

Pliocene and Early Pleistocene paleoenvironmental conditions in the Pannonian Basin (Hungary, Slovakia): Stable isotope analyses of fossil proboscidean and perissodactyl teeth



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ABSTRACT

Stable carbon and oxygen isotope values of structural carbonate ($\delta^{13}\text{C}$, $\delta^{18}\text{O}_{\text{CO}_3}$) and phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) in bioapatite were measured for fossil mammalian teeth from Slovakia and Hungary. Oxygen isotope compositions of enamel provide new quantitative records of the Pliocene and Early Pleistocene paleoclimate in the Pannonian Basin (PB). The $\delta^{18}\text{O}_{\text{PO}_4}$ values were used to study the temporal variations in the oxygen isotope compositions of precipitation and the changes in temperature over the PB. The new O-isotope data suggest that surface air temperatures between 4.5 and 2.0 Ma were 1 to 4 °C warmer with about 700 mm/yr more precipitation compared to the present. C-isotope analyses of samples from proboscideans (*Anancus* sp., *Mammot* sp.) and perissodactyls (*Stephanorhinus* sp., *Tapirus* sp.) from the Pliocene (MN15–MN16) and Early Pleistocene (MN17) suggest that they were primarily C₃ browsers. The mean $\delta^{13}\text{C}$ value is high at 4.5 to 3.7 Ma (MN14–15) during the Pliocene Warm Period and decreases at about 3.5 to 3.0 Ma (MN16; mid-Pliocene Warm Period), with the onset of more humid conditions in Europe. The $\delta^{13}\text{C}$ values return to higher values from 2.5 Ma onwards (MN17), most likely reflecting more arid conditions as a consequence of the onset of the Northern Hemisphere glaciation.

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1. Introduction

Investigating the changes in Earth's past climate provides a context to better understand current changes in climate and can help to predict future climatic and environmental conditions. The Pliocene–Pleistocene transition (about 2.6 Ma) is undoubtedly one of the most important episodes for the evolution of mankind (deMenocal, 2004; Trauth et al., 2010; Maslin et al., 2014, 2015). Investigations of the stable isotope compositions of biomineralized tissues have added greatly to our knowledge of changes in past climates and dietary behaviors of mammals (e.g., Sullivan and Krüger, 1983; Luz et al., 1984, 1990; Luz and Kolodny, 1985; Ayliffe et al., 1992, 1994; Coplen, 1994; Bryant and Froelich, 1995; Delgado Huertas et al., 1995; Bocherens et al., 1996; Iacumin et al., 1996; Fricke et al., 1998; Cerling and Harris, 1999; Kohn et al., 1999; Kohn and Cerling, 2002; Zazzo et al., 2004a, 2004b;

Arppe and Karhu, 2006; Levin et al., 2006; Tütken et al., 2006; Martin et al., 2008; Kohn, 2010; Pushkina et al., 2014). Quantitative paleoclimatological and paleoecological records based on stable isotope analyses of mammal teeth from the time period prior to the Pliocene and Early Pleistocene are scarce and fragmentary, and particularly poor in the region of East Central Europe (e.g., Kovács et al., 2012).

Mammal teeth and bones are mineralized as bioapatite, a calcium phosphate mineral, with a simplified chemical formula of $\text{Ca}_5(\text{PO}_4)_3(\text{OH}, \text{CO}_3)$ (Skinner, 2005). Carbonate ion (CO_3^{2-}) is substituted in two structural sites, replacing the phosphate (PO_4^{3-}) and hydroxyl (OH^-) ions, and for mammals it is a main constituent of the biomineral. The stable carbon isotope composition of this structural carbonate is known to record the diet of the mammals, hence can be linked to past vegetation (e.g. Sullivan and Krueger, 1983; Cerling and Harris, 1999; Passey et al., 2005). The stable oxygen isotope composition of both structural carbonate ($\delta^{18}\text{O}_{\text{CO}_3}$) and phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) can be linked to the body water of the animals, and its isotopic composition is related to climate and ecophysiological factors (e.g., Longinelli, 1984; Luz and Kolodny, 1985; Kohn et al., 1996). Because of the strong P–O bonds

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the phosphate oxygen is considered more resistant to low temperature inorganic alteration processes compared to carbonate oxygen (e.g., Kohn et al., 1999; Vennemann et al., 2002), hence it is preferentially analyzed for climatic reconstruction. However, during microbiological reactions oxygen isotope exchange between PO_4^{3-} and water is possible due to enzymatic catalysis. In these cases the oxygen isotope composition of the phosphate can also be changed during diagenesis (e.g., Blake et al., 1997; Zazzo et al., 2004a, 2004b; Liang and Blake, 2007). For this reason, tooth enamel rather than bone or dentine is the preferred phase for analysis because it is more resistant to diagenesis (e.g., Lee-Thorp and van der Merwe, 1987; Quade et al., 1992; Ayliffe et al., 1994; Wang and Cerling, 1994; Koch et al., 1997), even in a microbially mediated environment (Zazzo et al., 2004a, 2004b). Compared to bone and dentine, enamel has a larger average crystal size and a lower porosity and lower organic matter content (Skinner, 2005). As a result, the recrystallization of bioapatite and the pore-space infilling by secondary minerals are more limited in enamel compared to bone and dentine in the same taphonomic context (Kohn et al., 1999).

To gain reliable information about the past dietary, paleoclimatic and paleoenvironmental changes, it is important for the samples to have preserved their primary compositions throughout diagenesis and/or low grade metamorphism. Comparing the oxygen isotopic compositions of the structural carbonate to that of the phosphate itself can often help constrain the impacts of diagenesis (e.g., Iacumin et al., 1996). Hence, an approach of using, where possible, enamel rather than dentine and analyzing the stable isotope compositions of carbonate and phosphate within bioapatite, has a good potential of constraining the past changes in terrestrial vegetation and climate, including rainfall and temperature (e.g., Kohn and Cerling, 2002; Kohn, 2010).

From the Pliocene to Early Quaternary period in Central Europe so far only very sporadic stable isotope data exist from mammals, and most of the analyses were done on proboscideans (Kovács et al., 2012; Virág et al., 2014). Rhinoceros have not been specifically investigated in this region, a gap that is to be filled by this study. The sampling localities (Fig. 1) are dated from the late-Early Pliocene to Early Pleistocene. Fossil teeth of large herbivores were selected according to their abundance in the deposits and their appearance of preservation. Altogether, twenty-nine Pliocene and Early Pleistocene samples of fossil

proboscideans ($n = 9$), rhinoceroses ($n = 19$) and one of tapir from the Pannonian Basin (Slovakia and Hungary; Fig. 1) were studied. The carbon and oxygen isotope compositions of carbonate ($\delta^{13}\text{C}$, $\delta^{18}\text{O}_{\text{CO}_3}$) and the oxygen isotope composition of phosphate ($\delta^{18}\text{O}_{\text{PO}_4}$) in enamel were used to explore spatial patterns and temporal variations of $\delta^{18}\text{O}_w$ (oxygen isotope values of precipitation) in Central Europe prior to and after the Pliocene, during the MN15, MN16, and MN17 mammal biozones (about 4.5 to 2.0 Ma).

The goals of this paper are: (1) to reconstruct $\delta^{18}\text{O}_w$ and (2) surface air temperature on the basis of $\delta^{18}\text{O}_{\text{PO}_4}$ values of fossil tooth enamel from two Slovakian and eight Hungarian localities, (3) to interpret the diet of the animals, and (4) their paleoenvironment based on tooth enamel carbon isotope compositions.

2. Background

2.1. Carbon isotopes and diet

The stable carbon isotopic values of teeth reflect the isotopic composition of plants at the base of the food chain in an ecosystem. C_4 plants (warm climate grasses) and C_3 plants (trees, shrubs and high-latitude grasses) are important in the case of paleodiet research. Because of different photosynthetic pathways, the C_3 and C_4 plants have different carbon isotope compositions (-27 and -13‰ for average C_3 and C_4 modern plants, respectively). CAM plants (largely succulents and few aquatic plants) have values intermediate between C_3 and C_4 plants (O'Leary, 1988; Farquhar et al., 1989; Martinelli et al., 1991). Bioapatite carbonate $\delta^{13}\text{C}$ values of large herbivores are offset from the plant isotope values by about 14‰ (e.g., Cerling and Harris, 1999). Thus, animals feeding on modern C_3 vegetation have bioapatite carbonate $\delta^{13}\text{C}$ values from -20 to -8‰ , with mean values of around -13 to -12‰ . Correspondingly, C_4 consumers usually have $\delta^{13}\text{C}$ values ranging from 0 to $+5\text{‰}$ for their enamel (e.g., Kohn and Cerling, 2002; Kohn, 2010; Arppe et al., 2011). Because these animal's $\delta^{13}\text{C}$ values are directly related to those of the diet and hence to their environment, the analysis of the carbon isotope ratios in bioapatite has been applied to address a variety of paleodietary, paleoecological, and paleoenvironmental problems (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; Montanari et al., 2013; Kocsis

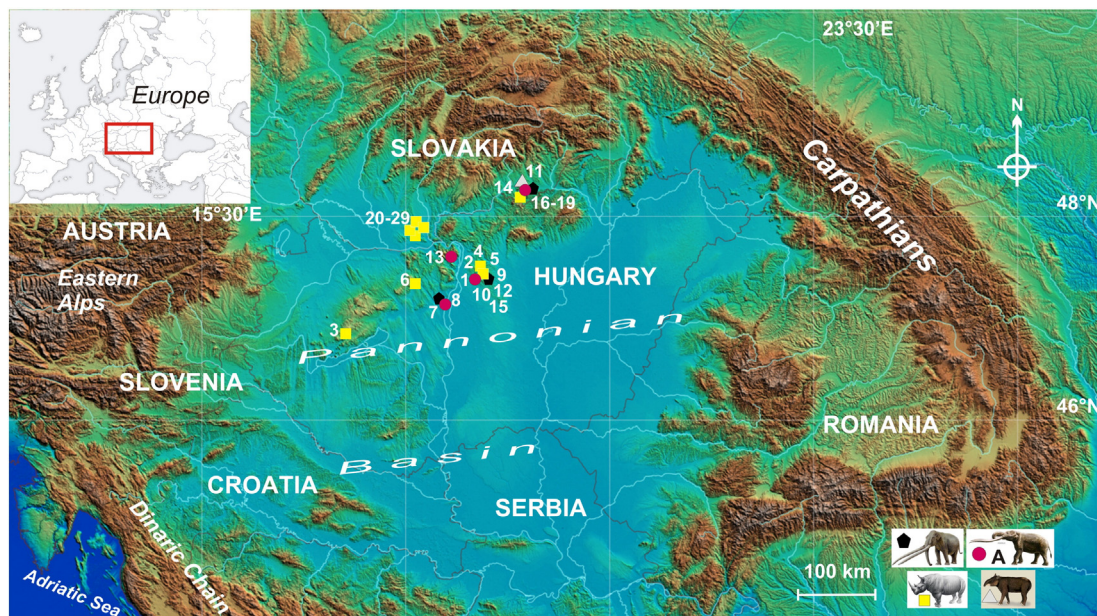


Fig. 1. Location of paleontological sites cited in Table 1.

et al., 2014; Scherler et al., 2014; Zanazzi et al., 2015). In C₃ ecosystems variations in $\delta^{13}\text{C}$ values within C₃ plant groups can provide further information about the type of vegetation, relative humidity or MAP (Mean Annual Precipitation) and habitat differences or niche partitioning between animals (Feranec and MacFadden, 2006). This variability of $\delta^{13}\text{C}$ values is due to variations in light and water availability, as well as location within the forest canopy, or habitat temperature, depending on latitude and altitude (Van der Merwe and Medina, 1991; Kohn, 2010). Generally the $\delta^{13}\text{C}$ values increase as the climate gets drier and the values are lower in humid climate (Kohn, 2010; Montanari et al., 2013). In the forest undergrowth the limited sunlight, increased relative humidity, and mixing of atmospheric CO₂ with CO₂ from decaying litter of the soil organic matter lowers the $\delta^{13}\text{C}_{\text{CO}_2}$ values (Bocherens et al., 1996; Cerling and Harris, 1999; Drucker et al., 2008). This is called the canopy effect. During the Pliocene, the $\delta^{13}\text{C}$ value of atmospheric CO₂ was different from today, which will also have an effect on $\delta^{13}\text{C}$ values of the plants. On the basis of isotopic data from marine foraminifera, the reconstructed $\delta^{13}\text{C}$ value of atmospheric CO₂ for the Late Pliocene is about -6.3% and for the Early Pleistocene it is -6.5% (Tipple et al., 2010; Domingo et al., 2013) while the modern (the year of 2000) value was referenced to -8% (Kohn, 2010), respectively. These differences have to be taken into account when comparing the results of fossil tooth enamel to that of similar species today.

