



Stable isotope compositions of mammoth teeth from Niederweningen, Switzerland: Implications for the Late Pleistocene climate, environment, and diet

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Abstract

Oxygen and carbon isotope compositions of well-preserved mammoth teeth from the Middle Würmian (40–70 ka) peat layer of Niederweningen, the most important mammoth site in Switzerland, were analysed to reconstruct Late Pleistocene palaeoclimatic and palaeoenvironmental conditions. Drinking water $\delta^{18}\text{O}$ values of approximately $-12.3 \pm 0.9\%$ were calculated from oxygen isotope compositions of mammoth tooth enamel apatite using a species-specific calibration for modern elephants. These $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values reflect the mean oxygen isotope composition of the palaeo-precipitation and are similar to those directly measured for Late Pleistocene groundwater from aquifers in northern Switzerland and southern Germany. Using a present-day $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ -precipitation–air temperature relation for Switzerland, a mean annual air temperature (MAT) of around 4.3 ± 2.1 °C can be calculated for the Middle Würmian at this site. This MAT is in good agreement with palaeotemperature estimates on the basis of Middle Würmian groundwater recharge temperatures and beetle assemblages. Hence, the climatic conditions in this region were around 4 °C cooler during the Middle Würmian interstadial phase, around 45–50 ka BP, than they are today.

During this period the mammoths from Niederweningen lived in an open tundra-like, C_3 plant-dominated environment as indicated by enamel $\delta^{13}\text{C}$ values of $-11.5 \pm 0.3\%$ and pollen and macroplant fossils found in the embedding peat. The low variability of enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from different mammoth teeth reflects similar environmental conditions and supports a relatively small time frame for the fossil assemblage.

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1. Introduction

1.1. The mammoths

The mammoth lineage developed in Africa and appeared in Europe about 3 Ma ago, evolving over several stages from *Mammuthus meridionalis*, *Mammuthus trogontherii* to the woolly mammoth *Mammuthus primigenius* (Lister and Sher, 2001). *M. primigenius* appeared in central Europe during the Early Pleistocene glaciation after 200 ka but originated in NE Siberia considerably earlier, probably around 800 ka (Lister and Sher, 2001). *M. primigenius* was

present over most of Europe during much of the Last Cold stage from ca. 115–10 ka BP while around 9.6 ka BP the last mammoths disappeared from the Eurasian mainland (MacPhee et al., 2002; Stuart et al., 2002). Isolated dwarf forms of mammoths survived into the Holocene on St. Paul Island, Alaska until 7.9 ka BP (Guthrie, 2004) and even until 3.7 ka BP on the Wrangel Islands in the eastern Arctic Ocean (Vartanyan et al., 1993, 1995; Kuzmin and Orlova, 2004). The mammoth with its thick fur, isolating fat layer and small ears was essentially an elephant species adapted to the cold climate and open habitat of the tundra-like Mammoth Steppe environment (Guthrie, 1982; Kubiak, 1982). They were large herbivores capable of digesting large quantities (~150–300 kg/day) of nutrient-poor plants with low-protein and high-fibre content (Guthrie, 1982). Mammoths fed dominantly on grasses and sedges but

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additionally some shrubs, mosses and young twigs and bark of trees and bushes like *Larix*, *Salix*, *Alnus* and *Betula* that have been encountered in mammoth stomach and intestine contents from frozen carcasses (Vereshchagin and Baryshnikov, 1982; Olivier, 1982; Joger and Koch, 1995) as well as dung boluses (Mead et al., 1986).

Skeletal remains of mammoths are abundant in Late Pleistocene deposits of Europe, Siberia and North America. In most cases only single disarticulated skeletal elements of mammoths, especially teeth or tusks are found in Quaternary fluvio-glacial sediments but also in loess, swamp deposits, sinkhole and fissure fillings and permafrost soils. Articulated skeletal remains or even whole mammoth skeletons are rare. Only a few finds are known from central Europe (Lang, 1892; Weidmann, 1970; Coope and Lister, 1987; Ziegler, 1994, 2001; Koenigswald, 2002 and references therein) and from the permafrost sediments of Siberia and Alaska as frozen mammoth carcasses (Farrand, 1961; Guthrie, 1990; Vasil'chuk et al., 1997; MacPhee et al., 2002; Kahlke and Mol, 2005). The site of Niederweningen, northern Switzerland, yielded skeletal remains of at least 9 mammoth individuals, including one neonate calf of about 2 months age, and one articulated half mammoth skeleton (Lang, 1892; Hünemann, 1985; Furrer, 2005; Furrer et al., this volume). These were all found in a Middle Würmian (70–40 ka BP) peat layer (Furrer et al., this volume; Hajdas et al., this volume). Niederweningen is thus an exceptional site, which offers a unique possibility to analyse the isotopic composition of skeletal remains of probably sympatric mammoth individuals from a single taphocoenose.

In this study, we analysed mammoth teeth from the Middle Würmian peat layer of Niederweningen for their carbon isotope values ($\delta^{13}\text{C}$), which track variations in diet and local vegetation and for their oxygen isotope values ($\delta^{18}\text{O}$), which track local climatic conditions. From the oxygen isotopic composition of mammoth tooth enamel, the oxygen isotopic composition of their respective drinking water ($\delta^{18}\text{O}_{\text{H}_2\text{O}}$) and from that the mean annual air temperatures (MAT) were calculated for the period around 45–50 ka BP.

1.2. Oxygen isotope composition of skeletal apatite as palaeoclimate proxy

The oxygen isotope composition of mammalian tooth enamel is a well established proxy for terrestrial palaeoclimate conditions (Longinelli, 1984; Fricke and O'Neil, 1996; Koch, 1998; Kohn and Cerling, 2002). For large mammals $\delta^{18}\text{O}$ values of body water depend mainly on the $\delta^{18}\text{O}$ values of the meteoric water ingested during drinking and feeding as well as their physiology and metabolic rate (Luz et al., 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996). The $\delta^{18}\text{O}$ values of meteoric water, in turn, are a function of air temperature and humidity, and hence of the prevailing climate (Dansgaard, 1964; Rozanski et al., 1993; Clark and Fritz, 1997; Fricke and O'Neil,

1999). The oxygen isotopic composition of both carbonate in apatite ($\delta^{18}\text{O}_{\text{CO}_3}$) as well as phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) that form in isotopic equilibrium from the same body water reservoir are offset by about 8.5–9.0‰ and thus are both related to drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values (Iacumin et al., 1996; Bryant et al., 1996). Therefore, $\delta^{18}\text{O}$ values of bones and teeth from fossil mammals can be used as a proxy for paleoclimate reconstructions (e.g., Longinelli, 1984, 1995; Fricke and O'Neil, 1996; Fricke et al., 1998; Sharp and Cerling, 1998; Kohn and Cerling, 2002; Kohn et al., 2004; Grimes et al., 2005; Tütken et al., 2006).

