT 28.6

months, efforts to gnaw bones generally are relatively slight. When food is scarce, the bones may be partly consumed and fragmented.''

Bones on the surface near watering-places (minor and abandoned channels, etc.) or on the alluvial plain have a larger probability of being gnawed than those that are rapidly buried in the active channel. However, there seems be no clear relationship between the amount of gnawing and the time span the bones were exposed as deduced by the weathering rate. Assemblage Zemst IIIC for instance, has a low percentage of gnawed bone but belongs to weathering group 3 and was exposed a relatively long time at the surface, while assemblage Hofstade II was buried quite quickly (weathering group 1) and yet belongs to scavenged group 3.

From the foregoing it can be concluded that the interpretation of gnawing traces on bones is a delicate matter. Many parameters play a role such as abundance, vulnerability and concentration of prey, concentration and location of carcasses (far or near the water course), the behaviour of predators, etc.

However, it is remarkable that all assemblages dating from the Pleniglacial belong to scavenged group 3. Maybe this indicates that, at least locally or temporarily, abundance of prey was lower during the Pleniglacial than during the Early Weichselian, so their remains were more extensively used by scavengers.

Not only carnivores gnaw bones but also ungulates use bony skeletal material to supplement the mineral content of their diet. In assemblage Hofstade II a metatarsal bone of horse was found that shows the forked pattern typical for ungulate chewing (SUTCLIFFE, 1977, pers. comm. 1992) (Plate 4, Fig. C). It is very similar to a forked canonbone of horse from middle Palaeolithic levels in the Wannen volcano, Germany described by JUSTUS & TURNER (1990).

TRANSPORT OF THE MATERIAL

Hydraulic selection:
Voorhies Groups versus associated skeletons

Bones of some assemblages (Zemst A, Zemst IIB, Zemst IIIC, Dendermonde I, Overmere II, Hofstade I) were recovered *in situ* in 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. Disarticulation of carcasses probably happened before the skeletal elements entered the active tracts. Carcasses, in various states of disintegration, picked up by the river, may have acted as a source of isolated skeletal elements. Nevertheless few cases of association occur. At Zemst, two vertebrae of a hog

probably belong to the same individual on the basis of the degree of fusion, weathering stage, etc. Although not *in situ* they were discovered the same day at the sieve. Furthermore a skull, mandibula and rib of a woolly mammoth were found in associated position. An unfused metatarsal of a subadult mammoth was found articulated in the blue grey sands indicating minimal reworking of the material (Plate 2, Fig. B).

At Overmere one remarkable case of association is known: a more or less complete skeleton of *Mammuthus primigenius* was discovered *in situ* by Mr. Verdonck (pers. com.) (Plate 3). Preservation of this skeleton indicates carcass flotation and stranding, unless the animal died on the spot. In both cases rapid burial followed (weathering stage 1, articular surfaces: fresh), without postdepositional exhumation and reworking.

According to RUTOT (1909a: 243) at Hofstade no associated skeletal elements were collected: "Les ossements ne se trouvent pas en connexion anatomique".

In general, mammalian fossils occur dispersed and scattered in the sediment. For Zemst the spatial density is below 0.1 bone/m². Articulated and associated remains are rare; bone concentrations were not found at Zemst and Overmere nor are there any such records at Hofstade and Dendermonde. The assemblages contain a high percentage of weathered bones (Table 3); during the time the remains spend at the surface chances were high for disarticulation by scavenging, trampling, etc. All this evidence indicates that the skeletal remains were collected by fluvial agencies as essentially disarticulated bones. After deposition reworking was probably minimal since high bone concentrations often imply reworking of the material (KOSTER, 1987) (see also section abrasion p. 284).

Sorting by water current occurs because bones differ in size, shape and density. VOORHIES (1969) examined the behaviour of different skeletal elements of coyote and sheep in controlled current velocities up to 150 cm/s. He defined three groups of skeletal elements on the basis of their similar potential for hydraulic dispersal. The Voorhies Groups, although based on rather small mammals, can give an estimate of the degree of transportation and sorting of an assemblage. Voorhies Group 1 contains elements such as ribs and vertebrae which are quickly removed by slight currents; Voorhies Group 2 (long bones and pelvis) are removed gradually by moderate currents; skull and mandible which constitute Voorhies Group 3, remain behind as a lag deposit and are transported only by high-velocity currents (VOORHIES, ibid.; BEHRENSMEYER, 1975; SHIPMAN, 1981)

For those species represented by 25 or more specimens, the relative frequency of the Voorhies Groups was calculated. The number of fragments in each Voorhies Group is expressed as the percentage of the possible maximum number of skeletal elements in the concerned group. Finally the relative proportions of

the three Voorhies Groups were calculated (Table 5).

In general, the distribution of the Voorhies Groups of most species is comparable, with a preponderance of Voorhies Groups 3 and 2. The frequency of Voorhies Group 1 lies almost in all cases below 10% which points to a removal of bones, like ribs and vertebrae, that are affected by slight currents. In assemblage Overmere II, however, the frequency of Voorhies Group I mounts to 17.7% for mammoth. Moreover, the Voorhies Groups of this animal are more evenly represented than for the other assemblages with exception of Dendermonde I. The high percentage of Voorhies Groups 1 & 2 at Overmere II is probably due to the find of an associated mammoth skeleton, an interpretation that can also be put forward to explain the more even Voorhies distribution of mammoth from Dendermonde I.

Voorhies Group 3, the group with the least transportable elements, is for most species the best represented. For horse however this does not work: the frequency of Voorhies Group 3 varies between 4 and 56%, which is a much lower figure than that for other species where the lowest frequency lies above 50%. Horse has in comparison with mammoth and rhinoceros a much smaller skull. The cranium of bovids and male deer (and of female reindeer) is much stronger than the skull of the equids thanks to the presence of horncores or pedicles. However, complementary explanation can be put forward not referring to differential preservation (see section root traces p. 286).

The Voorhies distributions of assemblage Dendermonde II is notable for the absence of Voorhies Group 3.

The prepondarance of Voorhies Group 3 and 2 in all assemblages, with exception of Dendermonde II, points to deposition in a channel and floodplain environment (BEHRENSMEYER, 1975), which confirms the supposed fluvial origin of the assemblages Overmere III, Hofstade II and Hofstade III. Assemblage Dendermonde II, with its preponderance of Voorhies Groups 1 and 2, represents a transported assemblage which is biased by the velocity of the current and the distance to the source area. According to BEHRENSMEYER (ibid.) an assemblage composed of Voorhies Group 3 has more paleoecological significance than a Voorhies Group 1 - assemblage.

For those species represented by at least 25 skeletal elements, the minimal number of individuals (MNI) and the corrected number of specimens per individual (CSI), as defined by SHOTWELL (1958) and which gives an estimate of the skeletal completeness of a species, were calculated (Table 6). In Table 6, the CSI is based on all skeletal elements with exception of the teeth. The CSI shows for all species a value below 25%, indicating that many of skeletal elements were destroyed prior to burial, washed out during transport and/or overlooked during sampling. Even for those assemblages known or presumed to contain an associated skeleton (mammoth in Overmere II and Dendermonde I) the CSI scores not very high. On the other hand, Dendermonde II, which

Table 5 — Relative frequency of the Voorhies Groups (VG) for species of the Weichselian assemblages

		DI %	OVII %	ZIIB %	ZIIIC %	OVIII %	HSI %	HSII %	HSIII %	DII %
Mammuthus primigenius	VG1	12.4	17.7	6.0	7.2	4.9	4.1	4.8	9.7	31.3
	VG2	34.4	20.6	8.3	14.7	12.6	11.3	4.5	17.9	68.7
	VG3	53.2	61.7	85.6	78.1	82.4	84.6	90.8	72.5	0.0
Coelodonta antiquitatis	VG1	3.7	2.9	8.4	7.6	9.3	2.7	1.5	6.8	9.3
	VG2	24.0	14.1	22.4	23.9	28.1	24.2	15.8	36.2	90.7
	VG3	72.3	83.0	69.2	68.4	62.5	73.1	82.7	57.0	0.0
Equus sp.	VG1	*	3.7	8.3	1.5	*	6.3	1.4	*	*
	VG2	*	65.6	87.6	42.5	*	43.9	75.6	*	*
	VG3	*	30.7	4.1	56.0	*	49.7	23.0	*	*
Bison priscus	VG1	*	3.8	6.0	6.1	*	2.5	*	*	*
	VG2	*	42.5	21.2	21.0	*	29.2	*	*	*
	VG3	*	53.7	72.8	69.8	*	67.2	*	*	*
Megaloceros giganteus	VG1	*	*	1.5	*	*	*	*	*	*
	VG2	*	*	13.4	*	*	*	*	*	*
	VG3	*	*	85.1	*	*	*	*	*	*
Cervus elaphus	VG1	*	*	4.7	*	*	*	*	*	*
	VG2	*	*	33.8	*	*	*	*	*	*
	VG3	*	*	61.4	*	*	*	*	*	*
Rangifer tarandus	VG1	*	*	7.4	*	*	*	*	*	*
	VG2	*	*	23.1	*	*	*	*	*	*
	VG3	*	*	69.4	*	*	*	*	*	*

