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Reconstructing the paleoenvironment of East Central Europe in the Late Pleistocene using the oxygen and carbon isotopic signal of tooth in large mammal remains

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A B S T R A C T

Stable carbon and oxygen isotope values ($\delta^{13}C$, $\delta^{18}O$) of structural carbonate were determined in the bioapatite component of fossil teeth from the Czech Republic, Slovakia and Hungary. Oxygen isotope compositions of enamel and dentin samples provide new quantitative records of the Late Pleistocene climate in East Central Europe (ECE). These $\delta^{18}O$ data were combined with records of oxygen isotope values of recent and paleogroundwaters to study the spatial patterns and temporal variations in the oxygen isotope composition of precipitation and the thermal climate over ECE. The new isotopic data suggest that surface air temperatures in the study region between 33 and 12 ka were 2–9 °C colder than present. Specimens of woolly mammoth, rhino and horse from the Late Pleistocene were primarily C_3 grazers.

1. Introduction

Investigations of stable isotope compositions of mineralized tissues have added greatly to knowledge of past climates and dietary behaviors of organisms. Quantitative paleoclimatological and -ecological records based on stable isotope analyses from the time period prior to the Late Glacial Maximum (LGM) in marine isotope stages (MIS) 3 and 2 (*ca.* 33–12 ka cal BP) are scarce and fragmentary, and particularly poor in the central region of East Central Europe. In this area, the paleoenvironmental information recorded in mammal skeletal remains can prove invaluable. Thirteen Late Pleistocene samples of fossil mammoth and four of horse and one of woolly rhino from the Central European area (Czech Republic, Slovakia and Hungary; Fig. 1) were studied for their C and O stable isotope compositions of enamel and dentin (in tusk) hydroxyapatite carbonate to explore spatial patterns and temporal variations of glacial $\delta^{18}O_W$ (oxygen isotope value of precipitation) in Central Europe prior to and after the LGM during MIS 3 and 2.

Terrestrial vegetation and past climatic parameters (rainfall, temperature) can be inferred from carbon ($\delta^{13}C$) and oxygen isotopic ratios ($\delta^{18}O$) respectively, measured in mammal tooth enamel. The skeletal parts of mammals form at a constant temperature of ~37 °C. Therefore, the oxygen isotope composition of the precipitating skeletal apatite is determined solely by the isotopic composition of the animal's body water (Longinelli, 1984; Luz et al., 1984). In large mammals, the $\delta^{18}O$ value of body water is mainly dependent on that of ingested environmental waters (Bryant and Froelich, 1995), which usually corresponds to the mean $\delta^{18}O$ value in regional precipitation ($\delta^{18}O_{ppt}$). The link between the $\delta^{18}O$ values of mammal bioapatite ($\delta^{18}O_{ap}$) and ingested meteoric waters ($\delta^{18}O_W$), and the strong relationship between temperature and the $\delta^{18}O_{ppt}$ value provide a basis for using $\delta^{18}O$ values recovered from mammal skeletal remains in paleoclimatological research.

The carbon stable-isotopic composition of teeth closely follows diet consisting mostly of two types of plants: C_4 plants (warm climate grasses) and C_3 plants (trees, shrubs and high-latitude and high-elevation grasses). Because of different photosynthetic mechanisms, these different types of plants have different carbon isotope compositions (−27 and −13‰ for average C_3 and C_4 modern plants, respectively). Bioapatite $\delta^{13}C$ values of large herbivores are offset from the plant isotope values by about 14‰ (Cerling and Harris, 1999). Thus, animals feeding on modern C_3-vegetation can display bioapatite $\delta^{13}C$ levels from −20 to −8‰, with mean values of *ca.* −13 to −12‰. Correspondingly, C_4 consumers usually show bioapatite $\delta^{13}C$ values ranging from 0 to +5‰ (Kohn and Cerling, 2002; Arppe et al., 2011). Because of the links between animal $\delta^{13}C$ values, diet and environment, the analysis of the carbon isotope ratios in bioapatite has been applied in a variety of paleodietary, paleoecological and paleoenvironmental investigations

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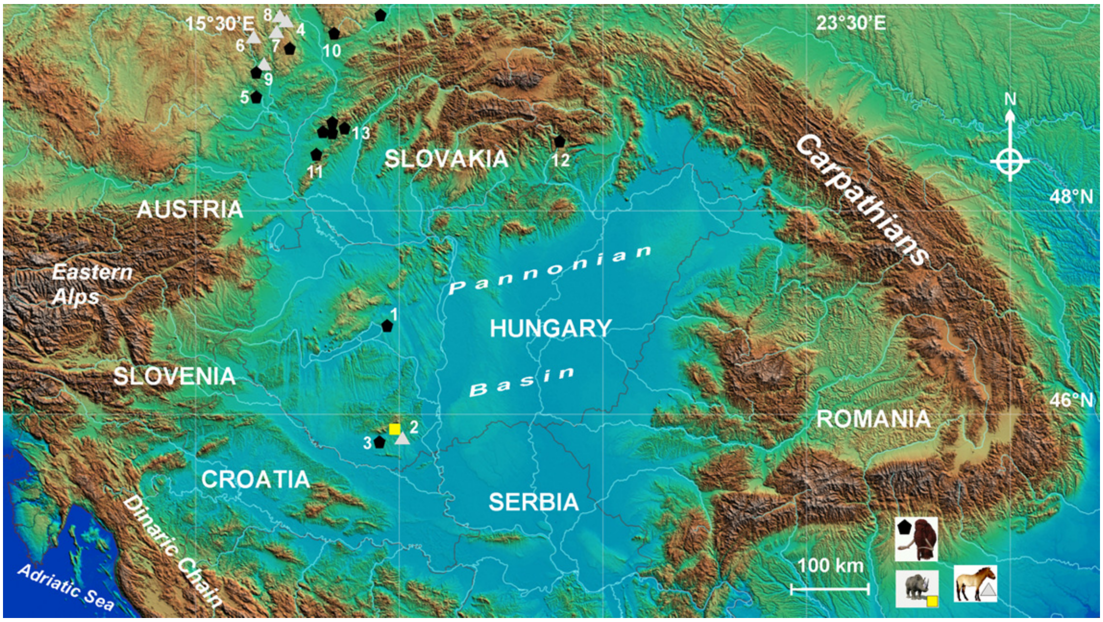

Fig. 1. Location of paleontological and archaeological sites cited in Table 1. The white arrows indicate generally accepted migrations of large mammals in the Late Pleistocene (Kahlke, 1999; Svoboda et al., 2005).