This is especially true for modern elephants, which are closely related to mammoths, because they are known to drink about 200 ± 100 L of water per day from surface water sources while only 1/3rd of their body water comes from the daily intake of 100–200 kg of fresh food (Sikes, 1971; Eltringham, 1982; Ayliffe et al., 1992). Furthermore, elephants have a large body mass and body water reservoir which is only to a small degree influenced by relative humidity and physiological effects (Ayliffe et al., 1992; Bryant and Froelich, 1995; Kohn, 1996). Thus the oxygen isotopic composition of bones and teeth, especially tooth enamel, from mammoths is well suited for palaeoclimatic reconstructions (Ayliffe et al., 1992, 1994; Genoni et al., 1998; Tütken et al., 2002; Arppe and Karhu, 2006) assuming a physiology and drinking behaviour similar to that of modern elephants.

1.3. The carbon isotope composition of skeletal apatite as dietary proxy

The $\delta^{13}\text{C}$ values of plants vary with photosynthetic pathway (O'Leary, 1981). C_3 and C_4 photosynthetic pathways fractionate carbon isotopes to different degrees, hence the C_3 and C_4 plants have distinct mean $\delta^{13}\text{C}$ values of -27 ± 3 and -13 ± 2 ‰, respectively (O'Leary, 1981; Farquhar et al., 1989). Most trees, shrubs, and temperate/arctic grasses are C_3 plants. Tropical grasslands, with warm season grasses, or mid-latitude xeric/saline and well-irradiated environments commonly have a considerable proportion of C_4 species. The carbon isotopic composition of food plants are reflected in the tissues of their consumers, with an isotopic shift, which is mainly linked to the analysed tissue (DeNiro and Epstein, 1978). For skeletal apatite of bones and teeth the carbon isotopic composition of the carbonate bound in the phosphate is related to that of the bulk diet while that of the collagen reflects mainly dietary protein intake (Tieszen and Fagre, 1993; Ambrose and Norr, 1993). For large herbivorous mammals, including elephants, the carbon isotopic composition of the carbonate in biogenic apatite of tooth enamel is enriched by 14.1‰ relative to that of the plant diet (Cerling and Harris, 1999; Cerling et al., 1999). Thus, the carbon isotopic composition of mammalian tooth enamel reflects the proportion of C_3/C_4 plants in their respective diet (e.g., Quade et al., 1992; Cerling et al., 1997, 1999) and/or the variation of $\delta^{13}\text{C}$ values in the food plants

due to differences in environmental and climatic parameters (e.g., Heaton, 1999). The carbon isotopic composition of elephant teeth hence allows for a reconstruction of the diet of extant and extinct elephants (Cerling et al., 1999; Fox and Fisher, 2001).

2. Setting of the Niederweningen fossil site

2.1. Geology, palaeontology and stratigraphic age

The so-called “Mammutloch” from Niederweningen in the Wehn Valley 20 km northwest of Zurich (Fig. 1) is the richest Pleistocene vertebrate fossil and most important mammoth site in Switzerland. Fossil skeletal remains of at least nine individual mammoths, including remains of a 2-month-old mammoth calf, as well as other vertebrates such as woolly rhinoceros, horse, bison, wolf, cave hyena, grass frog, vole, shrew, lemming and birds were found during several excavations in 1890/91, 2003, and 2004 in different locations of a Late Pleistocene peat layer (Lang, 1892; Hünemann, 1985, 1987; Furrer, 2005; Furrer et al., this volume). An exciting new find was the articulated half skeleton of an approximately 40-yr-old mammoth bull in 2003 (Furrer et al., this volume). In addition to these fossil vertebrate remains, a rich fossil insect fauna with more than 142 beetle taxa and remains from other insects (Coope, this volume). Likewise, a fossil flora with the remains such as wood, twigs, mosses, leafs, seeds, pine cones, as well as pollen (dominantly pine, *Picea* sp.) and spores of more than 60 taxa of terrestrial and aquatic plants (Drescher-Schneider et al., 2007) that lived within the vicinity of the swamp were found. The fossiliferous peat layer of Niederweningen is part of a 20 m succession of Middle Pleistocene to Holocene lake and meltwater sediments with intercalated Eemian and Late Pleistocene peat layers (Furrer et al., this volume). All fossil remains were found in the Middle Würmian upper peat complex of the sedimentary sequence, while a lower peat complex is probably of Eemian age (Welten, 1988; Furrer et al., this volume). Infrared stimulated dating of the aquatic sediments overlying the fossil-bearing peat layer yield ages

between 36 ± 3 and 43 ± 3 ka, while those underlying the peat yield ages between 62 ± 5 and 79 ± 6 ka (Preusser and Degering, this volume). The peat formation started around 55 ka BP (Preusser, personal communication, 2006) during an interstadial period of the Middle Würmian in the marine oxygen isotope stage 3 and ended around 40 ka BP due to flooding of the peat swamp and deposition of grey silty lake deposits (Furrer et al., this volume). ^{14}C -AMS radiocarbon dating of the peat ($45,430 \pm 1020$ yr BP), a wood fragment ($>40,480$ yr BP), and a mammoth bone ($45,870 \pm 1080$ yr BP) of the partial skeleton found in 2003 gives a consistent calendar age between 45–50 cal ka BP for the upper part of the mammoth-bearing peat layer and indicates that the mammoth died around 45 ka BP in the last phase of peat formation (Hajdas et al., this volume).

