Unexpected palaeoecological features of the Middle and Late Pleistocene large herbivores in southwestern Germany revealed by stable isotopic abundances in tooth enamel

Diana Pushkina [a,b,][*], Hervé Bocherens [c], Reinhard Ziegler [d]

[a] iPHEP, UMR CNRS 6046, Université de Poitiers SFA, 40 avenue du Recteur Pineau, F-86022 Poitiers, France
[b] Department of Geography and Geology, University of Helsinki, P.O. Box 64, FIN-00014 Helsinki, Finland
[c] Universität Tübingen, Fachbereich Geowissenschaften − Biogeologie, Hölderlinstrasse 12, 72074 Tübingen, Germany
[d] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany

ARTICLE INFO

ABSTRACT

Species flexibility in diet and habitat and their ability to tolerate a range of unfavourable ecological conditions and survive in unusual habitats accompanied by unexpected faunal components has been determined from various research fields. We present the dietary and environmental reconstructions of interglacial and glacial large mammals from central Germany (Bockstein and Vogelherd caves, Steinheim and Mauer) during the Middle and Late Pleistocene, using carbon and oxygen stable isotope relative abundances in the carbonate fraction of tooth enamel. The same species existed in central Europe during different temperature and ecosystem regimes. It appeared that the species during the glacial periods demonstrated much narrower ranges $\delta^{13}C$ and $\delta^{18}O$ than during the interglacial periods and at the dawn of the species origination. Intriguingly, the early woolly mammoth *Mammuthus primigenius fraasi* apparently lived in much milder conditions than the late woolly mammoth *Mammuthus primigenius primigenius*, and shared similar diet and habitat with the straight-tusked forest elephant *Palaeoloxodon antiquus*. Bovids existed in extremely open habitat at Steinheim, probably during the Saalian glacial, compared to other glacial species. Woolly rhinoceros *Coelodonta antiquitatis* and the early woolly mammoth came to occupy similar environments only later, during the Weichselian glacial period in Bockstein and Vogelherd caves. A so-called "steppe rhinoceros" *Stephanorhinus hemitoechus* occurred in the forested habitat, along with the Merck's rhino *Stephanorhinus kirchbergensis*. The horses appear to have preferred warmer and denser habitat than the woolly rhinoceros during the Pleistocene. The Pleistocene donkeys shared the ecological niches between bovids and horses. These new results demonstrate that stable isotope analyses can be extremely helpful to determine more detailed paleodiet and paleohabitat of extinct species. It appears that the deviation of the inferred palaeoecological patterns from the patterns deduced from modern survivors' ecology increases with increasing age, and species appeared more flexible at their origin.

1. Introduction

1.1. Background on changing European faunal assemblages

Climatic fluctuations of the last 2 million years during the Pleistocene and Holocene brought about dramatic changes in the faunal composition in Europe. A general scenario of shifts in the large mammal composition has been proposed for Central Europe, using diverse palaeoclimatic indicators, fossil morphological adaptations and ecological analogy with extant taxa. The two typical large mammal assemblages, best recognized in Europe and Siberia during the late Middle and Late Pleistocene, were drastically alternating in central Europe during interglacial and glacial periods: a more ancient interglacial assemblage with the straight-tusked or forest elephant *Palaeoloxodon antiquus* and Merck's rhinoceros *Stephanorhinus kirchbergensis* that permanently inhabited the Mediterranean region; and a more recent glacial assemblage with the woolly mammoth *Mammuthus primigenius* and woolly rhinoceros *Coelodonta antiquitatis*, adapted to cold climates and tundra steppes that inhabited eastern Europe and Siberia (Kowalski, 1980; Vereshchagin and Baryshnikov, 1980, 1985; Stuart,

* Corresponding author. Department of Geography and Geology, University of Helsinki, P.O. Box 64, FIN-00014 Helsinki, Finland.
E-mail address: diana.pushkina@gmail.com (D. Pushkina).