(e.g. Lee-Thorp et al., 1989; Quade et al., 1992; Bocherens et al., 1996; Cerling and Harris, 1999; Iacumin et al., 2000; Feranec, 2004; Metcalfe et al., 2009; Arppe et al., 2011).

Information on the vegetation and environmental conditions relating to mammoth steppe habitats in the study region has been obtained from earlier and recently published biostratigraphical (Vörös, 1987; Kovács, 2012), paleoecological (Pazonyi, 2004, 2011), paleolimnological (Břízova, 2009; Buczkó et al., 2009; Hetényi et al., 2010), paleobotanical (Rudner and Sümegi, 2001; Willis and van Andel, 2004), paleoenvironmental (Sümegi and Krolopp, 2002; Kovács et al., 2007; Demény et al., 2011; Musil, 2011; Schatz et al., 2011; Sümegi et al., 2011; Nývltová Fišáková, in press), and archaeological (Beresford-Jones et al., 2011; Budek et al., in press) records. Unlike many regions, the stable isotope composition of the Quaternary megafauna from the Czech Republic and Slovakia was studied and used in very sporadic cases up to the present; for specimens from Hungary these are the first analyses that have been carried out. Only a few scientists in the Czech and Slovak Republics have published any results (e.g. Ábelová, 2007a, 2007b; Moravcová (Ábelová) and Sabol, 2009, 2011; Moravcová (Ábelová), 2010; Vlačiky et al., in press; Nývltová Fišáková et al., 2009).

This paper provides paleotemperature, paleodiet and paleoenvironmental reconstructions of the Late Pleistocene on the basis of oxygen and carbon isotope analyses of mammoth (*Mammuthus primigenius*) tusk dentin, rhinoceros (*Coelodonta antiquitatis*), and horse (*Equus* sp.) tooth enamel samples. This study demonstrates how isotopic data can be employed along with other forms of evidence to deepen understanding of even the remote past, making it relevant to the Paleolithic where there is a wealth of material available for potential future studies. This paper was primarily aimed at reconstructing $\delta^{18}O_W$ and surface air temperature on the base of $\delta^{18}O_C$ of *M. primigenius* tusk dentin, *C. antiquitatis* and *Equus* sp. enamel from three Slovak, seven Moravian and three Hungarian Late Paleolithic localities. Another important goal was the interpretation of the diet of these animal species and the paleoenvironment based on tusk dentin and tooth enamel carbon isotope analyses. Isotopic analyses provide a way of identifying paleoenvironments without relying on archaeological proxies such as species lists (recording organisms found at a site) – meaning that such a study is immune to the factors that can affect a bone assemblage of a site, upon which more traditional dietary analyses are based. Bone assemblages at sites represent "a biased average of the dietary refuses of the group" (Bocherens et al., 2005).

2. Samples and location

2.1. Fossil material from the Czech Republic and Slovakia

In this research, bulk samples of tooth enamel and dentin of *M. primigenius* and *Equus* sp., from ten Slovak and Moravian localities (Fig. 1, Table 1) have been analyzed. All analyses of oxygen and carbon isotopes have been conducted in laboratories of the Czech Geological Survey in Prague, Czech Republic. All teeth belonged to adult individuals. Samples included in these studies were acquired from Moravian Museum (Brno, Czech Republic); Institute of Archaeology of the Academy of Sciences (Brno, Czech Republic); Institute of Archaeology of the Slovak Academy of Sciences (Košice, Slovak Republic); Slovak National Museum–Natural History Museum (Bratislava, Slovak Republic) and Department of Geology and Paleontology of the Faculty of Natural Sciences, Comenius University (Bratislava, Slovak Republic). All original specimens are housed in the collections of these institutions.

2.2. Hungarian samples

All fossil samples have been collected at recent excavations (Fig. 1, Table 1). All teeth belonged to adult individuals. Samples of *M. primigenius* tusk dentin are from Csajág and Zók. Sample of *C. antiquitatis* tooth enamel is from Kozármisleny. All original specimens are housed in the collections of the Department of Geology, University of Pécs, and the Natural History Museum of Bakony Mountains, Zirc (see in Konrád et al., 2010; Katona et al., 2012.)

Table 1
Carbon and oxygen isotopic composition of fossil remains. All samples are AMS dates unless otherwise stated. Calibrated using CalPal.