2.2. Late Pleistocene environmental conditions around Niederweningen

The peat swamp of Niederweningen developed in a relatively open landscape with marshes and wet meadows in a periodically flooded valley plain at the edge of a silting up lake in the Wehn Valley during an interstadial period (Furrer et al., this volume). At the beginning of the peat formation climate conditions were not favourable for tree growth as indicated by the low content and assemblage of tree pollen with *Juniperus*, *Betula* and *Salix* being the main species, which suggests vegetation similar to that of the modern transition of Taiga to treeless Tundra (Drescher-Schneider et al., this volume). This is also reflected in the beetle assemblage that contains species adapted to extreme coolness typical for the northernmost Taiga of Siberia (Coope, this volume). During consecutive climate amelioration, the dryer areas of the swamp surroundings were covered by loose mixed forests of *Picea*, *Betula*, and *Larix*. The swamp itself offered local aquatic habitats for different water plants such as *Menyanthes*, *Potamogeton*, *Ranunculus* and the characean algae *Chara*, indicated by abundant seeds, respectively oogonians, as well as for the frog *Rana temporaria*, from which abundant bones were found (Furrer et al., this volume). Palaeotemperature estimates for the lower part of the mammoth peat based on the beetle assemblage yield warmest month (July) temperatures (T_{\max}) between 8 and 11 °C and coldest month (January/February) temperatures (T_{\min}) between –20 and –9 °C. For the mammoth-bearing upper part of the peat layer T_{\max} between 12 and 13 °C and T_{\min} between –12 and –5 °C can be estimated (Coope, this volume). These are similar to palaeotemperature estimates based on beetle remains from the peat of the contemporaneous nearby Gossau-Interstadial-Complex (Jost-Stauffler et al., 2005; Coope, this volume). The formation of the Middle Würmian peat layer of Niederweningen is thus correlated with the warm interstadial period of the Dansgaard-Oeschger event 12 of the Greenland ice core record (Hajdas et al., this volume).

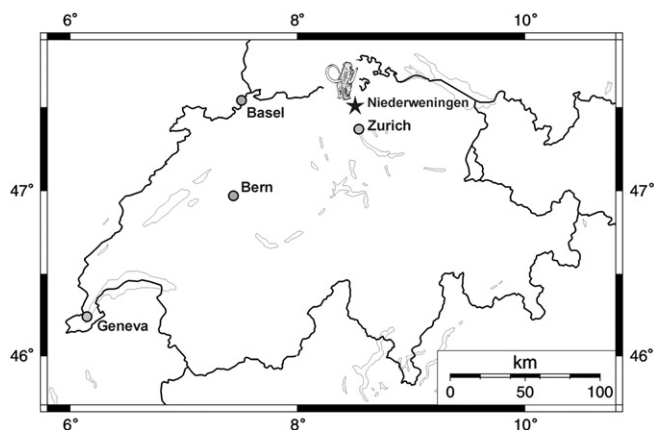


Fig. 1. Map of Switzerland with the mammoth locality Niederweningen.

Within the top of the mammoth peat layer, changes in tree pollen composition with a prominent decrease of tree pollen from about 60–20% indicate declining climate conditions (Drescher-Schneider et al., this volume). The overlying grey, fine-grained lake sediments and the tree and shrub pollen therein reflect further cooling at around 40 ka BP (Preusser and Degering, this volume; Drescher-Schneider et al., this volume). After the end of peat formation, the sedimentary sequence of peat and lacustrine sediments has been intensely deformed due to cryoturbation under permafrost conditions (Schlüchter, 1988, 1994). Although the peat layer is compacted, the Niederweningen site was never reached and overlain by glaciers (Furrer et al., this volume).

3. Material and methods

3.1. Fossil skeletal remains

Several skeletal remains from Niederweningen were analysed for their carbon and oxygen isotope composition. A molar (FZ MA ND 1) and a bone (FK MA ND 1) from *M. primigenius* were taken from the partial skeleton of the approximately 40-yr-old mammoth bull found in 2003 and now exhibited in the Mammutmuseum of Niederweningen. Furthermore, 9 mammoth molars (FZ MA ND 2–10) from different individuals of *M. primigenius*, one woolly rhinoceros tooth (FZ RH ND 1) of *Coelodonta antiquitatis*, one horse tooth (FZ EQ ND 1) of *Equus germanicus*, and two bison bones (FK BI ND 1 and 2) of *Bison priscus* were also analysed (Table 1). These skeletal remains were all found in 1890/91 (Lang, 1892; Hünermann, 1985) and lack exact documentation of their stratigraphic context but originate from the same peat layer of Middle Würmian age as the 2003 finds, found about 100 m further west (Furrer et al., this volume). Only one bison bone (FK BI ND 2) was found in the silty lake sediments immediately on top of the peat layer.

The age of the mammoth-bearing peat layer was ^{14}C -dated to around 45 ka using the peat itself and embedded wood remains (Hajdas et al., this volume). However, the first ^{14}C -AMS dates of bone material from 1890/91 and 1987 yielded ages between 34.6 and 33.3 ka BP (Schlüchter, 1994; Furrer et al., this volume). These ^{14}C -ages are likely to be too young due to humic acid contaminations not removed during conventional collagen preparation (Hajdas et al., this volume). Therefore, the conventional ^{14}C -ages of the analysed bison skull bone (FK BI ND 1: $34,590 \pm 480$ BP) and the horse tooth (FZ EQ ND 1: 31,000 BP) given in Table 1 are possibly too young. Using a modified Longin gelatine preparation technique with a base cleaning step to remove humic acid contamination the mammoth bone (FK MA ND 1) from the 2003 find was ^{14}C -dated to $45,870 \pm 1080$ yr BP (Hajdas, this volume). This ^{14}C -age is well in accordance with the ^{14}C -ages of around 45 ka BP for the embedding peat and wood therein (Hajdas et al., this volume).

For comparison with the mammoth remains from Niederweningen, a ^{14}C -dated mammoth bone (FK MA SIG 1) from Siegsdorf, Bavaria in Germany, was also analysed (Table 1). This bone belongs to a nearly complete skeleton from an adult mammoth bull of about 50 yr of age (Ziegler, 1994) and has a similar ^{14}C -age of $45,180 + 1130 / -990$ yr BP (KIA 14407 SIMAMM-1, Robert Darga, personal communication, 2005) as the Niederweningen specimen found in 2003 (Hajdas et al., this volume). All the analysed skeletal materials were not treated with any preservatives.