2.2. Oxygen isotopes and environmental water

The $\delta^{18}\text{O}_{\text{PO}_4}$ values of biogenic bone or tooth apatite of vertebrates are preferably used for reconstructing terrestrial paleoclimatic conditions (e.g., Longinelli, 1984; Bryant et al., 1996; Fricke and O'Neil, 1996; Fricke et al., 1998). The basis for these reconstructions is that the oxygen isotope composition of mammalian teeth reflects the animal's body water that in case of large herbivores is linked to the drinking water and/or water derived from food source. Both drinking water and the water in the consumed plants are influenced by climatic factors and the $\delta^{18}\text{O}_{\text{PO}_4}$ values often can be linked to the isotopic composition of local meteoric water. This latter, at mid-latitudes, correlates with several factors including the mean annual air temperature (MAT), moisture source, and air mass trajectories (Zanazzi et al., 2015). The $\delta^{18}\text{O}$ values of local meteoric precipitation are controlled by several factors, including the MAT, latitude, altitude, continental and/or amount effects. At mid and high latitudes, low elevations but distant from the oceans, and if precipitation amount and humidity are relatively low, the MAT has the greatest effect on the $\delta^{18}\text{O}$ values of the precipitation (Dansgaard, 1964). This is not the case for regions under monsoonal effects or tropical coastal or island stations where the amount or rain-out effect may dominate (Dansgaard, 1964; Rozanski et al., 1993).

Large terrestrial mammals do not directly ingest precipitation; instead, their water is ingested from streams, ponds, lakes, and leaves, and this is directly related to their body water. Each of these reservoirs can have different $\delta^{18}\text{O}$ values relative to precipitation, due to variable mixing of temporally different precipitation and potential evaporative effects on the different reservoirs (e.g., Montanari et al., 2013).

The skeletal parts of mammals form at a constant temperature of 36 to 39 °C (Clarke and Rothery, 2008). Therefore, the oxygen isotope composition of the newly formed skeletal apatite is determined solely by the isotopic composition of the animal's body water with a constant fractionation factor between apatite and body water (Longinelli, 1984; Luz et al., 1984). In large mammals, the $\delta^{18}\text{O}$ value of body water mainly depends on that of ingested environmental waters (Bryant and Froelich, 1995), which often corresponds to the mean $\delta^{18}\text{O}$ value of the regional precipitation ($\delta^{18}\text{O}_{\text{ppt}}$). Large (> 100 kg), obligate drinking animals track the average weighted $\delta^{18}\text{O}$ value (weighted for the seasonal changes and the relative amounts of precipitation and/or mixing ratios of the water sources) of ingested water most closely (Ayliffe et al., 1992; Bryant and Froelich, 1995; Koch, 1998). In the case of elephants the

ratio is approximately 2:1 (~65%) of water ingested via drinking compared to that ingested by consumption of plant matter (Ayliffe et al., 1992). In the case of rhinoceros ~80% of their ingested water comes from drinking water (Clauss et al., 2005; Martin et al., 2008). Thus tooth enamel of these two groups is potentially a good indicator of the $\delta^{18}\text{O}$ values of local meteoric waters (e.g., Martin et al., 2008). The remaining dependence on ingested food water and metabolic water from food processing can give further information on the behavior of different taxa. The link between the $\delta^{18}\text{O}$ values of mammal bioapatite ($\delta^{18}\text{O}_{\text{ap}}$) and ingested meteoric waters ($\delta^{18}\text{O}_{\text{w}}$), and the strong relationship between temperature and the $\delta^{18}\text{O}_{\text{ppt}}$ value provide the basis for using $\delta^{18}\text{O}$ values recovered from mammal skeletal remains in paleoclimatological research.

3. Materials and methods

3.1. Fossil materials from Slovakia and Hungary

The geographic distribution of fossil localities, associated faunas and estimates of their geochronologic ages are shown in Fig. 1 and Table 1. Age estimates are based on the assignment of fauna to biochronologic subdivisions of the Ruscinian and Villányian/Villafranchian (4.5 to 2.0 Ma, Kretzoi, 1985; Agustí et al., 2001; Van Dam et al., 2006; Kahlke, 2007; Rook and Martínez-Navarro, 2010; Hilgen et al., 2012, among others). European land-mammal ages are from Hordijk and de Bruijn (2009), Tesakov et al. (2007) and Vangengeim et al. (2005). Land-mammal ages and their subdivisions are biochronologic units, usually based on the first and last appearances of taxa (De Bruijn et al., 1992). Boundaries are from Hilgen et al. (2012).

All teeth belonged to adult individuals. Given that the samples were taken from disturbed sediments, each fossil or fossil fragment probably represents a different individual. Samples of tooth enamel of gomphothere, mastodon, rhinoceros, and tapir from two Slovakian and eight Hungarian localities (Fig. 1, Table 1) were collected. Samples included in this study were acquired from the Slovakian National Museum–Natural History Museum (Bratislava), Comenius University, Department of Geology and Palaeontology (Bratislava), and Gemer–Malohont Museum (Rimavská Sobota). Samples from Hungary were obtained from the Hungarian Natural History Museum, Department of Palaeontology and Geology (Budapest) and the Geological and Geophysical Institute of Hungary, Department of Geological and Geophysical Collections (Budapest). All original specimens are housed in the collections of these institutions.

All teeth sampled in this study are from deposits of fluvial, fluviolacustrine (Gödöllő, Pécel, Vecsés, Pilisvörösvár, Szár, Pestszentlőrinc, Százhalombatta, and Nová Vieska), and maar (Pula, Hajnáčka) settings (Kováč et al., 2011). Although these deposits vary in their taphonomic histories, they appear to represent a limited range of fluvial floodplain settings in areas of low relief. These specimens of the ten localities come from three periods (see Table 1): four from the late-Early Pliocene (MN14 to 15 and MN15, 4.5 to 3.7 Ma), five from mid-Pliocene (MN16, 3.6–2.5 Ma), and only one from the Early Pleistocene (MN17, 2.5–2.0 Ma). The MN14–15 and MN15 mammal biozone contains the Gödöllő, Pula, Szár, and Százhalombatta sites (Kormos, 1917; Mottl, 1939; Kretzoi, 1985; Jánossy, 1986; Gasparik, 2001, 2007; Virág and Gasparik, 2012; Főzy et al., 2014). Among these localities only the Pula maar fossiliferous deposit has a radiometric age of 4.3 ± 0.17 Ma (Balogh et al., 1982; Németh et al., 2008). The MN16 mammal biozone includes the sites of Pécel, Vecsés, Hajnáčka, Pilisvörösvár, and Pestszentlőrinc (Kormos, 1917; Fejfar, 1964; Jánossy, 1986; Fejfar et al., 1990, 2012; Gasparik, 2001, 2007; Sabol et al., 2006; Virág and Gasparik, 2012; Főzy et al., 2014). Among these localities only the Hajnáčka maar fossiliferous deposit has been dated at between 3.43 ± 0.4 Ma and 3.06 ± 0.03 Ma (Hurái et al., 2012). The MN17 mammal biozone is represented only by the site of Nová Vieska (Schmidt and Halouzka, 1970; Holec, 1996; Vlačiky et al., 2008).

Table 1
Carbon and oxygen isotopic compositions of fossil proboscidean and perissodactyl teeth.

Museum code, other code	Our code	Species	Sampling Site	Country	Age	$\delta^{13}\text{C}$ (V-PDB)	$\delta^{18}\text{O}_{\text{CO}_3}$ (V-PDB)	$\delta^{18}\text{O}_{\text{CO}_3}$ (V-SMOW)	$\delta^{18}\text{O}_{\text{PO}_4}$ (V-SMOW)	$\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ difference	
ob 5402	1	<i>A. arvernensis</i>	GGIH	Gödöllő	HU	MN15	−12.80	−8.50	22.10	13.87	8.23
ob 5393	2	<i>Stephanorhinus</i> sp.	GGIH	Gödöllő	HU	MN15	−13.00	−7.70	23.00	15.09	7.91
V-18520	3	<i>S. jeanvireti</i>	GGIH	Pula	HU	MN15	−10.10	−6.20	24.50	15.19	9.31
ob 5395	4	<i>S. jeanvireti</i>	GGIH	Gödöllő	HU	MN15	n.a.	n.a.	n.a.	14.71	n.a.
ob-5396	5	<i>S. jeanvireti</i>	GGIH	Gödöllő	HU	MN15	−10.70	−7.80	22.90	14.22	8.68
V.11130	6	<i>Stephanorhinus</i> sp.	GGIH	Szár II	HU	MN15	−11.10	−7.20	23.50	14.99	8.51
V.74.05	7	<i>M. borsoni</i>	HNHM	Százhalombatta	HU	MN14-MN15	−11.50	−8.10	22.60	14.19	8.41
V.62/121	8	<i>A. arvernensis</i>	HNHM	Százhalombatta	HU	MN14-MN15	−11.10	−8.30	22.30	14.80	7.50
V.60/207 E	9	<i>Stephanorhinus</i> sp.	HNHM	Pécel	HU	MN16	−11.30	−9.40	21.20	11.93	9.27
V.74.01.	10	<i>M. borsoni</i>	HNHM	Vecsés	HU	MN16	−11.90	−7.90	22.80	14.45	8.35
V.93.9	11	<i>M. borsoni</i>	HNHM	Hajnáčka	SK	MN16a	−11.40	−8.90	21.80	13.49	8.31
V.67/360	12	<i>A. arvernensis</i>	HNHM	Vecsés	HU	MN16	−14.00	−9.30	21.30	13.68	7.62
V.77.146.	13	<i>A. arvernensis</i>	HNHM	Pilisvörösvár	HU	MN16	−15.20	−9.50	21.10	12.58	8.52
n.a.	14	<i>A. arvernensis</i>	GMM	Hajnáčka	SK	MN16a	−14.07	−8.10	22.56	13.20	9.37
V.63/624	15	<i>A. arvernensis</i>	HNHM	Pestszentlőrinc	HU	MN16	−14.80	−8.70	22.00	13.31	8.69
B-3031/PZ	16	<i>Stephanorhinus</i> sp.	SNM	Hajnáčka	SK	MN16a	−13.18	−8.69	21.95	13.55	8.41
H-BT-2	17	<i>S. jeanvireti</i>	GMM	Hajnáčka	SK	MN16a	−11.03	−8.97	21.66	12.20	9.46
H-BT-1	18	<i>S. jeanvireti</i>	GMM	Hajnáčka	SK	MN16a	−11.66	−7.62	23.06	14.86	8.20
H-BT-3	19	<i>Tapirus arvernensis</i>	GMM	Hajnáčka	SK	MN16a	−12.81	−9.12	21.50	13.11	8.39
A 34	20	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−12.02	−8.32	22.33	13.67	8.66
A 36	21	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−11.63	−9.23	21.39	12.60	8.79
A 44	22	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−11.72	−8.16	22.50	13.69	8.81
A 40	23	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−12.73	−8.34	22.31	13.17	9.15
5.	24	<i>S. jeanvireti</i>	SNM	Nová Vieska	SK	MN17	−12.56	−8.28	22.37	12.96	9.41
A 35	25	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−12.58	−7.98	22.69	13.06	9.62
6.	26	<i>S. jeanvireti</i>	SNM	Nová Vieska	SK	MN17	−12.77	−8.15	22.51	13.00	9.50
A 43	27	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−12.55	−8.28	22.38	13.85	8.53
NV-17-4	28	<i>S. jeanvireti</i>	SNM	Nová Vieska	SK	MN17	−12.67	−8.07	22.59	13.37	9.23
A16	29	<i>S. jeanvireti</i>	DGP-CU	Nová Vieska	SK	MN17	−12.70	−7.82	22.85	12.95	9.90

3.2. Sampling

In the first step of sampling the enamel surface was mechanically cleaned. About 10 mg of bulk enamel was then sampled using a Dremel diamond-studded drill. Where possible, enamel was drilled along a vertical line over the whole length of the tooth from the crown to the root to get a representative mean sample of the period of enamel formation. Tooth enamel of proboscideans and rhinos can represent 2–3 years of growth, so this sampling method can provide an overall average isotope record for a longer period (Tafforeau et al., 2007; Metcalfe and Longstaffe, 2012). Due to sample limitations, in many cases enamel was collected only from tooth fragments, so these samples represent a relatively short time period, still giving an average composition for the part of the tooth analyzed. Where possible, the third or fourth molars were sampled for all species. This is important because of physiological effects, such as weaning that can change the isotopic compositions of apatite. Early-formed molars may be ^{13}C depleted compared to molars formed later, due to the shift from milk to solid food in the diet (Metcalfe et al., 2010). The $\delta^{13}\text{C}$ values of the third and fourth molars reflect the plant diet and are no longer affected by milk consumption. Where it was possible, several samples were collected from each site.