1991; Sher, 1992, 1997; Kahlke, 1999; Von Koenigswald, 1999, 2002, 2003, 2007; Pushkina, 2007) (Fig. 1) The interglacial assemblage was represented by the straight-tusked or forest elephant *P. antiquus*, Merck's rhinoceros *S. kirchbergensis*, narrow-nosed rhinoceros *Stephanorhinus hemitoechus*, hippopotamus *Hippopotamus amphibius*, water buffalo *Bubalus murrensis*, aurochs *Bos primigenius*, giant deer *Megaloceros giganteus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus*, and European wild boar *Sus scrofa*, because they were characteristic of the interglacial stages in central Europe (Stuart, 1986, 1991; Von Koenigswald, 1999; Van Kolfschoten, 2000; Currant and Jacobi, 2001; Bradshaw et al., 2003). The glacial assemblage was composed of the woolly mammoth *M. primigenius*, woolly rhinoceros *C. antiquitatis*, steppe bison *Bison priscus*, musk ox *Ovibos moschatus*, reindeer *Rangifer tarandus*, and saiga antelope *Saiga tatarica* (Alexeeva, 1980; Stuart, 1991; Sher, 1997; Kahlke, 1999).

In fossil localities, both types of species can occur together, creating the so-called "non-analogous" assemblages with no modern interglacial ecological analogues and atypical to fossil interglacial and glacial assemblages, species of which seemed to have been adapted to warm or cold environmental conditions and were not supposed to coexist (Guthrie, 1984; Aaris-Sørensen, 2009). This fact was often interpreted as a consequence of sampling bias or time averaging within a period of rapid climate

fluctuation (e.g. Stewart, 2008). However, an increasing amount of evidence suggests an alternative interpretation that large mammal species may have been more ecologically flexible than expected (e.g. Kaiser and Franz-Odendaal, 2004; Pushkina, 2007; Rivals et al., 2008; Pushkina et al., 2010), supporting the possibility that some of these species may have coexisted.

This uncertainty can be solved if accurate dating can firmly establish the contemporaneity of the different species (e.g. Stafford et al., 1999) but it is increasingly difficult with increasing geological age. Another possibility is to establish ecological preferences by using phenotypic tracers, i.e. indicators of the life conditions of fossil individuals independently of their species status. Stable isotopic analyses of tooth enamel have been shown to be a good proxy for reconstructing diet and habitat of modern and fossil species, and, thus, the changes in terrestrial paleoenvironments (e.g. Lee-Thorp and van der Merwe, 1987; Quade et al., 1995; Cerling et al., 1997; Koch, 1998; Cerling and Harris, 1999; MacFadden and Higgins, 2004; Bocherens, 2009, 2011).

1.2. Isotopes, diet and habitat

Carbon isotopic composition in herbivores reflect the source of carbon in their diet, indicating the photosynthetic pathways and the presence of C3 and C4 vegetation in their habitat as well

Mag Pol	Stratigraphy Geochron	Mammal ages	OIS, absolute ages ka			Western climatostrat	Eastern Europe/ Siberia	Faunal complexes and fossil bearing horizons	Alpine scale
	Holocene			0	10	Flandrian	Holocene	"Modern"	
Brunhes	PLEISTOCENE — LATE	Oldenburgian	OIS2	11	20	Weichselian Glaciation	Valdaj (Sartanian, Karginian, Zyrjanian)	Mammoth or Upper Palaeolithic: Sartanian (late Weichselian, 0.3-0.11) Zyrjanian (early- middle Weichselian) *Shkurlat (Eastern Europe) (0.075-0.128)*	Wurm
			OIS3	24	60				
			OIS4	57	70				
			OIS5ad	71	115				
			OIS5e	115	125	Eemian	Mikulino/ Kazantsevo	Shkurlat (Eastern Europe) Karangat (Black Sea) Upper Khazarian (Caspian Sea)	Riss-Wurm
			OIS6	129	190	Saalian Glaciation	Moskovian/ Tazovian	early Mammoth or Upper Palaeolithic (Pavlovian)	Riss
			OIS7	186	240		Odintsovian	Khazarian (or Chozarian) Priirtyshskij (Kazakhstan)	
			OIS8	242	300		Dneprovian/ Samara		
	PLEISTOCENE — MIDDLE		OIS9	301	330		Kamenka	Singilian	Mindel - Riss
			OIS10	334	360				
			OIS11	364	430	Holsteinian interglacial	Likhvin/ Tobolian		
			OIS12	427	470	Elsterian Glaciation	Oka Glac.		Mindel
		Biharian	OIS13	474	530	Cromerian (Galerian)	Muchkapian	Tiraspolian (European Russia, Ukraine) Koshkurgan (Kazakhstan) Vyatkinskij (Western Siberia) late Olyorian (north-eastern Siberia) - Aldan / Viljuj fauna	Gunz-Mindel
			OIS14	528	570				
			OIS15	568	620				
			OIS16	621	660		Don Glac.		
			OIS17	659	710		Iljinka		
			OIS18	712	760		Pokrovka		
			OIS19	760	790				
Matuyama	PLEISTOCENE — EARLY			800	1.1	Bavelian (Galerian)	Balashovsk Petropavlovian	Tamanian (European Russia, Ukraine), Odessa (*0.95-1.8*)	
				1.1	1.8	Menapian; Waalian; Eburonian (Villafranchian)		Khorgoss suite 0.73-0.1, Ilijskij (Kazakhstan) Razdoljinskij (Western Siberia) early Olyorian (0.8-1.2) (north-eastern Siberia) - ?Aldan / Viljuj fauna	
Gauss	Pliocene — Villanyan			1.8	2.5	(Villafranchian)		Khaprovian 1.5/1.8-2.5	
				2.5	3.4			Moldavian (2.5-3.4 Ma)	