3.2. Oxygen and carbon isotope analysis of skeletal apatite

For the oxygen and carbon isotope analysis about 50 mg of enamel, dentine or bone was sampled manually with a diamond studded 0.7 mm miniature drill from each skeletal element. The sample powder was pre-treated according to the procedure of Koch et al. (1997). Ten milligram of bone and enamel powder were washed with a 2% NaOCl solution to remove organic matter, followed by a 1 M Ca-acetate acetic acid buffer solution (pH = 4.5) to remove diagenetic carbonates. The powder/solution ratio was kept constant to 0.04 g/ml for both treatments. Each treatment lasted for 24 h and samples were rinsed five times with distilled water afterwards. Only the bone and dentine samples were treated two times 24 h with NaOCl. From the pre-treated enamel or bone powder a 3 mg aliquot was taken for analysis of the carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}_{\text{CO}_3}$) isotopic composition of the carbonate in the phosphate and the phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) itself. The carbon and oxygen isotopic compositions are expressed as δ -values in ‰ relative to the international standards Vienna Pee Dee Belemnite (VPDB) for carbonate and Vienna Standard Mean Ocean Water (VSMOW) for the phosphate according to $\delta = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$ with $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, respectively.

The samples were analysed at the University of Tübingen using a Thermo Finnigan Gasbench II following a procedure adapted after Spoetl and Vennemann (2003). Ten drops of 100% orthophosphoric acid were added allowing the samples to react at 70 °C for 1 h under a He atmosphere before starting 10 measurement cycles of the isotopic composition of the produced CO_2 on a Finnigan MAT 252 continuous flow isotope ratio gas mass spectrometer. The measured carbon and oxygen isotopic compositions were normalised to the in-house Laaser marble calcite standard, which has been calibrated against the NBS-19 calcite standard. The normalization incorporates the CO_2 -carbonate acid fractionation factor for calcite, which was assumed to be similar to that of the carbonate in phosphate. External reproducibility for carbonate in the phosphate was checked with NBS 120c Florida phosphate rock standard pre-treated the same way as the samples giving values of $\delta^{13}\text{C}_{\text{VPDB}} = -6.29 \pm 0.08\text{‰}$ and $\delta^{18}\text{O}_{\text{VPDB}} = -2.32 \pm 0.14\text{‰}$ ($n = 13$). The external reproducibility for the carbon and oxygen isotopic composition

Table 1
C and O isotopic composition of mammoth teeth and other skeletal remains

Sample	Specimen no.	Locality	Species	Skeletal tissue (element)	¹⁴ C age BP	$\delta^{13}\text{C}$		$\delta^{18}\text{O}_\text{C}$		$\delta^{18}\text{O}_\text{P}$		$\delta^{18}\text{O}_{\text{H}_2\text{O}}$		MAT (°C)	
						VPDB	VSMOW	VSMOW	VSMOW	VSMOW	VSMOW	Calculated ^a	Calculated ^b		
FK MA ND 1	PIMUZ A/V 4431	Niederweningen	<i>Mammuthus primigenius</i>	Bone	45.870 ± 1.080	-8.3	20.5	13.1	-10.9				7.5		
FD MA ND 1	PIMUZ A/V 4431	Niederweningen	<i>Mammuthus primigenius</i>	Dentine (M3)	45.870 ± 1.080	-8.7	21.4	13.0	-11.0				7.3		
FZ MA ND 1	PIMUZ A/V 4431	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M3)	45.870 ± 1.080	-11.7	19.9	12.8	-11.2				6.8		
FD MA ND 2	PIMUZ A/V 1263	Niederweningen	<i>Mammuthus primigenius</i>	Dentine (M2)		-11.7	20.0	10.8	-13.3				2.1		
FZ MA ND 2	PIMUZ A/V 1263	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M2)		-11.8	20.0	11.3	-12.8				3.2		
FZ MA ND 3	PIMUZ A/V 1355	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M)		-11.5	21.3	13.3	-10.7				8.0		
FZ MA ND 4	PIMUZ A/V 1354	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M)		-11.5	19.5	11.8	-12.2				4.5		
FZ MA ND 5	PIMUZ A/V 1360	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M2)		-11.3	18.4	10.8	-13.3				1.9		
FZ MA ND 6	PIMUZ A/V 1362	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M3)		-11.1	20.1	11.9	-12.1				4.7		
FZ MA ND 7	PIMUZ A/V 1363	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M2)		-11.7	20.0	10.3	-13.8				0.9		
FZ MA ND 8	PIMUZ A/V 1364	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M2)		-11.6	19.7	11.6	-12.5				3.8		
FZ MA ND 9	PIMUZ A/V 1358	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M3)		-11.5	20.4	12.2	-11.8				5.3		
FZ MA ND 10	PIMUZ A/V 1361	Niederweningen	<i>Mammuthus primigenius</i>	Enamel (M3)		-10.9	19.7	11.4	-12.7				3.4		
FK BI ND 1	PIMUZ A/V 1385	Niederweningen	<i>Bison priscus</i>	Bone (skull)	34.590 ± 480	-9.4	20.6	13.9	-10.4				8.5		
FK BI ND 2	PIMUZ A/V 1388	Niederweningen	<i>Bison priscus</i>	Bone		-10.7	21.5	12.9	-11.9				5.3		
FZ EQ ND 1	PIMUZ A/V 1373	Niederweningen	<i>Equus caballus</i>	Enamel (M)	31.000	-10.8	21.2	12.6	-12.9				2.9		
FZ RH ND 1	PIMUZ A/V 1795	Niederweningen	<i>Coelodonta antiquitatis</i>	Enamel (M)		-11.0	21.5	13.2	-						
FK MA SIG 1	KIA 14407	Siegsdorf	<i>Mammuthus primigenius</i>	Bone (humerus)	45.180 + 1.130/-990	-10.1	19.8	11.7	-12.4				4.1		

^aThe $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ VSMOW values were calculated with species-specific $\delta^{18}\text{O}_{\text{H}_2\text{O}} - \delta^{18}\text{O}_{\text{PO}_4}$ calibrations for modern elephants (Ayliffe et al., 1992), bisons (Hoppe, 2006) and horses (Huertas et al., 1995).