Sample code	Site (location numbers, see in Fig. 1)	Country	Species	Material for ^{14}C dating	Material for isotopic analysis	^{14}C age $\pm$ 1σ (uncal BP)	Lab no.	Source of dating	^{14}C age $\pm$ 1σ (cal BP)	$\delta^{13}C_C$ (V-PDB)	$\delta^{18}O_C$ (V-PDB)	$\delta^{18}O_C$ (V-SMOW)	$\delta^{18}O_P$ (V-SMOW)	$\delta^{18}O_W$ (V-SMOW)	T_{air} (°C)	$\delta^{13}C_{PV}$	Source of isotope data
CZ1	1. Csajág	HU	*M. primig.*	tusk	dentin	13 315 ± 35	GdA-2011	Katona et al. (2012)	16 249 ± 413	−11.4	−8.7	21.9	13.1	−10.3	8.1	−25.4	This study
KR4	2. Kozármisleny	HU	*C. antiq.*	tooth	enamel	10 080 ± 40	GdA-2012	This study	11 638 ± 172	−12.4	−6.4	24.3	15.3	−8.5	11.5	−26.4	This study
Z1	3. Zók	HU	*M. primig.*	tusk	dentin	17 760 ± 200	AA-80678	Konrád et al. (2010)	21 250 ± 450	−10.8	−12.0	18.5	9.8	−13.4	2.4	−24.8	This study
EB 1[a]	4. Balcarka Cave	CZ	*Equus* sp.	bone	enamel, M_3 inf.	13 930 ± 100	GrN-28448	Valoch and Neruda (2005)	17 186 ± 223	−7.6	−6.6	24.1	15.4	−9.3	10.1	−21.6	Ábelová (2008)
MP VU 1[a]	5. Brno – Vídeňská street	CZ	*M. primig.*	charred bone	tusk dentin	14 450 ± 90	GrN-9350	Valoch (1996)	17 588 ± 257	−9.9	−7	23.7	14.8	−8.7	11.0	−23.9	Ábelová (2008)
E BS 1	6. Býčí skála Cave	CZ	*Equus* sp.	bone	enamel, M_3 inf.	12 910 ± 60	GrA-29910	unpubl. data (J. van der Plicht)	15 652 ± 366	−9.5	−6.6	24.1	15.4	−9.3	10.1	−23.5	Ábelová (2008)
E K 1	7. Kolíbky Cave	CZ	*Equus* sp.	antler	enamel, M_3 inf.	12 680 ± 110	OxA-5973	Valoch and Neruda (2005)	15 053 ± 339	−10.7	−8.3	22.4	13.7	−11.4	6.8	−24.7	Ábelová (2008)
MP K 1[a]	8. Kůlna Cave	CZ	*M. primig.*	charcoal	tusk dentin	11 590 ± 80	GrN-5097	Valoch and Neruda (2005)	13 472 ± 127	−9.7	−6.9	23.8	14.9	−8.6	11.2	−23.7	Ábelová (2008)
MP P1	9. Pekárna Cave	CZ	*M. primig.*	antler	tusk dentin	12 500 ± 110	OxA-5972	Valoch and Neruda (2005)	14 803 ± 338	−10.5	−7.5	23.2	14.3	−9.2	10.3	−24.5	Ábelová (2008)
E P 1[a]		CZ	*Equus* sp.	horse bone	enamel, M_3 inf.	12 940 ± 250	Ly-2553	Valoch (1988)	15 701 ± 622	−8.8	−8.6	22.0	13.4	−11.8	6.2	−22.8	Ábelová (2008)
MP Pr 2[a]	10. Předmostí	CZ	*M. primig.*	charred bone	tusk dentin	26 320 ± 240 26 870 ± 250	GrN-6852, GrN-6801	Svoboda et al. (2002)	31 142 ± 374 31 620 ± 240	−8.2	−2.9	27.9	18.9	−4.9	16.9	−22.2	Ábelová (2008)
MP DS 1	11. Dzeravá skala Cave	SK	*M. primig.*	bone	tusk dentin	24 760 ± 130	OxA-13861	Kaminská et al. (2005)	29 809 ± 320	−8.4	−5.1	25.7	16.7	−6.9	13.8	−22.4	Ábelová (2008)
MP SJ 1[a]	12. Slaninová Cave	SK	*M. primig.*	bone	tusk dentin	27 950 ± 270	GrN-14832	Kaminská (1993)	32 469 ± 342	−8.7	−2.6	28.2	19.2	−4.6	17.4	−22.7	Ábelová (2008)
1. MP TB 1	13. Trenčianske Bohuslavice	SK	*M. primig.*	charcoal	tusk dentin	25 130 ± 170	GrA-16163	Verpoorte (2002)	30 053 ± 258	−8.8	−6.4	24.3	15.4	−8.1	11.9	−22.8	Ábelová (2008)
2. MP TB 2		SK	*M. primig.*	charcoal	tusk dentin	25 130 ± 170	GrA-16163	Verpoorte (2002)	30 054 ± 258	−8.7	−5.7	25.0	16.1	−7.5	12.9	−22.7	Ábelová (2008)
3. MP TB 3		SK	*M. primig.*	charcoal	tusk dentin	25 130 ± 170	GrA-16163	Verpoorte (2002)	30 055 ± 258	−8.3	−6.3	24.4	15.5	−8.0	12.0	−22.3	Ábelová (2008)
4. MP TB 4		SK	*M. primig.*	charcoal	tusk dentin	25 130 ± 170	GrA-16163	Verpoorte (2002)	30 056 ± 258	−9.2	−7.2	23.5	14.6	−8.9	10.7	−23.2	Ábelová (2008)
5. MP TB 5		SK	*M. primig.*	charcoal	tusk dentin	25 130 ± 170	GrA-16163	Verpoorte (2002)	30 057 ± 258	−10.8	−7.4	23.3	14.4	−9.1	10.4	−24.8	Ábelová (2008)

All isotopic data are given in permil (‰).
For the details of isotopic calculations see the Methods section.
HU – Hungary; CZ – Czech Rep.; SK – Slovakia.
[a] Conventional dating.

3. Methods

3.1. Radiocarbon dating

Tooth ($n = 3$), bone ($n = 5$), charred bone ($n = 2$) antler ($n = 2$) and charcoal ($n = 6$) have all been radiocarbon dated (AMS and conventional), and have calendar dates ranging from 33 to 12 ka (Table 1). Most of the specimens (13) were dated using accelerator mass spectrometry (AMS) and 5 using conventional radiocarbon dating. Radiocarbon ages are quoted both uncalibrated and in calendar years (calibrated using CalPal-2007$^{\text{online}}$; Danzeglocke et al., 2011). The results are summarized in Table 1. Because the specimens were dated in different laboratories over a period of time, the methods used for pre-treatment and dating vary. This adds an element of uncertainty in comparing dates. On the other hand, compiling results from different dating laboratories maximizes the information content in the study. It is also known that the reliability of radiocarbon dates decreases beyond 30 ka, so such dates should be treated with caution. The problem should be less critical for dates performed more recently, especially by AMS; but there are always exceptions. A recent study by Price et al. (2011) found major problems with AMS dating beyond 30 ka.

3.2. Sampling and pretreatment

Samples were taken from *M. primigenius* tusk dentin and enamel from lower teeth (M_3) of *Equus* sp. (Table 1) from three Slovak and seven Moravian localities (Fig. 1, Table 1). Five samples (MP TB 1–5) belong to one individual of *M. primigenius* from Trenčianske Bohuslavice. These bulk samples are from five fracture-bounded portions of tusk dentin, however it is not beyond doubt that each sample represents a comparable portion of the successive years. Samples were taken by drilling from the tusk surface towards the pulp cavity. MP TB 1 is from the tusk surface and MP TB 5 is from the inside of the tusk. Besides the samples from the Czech and Slovak Republic, bulk samples of *M. primigenius* tusk dentin (CZ1 and Z1 samples) and enamel (KR4) from lower cheek teeth (M_3) of *C. antiquitatis* (Table 1) have also been analyzed from three Hungarian localities.

The samples were taken either by tweezers and dental tools or by detaching fragments from the horse tooth enamel (after removing the outermost surface of the tooth) or from the mammoth tusk dentin. Typically, sampled enamel fragments measured 3–5 mm in diameter and sampled dentin fragments were within the 5–8 mm range. Samples were then sonicated in distilled water 2–3 times, and dried at room temperature. All samples were examined under an optical microscope prior to being finely ground using a mortar and pestle. Approximately 5–15 mg of enamel and dentin was treated with ~2.5% NaOCl at room temperature for ~24 h, rinsed 5 times with de-ionized water, processed with 0.1 M acetic acid for 4 h, rinsed 5 times again with de-ionized water, then freeze-dried (Koch et al., 1997; Garvie-Lok et al., 2004).