Table 6 — Minimal number of individuals (MNI) and corrected number of specimens per individual (CSI) for species of the Weichselian assemblages

		DI	OVII	ZIIB	ZIIIC	OVIII	HSI	HSII	HSIII	DII
Mammuthus primigenius	MNI	3	4	18	4	2	17	3	2	3
	CSI	13.6	21.5	22.5	13.7	4.9	16.2	9.0	8.7	4.1
Coelodonta antiquitatis	MNI	5	4	16	7	3	28	5	5	5
	CSI	8.6	6.5	22.7	11.5	6.2	9.8	5.3	6.5	4.6
Equus sp.	MNI	*	3	20	3	*	12	4	*	*
	CSI	*	11.5	15.3	7.9	*	5.9	4.6	*	*
Bison priscus	MNI	*	2	8	2	*	7	*	*	*
	CSI	*	12.3	20.6	15.9	*	5.9	*	*	*
Megaloceros giganteus	MNI	*	*	7	*	*	*	*	*	*
	CSI	*	*	8.2	*	*	*	*	*	*
Cervus elaphus	MNI	*	*	5	*	*	*	*	*	*
	CSI	*	*	11.5	*	*	*	*	*	*
Rangifer tarandus	MNI	*	*	6.0	*	*	*	*	*	*
	CSI	*	*	12.9	*	*	*	*	*	*

Table 7a — Number (N ab) and relative frequency of abraded bones of the Weichselian assemblages (WG: weathering group)

		WG1		WG2			WG3			
		DI	HSII	OVII	ZIIB	HSI	ZIIIC	OVIII	HSIII	DII
Mammuthus primigenius	N ab	5	0	2	46	23	13	2	0	10
	% sp	6.7	0.0	3.2	6.2	4.5	12.9	*	0.0	40.0
Coelodonta antiquitatis	N ab	9	2	1	63	38	27	5	10	13
	% sp	11.8	4.7	1.8	10.7	8.6	20.8	16.1	18.5	33.3
Equus sp.	N ab	3	0	5	56	9	11	3	3	2
	% sp	*	*	11.1	14.0	9.7	35.5	*	*	*
Bison priscus	N ab	1	0	2	22	1	3	2	0	1
	% sp	*	*	6.5	10.5	1.9	7.5	*	*	*
Megaloceros giganteus	N ab	0	0	0	15	4	0	1	1	0
	% sp	*	*	*	21.3	*	*	*	*	*
Cervus elaphus	N ab	0	*	1	6	*	0	*	*	*
	% sp	*	*	*	7.6	*	*	*	*	*
Rangifer tarandus	N ab	1	*	*	13	0	3	0	0	1
	% sp	*	*	*	15.5	*	*	*	*	*
Unidentifiable	N ab	1	0	5	49	2	19	3	1	3
TOTAL	N ab	20	2	21	270	77	76	17	15	30
	% TOT	9.2	1.7	5.3	7.9	6.1	11.8	14.2	11.8	33.3

has a Voorhies distribution different from that of the other assemblages, has extremely low CSI values (<5% for mammoth and rhino).

Modification by abrasion

During the transition from thanatocoenosis (community of dead organisms) to taphocoenosis (community of buried dead organisms), bone can be scoured and rounded by the impact of sediment grains. The distance necessary for abrasion of bones depends on local circumstances such as the grain size in the river system, the velocity of the current, the discharge and slope. BEHRENSMEYER (1982) discovered that bones transported by the East Fork River (Wyoming, USA) showed traces of abrasion after 1.5 to 3 km distance.

Table 7a shows the number of abraded bones in each assemblage. The percentages are low: less than 15%, except for Dendermonde II where 33% of the bones have been abraded. Probably at Zemst (Bos van Aa Member) and Hofstade (Lembeke Member) extensive erosion and reworking of sediments was rather limited (BOGEMANS, 1993). The outer surface layer of the bones, especially of the fresh bones, is very smooth and the weathering stages can be confidently identified;

removal of bony surface layer is virtually non existant. Abrasion consists in general of the rounding of the edges of the articular surfaces. Very rounded bones or bone pebbles were not found. Although longer transport of the carcasses can not be excluded, the bones were probably only carried over a relatively short distance and therefore not heavily reworked. At Dendermonde II however, the high frequency of abraded bones and the absence of Voorhies Group 3 of mammoth and rhino point to a transported assemblage.

Correlation between the Behrensmeyer Stages and the frequency of abrasion appears to be possible. The higher the weathering, the more bones are abraded (Table 7b). Fresh bones will resist better, bones in Behrensmeyer Stage 1 or 2 have small cracks and will probably be more easily rounded. There are not enough bones in Behrensmeyer Stage 3 to conclude whether bones in this stage will be more easily abraded with transport or rather splinter or break. According to ANDREWS & ERSOY (1990) there exists also a correlation between the degree of rounding and the degree of weathering of skeletal material. This correlation influences the assemblages as a whole: in general the most weathered assemblages (weathering group 3) are the most abraded (Table 7a).

POST-BURIAL MODIFICATONS

Root action

Bones with root marking occur in small quantities in the Flemish Valley, the frequency lies between 1.7% (assemblage Hofstade II) and 7.9% (assemblage Zemst IIIC) (Table 8). Bones with root traces were buried in the grassroot zone probably on vegetated bars, near minor channels or in the alluvial plain. Probably root marking is not a recent phenomenon in the Flemish Valley assemblages since it occurs on deeply buried

Table 7b — Number (N ab) and relative frequency of abraded bones per weathering stage

		DI	OVII	ZIIB	ZIIIC	OVIII	HSI	HSII	HSIII	DII
Behrensmeyer Stage 0	N ab	2	3	29	10	2	0	0	0	2
	% st	1.4	2.1	1.8	6.8	9.5	0.0	0.0	0.0	6.1
Behrensmeyer Stage 1	N ab	11	12	200	45	10	38	2	9	18
	% st	19.6	5.2	12.0	10.9	13.5	5.9	6.1	14.5	40.9
Behrensmeyer Stage 2	N ab	7	6	40	20	4	35	0	6	10
	% st	46.7	42.9	36.7	25.6	18.2	31.3	0.0	25.0	71.4
Behrensmeyer Stage 3	N ab	0	0	0	1	1	4	0	0	0
	% st	*	*	*	*	*	*	*	*	*
TOTAL	N ab	20	21	270	76	17	77	2	15	30
	% TOT	9.2	5.3	7.9	11.8	14.2	6.1	1.7	11.8	33.3

Table 8 — Number (N rm) and relative frequency of bones with root marks of the Weichselian assemblages

		DI	OVII	ZIIB	ZIIIC	OVIII	HSI	HSII	HSIII	DII
Mammuthus primigenius	N rm	0	1	26	8	1	12	1	0	2
	% sp	0.0	0.6	3.5	8.0	5.0	2.4	2.3	0.0	8.0
Coelodonta antiquitatis	N rm	4	0	26	9	2	26	1	0	3
	% sp	5.7	0.0	4.4	7.0	6.5	5.9	2.3	0.0	7.7
Equus sp.	N rm	6	3	90	6	1	21	0	3	1
	% sp	*	6.7	22.6	19.4	*	22.6	*	*	*
Bison priscus	N rm	2	1	26	4	0	6	0	0	0
	% sp	*	3.2	12.5	10.0	*	11.5	*	*	*
Megaloceros giganteus	N rm	0	0	13	5	0	1	0	0	1
	% sp	*	*	17.3	*	*	*	*	*	*
Cervus elaphus	N rm	0	0	10	0	*	*	*	*	*
	% sp	*	*	12.7	*	*	*	*	*	*
Rangifer tarandus	N rm	1	0	11	0	0	2	*	0	0
	% sp	*	*	13.1	*	*	*	*	*	*
Unidentifiable	N rm	2	2	43	19	5	6	0	1	0
TOTAL	N rm	15	7	245	51	9	74	2	4	7
	% TOT	6.9	1.8	7.3	7.9	7.6	5.9	1.7	3.1	7.9

bones; furthermore, the etched surfaces do not differ in colour from the unaffected surrounding bone pointing to a root mark formation before fossilisation started (Plate 5, Fig. A and B). According to POPLIN (1973) plant roots are chemotactically attracted to buried bones. How long bones will attract plant roots is not clear. ANDREWS & ERSOY (1990) found that recent roots penetrating into a Miocene deposit, were not associated with fossil bones found in the sediment. However, according to BEHRENSMEYER (1991) root marking can also happen after mineralization.