Fig. 1. Chronology and general climatic trends in Europe within a summarising stratigraphical table of Northern Eurasia with the representative large species during the times of their greatest commonness (pictures of species), the woolly mammoth *Mammuthus primigenius* (Weichselian) and the straight-tusked elephant *Palaeoloxodon antiquus* (Holsteinian) (Pushkina, 2007).

as a degree of canopy closure versus openness in wooded habitats. The C3 plants consist of most woody vegetation and grasses that have a cool growing season, such as ones growing in the temperate winter-rainfall zones and cool high-altitude summer rainfall regions (Vogel et al., 1978; Alcocks, 1988). The $\delta^{13}C$ values for C3 plants range between −34‰ and −23‰, with a mean of −26‰ (Calvin and Benson, 1948; Hatch et al., 1967; Smith and Epstein, 1971). The differences in $\delta^{13}C$ composition are also observed in the forest environments, known as the canopy effect. These differences result in a vertical $\delta^{13}C$ gradient in the trees and depletion of ^{13}C at the bottom of the canopy compared to the top (Van der Merwe and Medina, 1989; Bocherens et al., 1999). This effect occurs due to the forest soil respiration and decomposition of CO_2 and recycling of already-depleted organic carbon within an enclosed heavily wooded environment at the ground surface, and increased isotopic fractionation of carbon by plants performing their photosynthesis under shaded conditions (Van der Merwe and Medina, 1991; Rodière et al., 1996; Drucker et al., 2008) in comparison to woodland and more open forest environments with higher evapotranspiration. Canopy effect can produce up to 5‰ differences in $\delta^{13}C$ at one site in the same species, feeding on plants from different tree elevation, such as pigs and porcupine (Van der Merwe and Medina, 1991). The canopy effect has been also observed in pure C3 environments between herbivores feeding in a heavily enclosed wooded environment and those feeding in more open parkland or grassland environments with higher evapotranspiration (Feranec and MacFadden, 2006; Drucker et al., 2008). The carbon isotopic composition of the carbonate fraction of bioapatite in large herbivores is higher than or enriched by 14‰ from their diet (Cerling et al., 1999). In temperate and cold environments, $\delta^{13}C$ higher than −13‰ in herbivore enamel indicates open landscapes, such as grasslands and steppes, higher than −27‰ in diet or ecosystem $\delta^{13}C$ values. $\delta^{13}C$ values lower than −13‰ indicate woodlands and denser forests (Bocherens and Rousseau, 2008).