3.3. Isotopic analyses of the samples from the Czech Republic and Slovakia

Stable carbon and oxygen isotope analyses of tusk dentin and tooth enamel (and dentin) were performed using the procedure of McCrea (1950). All isotopic analyses were conducted at the Czech Geological Survey, Prague, Czech Republic. Powdered samples (10–30 mg) were treated with 100% anhydrous phosphoric acid (H_3PO_4) at 25 °C in evacuated vessels for at least 12 h. Carbon dioxide gas generated in the acid–carbonate reaction was then cryogenically separated into a second evacuated vessel and was subsequently analyzed employing a Finnigan MAT 252 mass-spectrometer. The precision of stable-isotopic analyses is 0.02 for $\delta^{13}C$ and 0.03 for $\delta^{18}O$, achieved by comparing results from a calcite standard (Carresian marble). Duplicate analyses of samples imply a reproducibility of ±0.05‰ for both oxygen and carbon. Radiocarbon dating was not done on the same specimens as the stable isotope analyses.

3.4. Isotopic analyses of Hungarian samples

After the pre-treatment, samples were processed with orthophosphoric acid at 70 °C to release CO_2. The resultant carbon dioxide was analyzed for both carbon and oxygen isotopes using a GasBench II interfaced to a Thermo-Finnigan Delta$^{\text{Plus}}$ XP IRMS in the Stable Isotope Geosciences Facility at TAMU, USA. Carbon and oxygen isotope values were expressed in the δ-notation as permil (‰) versus V-PDB and corrected through the NBS-19 calcite standard. Replicate analyses ($n = 16$) of this standard gave a mean $\delta^{13}C$ (V-PDB) value of 1.95 ± 0.05‰, and a $\delta^{18}O$ (V-PDB) value of −2.20 ± 0.02‰. Three samples were measured in double (CZ1, KR4, Z1), the reported values being the mean of two measurements. These duplicate analyses indicate a reproducibility of ±0.1‰ for carbon and ±0.15‰ for oxygen isotopes. Radiocarbon dating was done on the same specimens as the stable isotope analyses.

3.5. Calculations

$\delta^{13}C$ values of diet (i.e. paleovegetation) were estimated from measured $\delta^{13}C$ data of tooth bioapatite and using an isotopic offset of 14‰ (Kohn and Cerling, 2002):

$$\delta^{13}C_{PV} = \delta^{13}C_{C} - 14(‰) \tag{1}$$

$\delta^{18}O_C$ vs. V-PDB values were converted to the V-SMOW scale using the equation given by Coplen et al. (1983). As the intent was to obtain estimates on the oxygen isotopic composition of meteoric water ($\delta^{18}O_W$) and most equations are based on the relationship between the oxygen isotopic composition of bone phosphate in animals and that of local precipitation, it was necessary to convert $\delta^{18}O_C$ values to $\delta^{18}O_P$. Both Bryant et al. (1996) and Iacumin et al. (1996) demonstrated the relationship between oxygen isotopes in co-existing carbonate and phosphate fractions of biological apatite in mammalian teeth. It must be emphasized here that despite the fact that a fixed ~8.9‰ $\delta^{18}O_C$–$\delta^{18}O_P$ offset for these conversions is widely applied in $\delta^{18}O_C$-based paleoclimate reconstructions, this offset may range from 6 to 12‰ for intra-tooth sub-samples causing large uncertainties in the calculation of environmental water $\delta^{18}O$ (Pellegrini et al., 2011). The lack of measured $\delta^{18}O_P$ data from the studied fossil material required relying on these published relationships between $\delta^{18}O_C$ and $\delta^{18}O_P$. For the recalculation of $\delta^{18}O_C$ data coming from fossil remains of rhinoceros the equation of Iacumin et al. (1996)

$$\delta^{18}O_P = 0.98 \times \delta^{18}O_C - 8.5 \tag{2}$$

was used, as an equation specifically adjusted for the given species could not be derived due to the lack of appropriate datasets. By contrast, for the conversion of fossil horse and mammoth $\delta^{18}O_C$ data two equations were deduced from published data (see Fig. 2) thereby eliminating the effect of inter-species $\Delta^{18}O_{C-P}$ variability (Iacumin et al., 1996; Martin et al., 2008). For *Equus* sp. the recalculations have been executed using the equation

$$\delta^{18}O_P = 0.97 \times \delta^{18}O_C - 7.94 \left(R^2 = 0.99\right) \tag{3}$$

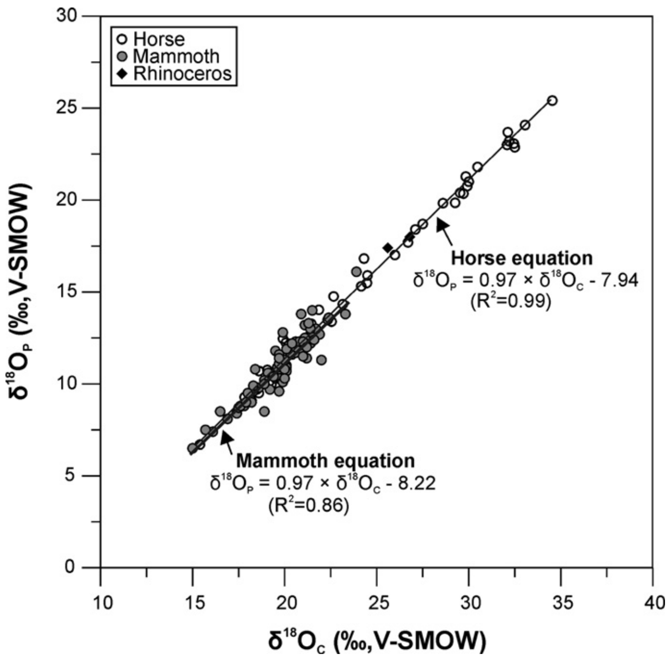

Fig. 2. Relationship between the oxygen isotopic composition of structural carbonate ($\delta^{18}O_C$) and phosphate ($\delta^{18}O_P$) in bioapatite of mammalian tooth. Data sources: horse – Bryant et al. (1996), Iacumin et al. (2010), and Pellegrini et al. (2011); mammoth – Arppe and Karhu (2006), Tütken et al. (2007), Ukkonen et al. (2007), Arppe and Karhu (2010), Iacumin et al. (2010), and Skrzypek et al. (2011); rhinoceros – Martin et al. (2008).