^bThe mean annual air temperature (MAT) was calculated using the present-day $\text{MAT} - \delta^{18}\text{O}_{\text{H}_2\text{O}}$ relation for Switzerland based on NISOT data (Schürch et al., 2003; unpublished NISOT data) using Eq. (2) given in the text.

of carbonate in the phosphate is better than $\pm 0.1\%$ and $\pm 0.15\%$, respectively.

Enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values were determined from the same pre-treated samples used for the $\delta^{18}\text{O}_{\text{CO}_3}$ measurement. An aliquot of 4 mg was dissolved in 2 M HF and after neutralisation with 25% NH_4OH , 2 M AgNO_3 solution was added for an instantaneous precipitation of the PO_4^{3-} ions in solution as Ag_3PO_4 according to a technique described in Tütken et al. (2006). Resultant Ag_3PO_4 were measured at the Universities of Lausanne and Tübingen by a TC-EA coupled to a Finnigan DeltaPlus XL mass spectrometer in triplicate with an external reproducibility for the oxygen ($\delta^{18}\text{O}_{\text{PO}_4}$) isotopic composition of the phosphate better than $\pm 0.3\%$ (Vennemann et al., 2002). Samples from pre-treated NBS 120c Florida phosphate rock standard precipitated as Ag_3PO_4 in the same way as the samples gave a $\delta^{18}\text{O}_{\text{PO}_4}$ value of $21.6 \pm 0.4\%$ ($n = 25$).

4. Results

4.1. Carbon isotope composition

The results of the carbon isotopic composition of the carbonate in the phosphate of all analysed skeletal remains are given in Table 1. The enamel $\delta^{13}\text{C}$ values for all analysed mammoth molar teeth of Niederweningen range from -11.8% to -10.9% , with a mean $\delta^{13}\text{C}$ value of $-11.5 \pm 0.3\%$ ($n = 10$). From the partial mammoth skeleton found in 2003 different skeletal tissues were analysed yielding $\delta^{13}\text{C}$ values of -11.7% for the enamel (FZ MA ND 1) and -8.7% for the dentine (FD MA ND 1) from the same third molar tooth and -8.1% for the bone (FK MA ND 1). The $\delta^{13}\text{C}$ value of enamel from the horse tooth (FZ EQ ND 1) is -10.8% , that of the woolly rhinoceros tooth (FZ RH ND 1) -11.0% , and two bison bones (FK BI ND 1) and (FK BI ND 2) have values of -9.4% and -10.7% , respectively. These are all similar to or slightly higher than those of the enamel of mammoth molar teeth. The humerus bone (FK MA SIG 1) of a contemporaneous mammoth skeleton from Siegsdorf, Bavaria, in southern Germany, has a $\delta^{13}\text{C}$ value of -8.3% .

4.2. Oxygen isotope composition

Results of the oxygen isotope composition of phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) and carbonate in the phosphate ($\delta^{18}\text{O}_{\text{CO}_3}$) of all analysed skeletal remains are given in Table 1. The enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values for all analysed mammoth molar teeth of Niederweningen range from 10.3% to 13.3% with a mean $\delta^{18}\text{O}_{\text{PO}_4}$ value of $11.7 \pm 0.9\%$ ($n = 10$). Samples from the partial mammoth skeleton found in 2003 have similar $\delta^{18}\text{O}_{\text{PO}_4}$ values of 12.8% for the enamel (FZ MA ND 1) and 13.0% for the dentine (FD MA ND 1) from the same third molar tooth, and 13.1% for the bone (FK MA ND 1). $\delta^{18}\text{O}_{\text{PO}_4}$ values of enamel of the horse tooth (FZ EQ ND 1), a woolly rhinoceros tooth and two bison bones (FK BI ND 1 and 2) are similar or slightly higher than those of the sympatric mammoth teeth (Table 1). The mammoth bone

(FK MA SIG 1) of a contemporaneous mammoth skeleton from Siegsdorf, Bavaria, in southern Germany, has a $\delta^{18}\text{O}_{\text{PO}_4}$ value of 11.7% , identical to the mean value for the mammoth teeth from Niederweningen, indicating the ingestion of water with similar oxygen isotopic composition as the mammoths from Niederweningen.

5. Discussion

5.1. Climatic reconstruction based on the oxygen isotope composition of the mammoth teeth

Biogenic apatite of tooth enamel is the most robust skeletal tissue with regard to diagenetic alteration because of its low content of organic matter, low porosity, large crystal size, and low solubility. It is thus the most appropriate skeletal tissue for reliable palaeoenvironmental reconstructions (e.g., Ayliffe et al., 1994; Kohn et al., 1999; Tütken, 2003). The carbonate in phosphate of tooth enamel can preserve its original C and O isotope composition for several 100 ka and even up to several million years (Lee-Thorp, 2000; Fox and Fisher, 2001; Tütken et al., 2006). The $\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values for all the tooth enamel samples (Table 1) have an average offset of $8.4 \pm 0.5\%$, which is close to that expected for isotopic equilibrium between both (Iacumin et al., 1996). This would support preservation of primary $\delta^{18}\text{O}$ values of the fossil enamel, which can then be used to estimate the mammoth drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values. However, for the two dentine samples and one bison bone (FK BI ND 1) the $\delta^{18}\text{O}_{\text{CO}_3} - \delta^{18}\text{O}_{\text{PO}_4}$ offset is $< 7.5\%$ indicating some diagenetic alteration. These samples are not considered for the reconstruction of drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$.