Oxygen isotopic composition of the herbivores' enamel apatite is related to the source and amount of body-water ingested, either free drinking water or obtained from food and plants, which is a proxy for $\delta^{18}O$ values of meteoric water, variable due to the source of precipitation and effects of latitude, altitude, continentality, temperature, and evaporation (Dansgaard, 1964; Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Bryant et al., 1996; Kohn, 1996; Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). $\delta^{18}O$ values of meteoric water are higher in warmer or drier environments (Dansgaard, 1964). Thus, herbivores feeding in open steppe habitats are expected to have more enriched $\delta^{18}O$ values than species from forested cooler and more humid habitats. Species in warm environments that obtain most of their ingested water from leaves, or non-obligate drinkers (e.g. giraffes, roe deer), tend to have higher $\delta^{18}O$ values due to evapotranspiration than those of the obligate drinkers, or species that drink, and aquatic mammals (hippopotamus), which are evaporation insensitive in isotopic results (Sponheimer and Lee-Thorp, 1999, 2001). Seasonal variation in rainwater in mid- and high latitude environments and species migration can be significant, producing intra-tooth variations of 3−4‰, or more (e.g. in high-crowned ungulates, horses and bison, Hoppe et al., 2004; Feranec et al., 2009). Oxygen isotopic composition can be affected not only by daily ecology and migration but also by life history and physiology of mammals. Oxygen isotopic compositions are higher in nursing animals during lactation and weaning periods because of milk consumption, which is related to the body water of the mother, and more enriched in ^{18}O due to the preferential loss of ^{16}O through sweat, urine, and expired water vapour (Bryant and Froelich, 1995; Kohn, 1996).

Measuring biogenic isotopic signatures in fossil skeletal tissues requires that these tissues have not been significantly modified post-mortem. Two different bone and tooth fractions potentially record unaltered isotopic signatures: collagen and the carbonate fraction of bioapatite. Bones with well-preserved collagen are exceptionally rare in sites older than the Late Pleistocene, with notable exceptions in the Middle Pleistocene (Jones et al., 2001; Kuitems et al., 2012). Fortunately, preservation of biogenic isotopic signatures has been demonstrated in tooth enamel of the fossils of millions years old (e.g. Bocherens et al., 1996; Lee-Thorp and Sponheimer, 2003). Therefore, we will focus on carbon and oxygen isotopic composition of carbonate fraction of bioapatite in tooth enamel.

1.3. Previous isotopic work on glacial and interglacial large mammals

Intriguing stable isotope results have already indicated species' habitual variations, suggesting that the large mammals were rather flexible in their ecology in Europe (e.g. Bocherens et al., 1999; Drucker et al., 2003; García García et al., 2009; Feranec et al., 2010; Britton et al., 2012), South-eastern Asia (Pushkina et al., 2010), Eastern Africa (e.g. Bibi et al., 2013) and North America (Koch et al., 1998; DeSantis et al., 2009). Studies have shown that European large ungulates, such as horses and aurochs, retreated into dense forest habitats during the Holocene interglacial (Bocherens et al., 2005; Drucker and Bocherens, 2009) and the late Middle Pleistocene (Van Asperen, 2010). Fauna adapted to open steppe environments could survive and forage in the forest and, vice versa. For example, the forest elephant was able to persist in open environments during the Late Weichselian Glaciation (Cerling et al., 1999; Markova, 2000; Bocherens et al., 2005; Pushkina, 2007).

The association of ecological changes with climatic fluctuations between glacial and interglacial periods in the Pleistocene of North America has been evaluated using carbon and oxygen isotopic composition of fossil herbivore tooth enamel (e.g. Koch et al., 1998; DeSantis et al., 2009). These works have shown that some species were conservative in their ecology despite climatic and environmental changes, whereas others were able to shift their diet and habitat. In Europe, such studies are not so common for the Middle Pleistocene. Most studies used carbon and nitrogen stable isotopic composition of bone and tooth collagen because the combination of these two isotopic tracers is powerful in deciphering habitat use and its trophic position in the food chain of past ecosystems (e.g. Bocherens et al., 1994, 2005, 2011; Drucker et al., 2003, 2008; Münzel et al., 2011; Yeakel et al., 2013). Due to collagen loss in fossil bones through time, published studies are mostly limited to the last 60,000 years. Only in a few exceptional cases was it possible to use this approach in older sites (e.g. Bocherens et al., 1999; Jones et al., 2001; Palmqvist et al., 2003; Britton et al., 2012; Kuitems et al., 2012). In mammal fossil remains devoid of collagen, it is still possible to obtain an isotopic signature with biological meaning from carbonate.