3.3. Pretreatment and isotope measurements

Sample powder was pre-cleaned according to the method given in Koch et al. (1997). NaOCl was used to remove soluble organic material and acetic acid–Ca–acetate buffer to remove exogenous carbonates (Koch et al., 1997; Kocsis, 2011). A recent study confirms that this treatment protocol produces highly reproducible results (Crowley and Wheatley, 2014). The carbonate isotopic composition was measured on a Gasbench II coupled to a Finnigan MAT Delta Plus XL mass spectrometer. The samples were reacted with 99% orthophosphoric acid and the product CO_2 introduced to the mass spectrometer with He-carrier gas. The carbon isotope compositions are expressed relative to

VPDB standard (Vienna Pee Dee Belemnite), while the oxygen either to VPDB or VSMOW (Vienna Standard Mean Ocean Water).

Carrara Marble in-house standards ($\delta^{18}\text{O} = -1.70\text{‰}$, VPDB; $\delta^{13}\text{C} = 2.05\text{‰}$, VPDB) were run in the same sequence with the samples (2 standards at the beginning and the end of the runs and regularly 1 after each 6–8 samples) and used for normalizing the data. The reproducibility of the in-house standard is $<0.1\text{‰}$ (1σ) for both oxygen and carbon isotopic compositions and it has been calibrated against NBS-19, using also NBS-18 as a linearity test calibration point. The GasBench analyses of carbonates in our laboratory do not show a scale compression between the values given by NBS-19 and NBS-18. NBS120c reference material was run parallel with the samples that yielded values of $\delta^{13}\text{C}$ of $-6.3 \pm 0.1\text{‰}$ ($n = 6$) and $\delta^{18}\text{O}$ of $-2.3 \pm 0.2\text{‰}$ ($n = 6$) on VPDB scale. These values are identical to that of long-term average values of NBS120c in our lab.

For the $\delta^{18}\text{O}$ analyses in the phosphate fraction further preparation was required on the pre-cleaned sub-samples (see above). The cleaned sample powders were dissolved in 2 M HF overnight. The solution was separated from precipitated CaF_2 and neutralized with NH_4OH . 2 M AgNO_3 was then added to the solution, which allowed the rapid precipitation of Ag_3PO_4 (Dettman et al., 2001). The silver-phosphate was analyzed via reduction with graphite in a TC/EA (high-temperature conversion elemental analyzer) coupled to a Finnigan MAT Delta Plus XL mass spectrometer according to the values and method given in Vennemann et al. (2002). The results were corrected to in-house Ag_3PO_4 phosphate standards (LK-2L: 12.1‰ and LK-3L: 17.9‰) that had better than $\pm 0.3\text{‰}$ (1σ) standard deviations during the measurements of the complete sequence of samples. These in-house standards were calibrated by TC/EA to TU-1 (21.11‰) and TU-2 (5.45‰) standards using values defined by the conventional fluorination method (CF) (cf. Vennemann et al., 2002) and were also calibrated with laser-fluorination measurements, giving identical values to that of the TC/EA calibration. International NBS-120c Florida phosphate rock standard was prepared and run together with the samples in order to test sample preparation. The analyses gave an average $\delta^{18}\text{O}$ value of $21.2 \pm 0.3\text{‰}$,

Table 1 (continued)

Museum code, other code	Type of vegetation	Calculated MAP	Environmental water, elephant (Ayliffe et al., 1992)	Environmental water, rhinoceros (Tütken et al., 2006)	Environmental water (relative humidity: 70%), herbivores (Kohn et al., 1996)	MAT based on Rozanski global (Domingo et al., 2013)	MAT based on (Kohn et al., 1996; Domingo et al., 2013)
ob 5402	Woodland to woodland-mesic C3 grassland	1155	-9.5		-8.8	8.7	10.7
ob 5393	Woodland to woodland-mesic C3 grassland	1279		-7.6	-7.2	14.0	15.2
V-18520	Woodland to woodland-mesic C3 grassland	180		-7.6	-7.1	14.2	15.5
ob 5395	n.a.	n.a.		-7.9	-7.7	13.2	13.8
ob-5396	Woodland to woodland-mesic C3 grassland	314		-8.3	-8.4	12.2	12.0
V.11130	Woodland to woodland-mesic C3 grassland	424		-7.7	-7.3	13.8	14.8
V.74.05	Woodland to woodland-mesic C3 grassland	553	-9.2		-8.4	9.6	11.9
V.62/121	Woodland to woodland-mesic C3 grassland	424	-8.7		-7.6	11.2	14.1
V.60/207 E	Woodland to woodland-mesic C3 grassland	486		-10.0	-11.4	7.3	3.6
V.74.01.	Woodland to woodland-mesic C3 grassland	705	-9.0		-8.1	10.2	12.8
V.93.9	Woodland to woodland-mesic C3 grassland	519	-9.9		-9.3	7.8	9.3
V.67/360	Woodland to woodland-mesic C3 grassland	2081	-9.7		-9.1	8.2	10.0
V.77.146.	Closed canopy forest	3596	-10.7		-10.5	5.4	6.0
n.a.	Woodland to woodland-mesic C3 grassland	2153	-10.2		-9.7	7.0	8.3
V.63/624	closed canopy forest	3006	-10.1		-9.6	7.3	8.7
B-3031/PZ	Woodland to woodland-mesic C3 grassland	1402		-8.8	-9.2	10.7	9.6
H-BT-2	Woodland to woodland-mesic C3 grassland	405		-9.8	-11.0	7.9	4.6
H-BT-1	Woodland to woodland-mesic C3 grassland	612		-7.8	-7.5	13.5	14.4
H-BT-3	Woodland to woodland-mesic C3 grassland	1162		-9.1	-9.8	9.8	8.0
A 34	Woodland to woodland-mesic C3 grassland	756		-8.7	-9.1	11.0	10.0
A 36	Woodland to woodland-mesic C3 grassland	600		-9.5	-10.5	8.7	6.1
A 44	Woodland to woodland-mesic C3 grassland	632		-8.7	-9.1	11.1	10.1
A 40	Woodland to woodland-mesic C3 grassland	1113		-9.1	-9.7	9.9	8.2
5.	Woodland to woodland-mesic C3 grassland	1018		-9.3	-10.0	9.5	7.4
A 35	Woodland to woodland-mesic C3 grassland	1028		-9.2	-9.9	9.7	7.8
6.	Woodland to woodland-mesic C3 grassland	1136		-9.2	-10.0	9.6	7.6
A 43	Woodland to woodland-mesic C3 grassland	1012		-8.6	-8.8	11.4	10.6
NV-17-4	Woodland to woodland-mesic C3 grassland	1077		-8.9	-9.5	10.4	8.9
A16	Woodland to woodland-mesic C3 grassland	1095		-9.3	-10.0	9.5	7.4

(n = 8), which is slightly lower than reported by others and also lower compared to the NBS-120c that was measured for the calibration of TU-1 and TU-2 (21.7 ± 0.3‰, e.g., Vennemann et al., 2002; Halas et al., 2011). Because there is no internationally accepted δ¹⁸O value for this material and as it is a sedimentary rock, the mammal teeth data were not corrected further. All analyses of oxygen and carbon isotopes were conducted in the stable isotope laboratory of the University of Lausanne.

3.4. Testing diagenetic effects

The best skeletal tissue for paleoenvironmental analyses is the inorganic fraction of enamel (hydroxylapatite) (Lee-Thorp and van der Merwe, 1987; Lee-Thorp et al., 1989; Ayliffe et al., 1994; Pellegrini et al., 2011; Clementz, 2012; Grimes and Pellegrini, 2013 and references therein). Powder X-ray diffraction patterns of all enamel samples are typical of carbonated hydroxyapatite, with no evidence of secondary mineral contamination. There is another method that is widely used to monitor diagenetic effects. Both the oxygen of apatite carbonate and phosphate form in isotopic equilibrium with body water and there is a linear relationship between them. Several studies have found a constant offset between δ¹⁸O_{CO3} and δ¹⁸O_{PO4} values for non-altered tooth enamel samples and the δ¹⁸O_{CO3}-δ¹⁸O_{PO4} slopes are similar for different species (Bryant et al., 1996; Iacumin et al., 1996; Arppe and Karhu, 2006, 2010; Tütken et al., 2007, 2008; Pellegrini et al., 2011; Domingo et al., 2013). Because it is rare to have altered skeletal remains that still show a good correlation between δ¹⁸O_{CO3}-δ¹⁸O_{PO4} values and a similar offset to modern samples, it is plausible to use the measurements of both these sites for oxygen as a monitor of diagenetic alteration. When a set of points lies on the equilibrium line or close to it, the δ¹⁸O values are hence usually considered to have preserved the original values (see Fig. 2; e.g., Iacumin et al., 1996; Pellegrini et al., 2011). Diagenetic processes can decrease or increase both the carbonate and the phosphate oxygen δ¹⁸O values between apatite and diagenetic

fluids (e.g., Zazzo et al., 2004b; Metcalfe et al., 2013). Iacumin et al. (1996) found that δ¹⁸O_{PO4} = 0.98 × δ¹⁸O_{CO3} - 8.5 for the isotopic equilibrium line with a mean offset of 9.1‰ between these different ions in the apatite. The correlation was good with a correlation coefficient R² = 0.98. Other studies showed an offset of 8.4 to 9.1‰ for modern, unaltered samples (Bryant et al., 1996; Martin et al., 2008). Martin et al. (2008) measured intra tooth differences in two upper molars (M1 and M2) of extant *Rhinoceros unicornis*. The mean value of the δ¹⁸O_{CO3} - δ¹⁸O_{PO4} difference was 8.4 ± 0.7‰, close to the literature values given

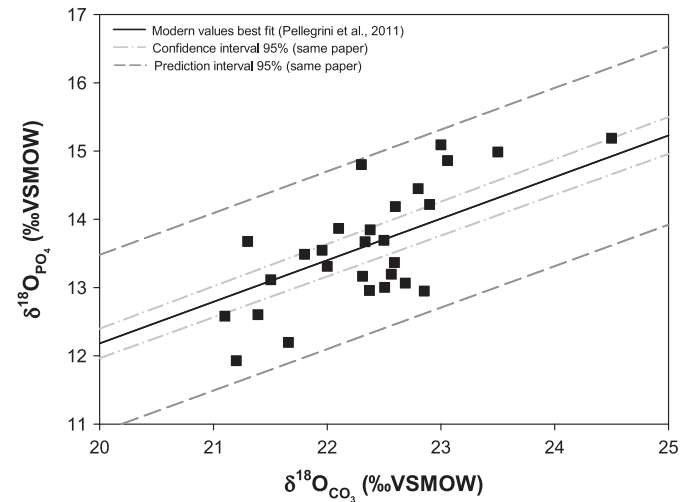


Fig. 2. Oxygen isotope compositions of the carbonate (δ¹⁸O_{CO3}) and phosphate (δ¹⁸O_{PO4}) from enamel apatite of all mammal teeth from the localities studied. The isotopic equilibrium line between carbonate and phosphate δ¹⁸O values is plotted for reference along with the 95% confidence interval and 95% prediction interval calculated by Pellegrini et al. (2011) on modern vertebrates.

for other species. However, the intra-tooth study of the two molars shows that $\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ differences can vary by about 2‰ within the same tooth (Martin et al., 2008). Further variations can be present due to environmental, physiological and tooth growth process differences. The final recommendation is that if the $\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ difference is in the range of 7.2 to 10.6‰ the values of the samples can be considered as unaltered (c.f. Martin et al., 2008). The preservation of the $\delta^{13}\text{C}$ values cannot be tested in a similar manner as the $\delta^{18}\text{O}$ values, because bioapatite holds only one pool of carbon. However, the oxygen is more sensitive to resetting during diagenetic alteration than the carbon within the carbonate as fluids contain more oxygen compared to dissolved carbon. Hence, it can be assumed that if the oxygen preserves the original values it is likely that this also applies to the carbon isotope composition.