The standard deviation $\pm 0.9\%$ of the enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values from the ten mammoth teeth from Niederweningen indicate that they drank from surface water sources with a relative homogeneous oxygen isotopic composition. For a direct comparison of the oxygen isotope compositions obtained from the tooth enamel of these mammoths and the skeletal remains of the other sympatric mammals in terms of palaeoclimate conditions, the $\delta^{18}\text{O}_{\text{PO}_4}$ values of the skeletal apatite can be converted to $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of drinking water. For this purpose empirical, species-specific $\delta^{18}\text{O}_{\text{H}_2\text{O}} - \delta^{18}\text{O}_{\text{PO}_4}$ calibrations for extant mammals were used to calculate the respective drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values for the fossil taxa. For the mammoth the empirical calibration (Eq. (1)) determined for extant elephants (*Loxodonta africana* and *Elephas maximus*) of Ayliffe et al. (1992) was used to calculate the $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of mammoth drinking water. This was done under the assumption that mammoths, which are closely related to modern elephants, have had a comparable ecological behaviour, diet, physiology and metabolic rate as modern elephants (Olivier, 1982; Haynes, 1991). A similar approach to reconstruct the oxygen isotope compositions of drinking water and hence palaeoclimate was applied to Late Pleistocene mammoth skeletal remains from the

Eurasian Arctic (Ayliffe, et al., 1992; Genoni et al., 1998; Tütken et al., 2002; Arppe and Karhu, 2006) as well as deer, horse, and cattle remains from southern Italy (Huertas et al., 1997).

$$\delta^{18}\text{O}_{\text{PO}_4} = 0.94 \times \delta^{18}\text{O}_{\text{H}_2\text{O}} + 23.3. \quad (1)$$

For the bison and horse remains the extant $\delta^{18}\text{O}_{\text{H}_2\text{O}} - \delta^{18}\text{O}_{\text{PO}_4}$ calibrations for *Bison bison* (Hoppe, 2006) and *Equus caballus* (D'Angela and Longinelli, 1990; Huertas et al., 1995) were used to calculate the $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values. The calculated drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values for all mammoth tooth enamel samples from Niederweningen range from -13.8‰ to -10.7‰ with a mean value of $-12.3 \pm 0.9\text{‰}$ ($n = 10$; Table 1). The two bison bones and the horse tooth enamel from Niederweningen give similar $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of -11.9‰ to -10.4‰ (Table 1). In comparison, the bone from the sympatric mammoth of Siegsdorf in southern Germany gave a $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ value of -12.4‰ , nearly identical to the mean value for the Niederweningen mammoths. Thus, all the investigated sympatric mammoths and other large herbivorous mammals drank water with a similar and relative homogeneous $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ value of about -12.3‰ . This oxygen isotope composition reflects that of the surface drinking water sources which were presumably mainly fed by precipitation, though they could have been modified by evaporation and/or surface or ground water inflow of different oxygen isotopic composition (e.g., meltwater, Schürch et al., 2003; Darling, 2004 and references therein). A surface water ^{18}O -enrichment due to evaporation is not a very likely scenario under cool glacial climate conditions. Also, the influence of ^{18}O -depleted meltwater is not very likely because no glaciers existed in the vicinity of the swamp in the Wehn Valley during the Middle Würmian (Graf and Müller, 1999). Even the most complete section of the Middle Würmian at Gossau, situated 35 km southeast near the northern front of the Alps, shows no sign of glaciation in the time between 50 and 32 ka BP (Schlüchter et al., 1987; Preusser et al., 2003). However, due to ^{18}O -depleted meltwater from snow and glaciers some modern rivers in Switzerland with Alpine catchments have lower $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values compared to the local precipitation (Schürch et al., 2003; Darling, 2004 and references therein). The meltwater influence on the mammoths drinking water ($\delta^{18}\text{O}_{\text{H}_2\text{O}} = -13.1 \pm 0.8\text{‰}$) seems negligible because Late Pleistocene (> 25 ka BP) groundwater from the Glatt Valley in the vicinity of Niederweningen has similar $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values between -11.5‰ and -12.8‰ (Beyerle et al., 1998). As the recharge of aquifers approximately represents the weighted mean of precipitation, $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values are often close to the long-term mean of local rainfall (e.g., Clark and Fritz, 1997; Darling, 2004). However, whether the mammoths drank locally from the swamp where they got trapped is unknown. The low abundance of dung beetles suggests the lack of a permanent population of large herbivore mammals around the swamp (Coope, this volume) and makes the extensive use of the swamp as a drinking water

source unlikely. Furthermore, modern and extinct elephants are known to migrate seasonally over large distances of up to more than 500 km (Sikes, 1971; Hoppe et al., 1999; Hoppe, 2004). Strong seasonality of climate and thus vegetation productivity in the Pleistocene (Guthrie, 1990) might have also forced mammoths to extensive seasonal migrations (Olivier, 1982) as has been shown for Late Pleistocene mastodonts and mammoths in North America (Hoppe et al., 1999; Hoppe, 2004). During such potential migrations, they would have made use of a variety of surface water sources which are mainly fed by precipitation (e.g., Darling, 2004) and integrated the respective oxygen isotopic compositions in their skeletal tissues. The assumption that the mammoth drinking water sources reflect the average oxygen isotopic composition of the Late Pleistocene precipitation in the area of northern Switzerland thus seems valid.

Based on this assumption, one can calculate the MAT at the time the mammoth lived using the linear relation between $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of the precipitation and the MAT. But instead of applying a global $\delta^{18}\text{O}_{\text{H}_2\text{O}} - \text{MAT}$ relationship (e.g., Dansgaard, 1964; Rozanski et al., 1993) a linear regression between the precipitation $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values and air temperature for Switzerland (Eq. (2)) was calculated based on the monthly mean precipitation $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ and air temperature data of the years 1993–2003 collected from 11 stations of the NISOT (National Isotope Measurement Network of Switzerland: Schürch et al., 2003, unpublished NISOT data, Fig. 2):

$$\delta^{18}\text{O}_{\text{H}_2\text{O}} = 0.44 \times T_{\text{air}} + 14.19 \quad (n = 1230) \quad R^2 = 0.68. \quad (2)$$