Root traces on mammoth and rhinoceros bones are not frequent in the assemblages (Table 8). In this subenvironment of vegetated bars, minor channels and alluvial plain, less opportunity for burial of the skeletal material of large-sized mammals exists. Being too far away from the active channels, not enough sediment will accumulate there during floods to cover the bones quickly enough. Bones of horse show the highest frequency of root traces in all assemblages. Why horse remains have more root traces than the bones of bison, red deer or reindeer, which are on the whole comparable in size or smaller, and therefore easily covered by sediment or trampled in the mud, can not be explained by body size. Perhaps horse bones occurred more frequently in the plain or near the minor channels since

horses died there more often and were thus better represented in these specific death assemblages. In the subenvironment of channel margins and ponds from the Siwalik rocks of Pakistan BADGLEY (1986) discovered that equids exhibit the highest specimen frequency of all mammals present there. It is remarkable in this respect that the Voorhies Group 3 values for horse point to a lesser occurrence of horse remains in channel lag environments (Table 6).

Corrosion

Pitting and dissolution of the bone surface can result from the attack of acids in ground water (MORLAN, 1980). The frequency of bones with this phenomenon is low, varying between 0% (Hofstade III) and 6.7% (Overmere III) (Table 9). Light, moderate and heavy corrosion occur (Plate 5, Fig. C, D and E).

AGE DISTRIBUTION

Mammuthus primigenius

Several authors use the eruption sequence and wear of the jugal teeth to reconstruct the age distribution of

Table 9 — Number (N cm) and relative frequency of corroded bones of the Weichselian assemblages

		DI	OVII	ZIIB	ZIIIC	OVIII	HSI	HSII	HSIII	DII
Mammuthus primigenius	N cm	1	1	14	2	0	1	1	0	0
	% sp	1.3	0.6	2.0	2.0	*	0.2	2.3	0.0	0.0
Coelodonta antiquitatis	N cm	2	1	20	2	3	0	0	0	0
	% sp	2.6	1.8	3.4	1.6	9.7	0.0	0.0	0.0	0.0
Equus sp.	N cm	0	0	12	0	0	1	0	0	0
	% sp	*	0.0	3.2	0.0	*	1.1	0.0	*	*
Bison priscus	N cm	0	0	15	1	3	0	0	0	0
	% sp	*	0.0	7.5	2.5	*	0.0	*	*	*
Megaloceros giganteus	N cm	0	0	5	0	0	0	0	0	0
	% sp	*	*	7.0	*	*	*	*	*	*
Cervus elaphus	N cm	0	0	7	0	*	*	*	*	*
	% sp	*	*	9.6	*	*	*	*	*	*
Rangifer tarandus	N cm	*	*	7	0	0	0	*	0	0
	% sp	*	*	8.3	*	*	*	*	*	*
Unidentifiable	N cm	2	3	18	2	2	0	0	0	1
TOTAL	N cm	7	9	98	7	8	2	1	0	1
	% TOT	3.2	2.3	2.9	1.1	6.7	0.2	0.8	0.0	1.1

recent and fossil proboscidean assemblages (SAUNDERS, 1977a, b, 1980; HAYNES, 1985, 1991; GERMONPRE, 1985, 1989; SCOTT, 1986; VAN NEER & GERMONPRE, 1991). The two modern elephants are very similar in the major aspects of their biology and behaviour. They possess identical dental formulae, they have a similar gestation period and birth rates and their maximum life span is estimated at about 60 years (OLIVIER, 1982; CONEYBEARE & HAYNES, 1984; HAYNES, 1988, 1991). The African elephant lives in family units of 5 to 12 individuals, composed of two or three related mother-offspring units: the oldest member or the matriarch and one or more mature daughters and their offspring; or in groups of usually sexually mature males (KINGDON, 1979). The Asian elephant has an almost identical social structure based on a matriarchal family unit (MCKAY, 1973). The closely related mammoths probably behaved in a similar way (SAUNDERS, 1980; OLIVIER, ibid.; CONEYBEARE & HAYNES, ibid.; 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 his relative age groups. This method has been criticised (FATTI et al., 1980; JACHMANN, 1988). LAWS' technique has however the advantage of being simple and is therefore used in GERMONPRE (1989) and here in an adapted form: LAWS' classes are combined into 6 groups (see Table 10) and are assigned an "African elephant year" age which is the corrected age given by CRAIG in HAYNES (1991 table A2, A8) for the African elephant. This age attribution facilitates calculations and comparisons without implying real absolute ages for the mammoths. Isolated teeth can also be assigned to the regrouped age classes. Furthermore, by regrouping the classes, the error in age attribution is reduced.

Table 10 — Age groups based on LAWS (1966) (GERMON-PRE, 1989) and their alleged ages (A.e.y.: African elephant years, CRAIG in HAYNES, 1991) for woolly mammoth (Mammuthus primigenius)

GROUP GERMONPRE (1989)	LAWS' classes (1966)	A.e.y.	Characteristics
A	I - III	0.0 - 1.9	M1 - M2
B	IV - VI	2.0 - 4.9	M2 - M3
C	VII - X	5.0 - 11.9	M3 - M4, plates M3 100% abraded
D	XI - XVI	12.0 - 21.9	M4 - M5, plates M4 100% abraded
E1	XVII - XX	22.0 - 34.9	M5 - M6, plates M5 100% abraded plates M6 < 50% abraded
E2	XXI - XXV	35.0 - 47.9	M5 - M6, plates M6 50 - 100% abraded
F	XXVI - XXX	48.0 - 60.0	M6, plates 100% abraded

Table 11a — Distribution of the age groups of woolly mammoth (Mammuthus primigenius) based on the teeth in the jaw (N: number of jaws)

GROUP	Zemst IIB N	%	Hofstade I N	%
A	1	5.0		
B	2	10.0	}1*	}6.7
C	2	10.0		
D	4	20.0	3	20.0
E1	7	35.0	3	20.0
E2	4	20.0	6	40.0
F	0	0.0	2	13.3
Total	20	100.0	14	100.0

* juvenile mandible without teeth

Table 11b — Distribution of the age groups of woolly mammoth (Mammuthus primigenius) based on all teeth (N: number of jaws)

GROUP	Zemst IIB N	%	Hofstade I N	%	Overmere II N	%
A	3	3.2			0	0.0
B	5	5.3	}1*	}2.0	2	10.5
C	9	9.6			0	0.0
D	10	10.6	7	14.0	5	26.3
E1	23	24.5	13	26.0	3	15.8
E2	21	22.3	20	40.0	6	31.6
F	23	24.5	9	18.0	3	15.8
Total	94	100.0	49	100.0	19	100.0