3.5. Calculations

The $\delta^{13}\text{C}$ values can provide information about the photosynthetic pathway of the consumed plant (i.e., diet) of the animals and the mean annual precipitation of the site. According to Domingo et al. (2013) the expected $\delta^{13}\text{C}_{\text{enamel}}$ cut-off values for different habitats in the Pliocene are the following: closed-canopy forest $<-14.3\%$; woodland to mesic C_3 grassland -14.3% to -9.3% , and open woodland-xeric C_3 grassland -9.3% to -6.3% . Values between -6.3% and -1.3% represent mixed C_3-C_4 feeding, while values $>-1.3\%$ indicate pure C_4 feeding (Domingo et al., 2013). As the ^{13}C isotope composition of the atmospheric CO_2 changed with time the Pleistocene offsets are about 0.2‰ lower for the given ranges. For pure C_3 ecosystems the MAP of the site can be calculated. For the calculations it has to be taken into account that the $\delta^{13}\text{C}$ value of atmospheric CO_2 was -6.3% during the Pliocene, -6.5% during the Early Pleistocene the value for the year of 2000 was -8.0% (Kohn, 2010; Tipple et al., 2010). A modern equivalent of diet composition ($\delta^{13}\text{C}_{\text{diet,meq}}$) can be calculated using the following equation (Domingo et al., 2013):

$$\delta^{13}\text{C}_{\text{diet,meq}} = \delta^{13}\text{C}_{\text{leaf}} + \left(\delta^{13}\text{C}_{\text{modern-atmCO}_2} - \delta^{13}\text{C}_{\text{ancient-atmCO}_2} \right), \quad (1)$$

where $\delta^{13}\text{C}_{\text{leaf}} = \delta^{13}\text{C}_{\text{tooth}} - 14.1\%$, $\delta^{13}\text{C}_{\text{modern-atmCO}_2} = -8\%$, and $\delta^{13}\text{C}_{\text{ancient-atmCO}_2} = -6.3\%$, -6.5% .

Estimating MAP from $\delta^{13}\text{C}$ values requires rewriting the relationship between modern plant $\delta^{13}\text{C}$ (referenced to $\delta^{13}\text{C}_{\text{atm}} = -8.0\%$) and MAP to solve for MAP as a function of $\delta^{13}\text{C}$, elevation (in meters), and latitude (absolute value in degrees). MAP was estimated based on the following equation provided by Kohn (2010):

$$\delta^{13}\text{C}_{\text{diet,meq}} (\text{‰, VPDB}) = -10.29 + 1.9 \times 10^{-4} \text{altitude (m)} - 5.61 \log_{10}(\text{MAP} + 300, \text{mm/yr}) - 0.0124 \text{Abs}(\text{latitude}, ^\circ). \quad (2)$$

It is assumed that the sites sampled were not high-elevation or mountainous regions during the Pliocene. An altitude of 150 m was substituted in the equation. The altitude does not have an important effect on the equation. For example substituting 800 or 1000 m, the calculated MAP does not change by more than the analytical error for the measurement. The latitude of the investigated sites is estimated at 48°N . The paleo-latitude of the sites was similar during the Pliocene (Fodor et al., 2005).

The MAP equation results and the vegetation cut-off values overlap for a precipitation between 500 and 2500 mm/yr. For example, the $\delta^{13}\text{C}$ values between -9.3 and -6.3% , the highest values for the pure C_3 ecosystems indicate open woodland-type C_3 grassland, the equation would give almost zero or negative MAP values. Taking into account both scales, $\delta^{13}\text{C}$ values higher than -9.3% could indicate an arid climate or mixed C_3-C_4 vegetation. On the other end of the scale, values under -14.3% indicate a closed canopy forest. For this value, where the canopy effect lowers the $\delta^{13}\text{C}$ values, the equation would give higher amounts of precipitation. It can hence be assumed that values under

-14.3% can represent more than about 2500 mm MAP and/or strong canopy effects.

Since the $\delta^{18}\text{O}_{\text{PO}_4}$ value of bioapatite is directly related to the oxygen isotope composition of body water, the $\delta^{18}\text{O}$ values of environmental water can be calculated. For proboscideans the species-specific equation of Ayliffe et al. (1992) was recalculated based on the original data for modern elephants:

$$\delta^{18}\text{O}_w = 0.93 \times \delta^{18}\text{O}_{\text{PO}_4} - 22.43 \left(R^2 = 0.86 \right), \quad (3)$$

while for the perissodactyls the equation from Tütken et al. (2006) was used:

$$\delta^{18}\text{O}_w = \left(\delta^{18}\text{O}_{\text{PO}_4} - 25.09 \right) / 1.31, \quad (4)$$

and for comparison the general herbivore equation (Kohn et al., 1996) was also used:

$$\delta^{18}\text{O}_w = \left(\delta^{18}\text{O}_{\text{PO}_4} - 26.8 + 8.9h \right) / 0.76, \quad (5)$$

where h is the relative humidity from 0 to 1 (0.7 was used in our equation following the calculations of Pound et al. (2014) and the dataset of Spinoni et al. (2015), see Table 1).

Because there is a correlation between the precipitation $\delta^{18}\text{O}$ value and mean annual temperature (MAT) (e.g., Dansgaard, 1964; Fricke and O'Neil, 1999), the MAT can be calculated for the given sites. There are different approaches to choose from. Using site-specific temperature-precipitation relationships based on data from the nearest IAEA meteorological station or the regional or global equations that use data of meteorological stations worldwide. The advantage of using global equations is that they represent an average mid-latitude climate regime. Using site-specific precipitation-temperature relationships can, however, give more precise estimates for a local area, notably if it is a mountainous area where local climate variability may be important (Pryor et al., 2014). Based on the data set of Rozanski et al. (1993), the following equation was chosen from the work of Domingo et al. (2013). This regression uses data from meteorological stations worldwide and as such represents a global average "climate" for mid-latitudes, rather than the polar extremes where the MAT is more sensitive to changes in $\delta^{18}\text{O}_w$:

$$\text{MAT} (^\circ\text{C}) = \left(\delta^{18}\text{O}_w (\text{VSMOW}) + 12.68 \right) / 0.36 \left(R^2 = 0.72 \right). \quad (6)$$

4. Results

The results of the carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{PO}_4}$) isotope compositions of tooth enamel of the large herbivores from Slovakia and Hungary are given in Table 1, along with the calculated $\delta^{18}\text{O}_w$ values and paleotemperatures (in $^\circ\text{C}$). Fig. 2 illustrates the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values of the four different taxa from all time periods (MN15, 4.5 to 3.5 Ma; MN16, 3.5 to 2.5 Ma; MN17, 2.5 to 2.0 Ma). The $\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ values seem to be in isotopic equilibrium for the majority of enamel samples (Fig. 2), as most of them plot in the predicted interval expected for modern vertebrates (Pellegrini et al., 2011). Most of the collected samples for this study satisfy the requirement (7.2–10.6‰; see in Table 1). Only one sample had a lower $\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ offset than 7.2‰. This sample was excluded from the environmental reconstruction.

4.1. $\delta^{13}\text{C}$ values and mean annual precipitation (MAP)

The $\delta^{13}\text{C}$ values for the fauna range from -10.1 to -15.2% (VPDB) (see Table 1). The MN14–15 and MN15 mean $\delta^{13}\text{C}$ values for

proboscideans from Gödöllő and Százhalombatta are -11.8% ; and for the rhinoceroses from Gödöllő, Pula and Szár -11.2% .

From Hajnáčka (MN16), samples of 2 proboscideans, 3 rhinoceroses, and one tapir, as well as one rhinoceros from Pécel (MN 16) were analyzed. Proboscideans represented the other MN16 sites from Hungary (Vecsés, Pilisvörösvár, and Pestszentlőrinc). The mean $\delta^{13}\text{C}$ value for the proboscideans is -13.5% , for the perissodactyls -11.9% . Averaging the results from all the species from any one site can give a better approximation for vegetation estimates of the environment. The mean $\delta^{13}\text{C}$ value for samples from the Nová Vieska site (MN17) is -12.3% . The average ^{13}C values for the different time periods are -11.5% for MN15, -12.9% for MN16, and -12.4% for MN17. F-tests for variances and two-tailed heteroscedastic t-tests for central values were performed on the data. Statistical significance is based on $p < 0.05$. The change between MN15 and MN16 values is statistically significant ($p = 0.04$) while that between MN16 and MN17 is not ($p = 0.35$).

The calculated average precipitation in the late-Early Pliocene (MN14–15 and MN15) is 565 mm ($n = 7$). The MAP value in the mid-Pliocene (MN16) is 1224 mm ($n = 11$) and for the Early Pleistocene (MN17) it is 862 mm ($n = 10$).

4.2. $\delta^{18}\text{O}_{\text{PO}_4}$ values and mean annual air temperature (MAT)

The $\delta^{18}\text{O}_{\text{PO}_4}$ values range from 11.9% to 15.2% (see Table 1). For the Hajnáčka site two proboscideans have a mean value of 13.3% and three rhinoceroses 13.5% . The average values and deviations (1σ) are $13.4 \pm 0.9\%$ ($n = 6$) for Hajnáčka, $13.2 \pm 0.4\%$ ($n = 10$) for Nová Vieska and $14.4 \pm 0.5\%$ ($n = 4$) in Gödöllő. The MN14–15 and MN15 mean $\delta^{18}\text{O}$ values for proboscideans from Gödöllő and Százhalombatta are 14.2% ; and for the rhinoceroses from Gödöllő, Pula and Szár 14.8% . The mean $\delta^{18}\text{O}_{\text{PO}_4}$ values from the MN16 sites for the proboscidean samples are 13.4% , for the perissodactyls 13.1% .

The mean $\delta^{18}\text{O}$ value in Nová Vieska site (MN17) is 13.2% . The average $\delta^{18}\text{O}$ values for the different time periods are 14.6% for MN15, 13.3% for MN16, and 13.2% for MN17. Significant change can be observed between MN15 and MN16 values ($p = 0.001$) while change between MN16 and MN17 is not significant ($p = 0.8$).

The calculated MAT values have a wide range from 5.4 to 14.2 °C. In the late-Early Pliocene (MN14–15 and MN15) the mean MAT values are 12.1 °C ($n = 7$), and that in the mid-Pliocene (MN16) is 8.7 °C ($n = 11$). The mean paleotemperature value for the Early Pleistocene (MN17) is 10.1 °C ($n = 10$). The two lowest values of 5.4 and 7.2 °C seem unrealistically low compared to other results and other proxies (Hably and Kvaček, 1998; Hably, 2002; Kovar-Eder, 2003; Erdei et al., 2007). These values are from samples of the Pestszentlőrinc and Pilisvörösvár sites.

5. Discussion

5.1. Paleoecology and diet of the fossil taxa indicated by $\delta^{13}\text{C}$ values

The $\delta^{13}\text{C}$ values of all the taxa from all the time periods are in the range expected for herbivores feeding on C_3 plants during the Pliocene and Early Pleistocene (O'Leary, 1988; Passey et al., 2002; Tütken et al., 2013; and Fig. 3, Table 1). Thus C_4 plants were not a significant part of the diet of these animals, compatible with earlier suggestions that C_4 grasses were absent in Europe during the Pliocene to Late Pleistocene (Kürschner, 2010).

Paleontological observations of *Anancus arvernensis*, *Mammuth borsoni*, *Tapirus arvernensis*, and *Stephanorhinus jeanvireti* suggest that they were browsers that lived in a forest or woodland (Brugal and Croitor, 2007; Kahlke et al., 2011; Rivals et al., 2015). Morphologically, the bunodont molars (*Anancus*) generally imply a soft diet of leaves, fruit and twigs. The feet were adapted to walk on soft soil, also suggesting that *Anancus* was an inhabitant of moist woodlands (Ji et al., 2002; Rivals et al., 2015). The dentition changes in the fossil record imply a

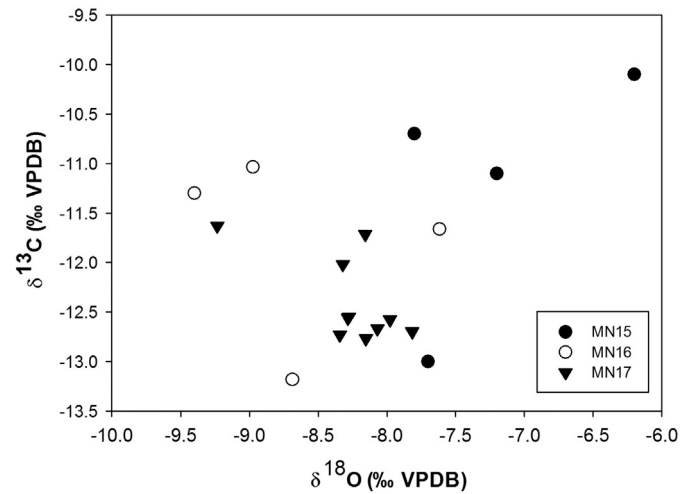


Fig. 3. $\delta^{13}\text{C}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{CO}_3}$ values of all 18 *S. jeanvireti* teeth from the six different localities Gödöllő, Pula, Szár (MN15); Pécel, Hajnáčka (MN16); Nová Vieska (MN17).

trend in the diet of *Anancus* from soft forest food toward the incorporation of grasses, requiring a grinding component to mastication (Rivals et al., 2015). Whether *S. jeanvireti* was C_3 browser or C_3 grazer cannot be inferred solely from their carbon isotope compositions. According to Lacombat and Mörs (2008), *S. jeanvireti* should be pledged to humidity not to the latitude or/and temperature.