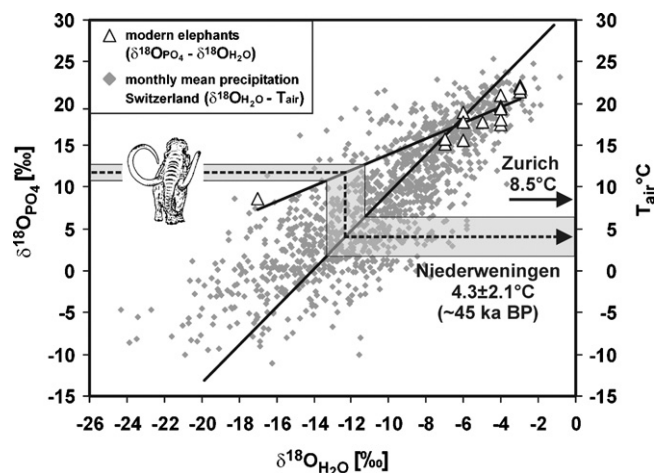


Fig. 2. $\delta^{18}\text{O}_{\text{PO}_4} - \delta^{18}\text{O}_{\text{H}_2\text{O}}$ species-specific calibration for modern elephants (Ayliffe et al., 1992) and monthly $\delta^{18}\text{O}_{\text{H}_2\text{O}} - T_{\text{air}}$ regression based on precipitation and air temperature measured at 11 Swiss stations for the years 1993–2003 based on unpublished data of the Swiss National Network for the Observation of Isotopes in the Water Cycle (NISOT; see Schürch et al., 2003). Using both regression lines, Late Pleistocene mean drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values and mean annual air temperatures of northern Switzerland are derived from the calculated $\delta^{18}\text{O}_{\text{PO}_4}$ values (Table 1) of the mammoth teeth of Niederweningen. Present-day air temperature from Zurich is the 30-years mean from 1961–90 (www.meteoschweiz.ch).

This modern-day $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ -MAT relationship (Eq. (2)) has a similar slope of around $0.44\text{‰}/^\circ\text{C}$, compared to $0.49 \pm 0.17\text{‰}/^\circ\text{C}$ for the Late Pleistocene $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ -groundwater recharge temperature relationship for northern Switzerland (Beyerle et al., 1998). Thus it can be used to calculate Late Pleistocene air temperatures from the drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values calculated for the mammoth teeth from Niederweningen. The calculated MAT of $4.3 \pm 2.1^\circ\text{C}$ for Niederweningen (~ 45 ka BP) is $1\text{--}2^\circ\text{C}$ warmer than groundwater recharge temperatures of 2.4 ± 1.4 and $3.2 \pm 1.7^\circ\text{C}$ calculated from noble gas contents of Late Pleistocene (25–30 ka BP) groundwater from the Glatt Valley aquifer (Beyerle et al., 1998), and about 4°C lower than modern-day MATs of $8.3\text{--}8.5^\circ\text{C}$ (Fig. 2) in the nearby Glatt Valley area and at Zurich Airport, respectively (Beyerle et al., 1998; MeteSchweiz and references therein; www.meteoschweiz.ch). Thus, both independent approaches of MAT reconstruction based on noble gas solubility in groundwater (Beyerle et al., 1998) and the oxygen isotopic composition of mammoth teeth used in this study indicate consistently about $>4^\circ\text{C}$ cooler climate conditions in northern Switzerland during the Middle Würmian period. These reconstructed MAT for the marine oxygen isotope stage 3 are well within the range of warmest month, i.e. July temperatures (T_{Max}) and coldest month(s), i.e. January and February temperatures (T_{Min}) calculated from the beetle assemblage of Niederweningen: $T_{\text{Max}} = 12\text{--}13^\circ\text{C}$ and $T_{\text{Min}} = -12$ to -5°C (Coope, this volume). Similar $T_{\text{Max}} = 12\text{--}13^\circ\text{C}$ and $T_{\text{Min}} = -15^\circ\text{C}$ to -7°C were calculated from beetle assemblages from lignite of the penecontemporaneous (30–54 ka BP) nearby Gosau-Interstadial-Complex (Preusser et al., 2003; Jost-Stauffer et al., 2005).

5.2. Diet and habitat of the mammoths—implications from the carbon isotopic composition

The mean enamel $\delta^{13}\text{C}$ value of $-11.4 \pm 0.3\text{‰}$ ($n = 10$) for the mammoth teeth from Niederweningen is similar to $\delta^{13}\text{C}$ values of Late Pleistocene mammoth skeletal remains from Alaska and Russia (Bocherens et al., 1994; Iacumin et al., 2000). The mean $\delta^{13}\text{C}$ value of -11.4‰ indicates that the mammoth from Niederweningen fed on plants with a $\delta^{13}\text{C}_{\text{diet}}$ value of $-25.5 \pm 0.3\text{‰}$. This calculated $\delta^{13}\text{C}_{\text{diet}}$ value is similar to those reconstructed for the diet of mammoths from soft tissues of frozen carcasses from Beringia ($\delta^{13}\text{C}_{\text{diet}} = -26.2 \pm 1.2\text{‰}$; Bombin and Muehlenbachs, 1985), mammoth bones and teeth from Eurasia ($\delta^{13}\text{C}_{\text{diet}} = -26.0 \pm 0.6$ to $-28.2 \pm 0.6\text{‰}$; Iacumin et al., 2000) and mammoth hair from Lyakhovsky Island, north Siberia ($\delta^{13}\text{C}_{\text{diet}} = -27.0\text{‰}$; Iacumin et al., 2005). The geographical variations in $\delta^{13}\text{C}$ values of dietary carbon intake between mammoth remains from Europe/Russian Plain and Siberia are probably due to environmental factors on plants and animals and/or different plant availabilities (Iacumin et al., 2000). Nevertheless, the dietary $\delta^{13}\text{C}$ values reconstructed for the mammoths of

Niederweningen from this study and other mammoth remains from western Europe and northern Eurasia (Bocherens et al., 1994, 1996; Iacumin et al., 2000, 2005) are indicative of an exclusive C_3 plant diet. C_4 plants were thus not an important part of the glacial landscape of the Mammoth Steppe, confirming results of Bombin and Muehlenbachs (1985), and are still not an important component in the flora of Europe today (Mateu Andrés, 1993). In such a C_3 -plant-dominated ecosystem it is impossible to determine the relative proportion of grazing and browsing on the basis of carbon isotopes, as can be done for modern and extinct elephants in subtropical–tropical ecosystems with an abundant C_4 -component in the vegetation (Cerling et al., 1999). Low enamel $\delta^{13}\text{C}$ values can indicate if animals lived in a closed canopy woodland environments (Drucker et al., 2003; Cerling et al., 2004; Kohn et al., 2005) and fed on plants with lower $\delta^{13}\text{C}$ values due to photosynthetic use of ^{13}C -depleted CO_2 from biomass recycling and lower light intensities (Medina et al., 1986; van der Merwe and Medina, 1989; France, 1996). No such canopy effect is detectable for the $\delta^{13}\text{C}$ values measured on the mammoth teeth from Niederweningen. It is thus likely that the mammoths fed on a relatively open tundra landscape with few trees, in agreement with pollen and plant macro remains (Drescher-Schneider et al., this volume) and the sympatric occurrence of other typical large grazing mammals like bison, horse and woolly rhinoceros. Pleistocene mammoths fed primarily on grass as indicated by gastro-intestine contents of frozen mammoth carcasses (Vereshchagin and Baryshnikov, 1982; Guthrie, 1990) and dung boluses (Mead et al., 1986) although tree bark and twigs constituted a small part of their winter diet (Olivier, 1982; Vereshchagin and Baryshnikov, 1982).