* juvenile mandible without teeth

The age distribution of the fossil remains of woolly mammoth of assemblages Zemst IIB, Hofstade I and Overmere II is given in Table 11 and Fig. 7 and 8. The distribution of assemblages Zemst IIB and Hofstade I is based on the teeth in situ and on isolated teeth, the one of assemblage Overmere II is based solely on isolated teeth. Juvenile mammoth remains are very scanty in assemblage Hofstade I. Why these age classes are less well represented in this assemblage than in assemblages Zemst IIB and Overmere II is not clear. One possible explanation could be scavenger activity which is higher during accumulation of assemblage Hofstade I (cf. high percentage of gnawing traces) than of assemblages Zemst IIB and Overmere II. Also, the collecting of the fossil bones of assemblage Hofstade I could be more biased. However, the assemblages of the Flemish Valley show in general a comparable trend. They are notable for their relatively high frequency of prime-age classes D, E1 and E2. They do not correspond with the classical catastrophic age profile, but they are also somewhat different from the classical attritional profile (VOORHIES, 1969; SHIPMAN, 1981). Attritional profiles are characterised by a high number of very young and old individuals; mortality is caused by juvenile weak-
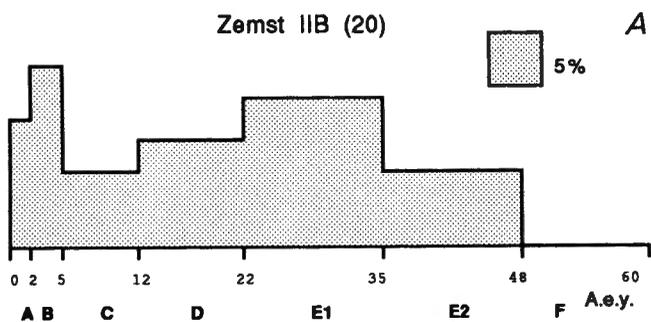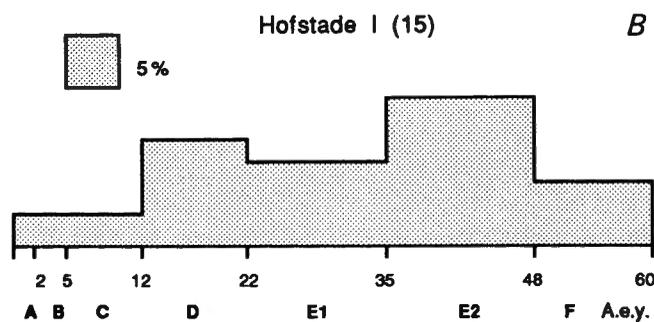
Zemst IIB (20)   A

Mammuthus primigenius

Hofstade I (15)   B

Mammuthus primigenius

Figure 7 — Age profiles based on mandibular dentition of woolly mammoth (*Mammuthus primigenius*) of assemblages Zemst IIB (A) and Hofstade I (B), groups based on regrouped age classes of LAWS (1966) (GERMONPRE, 1989)

ness, disease, predation and old age (KOSTER, 1987; BEHRENSMEYER, 1991). In mass mortalities or catastrophic profiles, representation diminishes with age, the profile reflects the age distribution of a living population which is essentially stable in size and structure. Mass mortality follows sudden changes in ecological conditions such as floods, droughts or epidemics (KLEIN, 1987; KOSTER, *ibid.;* BEHRENS-MEYER, *ibid.*).

The age distribution of recent African elephants based on jaws collected in the Murchison Falls Park and the Queen Elisabeth Park in Uganda shows a relative high percentage of age groups XI - XX (LAWS 1966: table 5). LAWS (*ibid.*) supposed that the elephants died in the period 1962 - 65. Remains of very young animals are underrepresented: they are less easily spotted and less resistant to weathering and scavengers. The clear preponderance of groups XI - XX (12 - 35 African elephant years) is noteworthy. The African elephant reaches sexual maturity at an age varying between 8 and 14 years (LAWS, 1966; FRADE, 1955; HAYNES, 1988), depending upon nutritional status. In Asian elephants, puberty occurs between the ages of 8 and 10 (MCKAY, 1973). The male animals leave the herd two or three years later and live alone or in temporary all-male

groups (OLIVIER, 1982). However, since the bonds in such groups are not strong, the animals more easily become victims of predators or poachers; this could explain the excessive representation of classes XI - XX in the age profile of LAWS (*ibid.*). According to COR-FIELD (1973) male elephants from about 25 years are especially vulnerable, for ivory poachers will select adult bulls where possible. According to MCKAY (*ibid.*) there is a higher mortality among subadult male Asian elephants since young males recently separated from the herd would be quite vulnerable.

Mass mortality of African elephant populations occurred in Tsavo National Park (Kenya) during the dry
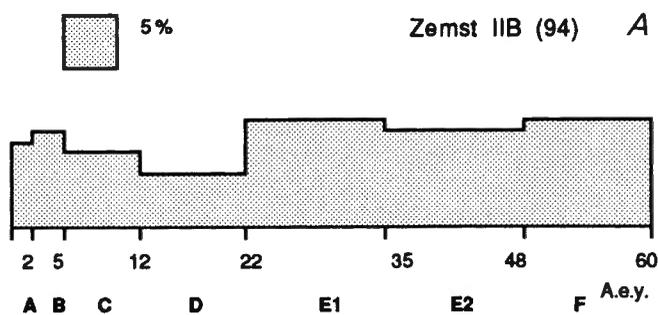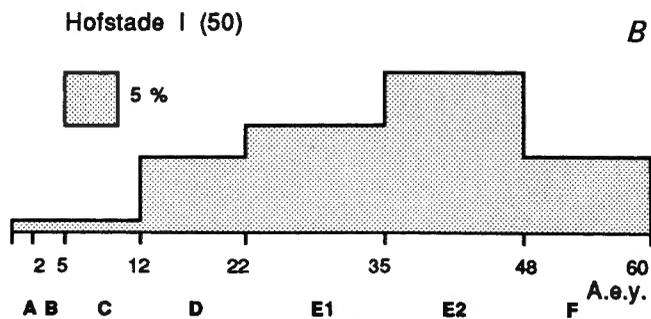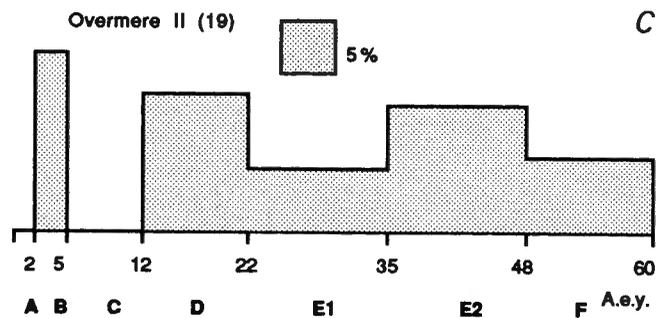
Zemst IIB (94)   A

Mammuthus primigenius

Hofstade I (50)   B

Mammuthus primigenius

Overmere II (19)   C

Mammuthus primigenius

Figure 8 — Age profiles based on all teeth of woolly mammoth (*Mammuthus primigenius*) of assemblages Zemst IIB (A), Hofstade I (B), Overmere II (C), groups based on regrouped age classes of LAWS (1966) (GERMONPRE, 1989)

years 1970 and 1971 (CORFIELD, 1973: table 5). Mortality was clearly concentrated along water courses and permanent waterbodies, and was age and sex-specific (CORFIELD, ibid.). HAYNES (1985) notes the same phenomenon during the two consecutive dry years 1982-1983 in Zimbabwe.

The age distributions of mammoths in the Flemish Valley, including the one of Rotselaar (VAN NEER & GERMONPRE, 1991), are clearly not in the range of mass mortality distribution of Tsavo National Park (CORFIELD, 1973) and Zimbabwe (HAYNES, 1985) but are more similar to the supposed attritional mortality profile of LAWS (ibid.). Also, they compare very well with the age distribution of the Middle Pleistocene Ambrona elephants (KLEIN, 1987: fig. 7). The Ambrosa mortality profile suggests death from accidents, disease and old age (KLEIN, ibid.).

The age profiles of assemblages Zemst IIB, Overmere II and Hofstade I correspond in general to the description of the type C profile of HAYNES (1991, 218): "In type C, subadults are conspicuously rare, and prime-age adults predominate. This type represents selective mortality over an extended period of time". Furthermore he adds (ibid., 231): "In North America, the largest mass assemblages of mammoths are of type C when artifacts are not present."

At Zemst (BOGEMANS & CASPAR, 1984; VAN PEER & SMITH, 1990) and Overmere a few stone artefacts were found. No artefacts, associated with assemblage Hofstade I, are known. The Zemst artefacts have been described and attributed to a "Moustérien typique" (VAN PEER & SMITH, ibid.). It is thought that groups of Middle Palaeolithic man visited regularly or seasonaly the area in search of meat which they obtained by hunting or scavenging. The small number of artefacts would indicate that the occupations were only of a limited duration (VAN PEER & SMITH, ibid.).

The foregoing indicates that hunting was not a primary cause of mammoth mortality in the Flemish Valley. Moreover, HAYNES (1991) argued convincingly that hunting elephants, and related pachyderms, was not a regular sport of Palaeolithic man. The few artefacts, found in the fossiliferous layers, could have been used by scavenging hominids.