The $\delta^{13}\text{C}$ values of the different taxa (presumably lived in different microhabitats) have similar $\delta^{13}\text{C}$ values while site and age differences are 2 to 2.9‰ (Fig. 3, Table 1). This could imply that taxonomic differences of the two/three groups have smaller effects on the isotope variances compared to the environmental factors.

5.2. Paleoprecipitation based on $\delta^{13}\text{C}$ values

The average $\delta^{13}\text{C}$ values of proboscideans and rhinos are statistically not different ($p = 0.13$), hence the data can be pooled for the investigated time periods. Fig. 4A shows how the $\delta^{13}\text{C}$ values relate to MAP (see background section and Table 1) between MN15 and MN17. Table 2 summarizes the data of different proxies compared to our results. Mean tooth enamel $\delta^{13}\text{C}$ values decreased from MN15 to MN16 (Fig. 4A). The decrease in $\delta^{13}\text{C}$ values during MN16 may be related to the Pliocene Warm Period that began at 5 Ma and introduced more humid conditions in Europe (Fortelius et al., 2006; Eronen et al., 2010, 2011). The high $\delta^{13}\text{C}$ values for the period of MN15 may be related to the late Neogene aridification and the more continental characteristic of the study area (Eronen et al., 2010, 2011, 2012). The decrease in $\delta^{13}\text{C}$ also corresponds to an increase in MAP values by about 660 mm/yr between MN15 (560 mm/yr) and MN16 (1220 mm/yr). After MN16, the $\delta^{13}\text{C}$ values increased during MN17 and the middle Pleistocene, but did not reach values as high as those observed in MN15, which corresponds to a decrease in MAP values of 360 mm/yr between MN16 (1220 mm/yr) and MN17 (860 mm/yr). This increase in $\delta^{13}\text{C}$ values corresponds to a global and regional climatic change and to faunal and environmental changes in Europe. The beginning of MN16 (3.5 Ma; Hilgen et al., 2012) predates the onset of Northern Hemisphere glaciation (Meyers and Hinnov, 2010; De Schepper et al., 2013; Woodard et al., 2014). At that time, the modern Mediterranean climatic regime was established and aridity in Europe was enhanced, which led to changes in mammalian fossil assemblages in such a way that, according to Agustí et al. (2001) and Rook and Martínez-Navarro (2010), the Villányian/Villafanchian mammal turnover occurred at this time with an increase in grazers, the appearance of morphological features associated with a highly cursorial lifestyle in some ungulates, and the diversification of pursuit carnivores. All of these changes point toward the development of prairies and grasslands in Europe (Pott, 1995;

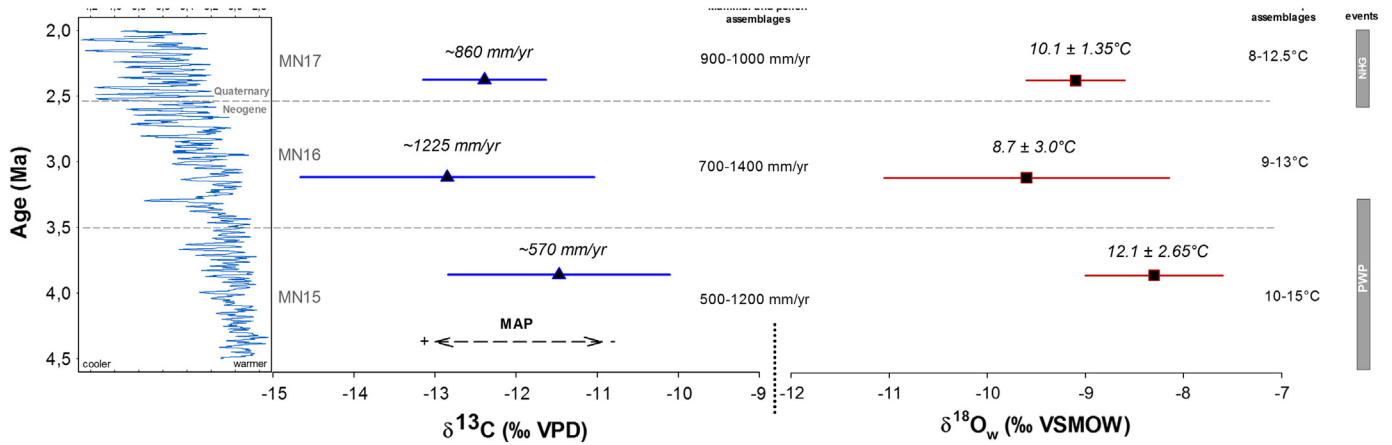


Fig. 4. Variation with time of average $\delta^{13}\text{C}$ values of tooth enamel and average $\delta^{18}\text{O}$ of meteoric water calculated from $\delta^{18}\text{O}_{\text{PO}_4}$ values for different time bins, compared to the benthic foraminiferal $\delta^{18}\text{O}$ record (Lisiecki and Raymo, 2005). (A) Mean and standard deviation $\delta^{13}\text{C}$ values and MAP (mm/yr) in each MN were calculated by applying Eqs. (3) and (4) of Ayliffe et al. (1992) and Tütken et al. (2006). MAP values based on pollen and mammal data are from Kovar-Eder (2003), Erdei et al. (2007), Eronen and Rook (2004) and Montuire et al. (2006). (B) Mean and standard deviation of $\delta^{18}\text{O}_{\text{Water}}$ and MAT ($^{\circ}\text{C}$) values are calculated by applying Eq. (6) Domingo et al. (2013). MAT values based on pollen and mammal data are from Mosbrugger et al. (2005), Fortelius et al. (2006), Eronen et al. (2010, 2011). Chronology according to Hilgen et al. (2012), the onset of the Quaternary according to the chronology confirmed in 2009 by the International Union of Geological Sciences. The ages of the global/regional events are not absolute, but approximate according to the MN chronology. NHG = Northern Hemisphere glaciation, PWP = Pliocene Warm Period.

Bredenkamp et al., 2002). Fortelius et al. (2006) evaluated the hypsodonty index in mammalian herbivores between the Late Miocene and the Pliocene in Eurasia and suggested that browsing taxa in MN15 were replaced by grazers in MN16 and MN17. Another important change occurred at 2.6 Ma (Dowsett et al., 2013; Woodard et al., 2014), when there was a replacement of forests by tundra-like vegetation in northern and steppe-like in central Europe (e.g., Pott, 1995; Bredenkamp et al., 2002).

The rhinoceros sample from Pula (4.25 ± 0.17 Ma) shows the lowest precipitation value; 180 mm/yr, although this is only one sample, in this case we cannot come to conclusions. Other proxies do show, however, that there were arid periods at that time in Pula (and in the Pannonian Basin). The alginite in Pula preserves the remains of a mesophytic arboreal coenosis. The predominant species were short-leaved, which indicates regionally drier climate (Hably and Kvaček, 1998; Hably, 2002; Erdei et al., 2007). Based on the micro-mammal studies of Jánossy (1986), certain parts of the Pannonian Basin experienced anomalously dry periods at that time. The surroundings of the Pula maar lake must have been more humid but the climate, in general, was presumably quite dry (Hably and Kvaček, 1998). It is conceivable that the time period when the rhinoceros fossils were buried in the Pula maar lake, the climate was more arid compared to the Pliocene average. Other unusual

$\delta^{13}\text{C}$ values are given by the two *A. arvernensis* specimens (-14.8‰ and -15.2‰) from two Late Pliocene sites Pestszentlőrinc and Pilisvörösvár with very high MAP. In this case, the 3600 mm/yr precipitation seems too high but decreases in $\delta^{13}\text{C}$ values may suggest increased atmospheric CO_2 , a wetter environment with greater canopy cover (Bocherens et al., 1999; Cerling and Harris, 1999; Drucker et al., 2008; Metcalfe and Longstaffe, 2012; Pushkina et al., 2014).

Current MAP within the Pannonian Basin is about 500 to 800 mm/yr (Spinoni et al., 2015). Only the MN15 gives a lower value (560 mm/yr), both the MN16 and MN17 are higher than the present day MAP. The well-studied site from MN16 is Hajnáchka, where the precipitation is estimated to be 400 to 2150 mm/yr and where the canopy effect was also present. The paleoenvironment in Hajnáchka was characterized by a bushy humid primeval forest belt with flowing streams and backwaters around a maar lake, surrounded by an open, drier habitat at higher elevations (Fejfar, 1964; Fejfar et al., 1990, 2012).

The above-mentioned higher MAP values are in good agreement with paleosol proxies from the region. Paleosols suggest 1100 to 1200 mm/yr for the Piacenzian (MN16) and 900 to 1200 mm/yr for younger MN17 at 2.5 to 1.8 Ma (Kovács et al., 2013).

During the Early Pliocene (MN14–MN15), the mean hypsodonty (crown height) values of large mammalian herbivores are compatible

Table 2

MAT and MAP reconstructions obtained from previous studies and the new results.

	Age (Ma)			Recent	Ref.
	5.2–3.2	3.2–2.5	2.5–1.8		
MN zone					
	MN14–15	MN16	MN17 (Nova Vieska)		
MAT ($^{\circ}\text{C}$) this study	12.1	8.7	10.1		
MAT ($^{\circ}\text{C}$) paleosol	13–15	10–13	8–10		1
MAT ($^{\circ}\text{C}$) mammals (primates, rodents)	10–15	–	10.6–12.4		2; 3; 4
MAT ($^{\circ}\text{C}$) paleogroundwater	15	6–7	6–7		5
MAT ($^{\circ}\text{C}$) paleoflora	10–13	9–13	8–12.5		6, 7, 8, 9, 10
MAT ($^{\circ}\text{C}$) recent				10–11	11
MAP (mm) this study	560	1225	860		
MAP (mm) paleosol	1200–1400	1100–1200	900–1000		1
MAP (mm) mammals (primates, rodents)	1150	700	990		2; 3; 4
MAP (mm) hypsodonty	700–800	1200–1500			12; 13
MAP (mm) recent				500–800	11

1 – Kovács et al., 2013; 2 – Eronen and Rook, 2004; 3 – van Dam, 2006; 4 – Montuire et al., 2006; 5 – Szöcs et al., 2013; 6 – Mosbrugger et al., 2005; 7 – Hably and Kvaček, 1998; 8 – Hably, 2002; 9 – Kovar-Eder, 2003; 10 – Erdei et al., 2007; 11 – Spinoni et al., 2015; 12 – Fortelius et al., 2006; 13 – Eronen et al., 2010.

with a uniform humidity in central Europe (700 to 800 mm/yr) with intermittent dry periods (Fortelius et al., 2006; Eronen et al., 2010). As stated by Eronen et al. (2010, 2011), the Late Pliocene shows similar patterns from the mean hypsodonty values and the precipitation estimates, which means the Hungarian/Slovakian area was humid, with about 1200 to 1500 mm per year.

The overall more humid climate is in good agreement with continental or global records as well (Salzmann et al., 2011). Based on the records above, the Pliocene was more humid compared to the present in the Pannonian Basin, but there were extended arid episodes such as that presented by the Pula maar.