which was based on the data of Bryant et al. (1996), Iacumin et al. (2010), and Pellegrini et al. (2011). The respective mammoth equation is

$$\delta^{18}O_P = 0.97 \times \delta^{18}O_C - 8.22 \left(R^2 = 0.86\right) \tag{4}$$

derived from data of Arppe and Karhu (2006), Tütken et al. (2007), Ukkonen et al. (2007), Arppe and Karhu (2010), Iacumin et al. (2010), and Skrzypek et al. (2011). The overall uncertainty (95% prediction interval) associated with the $\delta^{18}O_{C-P}$ conversion using the above linear equations is *ca.* 1–1.3‰, as calculated by

$$s_{y_p} = t_{\left(1-\frac{\alpha}{2}\right),n-2} \sqrt{\hat{\sigma}_0 \left(1 + \frac{1}{n} + \frac{(x_p - \bar{x}_i)^2}{\sum_i^n (x_p - \bar{x}_i)^2}\right)}, \tag{5}$$

where t is the t score equal to $n-2$ degrees of freedom from the Student's t–distribution, $\alpha = 1 - $ (confidence level/100), x_p is the $\delta^{18}O_C$ value for which y_p is calculated, $\bar{x}_i$ is the mean of $\delta^{18}O_C$ values, n is the number of x_i–y_i data pairs used for regression, while $\hat{\sigma}_0$ being the root mean square error of the regression.

Since the $\delta^{18}O_P$ in bioapatite is directly related to the oxygen isotopic composition of body water of mammals and hereby to that of ingested water (e.g. Longinelli, 1984; Luz and Kolodny, 1985) obtained by large mammals from the local precipitation and food (Luz et al., 1984; Ayliffe et al., 1992), there is a correlation between $\delta^{18}O_P$ and $\delta^{18}O_W$ (meteoric water) (Luz et al., 1984). For calculations of $\delta^{18}O_W$ from oxygen isotopic data of *M. primigenius* and *Equus* teeth published equations regarding the $\delta^{18}O_P$–$\delta^{18}O_W$ relationship for modern elephants (Ayliffe et al., 1992) and horses (Sanchez Chillón et al., 1994; Delgado Huertas et al., 1995) were recalculated based on the original data. In these recalculations data points from arid regions (eastern African samples) have been excluded from the elephant dataset as suggested by Ayliffe et al. (1992). The respective equations are

$$\delta^{18}O_W = 0.93 \times \delta^{18}O_P - 22.43 \left(R^2 = 0.86\right) \tag{6}$$

for elephants, and

$$\delta^{18}O_W = 1.25 \times \delta^{18}O_P - 28.59 \left(R^2 = 0.90\right) \tag{7}$$

for equids. To the authors' knowledge, such data for rhinoceros are not available in the literature, therefore the following equation was used

$$\delta^{18}O_W = \left(\delta^{18}O_P - 23\right) \Big/ 0.9 \tag{8}$$

given by Kohn and Cerling (2002) for vertebrates omitting turtles, deer, rabbits, and macropodids.

Finally, the mean surface air temperatures (T_{air} in °C) have been estimated by using present-day temporal $\delta^{18}O/T$ relationships from two proximal GNIP stations (monthly raw data at Vienna and Zagreb). Present-day and last glacial maximum (LGM) model simulations of water isotope geochemistry suggest that there is a fairly good agreement between spatial and temporal $\delta^{18}O/T$ slopes for most of Europe (Joussaume and Jouzel, 1993; Jouzel et al., 1994). Fricke and O'Neil (1999) emphasize, however, that present-day ('Greenhouse') $\delta^{18}O/T$ relationships cannot be used unambiguously directly to infer ice age surface air temperatures. However, the oxygen isotopic and noble gas compositions of paleogroundwaters in the Great Hungarian Plain revealed a temporal $\delta^{18}O/T$ slope of 0.37‰/°C for the last glacial/interglacial transition (Stute and Deák, 1989) which corresponds with present-day temporal slopes for Vienna (0.38‰/°C) and Zagreb (0.33‰/°C), thereby justifying this approach. Before calculating surface air temperatures, $\delta^{18}O_W$ values were compensated for the ^{18}O-enrichment of the glacial ocean (0.4‰ for samples with ages of 11.5–12.8 ka, 0.6‰ for those between 13 and 50 ka, and 0.8‰ for the LGM sample; Sowers et al., 1993; Schrag et al., 1996, 2002) and then these corrected values ($\delta^{18}O_{Wcorr}$) were used for T_{air} calculations. The respective equations are

$$T_{air\ (V)} = 1.55 \times \delta^{18}O_{Wcorr} + 25.43 \left(R^2 = 0.598\right) \tag{9}$$

for Vienna, and

$$T_{air\ (Z)} = 1.94 \times \delta^{18}O_{Wcorr} + 28.80 \left(R^2 = 0.649\right) \tag{10}$$

for Zagreb (Fig. 3). As the Hungarian sites of fossil remains are located at approximately the same distance from Vienna and Zagreb the surface air temperatures were calculated as the mean of $T_{air\ (V)}$ and $T_{air\ (Z)}$:

$$T_{air} = \left(T_{air\ (V)} + T_{air\ (Z)}\right) \Big/ 2. \tag{11}$$

For the calculation of T_{air} from fossil remains in the Czech Republic Equation (9) for Vienna was used in lack of appropriate, long isotopic record of precipitation in the given country.

4. Results

The carbon and oxygen isotope compositions of the carbonate fraction ($\delta^{13}C_C$, $\delta^{18}O_C$) are given in Table 1. Stable isotope results are presented in standard delta (δ) notation relative to V-SMOW (oxygen) and V-PDB (carbon), following Coplen (1994). The $\delta^{18}O_C$ values range from 18.5‰ to 28.2‰ for the mammoth samples with a mean value of 23.35‰. The enamel samples form a tight group with all $\delta^{18}O_C$ values falling between 22‰ and 24.1‰, whereas the dentin samples yielded more positive values. The mammoth

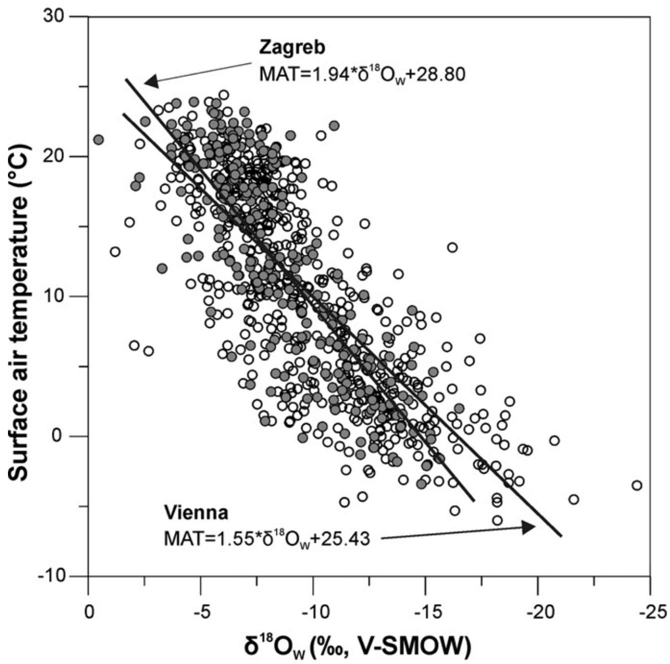

Fig. 3. Oxygen isotopic composition of precipitation versus surface air temperature plot for the Vienna and Zagreb GNIP stations (monthly raw data). Data source: IAEA/WMO (2006). Global Network of Isotopes in Precipitation. The GNIP Database. Accessible at: http://www.iaea.org/water, (last accessed: 08.03.2011).