The low variability of enamel $\delta^{13}\text{C}$ values ($\pm 0.3\text{‰}$) indicates a relatively uniform and possibly restricted diet for the mammoths (Bombin and Muehlenbachs, 1985; Bocherens, 2003). As low levels of carbon isotope variability were found to be the most diagnostic signal of a mammoth herd/family group association, especially in ecosystems with abundant C_4 grasses (Hoppe, 2004), this could also be an indicator for a non-time-averaged mammoth fossil assemblage and thus the possible death of a herd. But in C_3 -dominated ecosystems such as in Europe (Mateu Andrés, 1993) only a small variability of herbivore enamel $\delta^{13}\text{C}$ values is to be expected and indeed also found for mammoths elsewhere in Eurasia (Bocherens, 2003). Additional evidence is needed to test such a hypothesis.

5.3. Taphonomy of the mammoths from Niederweningen—a possible isotope approach

Like modern elephants, mammoths probably lived in family groups of 5–30 adult females with their immature offspring, while adult bulls presumably were solitary (Sukumar, 1989; Haynes, 1991). The skeletal remains of

at least 7 mammoth individuals found during 1890/91, including a 2-month-old calf with unworn teeth (Lang, 1892; Hünermann, 1985), raises the possibility that a small mammoth herd became mired in the peat swamp of Niederweningen. The occurrence of so many mammoth remains, including the still suckling calf, as well as the small intra-population variability in $\delta^{13}\text{C}$ values and $\delta^{18}\text{O}$ values (Table 1) might be a tentative indicator for such a hypothesis. The partial skeleton of the mammoth bull found in 2003 about 100 m further west, was isolated from the other mammoth remains (Furrer et al., this volume). As male elephants leave family groups upon reaching sexual maturity and roam as individuals (Sukumar, 1989; Haynes, 1991), the mammoth bull from Niederweningen probably died at a different time compared to the other mammoths. All the mammoths probably became mired and sunk into the unconsolidated swamp sediments during the summer thaw. The skeletal remains are not exactly contemporaneous with the embedding sediment as indicated by the scarcity of dung beetles in the beetle assemblage associated with the mammoth remains (Coope, this volume). Many of the bones and teeth were found disarticulated and the new outcrop in the area of the “Mammutloch” at Niederweningen in April 2004 showed clear evidence of erosion and re- sedimentation of peat and bone material (Furrer et al., this volume).

If all of these mammoths lived under the same climatic and environmental conditions in the same geographic area and thus belonged to the same population, herd or family group, they should display similar isotopic compositions in their skeletal remains. This can potentially be traced by a combined analysis of carbon, nitrogen, and strontium isotope ratios of teeth and tusks which has already been successfully applied to distinguish among separate populations of modern African elephants (Vogel et al., 1990; Van der Merwe et al., 1990; Koch et al., 1995) as well as mammoths (Hoppe, 2004). The carbon isotopes of mammal teeth vary with diet and local vegetation, oxygen isotopes vary with local climate, and strontium isotopes vary with local soil chemistry. If Pleistocene mammoths travelled together in small family groups, then their skeletal remains from sites where such family groups have been buried should have lower inter-individual isotopic variability than mammoths from sites containing unrelated individuals (Hoppe, 2004). Intra-tooth and -tusk variability of C, N, O, and Sr isotopic compositions of skeletal material of elephants mineralised during the last years of each individuals life can help to further constrain potential seasonal climatic and dietary changes as well as migratory movements and thus trace similar life histories of related animals and even the season of death (Koch et al., 1989, 1995; Hoppe et al., 1999). Such a combined isotope analysis would potentially help to constrain if the Niederweningen mammoth assemblage is a time-averaged accumulations of unrelated individuals or represents the death of a family group.

6. Conclusions

The isotope compositions of well-preserved biogenic apatite of mammoth skeletal remains, which are abundant finds in Late Pleistocene sediments in central Europe, can successfully be used as proxy archives to reconstruct Pleistocene palaeoclimate and palaeoenvironmental conditions. For mammoth teeth and skeletal remains of other sympatric large herbivores from the Middle Würmian peat layer of Niederweningen, northern Switzerland, and the sympatric mammoth specimen from Siegsdorf, Bavaria, drinking water $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values of around -12.3‰ were determined. These $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ values are similar to those directly measured for Late Pleistocene groundwater from aquifers in northern Switzerland and southern Germany and thus represent the mean oxygen isotopic composition of the palaeo-precipitation. Using a present-day $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ -air temperature relation for Switzerland, a MAT of around $4.3 \pm 2.1^\circ\text{C}$ during the Middle Würmian can be calculated. This MAT is in good agreement with palaeotemperature estimates for the Middle Würmian from other proxy archives such as groundwater recharge temperatures and contemporaneous beetle assemblages. The Late Pleistocene climate conditions in northern Switzerland during the Middle Würmian interstadial phase around 45–50 ka BP were thus about 4°C cooler than today.

The mammoths from Niederweningen fed on C_3 plants. The homogeneity of tooth enamel carbon isotopic composition supports a restricted diet, possibly dominated by C_3 -type grasses. Such an environment may well have been tundra-like, with swamps and marshes mainly covered by *Carex*. Growth of an open mixed forest of *Picea*, *Betula* and *Larix*, typical of a forest-tundra as found presently in eastern Siberia, was likely on the adjacent valley slopes (Drescher-Schneider et al., this volume).

To constrain the taphonomic setting of the Niederweningen mammoth further ^{14}C -dating and combined stable isotope (O, C, Sr) analysis of skeletal remains is needed. Such analyses may resolve the question of whether a complete herd of several mammoths got entrapped in the peat swamp and died at the same time or whether the skeletal remains represent a time-averaged fossil assemblage.

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