5.3. Paleotemperature records

Average $\delta^{18}\text{O}$ values of proboscideans and rhinos are not statistically different ($p = 0.71$), in this case all these data are pooled into one dataset. Fig. 4B shows the variations in $\delta^{18}\text{O}_W$ values calculated from the tooth enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values. In this study the age-average $\delta^{18}\text{O}_W$ values are directly linked to regional meteoric water, though some local environmental water sources might have had some offsets from local precipitation (e.g., rivers bringing glacial melt water or enhanced evaporation). Because different taxa from several localities were investigated and no statistical differences was measured among them (except Pula – see previous chapter), hence local water source with extreme isotopic composition could not have significant effect on the average $\delta^{18}\text{O}_W$ values. Therefore, from the $\delta^{18}\text{O}_W$ values mean annual temperatures were estimated using Eqs. (3)–(5) after Ayliffe et al. (1992), Tütken et al. (2006), and Kohn et al. (1996), respectively. Table 2 summarizes the data of different proxies in comparison to our results. Our estimate of MAT during MN15 is 12.1 ± 2.7 °C, similar to those based on primate (Eronen and Rook, 2004) and rodent (Montuire et al., 2006) fossil records from the Pannonian Basin (10 to 15 °C). The estimates of Kovács et al. (2013) based on clay mineralogical and geochemical proxies from the study area (13 to 15 °C) are also quite similar. Current MAT within the Pannonian Basin is 10 to 11 °C, with a seasonal range from 20 °C in July to -1 °C in January (Spinoni et al., 2015).

After MN15, MAT values decrease, reflecting global cooling with the strengthening of the Northern Hemisphere glaciation at about 2.6 Ma. Tooth enamel $\delta^{18}\text{O}$ values from MN16 and MN17 in this study correspond to MAT values of 8.7 ± 0.3 °C and 10.1 ± 1.4 °C, respectively, slightly cooler than MAT values estimated by Mosbrugger et al. (2005) between MN16 (9 to 13 °C) and MN17 (8 to 12.5 °C). Szócs et al. (2013), on the basis of isotope data of Early Pliocene groundwater in the southern part of the Pannonian Basin suggested a surface temperature of about 15 °C, while Late Pliocene to Early Pleistocene waters infiltrated at 6 to 7 °C. Plant macrofossil and palynological studies from the Pannonian Basin indicate a climate with 10 to 13 °C during the Early Pliocene, MN14 to MN15 (Hably and Kvaček, 1998; Hably, 2002; Kovar-Eder, 2003; Erdei et al., 2007). Overall, the MAT values estimated here using mammalian tooth enamel are hence in good agreement with data from palynology, rodent assemblages, primate fossils and the paleogroundwater analyses.

As was the case for the C-isotope compositions, the Pula samples are somewhat anomalous for the oxygen isotope compositions too, with a MAT as high as 14.2 °C. According to Levin et al. (2006), high $\delta^{18}\text{O}_{\text{enamel}}$ values could be related to evaporation, notably for animals that might be sensitive to such effects because of a high proportion of leaf to body water, with the leaf fraction becoming more important with increasing aridity. Kohn et al. (1996) gave an Eq. (5) for enamel–environmental water relationship for herbivores that incorporates the effect of relative humidity. In this equation a 10% shift in mean annual relative humidity can change the calculated environmental water by about 1.2‰ and the calculated MAT by about 3 °C (see Table 1). It can be assumed that in cases of the Pula, Pestszentlőrinc, and Pilisvörösvár

sites, this effect could change the $\delta^{18}\text{O}$ values rather than temperature itself.

Most of the proxies and models show that during the Pliocene the climate was, in general, warmer and more stable than during the Pleistocene. During the Piacenzian (3.6 to 2.58 Ma) global mean annual sea surface temperatures were generally 2 to 3 °C higher than today with a decreased equator to pole gradient (Dowsett et al., 1996, 2013; Haywood and Valdes, 2004; Hill et al., 2011; Salzmann et al., 2011; Haywood et al., 2013). In the Arctic regions sea surface temperatures could reach 18 ± 4 °C, which was higher than today, partly due to the reduced ice and the related feedback processes (Csank et al., 2011). The Pliocene world was not only warmer but on most continents also wetter than today; the southern Mediterranean is a rare example of a drier-than-modern Pliocene climate (Salzmann et al., 2011). Despite the generally stable climate there were also fluctuations during the Pliocene. The mid-Pliocene warm period from 3.3 Ma to 3.0 Ma was a warmer interval, while at approximately 2.6 Ma the Northern Hemisphere Glaciation strengthened (e.g., Haywood et al., 2002; Salzmann et al., 2011, 2013; Haywood et al., 2013). Some changes in climate were linked to events like changes in sea pathways, particularly the narrowing of the Indonesian Seaway and the final closure of the Central American Isthmus. The latter occurred at about 2.7 Ma and caused re-arrangements in the ocean currents (Bartoli et al., 2005). In Western Europe paleoflora proxies indicate 3 to 6 °C higher MAT and 230 to 400 mm higher MAP than today (Salzmann et al., 2011). Higher temperatures were also suggested for central and northern Europe: in the Pannonian Basin paleoflora and paleosol proxies indicate a warmer and wetter climate compared to the present with decreasing temperature and precipitation trends toward the end of the Pliocene (Hably and Kvaček, 1998; Hably, 2002; Erdei et al., 2007; Kovács et al., 2013). Knowing more about paleoclimate and paleoenvironments of this era is particularly important to help predict the impacts of global climate change today. This is because the atmospheric CO_2 concentrations, paleogeography, and paleobiology of the Pliocene were very similar to those of today (Salzmann et al., 2011).

6. Conclusions

This study was based on the analyses of the C- and O-isotope composition of structural carbonate and O-isotope composition of the phosphate of fossil bio-apatite. 29 samples of large mammal teeth were selected from Slovakia and Hungary, with the aim of reconstructing the past habitats in which the animals lived. The samples are well-preserved and the isotopic compositions of carbonates and phosphates of the enamel are suitable for paleoenvironmental interpretations ($\delta^{18}\text{O}_{\text{CO}_3}-\delta^{18}\text{O}_{\text{PO}_4}$ differences are between 7.2 and 10.6‰).

The analyzed fauna lived in the Pannonian Basin (East Central Europe) between 4.5 and 2.0 Ma, allowing for the reconstruction of environmental and climatic changes during the Late Neogene and Early Quaternary. In general, tooth enamel $\delta^{13}\text{C}$ values indicate that the analyzed taxa may have occupied woodland to mesic C_3 grassland or closed canopy forest, with no evidence of significant C_4 consumption for any of the genera studied.

Accordingly, the isotope data imply a warmer and possibly wetter habitat of open vegetation for the proboscideans and perissodactyls in the region compared to that of today. The isotopic data suggest that surface air temperatures in the region between 4.5 and 2.0 Ma were 1 to 4 °C warmer and, with about 700 mm/yr more precipitation, wetter than at present. A decrease in $\delta^{13}\text{C}$ values during MN16 is probably linked to the Pliocene Warm Period (with an associated increase in air moisture), whereas the higher $\delta^{13}\text{C}$ values from MN17 onwards may have been a consequence of the increased aridity in Europe related to the onset of Northern Hemisphere glaciation. The MAT pattern estimated using tooth enamel $\delta^{18}\text{O}_{\text{PO}_4}$ values agrees well with the thermal trend based on palynological records, mammal assemblages, and other isotopic studies from the Pannonian Basin, with a gradual decrease in MAT

from MN16 onwards in response to the progressive cooling observed since the mid-Pliocene and culminating in the increased Northern Hemisphere glaciation.

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References

- Agusti, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe: state of the art. *Earth-Sci. Rev.* 52, 247–260.
- Arppe, L.M., Karhu, J.A., 2006. Implications for the Late Pleistocene climate in Finland and adjacent areas from the isotopic composition of mammoth skeletal remains. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 231, 322–330.
- Arppe, L., Karhu, J.A., 2010. Oxygen isotope values of precipitation and the thermal climate in Europe during the middle to late Weichselian ice age. *Quat. Sci. Rev.* 29, 1263–1275.
- Arppe, L., Aaris-Sørensen, K., Daugnora, C., Lõugas, L., Wojtal, P., Zupičič, I., 2011. The palaeoenvironmental $\delta^{13}\text{C}$ record in European woolly mammoth tooth enamel. *Quat. Int.* 245, 285–290.
- Ayliffe, L.K., Lister, A.M., Chivas, A.R., 1992. The preservation of glacial–interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 99, 179–191.
- Ayliffe, L.K., Chivas, A.R., Leakey, M.G., 1994. The retention of primary oxygen isotope compositions of fossil elephant skeletal phosphate. *Geochim. Cosmochim. Acta* 58, 5291–5298.
- Balogh, K., Jámor, A., Partényi, Z., Ravaszné Baranyai, L., Solti, G., 1982. A dunántúli bazaltok K/Ar radiometrikus kora (K/Ar radiogenic age of Transdanubian basalts) (in Hungarian with English summary) *MÁFI Évi Jel. 1980-rólpp.* 243–259.
- Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D., Lea, D.W., 2005. Final closure of Panama and the onset of northern hemisphere glaciation. *Earth Planet. Sci. Lett.* 237, 33–44.
- Blake, R.E., Oneil, J.R., Garcia, G.A., 1997. Oxygen isotope systematics of biologically mediated reactions of phosphate. 1. Microbial degradation of organophosphorus compounds. *Geochim. Cosmochim. Acta* 61, 4411–4422.
- Bocherens, H., Pacaud, G., Lazarev, P.A., Mariotti, A., 1996. Stable isotope abundances (C-13, N-15) in collagen and soft tissues from Pleistocene mammals from Yakutia: implications for the palaeobiology of the Mammoth Steppe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 126, 31–44.
- Bocherens, H., Billiou, D., Patou-Mathis, M., Otte, M., Bonjean, D., Toussaint, M., Mariotti, A., 1999. Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of late interglacial Neandertal and mammal bones in Scaldina Cave (Belgium). *J. Archaeol. Sci.* 26, 599–607.
- Bredenkamp, G.J., Spada, F., Kazmierczak, E., 2002. On the origin of northern and southern hemisphere grasslands. *Plant Ecol.* 163, 209–229.
- Brugal, J.P., Croitor, R., 2007. Evolution, ecology and biochronology of herbivore associations in Europe during the last 3 million years. *Quaternaire* 18, 129–151.
- Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochim. Cosmochim. Acta* 59, 4523–4537.
- Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. *Geochim. Cosmochim. Acta* 60, 5145–5148.
- Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347–363.
- Clarke, A., Rothery, P., 2008. Scaling of body temperature in mammals and birds. *Funct. Ecol.* 22, 58–67.
- Clauss, M., Polster, C., Kienzle, E., Wiesner, H., Baumgartner, K., Houwald, F.V., Streich, W.J., Dierenfeld, E., 2005. Energy and mineral nutrition and water intake in the captive Indian rhinoceros (*Rhinoceros unicornis*). *Zoo Biol.* 24, 1–14.
- Clementz, M.T., 2012. New insight from old bones: stable isotope analysis of fossil mammals. *J. Mammal.* 93, 368–380.
- Coplen, T.B., 1994. Reporting stable hydrogen, carbon and oxygen isotopic abundances. *Pure Appl. Chem.* 66, 271–276.
- Crowley, B.E., Wheatley, P.V., 2014. To bleach or not to bleach? Comparing treatment methods for isolating biogenic carbonate. *Chem. Geol.* 381, 234–242.
- Csank, A.Z., Patterson, W.P., Eglinton, B.M., Rybczynski, N., Basinger, J.F., 2011. Climate variability in the Early Pliocene Arctic: annually resolved evidence from stable isotope values of sub-fossil wood, Ellesmere Island, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 339–349.
- Dansgaard, W., 1964. Stable isotopes in precipitation. *Tellus* 16, 436–468.
- De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsl. Stratigr.* 26, 65–118.
- De Schepper, S., Groeneveld, J., Naafs, B.D.A., Van Renterghem, C., Hennissen, J., Head, M.J., Louwyte, S., Fabian, K., 2013. Northern Hemisphere Glaciation during the Globally Warm Early Late Pliocene. *PLoS One* 8, e81508.
- Delgado Huertas, A., Iacumin, P., Stenni, B., Sánchez Chillón, B., Longinelli, A., 1995. Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. *Geochim. Cosmochim. Acta* 59, 4299–4305.
- deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth Planet. Sci. Lett.* 220, 3–24.
- Dettman, D.L., Kohn, M.J., Quade, J., Ryerson, F.J., Ojha, T.P., Hamidullah, S., 2001. Seasonal stable isotope evidence for a strong Asian monsoon throughout the past 10.7 m.y. *Geology* 29, 31–34.
- Domingo, I., Koch, P.L., Hernandez Fernandez, M., Fox, D.L., Domingo, M.S., Teresa Alberdi, M., 2013. Late Neogene and Early Quaternary paleoenvironmental and paleoclimatic conditions in southwestern Europe: isotopic analyses on mammalian taxa. *PLoS One* 8, e63739.
- Dowsett, H., Barron, J., Poore, R., 1996. Middle Pliocene sea surface temperatures: a global reconstruction. *Mar. Micropaleontol.* 27, 13–25.
- Dowsett, H.J., Foley, K.M., Stoll, D.K., Chandler, M.A., Sohl, L.E., Bentsen, M., Otto-Bliesner, B.L., Bragg, F.J., Chan, W.-L., Contoux, C., Dolan, A.M., Haywood, A.M., Jonas, J.A., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Nisancioglu, K.H., Abe-Ouchi, A., Ramstein, G., Riesselman, C.R., Robinson, M.M., Rosenbloom, N.A., Salzmann, U., Stepanek, C., Strother, S.L., Ueda, H., Yan, Q., Zhang, Z., 2013. Sea surface temperature of the mid-Piacenzian Ocean: a data-model comparison. *Sci. Rep.* 3. <http://dx.doi.org/10.1038/srep02013> (article num.: 2013).
- Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E., Bocherens, H., 2008. Can carbon-13 abundances in large herbivores track canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 69–82.
- Erdei, B., Hably, L., Kazmer, M., Utescher, T., Bruch, A.A., 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 115–140.
- Eronen, J.T., Rook, L., 2004. The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *J. Hum. Evol.* 47, 323–341.
- Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C., Fortelius, M., 2010. Precipitation and large herbivorous mammals II: application to fossil data. *Evol. Ecol. Res.* 12, 235–248.
- Eronen, J.T., Micheels, A., Utescher, T., 2011. A comparison of estimates of mean annual precipitation from different proxies: a pilot study for the European Neogene. *Evol. Ecol. Res.* 13, 851–867.
- Eronen, J.T., Fortelius, M., Micheels, A., Portmann, F.T., Puolamäki, K., Janis, C.M., 2012. Neogene aridification of the northern hemisphere. *Geology* 40, 823–826.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 503–537.
- Fejfar, O., 1964. The Lower Villafranchian vertebrates from Hajnáčka near Filákovo in Southern Slovakia. *Rozpravy Ústředního ústavu geologického* 30, 1–116.
- Fejfar, O., Heinrich, W.-D., Heintz, E., 1990. Neues aus dem Villafranchium von Hajnáčka bei Filákovo (Slowakei, ČSSR). *Quartärpaläontologie* 8, 47–70.
- Fejfar, O., Sabol, M., Tóth, C., 2012. Early Pliocene vertebrates from Ivanovce and Hajnáčka (Slovakia). VIII. Ursidae, Mustelidae, Tapiridae, Bovidae and Proboscidea from Ivanovce. *Neues Jahrb. Geol. Paläontol. Abh.* 264, 95–115.
- Feranec, R.S., 2004. Geographic variation in the diet of hypsodont herbivores from the Francholabrean of Florida. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 359–369.
- Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. *Paleobiology* 32, 191–205.
- Fodor, L., Bada, G., Csillag, G., Horváth, E., Ruszkiczay-Rüdiger, Z., Palotás, K., Sikhegyi, F., Timár, G., Cloetingh, S., Horváth, F., 2005. An outline of neotectonic structures and morphotectonics of the western and central Pannonian Basin. *Tectonophysics* 410, 15–41.
- Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z., 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 219–227.
- Főzy, I., Szente, I., Dyke, G., 2014. Fossils of the Carpathian Region. Indiana University Press, Bloomington.
- Fricke, H.C., O'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 126, 91–99.
- Fricke, H.C., O'Neil, J.R., 1999. The correlation between $^{18}\text{O}/^{16}\text{O}$ ratios of meteoric water and surface temperature: its use in investigating terrestrial climate change over geologic time. *Earth Planet. Sci. Lett.* 170, 181–196.
- Fricke, H.C., Clyde, W.C., O'Neil, J.R., 1998. Intra-tooth variations in $\delta^{18}\text{O}$ (PO_4) of mammalian tooth enamel as a record of seasonal variations in continental climate variables. *Geochim. Cosmochim. Acta* 62, 1839–1850.
- Gasparik, M., 2001. Neogene proboscidean remains from Hungary; an overview. *Fragm. Palaeontol. Hun.* 19, 61–77.
- Gasparik, M., 2007. “Elephants” in the cellar. A revision of the Neogene Proboscidean remains, damaged in the fire of the Hungarian Natural History Museum in 1956. *Fragm. Palaeontol. Hun.* 24–25, 83–91.
- Grimes, V., Pellegrini, M., 2013. A comparison of pretreatment methods for the analysis of phosphate oxygen isotope ratios in bioapatite. *Rapid Commun. Mass Spectrom.* 27, 375–390.