sample from Zók (Hungary) yields the lowest (18.5‰) and the one from Slaninová Cave (Slovakia) the highest (28.2‰) $\delta^{18}O_C$ values. Tusk dentin samples MP SJ1 and MP Pr2, of woolly mammoth specimens from Slaninová Cave (Slovakia) and Předmostí (Czech Rep.), yielded unusually high $\delta^{18}O_C$ values of 28.2‰ and 27.9‰. The $\delta^{18}O_C$ values of horses and woolly rhino vary between 22‰ and 24.3‰ with a mean value of 23.15‰ for the horses.

The $\delta^{13}C$ data indicate relatively high within-region variation, ranging from 0.1 to 4.8‰. The $\delta^{18}C_C$ values of *M. primigenius* vary from −8.2‰ to −11.4‰ and fall between −7.6‰ and −12.4‰ for horse and woolly rhino. The rhino sample from Hungary showed the lowest value, −12.4‰, while the horse sample from the Czech Rep. provided the highest −7.6‰. The mean $\delta^{13}C$ value of the mammoth dentin samples is −9.8‰.

5. Discussion

5.1. Preservation of the samples

The majority of the Late Pleistocene specimens investigated in this study are macroscopically well-preserved, commonly exhibit a dark (grey, black) crust covering part of their external surface and the inside of dentin fractures. These are mainly iron and manganese minerals. Samples are found in dry cave and loess sediments and as well as in fluvial sediments (sample KR4 only). Arppe and Karhu (2006) suggested that high concentrations of Fe or Mn do not cause a dramatic alteration of enamel. All these crusts were removed before sampling. Where possible, the least weathered samples were chosen for analysis.

5.2. $\delta^{18}O_P$, $\delta^{18}O_W$ and surface air temperatures

The converted $\delta^{18}O_P$ values range from 9.8‰ to 19.2‰ for the mammoth samples with a mean value of 14.5‰. The enamel samples displayed $\delta^{18}O_P$ values falling between 13.4‰ and 15.4‰, whereas the dentin samples yielded more positive values. The mammoth sample from Zók (Hungary) provides the lowest (9.8), while the one from the Slaninova Cave (Slovakia) the highest (16.7) $\delta^{18}O_P$ composition.

The $\delta^{18}O$ signature of the ECE samples presented in this study are amongst the highest values (Fig. 4) reported to date for woolly mammoth from the European Late Pleistocene (Ayliffe et al., 1992; Genoni et al., 1998; Tütken et al., 2008; Arppe and Karhu, 2010; García-Alix et al., 2012), except for the Z1 (Zók) sample from Hungary (9.8‰). The oxygen isotopic signal of pre-LGM mammoth samples correlates well with those values of fossil finds from the North Sea and Rhine River sediments (Tütken et al., 2008). The post-LGM fossil finds where comparative mammoth $\delta^{18}O$ data, are available are Eliscevichi and Mezhirich (14.3 ka BP; Genoni et al., 1998) from the Russian Plain; and Puurmani, Saare-Utsali (10.2 ka BP; Lõugas et al., 2002; Arppe and Karhu, 2010), Rucava (12.9 ka BP; Arppe and Karhu, 2010), Kaunas (river Jiesia 1, 13.8 ka BP; Arppe and Karhu, 2010) from the Baltic states, and Dzierżysław (12.6 ka BP; Arppe and Karhu, 2010) from Poland. The oxygen isotopic composition of the Csajág mammoth and the Brno – Vídeňská Street samples are provided 1.0–2.7‰ and 2.2–3.9‰ higher values than those of samples from Russia and Kaunas region (Lithuania), respectively. This is expected considering the latitudinal and longitudinal decreasing of $\delta^{18}O_W$ value upon growing distance from the ocean towards more continental areas. The only LGM fossil finds, where comparative mammoth $\delta^{18}O$ data are available, is Højballegård, Hansted (19.9 ka BP; Aaris-Sørensen, 2006; Arppe and Karhu, 2010) in Denmark. The $\delta^{18}O_P$ value of the Zók sample (age 18 ka BP) is ~3.5‰ lower than the Danish sample.

The oxygen isotopic signal of horse samples correlates well with those values of fossil finds from North Sea and Rhine river gravels (Tütken et al., 2008) and from French Jura (Fabre et al., 2011). The $\delta^{18}O_P$ of rhinoceros is also in accordance with values measured by Tütken et al. (2008) in samples from Rhine River gravels and from the North Sea.

Based on $\delta^{18}O_P$ of the enamel and dentin samples, the oxygen isotope composition of the mean annual Late Pleistocene precipitation in East Central Europe varied from −13.4‰ to −4.6‰, with an average value of −9‰ (Fig. 5). Based on the relationship of Equations (9)–(11), this would correspond to a surface air temperature of

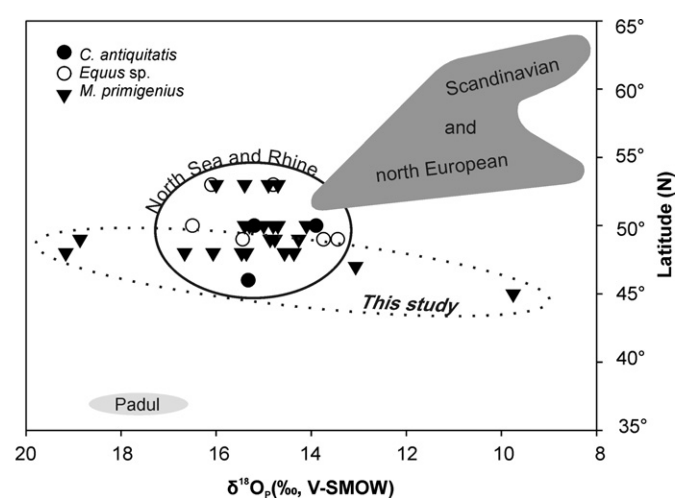

Fig. 4. Latitudinal variation of $\delta^{18}O_P$ values in European woolly mammoths (and some woolly rhinos and horses) ranging from 50 to 12 cal ka BP. Woolly mammoth data (except those from this study) from Ayliffe et al. (1992); Genoni et al. (1998); Arppe and Karhu (2006); Tütken et al. (2007, 2008); Ukkonen et al. (2007); Arppe and Karhu (2010); García-Alix et al. (2012); Pryor et al. (in press).