Four tusk fragments of assemblage Hofstade I show a remarkable shape (Plate 3, Fig. A). The scraps consist of polished, obliquely broken end points of tusks with a length of 200 to 250 mm. They can be compared with African elephant tusk fragments found near the natural water source Shabi Shabi in Zimbabwe (CONEYBEARE & HAYNES, 1984). According to HAYNES (1988, 1991) tip of tusks are frequently broken off during violent intraspecific encounters, they can also break by use in feeding and de-barking trees. Probably such breakage can only be during life, since it must result from excessive bending with a great load exerted on the tusk (HAYNES, pers. comm. 1986). Also according to KINGDON (1979) the ends of living ivory can snap off when stressed too far. According to VERESHCHAGIN &

BARYSHNIKOV (1982, 1991), mammoths could damage their tusks by breaking ice which they swallowed to releave their thirst during dry and snowless winters.The fragmentation of the Hofstade tusks could be caused during violent interaction of the animals, by breaking ice or some yet unknown behaviour of the animals.

Coelodonta antiquitatis

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. Furthermore, he assigned tentative and approximate mean ages to each class. The eruption of the definite mandibular teeth occurs in a specific sequence (GODDARD, ibid.): the first molar (M1) erupts while deciduous D2, D3, D4 are functional; in a next step permanent M2 and P2, P3 erupt; the last deciduous teeth disappear when P4 erupts; M3 is the last molar to appear. The same sequence for rhinoceros in general was described by GUERIN (1980) and FORTELIUS (1985). There are enough lower jaws (22) of woolly rhinoceros present in assemblage Hofstade I to check the sequence of dental eruption in this species (Plate 6). The pattern is very similar to the one of the black rhino. Although the woolly rhinoceros can not be considered as an ecological homologue to the black rhino the age classes of GODDARD (ibid.) can be used to subdivide the woolly rhino material. This was also done by SCOTT (1986) for the woolly rhinoceros of La Cotte de St. Brelade (Jersey). GODDARD's classes are regrouped into 8 groups to facilitate attribution of mandibules and to reduce the error in age assignment (GERMONPRE, 1989). The woolly rhino classes are attributed a "black rhino

Table 12 — Regrouped age groups of woolly rhinoceros (Coelodonta antiquitatis) (GERMONPRE, 1989) based on the classes defined by GODDARD (1970) and their alleged ages (b.r.y.: black rhinoceros years)

GROUP	GODDARD's Classes	b.r.y.	Characteristics of mandibular dentition
A	I - III	0 - 1	milk dentition present, bud M1 present
B	IV - VI	1.5 - 3	milk dentition in wear, M1 erupting, bud M2 present
C	VII - VIII	4 - 5	milk dentition in wear, P2, P3, M2 erupting P4 present as bud or erupting, bud M3 present
D	IX - X	6 - 7	P2, P3, P4 replaced milk dentition P2, M1: exposed dentine between cusps joined, M3 erupting
E	XI - XII	8 - 9	permanent dentition complet, P3, P4: exposed dentine cusps joined, often also of M2, M3 in slight wear
F	XIII - XIV	10 - 12	M1: exposed dentine between cusps of broadly joined, M3: exposed rarely joined
G	XV - XVII	14 - 21	P2, P3 sometimes missing, M1: dentine continuous or completely worn, M3: dentine between cusps joined
H	XVIII - XX	25 - 40	P2, P3, P4, M1: often missing M2: completely worn, M3: dentine broadly joined

year" age which does not imply an absolute age but enables a better visualisation of the age structure of the rhino assemblage. The characteristics of the regrouped groups are described in Table 12.
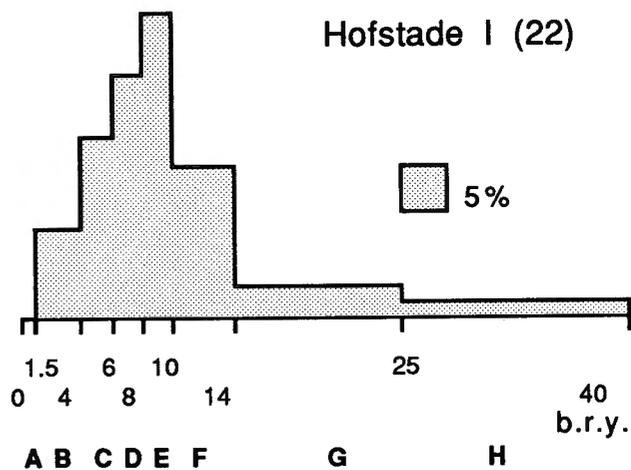
The age distribution of the woolly rhino of assemblage Hofstade I is given in Table 13 and Fig. 9. Fig. 10 shows the age distribution of 477 mandibules of black rhinoceros collected in Tsavo National Park (Kenya) at the end of the 1960s (GODDARD, *ibid*.) and is derived from the data compiled by GODDARD (*ibid*.: table 6). GODDARD (*ibid*.) assumed that his collection represented animals that died during the previous decade (1958-1968). Some years before the collecting started a severe drought occurred (1960-1961) which caused the starvation of about 300 black rhinoceros along the Athi river (TREMLETT, 1961 *fide* GODDARD, *ibid*.; FOSTER, 1965). The profile of the Tsavo rhinos is not of the attritional mortality type: the older age groups are not well enough represented and on the other hand the profile displays a subadult and prime adult peak.

HUNT (1990) described the age profile of rhinoceros remains, found in waterhole deposits and dating from the Early Miocene of Nebraska. The profile (HUNT, *ibid*.: fig. 27) shows, just as the Hofstade I profile, a good representation of subadults and prime adults and few aged individuals. According to HUNT (*ibid*.) the death of the animals was influenced by drought.

The age profile of the woolly rhinoceros of assemblage Hofstade I compares very well with the age distributions of Tsavo National Park, Kenya and of the Miocene of Nebraska. It is characterised by low frequency of aged rhinoceroses and a peak of subadult and prime adult animals (group D and E). The under-representation of material of very young rhinos is attributed to the greater susceptibility of juvenile remains to weathering and scavenging (carnivores were very active on this site, cf. the high percentage of gnawing traces). It is not clear what caused the
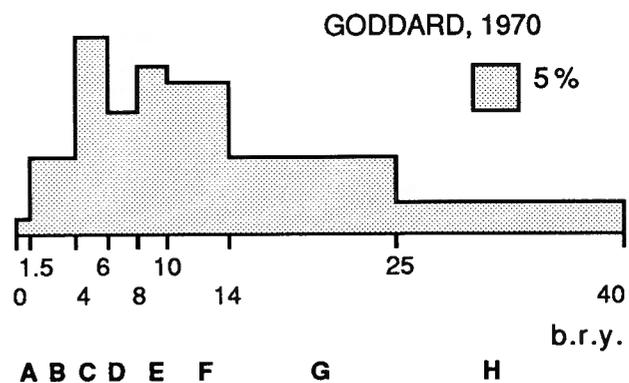

Coelodonta antiquitatis

Figure 9 — Age profile based on mandibular dentition of woolly rhinoceros (*Coelodonta antiquitatis*) of assemblage Hofstade I, groups based on regrouped age classes of GODDARD (1970) (GERMONPRE, 1989)

Diceros bicornis

Figure 10 — Age profile of black rhinoceros (*Diceros bicornis*) in Tsavo National Park, Kenya, based on GODDARD (1970, table 6), groups based on regrouped age classes of GODDARD (1970) (GERMONPRE, 1989)

Table 13 — Age profile of woolly rhinoceros (*Coelodonta antiquitatis*) of assemblage Hofstade I

GROUP	N	%
A	0	0.0
B	2	9.1
C	3	13.7
D	4	18.2
E	5	22.7
F	5	22.7
G	2	9.1
H	1	4.5
Total	22	100.0

preponderance of subadults and prime adults. The profile of rhinoceros from assemblage Hofstade I suggest that skeletons accumulated as a result of either single or regularly recurring events causing excessive deaths. More likely, the profile results from recurrent events. If the profile resulted from one event the burial of the remains of assemblage Hofstade I must have occurred over a very short period, otherwise attritional mortality would have overprinted the mass mortality profile.

Maybe a combination of harsh winter conditions preceded or followed by a prolonged drought period was fatal to many rhinos of Hofstade. Furthermore, sedimentary features of the Lembeke Member indicate a continental paleoclimate characterized by extreme temperatures and little precipitation (BOGEMANS, 1993). But the question remains why the event, causing mass mortality in the rhinos, is not reflected in the Hofstade I profile of mammoth (Figs 7 & 8, Table 11).