- Hably, L., 2002. Late Neogene vegetation and climate reconstruction in Hungary. *Acta Univ. Carol. Geol.* 46, 85–90.
- Hably, L., Kvaček, Z., 1998. Pliocene mesophytic forests surrounding crater lakes in western Hungary. *Rev. Palaeobot. Palynol.* 101, 257–269.
- Halas, S., Skrzypek, G., Meier-Augenstein, W., Pelc, A., Kemp, H.F., 2011. Inter-laboratory calibration of new silver orthophosphate comparison materials for the stable oxygen isotope analysis of phosphates. *Rapid Commun. Mass Spectrom.* 25, 579–584.
- Haywood, A.M., Valdes, P.J., 2004. Modelling Pliocene warmth: contribution of atmosphere, oceans and cryosphere. *Earth Planet. Sci. Lett.* 218, 363–377.
- Haywood, A.M., Valdes, P.J., Sellwood, B.W., 2002. Magnitude of climate variability during middle Pliocene warmth: a palaeoclimate modelling study. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 188, 1–24.
- Haywood, A.M., Hill, D.J., Dolan, A.M., Otto-Bliesner, B.L., Bragg, F., Chan, W.L., Chandler, M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Abe-Ouchi, A., Pickering, S.J., Ramstein, G., Rosenbloom, N.A., Salzmann, U., Sohl, L., Stapanek, C., Ueda, H., Yan, Q., Zhang, Z., 2013. Large-scale features of Pliocene climate: results from the Pliocene Model Intercomparison Project. *Clim. Past* 9, 191–209.
- Hilgen, F.J., Lourens, L.J., Van Dam, J.A., Beu, A.G., Boyes, A.F., Cooper, R.A., Krijgsman, W., Ogg, J.G., Piller, W.E., Wilson, D.S., 2012. The Neogene Period. In: Gradstein, F.M., Schmitz, J.G.O.D., Ogg, G.M. (Eds.), *The Geologic Time Scale*. Elsevier, Boston, pp. 923–978.
- Hill, D.J., Csank, A.Z., Dolan, A.M., Lunt, D.J., 2011. Pliocene climate variability: Northern Annular Mode in models and tree-ring data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 309, 118–127.
- Holec, P., 1996. A Plio-Pleistocene large mammal fauna from Strekov and Nová Vieska, south Slovakia. *Acta Zool. Cracov.* 39, 219–222.
- Hordijk, K., De Bruijn, H., 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina–Ptolemais–Servia Basin (Greece). *Hell. J. Geosci.* 44, 21–103.
- Hurai, V., Paquette, J.-L., Huraiova, M., Sabol, M., 2012. U–Pb geochronology of zircons from fossiliferous sediments of the Hajnacka 1 maar (Slovakia) – type locality of the MN 16a biostratigraphic subzone. *Geol. Mag.* 149, 989–1000.
- Iacumin, P., Bocherens, H., Mariotti, A., Longinelli, A., 1996. Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: a way to monitor diagenetic alteration of bone phosphate? *Earth Planet. Sci. Lett.* 142, 1–6.
- Iacumin, P., Nikolae, V., Ramigni, M., 2000. C and N isotope measurements on Eurasian fossil mammals, 40 000 to 10 000 years BP: herbivore physiologies and palaeoenvironmental reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 163, 33–47.
- Janossy, D., 1986. Pleistocene vertebrate faunas of Hungary. *Developments in Palaeontology & Stratigraphy*. Elsevier, p. 8.
- Ji, Q., Luo, Z.X., Yuan, C.X., Wible, J.R., Zhang, J.P., Georgi, J.A., 2002. The earliest known eutherian mammal. *Nature* 416, 816–822.
- Kahlke, R.D., 2007. Late Early Pleistocene European large mammals and the concept of an Epivillafranchian biochron. *Cour. Forschungs-Inst. Senckenberg*. pp. 265–278.
- Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacomat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quat. Sci. Rev.* 30, 1368–1395.
- Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annu. Rev. Earth Planet. Sci.* 26, 573–613.
- Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *J. Archaeol. Sci.* 24, 417–429.
- Kocsis, L., 2011. Geochemical compositions of marine fossils as proxies for reconstructing ancient environmental conditions. *Chimia* 65, 787–791.
- Kocsis, L., Ozsvárt, P., Becker, D., Ziegler, R., Scherler, L., Codrea, V., 2014. Orogeny forced terrestrial climate variation during the late Eocene–early Oligocene in Europe. *Geology* 42, 727–730.
- Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. *Proc. Natl. Acad. Sci. U. S. A.* 107, 19691–19695.
- Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. *Rev. Mineral. Geochem.* 48, 455–488.
- Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochim. Cosmochim. Acta* 60, 3889–3896.
- Kohn, M.J., Schoeninger, M.J., Barker, W.W., 1999. Altered states: effects of diagenesis on fossil tooth chemistry. *Geochim. Cosmochim. Acta* 63, 2737–2747.
- Kormos, T., 1917. Die pliozänen Schichten von Ajnacső und ihre fauna. *Jahresbericht der Königlich Ungarischen Geologischen Reichsanstalt 1915* pp. 564–582.
- Kováč, M., Synak, R., Fordinál, K., Joniak, P., Tóth, C., Vojtko, R., Nagy, A., Baráth, I., Maglay, J., Minár, J., 2011. Late Miocene and Pliocene history of the Danube Basin: inferred from development of depositional systems and timing of sedimentary facies changes. *Geol. Carpath.* 62, 519–534.
- Kovács, J., Moravcová, M., Újvári, G., Pintér, A.G., 2012. Reconstructing the paleoenvironment of East Central Europe in the Late Pleistocene using the oxygen and carbon isotopic signal of tooth in large mammal remains. *Quat. Int.* 276–277, 145–154.
- Kovács, J., Raucsik, B., Varga, A., Újvári, G., Varga, G., Ottner, F., 2013. Clay mineralogy of red clay deposits from the central Carpathian Basin (Hungary): implications for Plio-Pleistocene chemical weathering and palaeoclimate. *Turk. J. Earth Sci.* 22, 414–426.
- Kovar-Eder, J., 2003. Vegetation dynamics in Europe during the Neogene. *DEINSEA* 10, 373–392.
- Kretzoi, M., 1985. Sketch of the biochronology of the Late Cenozoic in Central Europe. *Problems of the Neogene and Quaternary in the Carpathian Basin. Stud. Geogr. Hung.* 19, 3–20.
- Kürschner, W.M., 2010. C-isotope composition of fossil sedges and grasses. *Geophys. Res. Abstr.* 12 (EGU2010-8012-1).
- Lacomat, F., Mörs, T., 2008. The northernmost occurrence of the rare Late Pliocene rhinoceros *Stephanorhinus jeanvireti* (Mammalia, Perissodactyla). *Neues Jahrb. Geol. Palaontol. Abh.* 249, 157–165.
- Lee-Thorp, J.A., van der Merwe, N.J., 1987. Carbon isotope analysis of fossil bones apatite. *S. Afr. J. Sci.* 83, 712–715.
- Lee-Thorp, J.A., Sealy, J.C., van der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone and collagen and bone apatite, and their relationship to diet. *J. Archaeol. Sci.* 16, 585–599.
- Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11201–11205.
- Liang, Y., Blake, R.E., 2007. Oxygen isotope fractionation between apatite and aqueous-phase phosphate: 20–45 degrees C. *Chem. Geol.* 238, 121–133.
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography* 20, PA1003.
- Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate – a new tool for paleohydrological and paleoclimatological research. *Geochim. Cosmochim. Acta* 48, 385–390.
- Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. *Earth Planet. Sci. Lett.* 75, 29–36.
- Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone phosphate and environmental drinking-water. *Geochim. Cosmochim. Acta* 48, 1689–1693.
- Luz, B., Cormie, A.B., Schwarcz, H.P., 1990. Oxygen isotope variations in phosphate of deer bones. *Geochim. Cosmochim. Acta* 54, 1723–1728.
- Martin, C., Bentaleb, I., Kaandorp, R., Iacumin, P., Chatri, K., 2008. Intra-tooth study of modern rhinoceros enamel $\delta^{18}\text{O}$: is the difference between phosphate and carbonate $\delta^{18}\text{O}$ a sound diagenetic test? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 183–189.
- Martinelli, L.A., Devol, A.H., Victoria, R.L., Richey, J.E., 1991. Stable carbon isotope variation in C3 and C4 plants along the Amazon River. *Nature* 353, 57–59.
- Maslin, M.A., Brierley, C.M., Milner, A.M., Shultz, S., Trauth, M.H., Wilson, K.E., 2014. East African climate pulses and early human evolution. *Quat. Sci. Rev.* 101, 1–17.
- Maslin, M.A., Shultz, S., Trauth, M.H., 2015. A synthesis of the theories and concepts of early human evolution. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140064.
- Metcalfe, J.Z., Longstaffe, F.J., 2012. Mammoth tooth enamel growth rates inferred from stable isotope analysis and histology. *Quat. Res.* 77, 424–432.
- Metcalfe, J.Z., Longstaffe, F.J., White, C.D., 2009. Method-dependent variations in stable isotope results for structural carbonate in bone bioapatite. *J. Archaeol. Sci.* 36, 110–121.
- Metcalfe, J.Z., Longstaffe, F.J., Zazula, G.D., 2010. Nursing, weaning, and tooth development in woolly mammoths from Old Crow, Yukon, Canada: implications for Pleistocene extinctions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 298, 257–270.
- Metcalfe, J.Z., Longstaffe, F.J., Hodgins, G., 2013. Proboscideans and paleoenvironments of the Pleistocene Great Lakes: landscape, vegetation, and stable isotopes. *Quat. Sci. Rev.* 76, 102–113.
- Meyers, S.R., Hinnov, L.A., 2010. Northern Hemisphere glaciation and the evolution of Plio-Pleistocene climate noise. *Paleoceanography* 25, PA3207.
- Montanari, S., Louys, J., Price, G.J., 2013. Pliocene paleoenvironments of Southeastern Queensland, Australia inferred from stable isotopes of marsupial tooth enamel. *PLoS One* 8.
- Montuire, S., Maridet, O., Legendre, S., 2006. Late Miocene–Early Pliocene temperature estimates in Europe using rodents. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 247–262.
- Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 14964–14969.
- Mottl, M., 1939. Die mittelpozäne Säugetierfauna von Gödöllő bei Budapest. *A Magyar Királyi Földtani Intézet Évkönyve*. 32 pp. 257–350.
- Németh, K., Goth, K., Martin, U., Csillag, G., Suhr, P., 2008. Reconstructing paleoenvironment, eruption mechanism and paleomorphology of the Pliocene Pula maar (Hungary). *J. Volcanol. Geotherm. Res.* 177, 441–456.
- O’Leary, M.H., 1988. Carbon isotopes in photosynthesis. *Bioscience* 38, 328–336.
- Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., Tucker, S.T., 2002. Environmental change in the great plains: an isotopic record from fossil horses. *J. Geol.* 110, 123–140.
- Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO_2 , and bioapatite in different mammals. *J. Archaeol. Sci.* 32, 1459–1470.
- Pellegrini, M., Lee-Thorp, J.A., Donahue, R.E., 2011. Exploring the variation of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ relationship in enamel increments. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 71–83.
- Pott, R., 1995. The origin of grassland plant species and grassland communities in Central Europe. *Fitosociologia* 29, 7–32.
- Pound, M.J., Tindall, J., Pickering, S.J., Haywood, A.M., Dowsett, H.J., Salzmann, U., 2014. Late Pliocene lakes and soils: a global data set for the analysis of climate feedbacks in a warmer world. *Clim. Past* 10, 167–180.
- Pryor, A.J.E., Stevens, R.E., O’Connell, T.C., Lister, J.R., 2014. Quantification and propagation of errors when converting vertebrate biomineral oxygen isotope data to temperature for palaeoclimate reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 99–107.
- Pushkina, D., Bocherens, H., Ziegler, R., 2014. Unexpected palaeoecological features of the Middle and Late Pleistocene large herbivores in southwestern Germany revealed by stable isotopic abundances in tooth enamel. *Quat. Int.* 339–340, 164–178.

- Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A., Lee-Thorp, J.A., van der Merwe, N.J., 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chem. Geol. (Isotope Geoscience Section)* 94, 183–192.
- Rivals, F., Mol, D., Lacomat, F., Lister, A.M., Sempere, G.M., 2015. Resource partitioning and niche separation between mammoths (*Mammuthus rumanus* and *Mammuthus meridionalis*) and gomphotheres (*Anancus arvernensis*) in the Early Pleistocene of Europe. *Quat. Int.* 379, 164–170.
- Rook, L., Martínez-Navarro, B., 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quat. Int.* 219, 134–144.
- Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 1993. Isotopic patterns in modern global precipitation. In: Swart, P.K., Lohmann, K.C., Mckenzie, J., Savin, S. (Eds.), *Climate Change in Continental Isotopic Records*. American Geophysical Union, Washington D.C., pp. 1–36.
- Sabol, M., Konečný, V., Vass, D., Kováčková, M., Ďurišová, A., Túnyi, I., 2006. Early Late Pliocene site of Hajnáčka I (Southern Slovakia) – geology, palaeovolcanic evolution, fossil assemblages and palaeoenvironment. *Cour. Forschungs-Inst. Senckenberg* 261–274.
- Salzmann, U., Williams, M., Haywood, A.M., Johnson, A.L.A., Kender, S., Zalasiewicz, J., 2011. Climate and environment of a Pliocene warm world. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 309, 1–8.
- Salzmann, U., Dolan, A.M., Haywood, A.M., Chan, W.L., Voss, J., Hill, D.J., Abe-Ouchi, A., Otto-Bliesner, B., Bragg, F.J., Chandler, M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Pickering, S.J., Pound, M.J., Ramstein, G., Rosenbloom, N.A., Sohl, L., Stepanek, C., Ueda, H., Zhang, Z., 2013. Challenges in quantifying Pliocene terrestrial warming revealed by data-model discord. *Nat. Clim. Chang.* 3, 969–974.
- Scherler, L., Tütken, T., Becker, D., 2014. Carbon and oxygen stable isotope compositions of late Pleistocene mammal teeth from dolines of Ajoie (Northwestern Switzerland). *Quat. Res.* 82, 378–387.
- Schmidt, Z., Halouzka, R., 1970. Nová fauna vertebrát villafranchienú zo Strekova na Hronskej pahorkatine (Podunajská nížina). *Geologické práce, Správy* 51, 173–183.
- Skinner, H.C.W., 2005. Biominerals. *Mineral. Mag.* 69, 621–641.
- Spinoni, J., Szalai, S., Szentimrey, T., Lakatos, M., Bihari, Z., Nagy, A., Németh, Á., Kovács, T., Mihic, D., Dacic, M., Petrovic, P., Kržič, A., Hiebl, J., Auer, I., Milkovic, J., Štěpánek, P., Zahradníček, P., Kilar, P., Limanowka, D., Pyrc, R., Cheval, S., Birsan, M.-V., Dumitrescu, A., Deak, G., Matei, M., Antolovic, I., Nejedlík, P., Štaštný, P., Kajaba, P., Bochníček, O., Galo, D., Mikulová, K., Nabyvanets, Y., Skrynyk, O., Krakovska, S., Gnatiuk, N., Tolasz, R., Antofie, T., Vogt, J., 2015. Climate of the Carpathian Region in the period 1961–2010: climatologies and trends of 10 variables. *Int. J. Climatol.* 35, 1322–1341.
- Sullivan, C.H., Krueger, H.W., 1983. Carbon isotope ratios of bone apatite and animal diet reconstruction. *Nature* 301, 177.
- Szöcs, T., Rman, N., Süveges, M., Palcsu, L., Tóth, G., Lapanje, A., 2013. The application of isotope and chemical analyses in managing transboundary groundwater resources. *Appl. Geochem.* 32, 95–107.
- Tafforeau, P., Bentele, I., Jaeger, J.-J., Martin, C., 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: potential implications for palaeoenvironmental isotopic studies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 246, 206–227.
- Tesakov, A., Vangengeim, E., Pevzner, M., 2007. Arvicolid zonation of continental Pliocene deposits of East Europe. *Cour. Forschungs-Inst. Senckenberg* 227–236.
- Tipple, B.J., Meyers, S.R., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO₂: a comparative evaluation of available geochemical proxies. *Paleoceanography* 25, PA3202.
- Trauth, M.H., Maslin, M.A., Deino, A.L., Junginger, A., Lesoloyia, M., Odada, E.O., Olago, D.O., Olaka, L.A., Strecker, M.R., Tiedemann, R., 2010. Human evolution in a variable environment: the amplifier lakes of Eastern Africa. *Quat. Sci. Rev.* 29, 2981–2988.
- Tütken, T., Vennemann, T.W., Janz, H., Heimann, E.P.J., 2006. Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany: a reconstruction from C, O, and Sr isotopes of fossil remains. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 241, 457–491.
- Tütken, T., Furrer, H., Vennemann, T.W., 2007. Stable isotope compositions of mammoth teeth from Niederweningen, Switzerland: implications for the Late Pleistocene climate, environment and diet. *Quat. Int.* 164–165, 139–150.
- Tütken, T., Vennemann, T.W., Pfretzschner, H.U., 2008. Early diagenesis of bone and tooth apatite in fluvial and marine settings: constraints from combined oxygen isotope, nitrogen and REE analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 254–268.
- Tütken, T., Kaiser, T.M., Vennemann, T., Merceron, G., 2013. Opportunistic feeding strategy for the earliest Old World hypsodont Equids: evidence from stable isotope and dental wear proxies. *PLoS One* 8, e74463.
- van Dam, J.A., 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: the use of small mammals paleoprecipitation proxies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 190–218.
- van Dam, J.A., Abdul Aziz, H., Álvarez Sierra, M.A., Hilgen, F.J., van den Hoek Ostende, L.W., Lourens, L., Mein, P., van der Meulen, A.J., Pelaez-Campomanes, P., 2006. Long-period astronomical forcing of mammal turnover. *Nature* 443, 687–691.
- Van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *J. Archaeol. Sci.* 18, 249–259.
- Vangengeim, E.A., Pevzner, M.A., Tesakov, A.S., 2005. Ruscianian and lower Villafranchian: age of boundaries and position in magnetochronological scale. *Stratigr. Geol. Correl.* 13, 530–546.
- Vennemann, T.W., Fricke, H.C., Blake, R.E., O'Neil, J.R., Colman, A., 2002. Oxygen isotope analysis of phosphates: a comparison of techniques for analysis of Ag₃PO₄. *Chem. Geol.* 185, 321–336.
- Virág, A., Gasparik, M., 2012. Relative chronology of late Pliocene and early Pleistocene mammoth-bearing localities in Hungary. *Hantkeniana* 27–36.
- Virág, A., Kocsis, L., Gasparik, M., Vasile, Ș., 2014. Palaeodietary reconstruction of fossil proboscideans from Hungary and Romania. *Sci. Ann. School Geol.* 102, 215–216.
- Vlačičky, M., Sliva, L., Tóth, C., Karol, M., Zervanová, J., 2008. Fauna a sedimentológia lokality Nová Vieska (vilafrank, SR). *Acta Mus. Morav.-Sci. Geol.* 93, 229–244.
- Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107, 281–289.
- Woodard, S.C., Rosenthal, Y., Miller, K.G., Wright, J.D., Chiu, B.K., Lawrence, K.T., 2014. Antarctic role in Northern Hemisphere glaciation. *Science* 346, 847–851.
- Zanazzi, A., Judd, E., Fletcher, A., Bryant, H., Kohn, M.J., 2015. Eocene–Oligocene latitudinal climate gradients in North America inferred from stable isotope ratios in perissodactyl tooth enamel. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 417, 561–568.
- Zazzo, A., Lecuyer, C., Mariotti, A., 2004a. Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions. *Geochim. Cosmochim. Acta* 68, 1–12.
- Zazzo, A., Lecuyer, C., Sheppard, S.M.F., Grandjean, P., Mariotti, A., 2004b. Diagenesis and the reconstruction of paleoenvironments: a method to restore original delta O-18 values of carbonate and phosphate from fossil tooth enamel. *Geochim. Cosmochim. Acta* 68, 2245–2258.