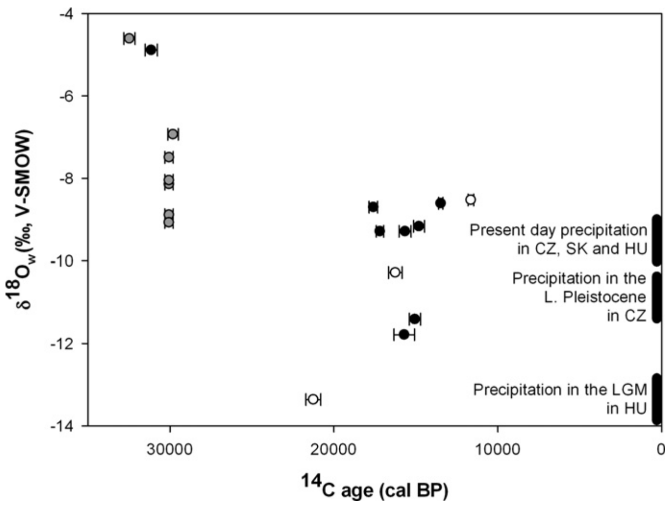

Fig. 5. Oxygen isotope composition of precipitation ($\delta^{18}O_W$) calculated from the samples. The range of present-day (Deák et al., 1996; Šanda et al., 2009) and LGM (Stute and Deák, 1989; Deák et al., 1996) oxygen isotope composition of precipitation in the areas of the fossil finds localities in ECE are indicated.

10 °C. The oxygen isotope composition of present-day precipitation in ECE ranges from −9‰ to −10.5‰ (Deák et al., 1996; Šanda et al., 2009; Jiráková et al., 2011; Varsányi et al., 2011), while the δ^{18}O composition of Late Pleistocene groundwater varies from −11.2‰ and −10.6‰ for the western part (Šilar and Šilar, 1995; Kadlec et al., 2000; Jiráková et al., 2010, 2011), and from −11‰ and −14‰ for the eastern part of the study region (Stute and Deák, 1989; Deák et al., 1996; Varsányi et al., 2011). The difference of 0–5‰ between Late Pleistocene and modern $\delta^{18}O_W$ values implies 0–9 °C lower surface air temperatures for the Late Weichselian period between 12 and 23 ka ago than present-day air temperature (Fig. 6). Compared with the model results of stable water isotopes in precipitation for the last glacial maximum (LGM), the presented $\delta^{18}O_W$ datum from the Zók locality (−13.3, T_{air}: 2.4 °C, age: 21 250 cal BP) is slightly lower than the simulated values of *ca.* −10 to 12 for the region (Jouzel et al., 1994). At the same time, the surface temperature (T_{air}) difference of 0–9 °C between the present-day and the LGM is in general accordance with the simulated values of *ca.* 4–7 °C for the region (Kageyama et al., 2006; Corcho Alvarado et al., 2011) and the measured noble gas data of the southern part of the Pannonian basin (3.3 °C; Varsányi et al., 2011).

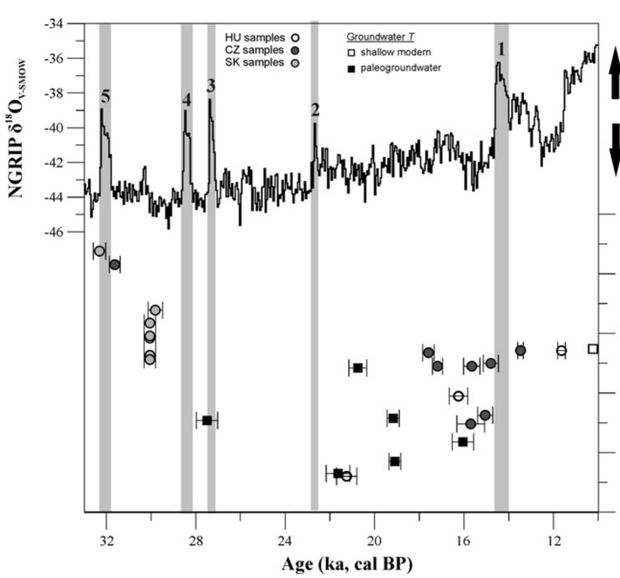

Fig. 6. Plot of paleotemperature data alongside the NGRIP ice core δ^{18}O record. numbers (1–5) – Dansgaard–Oeschger events. Data source for the isotopic record (NGRIP members 2004), for paleogroundwater (Stute and Deák, 1989; Deák et al., 1996; Varsányi et al., 2011).

According to Varsányi et al. (2011), the temperature difference between waters of cold and warm recharge of paleogroundwater (including the early Holocene samples), i.e. between the LGM and the Holocene, was found to be 9.1 ± 0.8 °C. This LGM to Holocene temperature change for the Carpathian Basin has the same magnitude as that calculated from the $\delta^{18}O_P$ value of the Zók sample ($T_{PRESENT\text{-}DAY} - T_{LGM} = 11 - 2.4 = 8.6$ °C). However, the range of $\delta^{18}O_W$ values (−4.6 to −11.4) reconstructed from the fossil remains differs from that indicated by paleogroundwater studies, since the latter lie at the negative end of the $\delta^{18}O_W$ spectrum defined by the studied mammals. As described by Williams and Elliot (1989) dentin, cementum and bone have higher organic composition than enamel and their inorganic phase can be altered more easily than that of enamel. It is possible, therefore, that the oxygen isotopic compositions of some dentin samples (MP Pr 2, MP DS 1, MP SJ 1) displaying $\delta^{18}O_W$ values of <*ca.* −7–8‰, are not well-preserved.