Discrepancies of age profiles have been observed in the fossil record, for example at the Miocene site of Paşalar (Turkey). Large mammals are in general better represented by adults than by juveniles, exceptions are the rhinocerotid *Begertherium* BELIAEVA, the suid *Listriodon* VON MEYER and the giraffid *Giraffokeryx* PILGRIM material which contain a high portion of juveniles. The presence of these age-structure anomalies are explained by predator activity (ANDREWS & ERSOY, 1990; FORTELIUS, 1990; FORTELIUS & BERNOR, 1990). Carnivores were quite active on the site of Hofstade, at least as scavengers, as can be judged by gnawing traces left on bone. Although the percentage of gnawed rhino bone lies almost 10% above the mean of the assemblage (Table 4), to hold carnivores responsible for killing subadult and young adult rhinos is doubtful. It is more likely that differential response to ecological stress accounts for the observed difference in age profiles. According to KINGDON (1979: 66) in periods of drought rhinoceroses are 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."

The fact that proboscideans are more mobile than rhinoceroses can also have played a role. CHURCHER (1978) noted that mammoths could cover distances up to 2500 km, but OLIVIER (1982) put forward a lower figure (650 km). Migrations of the African elephant are not well documented and movements are normally local and restricted to the home range. Also, elephants can go up to four days without drinking water as noticed by VILJOEN (1989) in the Namib desert. Recent African elephants, in at least part of the Tsavo area, Kenya, may move over distance of 80 km or more in response to localized rainfall, which brings out flushes of new vegetation (LEUTHOLD & SALE, 1973).

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, having a larger range, escaped. The mammoth tusks scraps, however, could indicate stress situations.

SEASONALITY

The presence of male deer (and female reindeer) at a certain season can be deduced by the condition of the antlers found at a site. Deer shed their antlers at a particular time of the year and start afterwards growing a new one which is at a certain period of the year fully grown and cleaned of velvet.

Cervus elaphus

The number of antler fragments of red deer found in the assemblages is given in Table 14. Male red deer cast their antlers at the end of winter (February) or beginning of spring (March-April) (BANFIELD, 1974; MITCHELL et al., 1976; BUTZLER, 1986). Antlers are full grown and free of velvet by the summer (July-September) (BANFIELD, ibid., BUTZLER, ibid.). Antlers in velvet are very prone to decay and probably do not fossilise (PAYNE, 1972, STURDY, 1975). Shed antlers were recovered from assemblages Overmere II, Zemst IIB and Zemst IIIC. Consequentially, stags visited these sites during spring. Skull remains with antlers attached were found in assemblages Overmere I, Overmere II and Zemst IIB. The stags could have died during the rut or fallen victim to harsh winter conditions. Due to the high energy demands of the rut, the stags enter this season weakened; as a result they are subject to a higher winter mortality than females (KITCHENER, 1991). At the time of the accumulation of assemblages Overmere II and Zemst IIB, red deer stags were present in spring, winter and/or autumn.
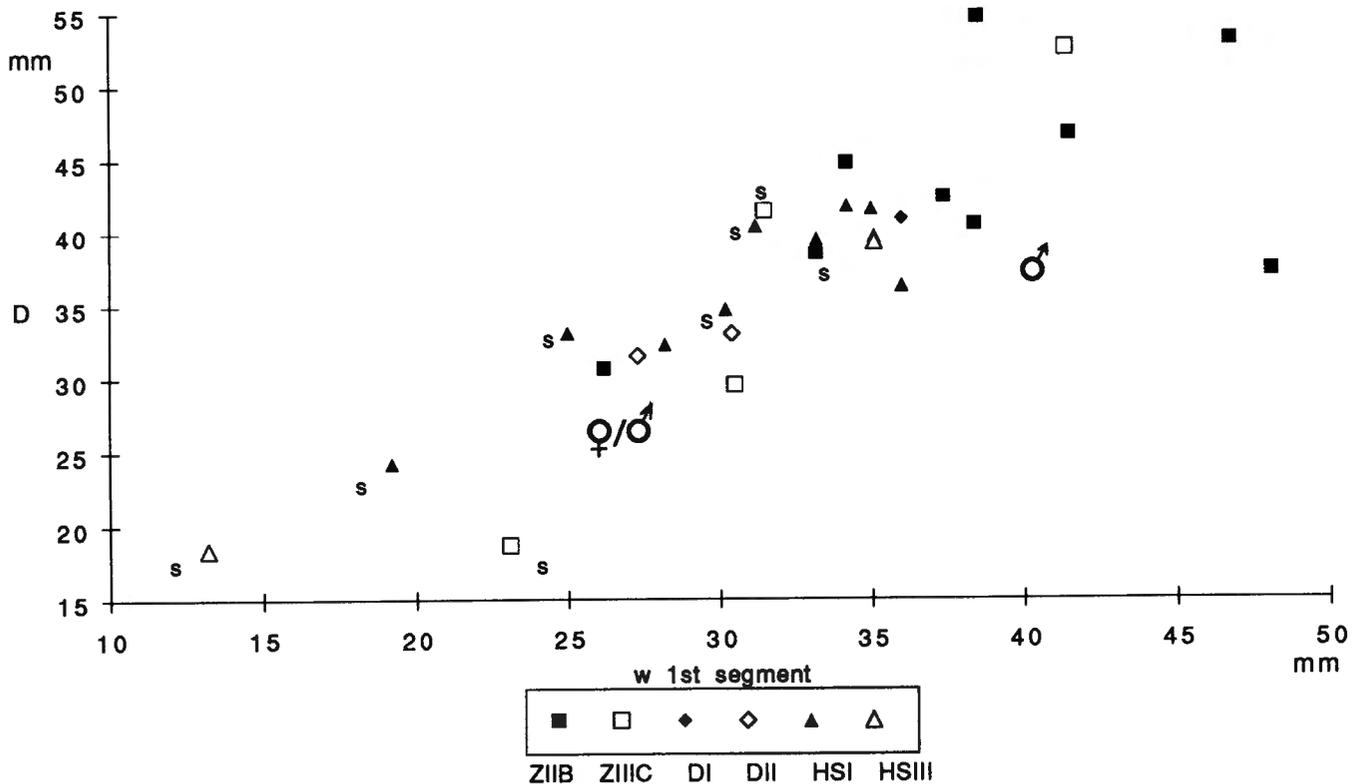
Rangifer tarandus

Reindeer are unique among the cervids in that the cows frequently grow antlers (BANFIELD, 1974). The antler of the male is much bigger than that of the female. The distinction between the antler of a female and of a young male reindeer is difficult to make. To distinguish the antlers of adult males and young adults/females the method of BOUCHUD (1966) as adapted by STURDY (1975) is used. The width is plotted against the thickness; the two diameters are measured between the first and second brow tine. The results are given in Table 15. Two groups can be recognized (Fig. 11). The sexing of the cast antlers on base of the concavity or convexity

Table 14 — Antlers of red deer (*Cervus elaphus*) of the Weichselian assemblages

	Shed	Unshed	Total
Overmere I	*	1	1
Overmere II	1	1	2
Zemst IIB	7	4	11
Zemst IIIC	3	*	3

Table 15 — Antlers of reindeer (*Rangifer tarandus*) of the Weichselian assemblages

	Shed		Unshed		?	Total
	male	female/male	male	female/male		
Zemst IIB	1	*	7	1	8	17
Zemst IIIC	1	1	1	1	2	6
Hofstade I	1	3	4	1	2	11
Hofstade III	*	1	1	*	*	2
Dendermonde I	*	*	1	1	*	2
Dendermonde II	*	2	*	*	*	2

Figure 11 — Beam measurements between first and second brow tine of adult male and young male/female antlers of reindeer (*Rangifer tarandus*) (absciss: width, ordinate: depth)

of the fracture (BOUCHUD, 1966) is somewhat confusing and has not been used here.

Recent European reindeer cows cast their antler in spring (April-May), after the birth of the calves. Older males shed their antler in November after the rut and young males in early spring (February-March) (BOUCHUD, *ibid.*, HERRE, 1986). According to BANFIELD (1974) the antlers of male Canadian caribous are clean of velvet by early autumn (September), later in autumn (November), the older bulls begin to drop their antlers and at the end of the winter (February) most of the younger males have shed theirs as well. Cows carry their antlers until late spring and lose them after the

birth of the calves (April-May), which are born on the summer pastures. After the rut, the Canadian caribou migrate to their winter pastures. According to HERRE (*ibid.*) the recent European reindeer do not really migrate.