Some studies investigated the carbon and oxygen of tooth enamel in diverse large mammal middle Pleistocene assemblages in southwestern Europe, in southern France, such as in Aldène and Escale caves (Bocherens et al., 1991, 1994) and in Payre (Ecker et al., 2013), as well as in Spain, in Atapuerca (García García et al., 2009). Very little work has been done in Central Europe using this approach on diverse large mammal assemblages. Kovács et al. (2012) analysed carbon and oxygen isotopes in teeth from late Pleistocene large mammals from Czech Republic, Slovakia and Hungary, essentially woolly mammoths, as well as a few horses and one woolly rhinoceros, from various sites. However, this study

includes only 4 enamel samples, with 12 additional measurements on dentine, a fossil tissue that is well known to be prone to diagenetic alteration (e.g. Koch et al., 1997; Bocherens et al., 2011). Due to these problems, the result of this study cannot be considered as valid unless convincing evidence is provided that diagenetic alteration did not have any significant impact on dentine stable isotopic composition. The studies of the carbon and oxygen isotopic composition of woolly mammoth tooth enamel in Eastern and Northern Europe reconstructed palaeoenvironment trends during the second half of the late Pleistocene, but did not consider the niche partitioning aspects, as they focus only on one species (Arppe and Karhu, 2010; Arppe et al., 2011). In contrast, two studies included more than one species, Jones et al. (2001) and Britton et al. (2012). Both investigated the carbon and nitrogen isotopic composition of bone and tooth collagen in England (Jones et al., 2001) and Germany (Britton et al., 2012), together with the carbon and oxygen isotopic composition of tooth enamel of proboscideans, bison and horse in the first study (Jones et al., 2001). Although the article by Britton et al. (2012) includes carbon isotopic data for horse and large bovines, it does not evaluate the implications of these results in terms of habitat, i.e. foraging in forested versus open landscape.

Our study is, therefore, unique for Central Europe as it considers diverse faunas of large herbivorous mammals and compares faunal assemblages occurring within different climatic and environmental contexts. The purpose of the present study is to assess the ecology of the large ungulates typical of the late Middle and Late Pleistocene interglacial and glacial stages in central Europe, using isotopic geochemistry (^{13}C, ^{18}O) of fossil tooth enamel, and testing, whether they had a more flexible ecology than previously assumed. Carbon and oxygen stable isotopic composition of fossil tissues can be used to test whether the same species experienced various climatic and environmental conditions despite being retrieved from the deposits of their expected climatic regime and species assemblage. Using this approach, we should find very different isotopic signatures, indicating that the species were able to tolerate different climatic conditions.

2. Materials and methods

2.1. Sites and the geological setting

We studied warm- and cold-adapted large ungulates from 4 sites in southwestern Germany: the interglacial locality of Mauer, the glacial caves of Vogelherd and Bockstein, analysed together, and the "mixed" interglacial and glacial, non-analogous locality of Steinheim an der Murr (hereafter, Steinheim). In Steinheim, the mixed faunal composition is demonstrated either due to the sampling bias because the vast majority of the bones have been collected by mine workers from different pits (or grube in German) around the site and their exact provenance is unknown, or due to real coexistence of some species with more flexible adaptations than anticipated. The majority of the species was analysed from Steinheim (Table 1; Fig. 2). These species were discovered in the layers associated with the Rissian glacial (correlated to the Saalian Glaciation) and Holsteinian interglacial deposits (Wahl et al., 2009). Many specimens were found from the pit of Sammet, which is considered to contain glacial deposits. Several specimens come from the pits of Fritz, Sigrist, Bauer, Gruber, and Müller, apparently associated with more temperate climates. However, many specimens could not be associated with any pit or correlated to the Holsteinian or Saalian. All specimens of *Mammuthus primigenius fraasi*, *P. antiquus*, and *S. kirchbergensis* are not associated with any pits. To establish a reference dataset corresponding to unambiguous glacial period conditions, we used