The two tusk dentin samples from Slaninová Cave (Slovakia) and Předmostí (Czech Rep.) yielded unusually high $\delta^{18}O_P$ values, with ages around 32 ka cal BP. These data may represent the warmer Dansgaard–Oeschger 5 event (see Fig. 6). Based on δ^{18}O values (Fig. 6), the reconstructed surface temperature (T_{air}) was between 17.4 and 10.4 °C (mean ∼13.2) in the study area in MIS 3 (32.5–29.5 ka cal BP), while during the LGM (∼21 ka cal BP), the T_{air} may have been quite low (*ca.* 2–3 °C) in the southern part of the Pannonian basin. The surface air temperature had begun to rise in MIS 2 (28–12 ka cal BP) after the LGM. In the western part of ECE (Czech Rep., Slovakia), the T_{air} was between 6.2 and 11.2 °C (∼9.4); and in the southern part it reached *ca.* 9.8 °C at the end of the Late Pleistocene (Fig. 6). The LGM to Holocene paleotemperature change of 8.5–9.5 °C, as reconstructed from the data and those of paleogroundwaters (Varsányi et al., 2011), refers to a prevailing subarctic/boreal (taiga) climatic regime (Köppen Dfc, Dwc, Dsc) in the basin.

5.3. $\delta^{13}C$ data

Mammals feeding on C_3 plants (fruit, leaves, etc.) characteristically have δ^{13}C values between about −20 and −8‰, while animals that eat C_4 tropical grasses (including blades, seeds, and roots) have δ^{13}C values between 0 and +5‰. Those on a mixed diet would fall somewhere between these two extremes (Lee-Thorp and van der Merwe, 1987; Quade et al., 1992; Kohn and Cerling, 2002). In these specimens, δ^{13}C values have been obtained from structural carbonate of hydroxyapatite (inorganic fraction). In general, European woolly mammoth followed a diet of C_3 plants during the latest Pleistocene glacial stage, and their δ^{13}C values usually correspond to the upper range of C_3 plants (Bocherens et al., 1996; Iacumin et al., 2000; Arppe et al., 2011). The mammoth dentin $\delta^{13}C_C$ values are typical for herbivores found in pure C_3 ecosystems. These values are in accordance with values measured in Siberian, Ukrainian and Russian mammoth remains by Iacumin et al. (2000) and in samples from Finland (Arppe and Karhu, 2006; Arppe et al., 2011) as well as from Poland (Pryor et al., in press) and Spain (García-Alix et al., 2012). The Polish, Swedish, Lithuanian and Estonian specimens provide intermediate regional mean values of −11.3 ± 0.4‰, −11.4 ± 0.4‰, −11.5 ± 0.3‰ and −11.6 ± 0.4, respectively (Arppe et al., 2011). The mean δ^{13}C value of the mammoth enamels from northern Switzerland (−11.5 ± 0.3‰, $n = 10$, Tütken et al., 2007) is similar to these. The ECE mammoth specimens' mean value is −9.8‰ ($n = 13$) while that of the Padul (southernmost record) mean is $-8.4‰$ ($n = 15$; García-Alix et al., 2012). In general, the strength of negative correlation with latitude is weak, but clear. Reported carbon isotopic data from the study region indicate that horses in the latest Pleistocene were primarily C_3 grazers. These $\delta^{13}C$ compositions for the studied fossil horse remains are in accordance with values measured in Yakutia (Bocherens et al., 1996), in Switzerland (Tütken et al., 2007) and Pampean Region, Argentina (Sánchez et al., 2006). The highest $\delta^{13}C$ value ($-7.6‰$) might be proportional to the C_3–C_4 ratio of the possible diet, however that was based on sample only. Regarding the rhinoceros sample, its $\delta^{13}C$ value (12.4‰) falls between the lower Russian −15.6 to −11.6‰ (Bocherens et al., 1996; Tiunov and Kirillova, 2010) and the higher Niederweningen −11.0‰ values (Tütken et al., 2007) as well as those from Scotland −10.2–10.8‰ (Jacobi et al., 2009). $\delta^{13}C$ values show a weak, but clear negative correlation with longitude in this case. Arppe et al. (2011) propose a SW–NE gradient based on the carbon isotopic composition of tooth enamel in central and northern European woolly mammoths, where higher $\delta^{13}C_C$ values were found in southwestern areas, implying warmer and drier conditions than those found in northeastern areas. The data of biogenic apatite are among the highest values (mean: $-9.6‰_{total}$, including rhino and horse specimens), close to the uppermost boundary implying that there was an important water stress in the vegetation, likely caused by drier conditions. This may indicate that the specimens lived occasionally under more arid conditions than others in the surrounding area.

The calculated paleovegetation ($\delta^{13}C_{PV}$, see in Table 1) values range from −26.4‰ to −21.6‰, which also indicate typical C_3-vegetation. In a recent study, Schatz et al. (2011) published soil carbon isotope values ranging from −24 to −25‰ from a loess profile near Tokaj (NE Hungary) and suggested that C_3 plants have been the main vegetation type in the Carpathian Basin during the Late Weichselian. Indications of C_4-vegetation in Europe during the Late Pleistocene have only been recorded from the Balkans (Willis and van Andel, 2004). The $\delta^{13}C$ values suggest warmer and drier conditions in ECE than in northeastern Europe (Arppe et al., 2011) while less warm and dry environments than in southwestern Europe (García-Alix et al., 2012).

6. Conclusions

This study was based on the analyses of the isotopic composition of structural carbonate in 18 subfossil large mammal skeletal samples from the Czech and Slovak Republics and Hungary, in order to reconstruct past habitat in which the specimens lived. The overall state of preservation of these samples suggested that the isotopic composition of carbonates of dentin and enamel was suitable for paleoenvironmental interpretations. These specimens lived in East Central Europe between ~33 and ~12 cal ka BP, coinciding with cold and dry phases, such as Greenland stadials 3 and 2, *ca.* 22.5–14.7 ka, including LGM; the warm Bølling/Allerød (Greenland interstadial 1) *ca.* 14.7–12.6 ka; the cold Younger Dryas (Greenland stadial 1) *ca.* 12.6–11.5 ka.

The $\delta^{13}C$ results point to the fact that the Late Pleistocene vegetation in the ECE was dominated by C_3 plants. The geographic pattern of $\delta^{13}C$ values suggests that the mammoths in the northeastern parts of Europe subsisted in a colder and moister environment than the ECE counterparts. Accordingly, the isotope data imply a warmer and possibly dryer living environment of open vegetation for the mammoths in the study region. Specimens of woolly mammoth, rhino and horse from the Late Pleistocene were primarily C_3 grazers.

The enamel and dentin-derived long-term mean glacial $\delta^{18}O_W$ values agree remarkably well with local glacial palaeogroundwater oxygen isotope levels in several East Central European locations. These isotopic data suggest that surface air temperatures in the study region between 33 and 12 ka were 2–9 °C colder than present.

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