During autumn, male reindeer visited the area of Zemst as is evidenced by the presence of seven large antlers with skulls attached in assemblage Zemst IIB. The bulls died here probably during the mating season. One skull shows asymmetric antler formation (GERMONPRE, 1986). A single male reindeer lost its antlers before moving to the winter grounds which the reindeer probably spent elsewhere. Cast antlers of the group

young adult/female reindeer were not found at Zemst IIB although a fragment of an unshed antler of this group occur. Assemblage Zemst IIB reindeer probably only used the Zemst grounds rather briefly.

Assemblage Hofstade I contains four unshed antlers of bulls pointing to the presence of reindeer during autumn. One cast antler of a male reindeer was found, extending the presence to early winter. The occurrence of three shed antlers of young adults/females is more problematic, if belonging to young males, the reindeer were at the site during winter. In the other case cows visited the area during spring.

The number of antlers present in assemblages Zemst IIIC, Dendermonde I, Dendermonde II and Hofstade III are too small to allow any interpretation.

Megaloceros giganteus

Table 16 gives the number of shed and unshed antlers that were recovered. According to BARNOSKY (1985) the giant deer lost it antlers during spring. Consequentially, male giant deer were present at the sites of Zemst (assemblage Zemst IIB) and Hofstade (assemblages Hofstade I and Hofstade III) during that season. Furthermore, in assemblage Zemst IIB skull fragments with full grown antlers were found belonging to male giant deer, which did not survive the hardships of autumn and/or winter.

Table 16 — Antlers of giant deer (*Megaloceros giganteus*) of the Weichselian assemblages

	Shed	Unshed	Total
Zemst IIB	6	3	9
Hofstade I	8	*	8
Hofstade III	1	*	1

Discussion and conclusion

The studied mammalian fauna of the Flemish Valley is clearly influenced by the deteriorating climatic conditions of the Weichselian. From the Early Glacial onwards large grazers dominate the fauna. Temperate species disappear in the course of the Early Glacial. Furthermore, microevolutinary trends in the dentition of woolly mammoth, such as an increase in the lamellar frequency and the shearing index, and the size reduction of horse (GERMONPRE, 1989; VAN NEER & GERMONPRE, 1991) could correspond to the declining ecological circumstances. Fossil remains of the main glaciation and of the Late Glacial have only been sparsely encountered in the Flemish Valley (GAUTIER, 1975; GAUTIER et al., 1986).

A first taphonomic model for the Last Glacial assemblages of the Flemish Valley was developed by GAUTIER (1974, 1985). According to this author, herbivores concentrated during winter in the valleys for protection and food. The mortality was relatively high. Due to the low temperatures decay of the carrion was postponed. In spring carcasses were contaminated by the blowfly *Protophormia terraenovae* ROBINEAU-DESVOIDY 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 which permitted the conservation of the puparia.

This scenario can now be extended. In general, it can be concluded that the occurrences of bones in the braided-fluvial deposits of the Flemish Valley are the result of gradual, long-term accumulations of skeletal remains of medium-sized to very large mammals that died within the confines of valleys by attritional death causes due to predation, disease, accident and aging. Probably most deaths occurred during winter which is the most difficult season for mammals. Food and water are limited and the weakened herbivores, which gathered in the valleys succombed to the harsh conditions or fell easily prey to carnivores. Some of the remains on the braided plain were scavenged and weathered before burial, which could have happened during floods if the rate of sedimentation was high enough. However, a large part of the bone sample underwent some degree of transport. Fluvial agencies, active in the braided plain, collected the remains, consisting of carcasses, fragmented body parts but particularly of isolated bones, and deposited them in accordance with their hydraulic properties and the prevailing flow conditions. Abrasion of the bones is in general rather limited. The distance of the source area of the bones is therefore thought not to be very far away from the site of deposition, perhaps at most a few kilometers. Carcasses however, could have been transported over longer distances.

The dispersed and isolated occurence of the remains, the frequencies of weathered and scavenged bones, the low CSI (corrected number of specimens per individual) values, the preponderance of Voorhies Group 3, the large number of ungulate remains and the age profiles of woolly mammoth confirm the foregoing model. However, the taphonomic history and the paleoecology of some assemblages can be refined. Zemst was, during the accumulation of assemblage Zemst IIB, visited by reindeer in autumn; giant deer were present during spring, winter and/or autumn as were also red deer. The presence of the latter combined with the scanty remains of beaver, roe deer, wild hogs and aurochs, points to rather mild conditions and to the existence of locally wooded areas or parkland. The preponderance of woolly mammoth, woolly rhinoceros, steppe bison and horse indicates widely spread grassland.

In assemblage Zemst IIIC beaver, roe deer, wild hog and aurochs are lacking. Only red deer persists. Again large grazers are most frequent indicating an open

environment. The composition of the fauna and the weathering rate of the bones seem to point to a colder and drier environment than during the accumulation of assemblage Zemst IIB.

From a taphonomic and biometric point of view assemblages Overmere II and Overmere III can be correlated respectively with assemblages ZIIB and Zemst IIIC (GERMONPRE, 1989); they pertain, just as Dendermonde I, to the Early Weichselian antidating the Amersfoort and Brörup s.s. interstadials. Furthermore, in the Early Weichselian, which is relatively warm compared to the Pleniglacial (STUART, 1991), a cooling and drying trend can be detected.

The remaining assemblages (Hofstade I, Hofstade II, Hofstade III, Dendermonde II) belong to the Pleniglacial, being limited to the early and middle part of it. Temperate species such as red deer, roe deer, wild hog and aurochs are lacking completely. The species present such as woolly mammoth, woolly rhino, horse and bison, indicate steppe-tundra. The relative high frequency of gnawed bones may point to lower abundance of prey and lower herbivore biomass. Harsher conditions are also indicated by the mass-mortality profile of woolly rhinoceros of assemblage Hofstade I, suggesting recurrent severe cold-dry periods causing catastrophic mortalities of rhinoceros.

The number of abraded bones and the absence of Voorhies Group 3 point to the transported character of assemblage Dendermonde II.

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PLATE 1

A: Zemst: outcrop of the blue-grey sands of the Bos van Aa Member in which assemblage Zemst IIB is found

B: Zemst: rib of woolly mammoth (*Mammuthus primigenius*) (assemblage Zemst IIB) *in situ* in the blue grey sands of the Bos van Aa Member

C: Zemst: detail of the rusty coarse gravelly sands of the Bos van Aa Member with a vertebra of woolly rhinoceros (*Coelodonta antiquitatis*) (assemblage Zemst IIIC)
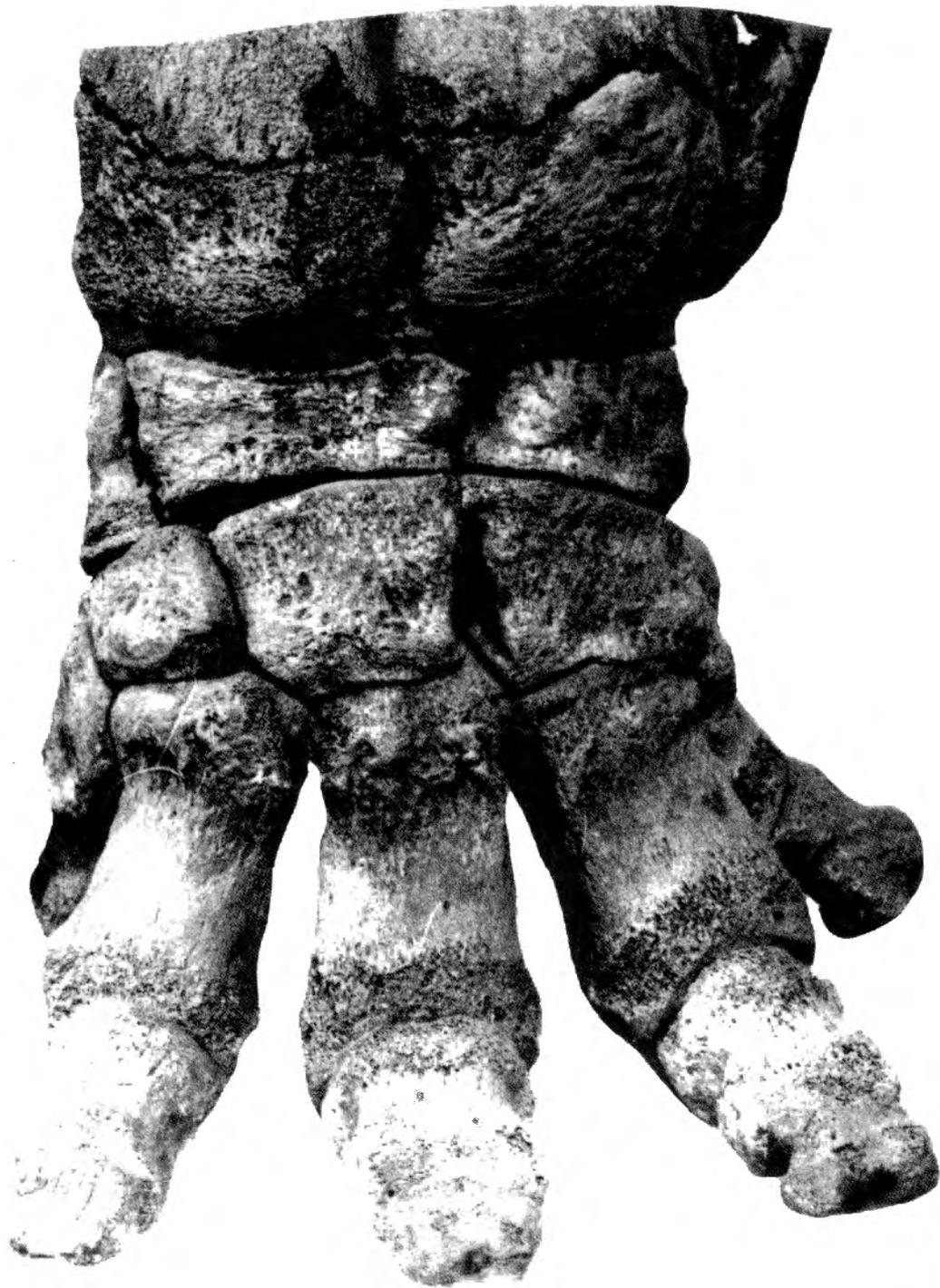
A

B

C

PLATE 2

Left forefoot of woolly mammoth (*Mammuthus primigenius*), part of an associated skeleton found *in situ* at Overmere (collection M. Verdonck)
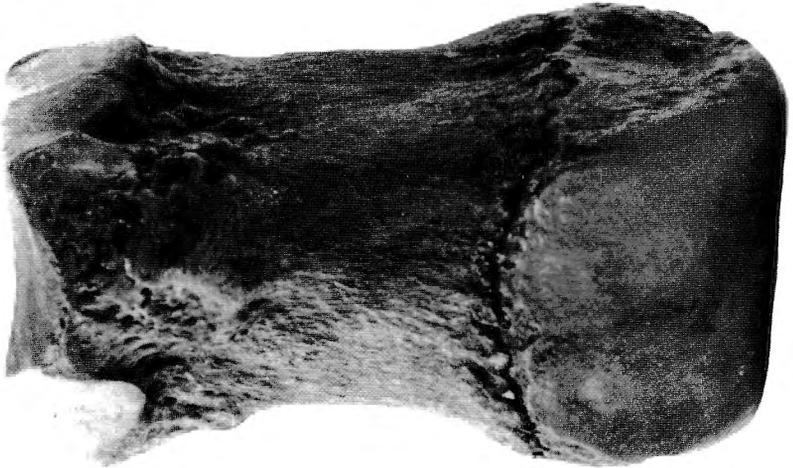
0   2   4   6   cm
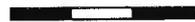
PLATE 3

A: Tusk tip of woolly mammoth (*Mammuthus primigenius*) (assemblage Hofstade I, collection KBIN, M1568)

B: Unfused metatarsal IV of woolly mammoth: distal epiphysis found *in situ* with the shaft (left: unfused bone parts, right: same bone articulated) (assemblage Zemst IIB, collection of M. G. Van der Elst)
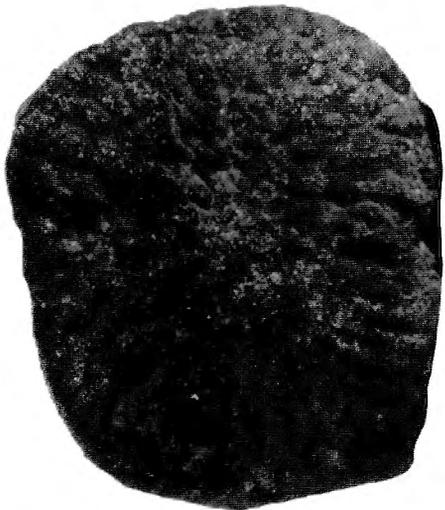
PLATE 4

A: Humerus of woolly rhinoceros (*Coelodonta antiquitatis*) showing gouging by spotted hyaena in proximal half (anterior view) (assemblage Zemst IIB, collection KBIN, M1569)

B: Humerus of woolly rhinoceros proximally and distally gnawed by spotted hyaena (lateral view) (assemblage Zemst IIB collection KBIN, M1570)

C: Forked metatarsus of horse (*Equus* cf. *ferus*) chewed by an artiodactyle (anterior view) (assemblage Hofstade II, collection KBIN, M1571)
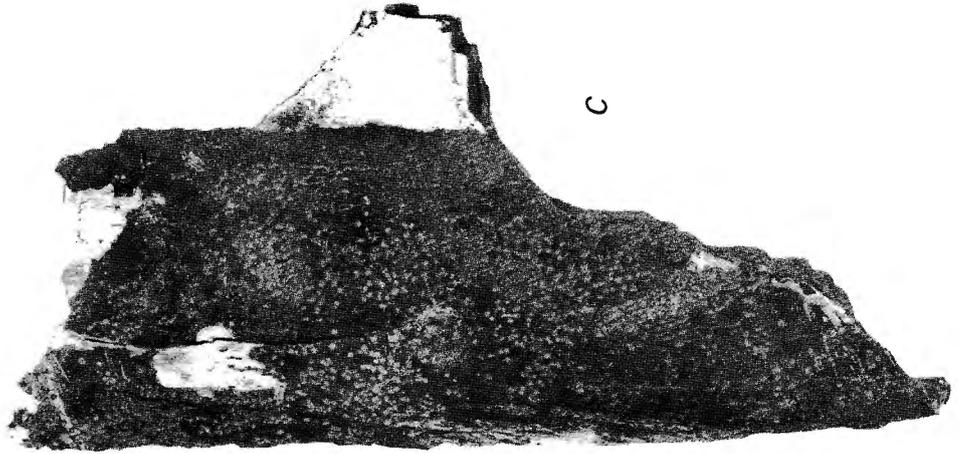
PLATE 5

A: Rib fragment showing extensive root marks (assemblage Zemst IIIC, collection KBIN, M1572)

B: Root marks on humerus fragment of red deer (*Cervus elaphus*); the proximal gnawing traces and the root marks in the bone cavity are not shown (lateral view) (assemblage Zemst IIB, collection KBIN, M1572)

C: Mammoth ivory showing light corrosion (assemblage Zemst IIB, collection KBIN, M1573)

D: Rib fragment showing moderate corrosion (assemblage Zemst IIB, collection KBIN, M1574)

E: Humerus of bison (*Bison priscus*) showing heavy corrosion (anterior view) (assemblage Zemst IIB, collection KBIN, M1575)
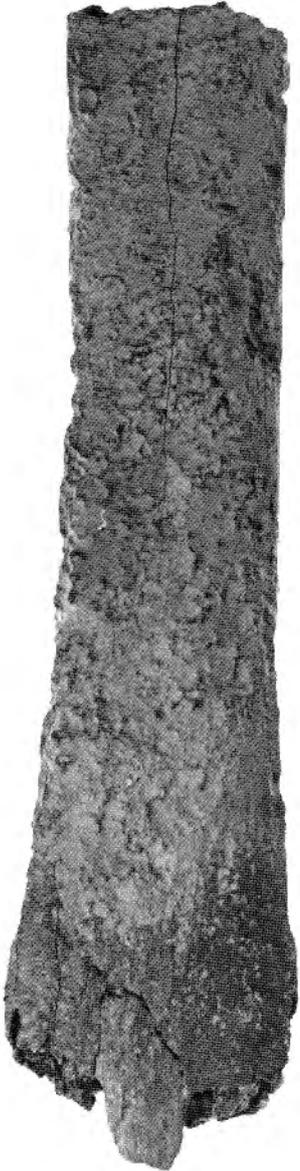
PLATE 6

Mandibles of woolly rhinoceros (*Coelodonta antiquitatis*) of assemblage Hofstade I, all were chewed by carnivores

A: Age group B (collection KBIN, M1576)
B: Age group D (collection KBIN, M1577)
C: Age group E (collection KBIN, M1578)
D: Age group G (collection KBIN, M1579)