cave deposits from the caves Bocksteinhöhle and Vogelherdhöhle in the Lone Valley in the Eastern part of the Swabian Alb, which correspond to the middle and late Weichselian (Bockstein – archaeological deposits of the Middle Paleolithic (Bosinski, 2001; Kronneck et al., 2004; Champion et al., 2009)). In contrast, the site of Mauer, situated in the valley of the Elsenz rivulet, the old bed of the Neckar River (today the Neckar runs north of Mauer) represents a relatively moderate climatic interval (presence of the hippopotamus), during the Cromerian interglacial. Germany's oldest human fragment, the jaw of *Homo heidelbergensis*, or Mauer jaw, was discovered in Mauer, making unveiling its ecological context more intriguing (Mounier et al., 2009). All of the sites are located in Baden-Württemberg (Germany) less than 270 km apart (Fig. 2).

Table 1
Studied sites and species per site.

Locality	Chronostratigraphy	Species
Steinheim an der Murr	Rissian (Saalian) Holsteinian (Sammet pit is Rissian, Sigrist pit is Holsteinian?)	*Palaeoloxodon antiquus* *Mammuthus primigenius fraasi* *Coelodonta antiquitatis* *Stephanorhinus kirchbergensis* *Stephanorhinus hemitoechus* *Megaloceros giganteus* *Cervus elaphus* *Dama dama* *Equus ferus* *Equus hydruntinus* *Bison/Bos genus*, species unidentified
Bocksteinhöhle, Vogelherdhöhle (in Vogelherd no *Megaloceros*)	Middle and Late Weichselian	*Mammuthus primigenius* *Coelodonta antiquitatis* *Equus ferus* *Megaloceros giganteus*
Mauer	Cromerian	*Palaeoloxodon antiquus* *Stephanorhinus hundsheimensis/etrusus* *Equus mosbachensis*

2.2. Selection and preparation of teeth enamel samples for isotope analyses

We sampled M3 for all elephants and mammoths. M3 were also available for two giant deer and one Merck's rhinoceros. For the other ungulates, we sampled the upper M1 or M2 teeth, which were sometimes undistinguishable from each other, because these were the most available teeth (Table 2). For *Equus hydruntinus* we sampled also P3, P4, P2, and for *Equus caballus* P3 teeth (Table 2). Although in many ungulates isotope composition in M1 or M2 would reflect nutrients from mother's milk and is more enriched in ^{18}O compared to isotopic composition of consequently P2, M3, P3 and P4 that reflect solid diet after weaning because M1 and M2 partially mineralize, while animals are nursing during the first 2 years of life (Ancrenaz and Delhomme, 1997; Hoppe et al., 2004; Ecker et al., 2013), we tried to be consistent in the isotopic offset relative to adult isotopic values by sampling the same teeth. It has been also shown that δ^{13}C values of nursing ungulates are not drastically different from the mothers' unlike δ^{15}N, even though milk is ^{13}C depleted by 2.1‰ relative to the mother's plasma (Jenkins et al., 2001) because of a high ^{13}C depleted lipid content (DeNiro and Epstein, 1977), and teeth formed before weaning may have lower δ^{13}C values than those formed after weaning by ~0.5‰ in humans (Wright and Schwarcz, 1998) to by ~2‰ in sea lions (Hobson and Sease, 1998).

Table 2
Isotopic results (See Supplemental material).

Taxon	Site	CO$_3$ (%CaCO$_3$)	δ^{13}C carb (‰ VPDB)	δ^{18}O (‰ VPDB)	δ^{18}O (‰ SMOW)	Ecosystem	dOph (after Lecyuer et al., 2010)	Owat (after Lecyuer et al., 2010)	Temperature (after Skrzipek et al., 2011), northern areas	Temperature (after Skrzipek et al., 2011), central Europe
Coelodonta antiquitatis	Bocksteinhöhle, Stuttgart	3.85	−11.82	−8.96	21.63	−24.32	12.85	−11.12003978	6.226340033	6.043928391
	Bocksteinhöhle, Stuttgart	5.21	−11.62	−9.12	21.46	−24.12	12.69	−11.29031486	5.905066302	5.737433252
	Bocksteinhöhle, Stuttgart	3.53	−11.38	−10.67	19.86	−23.88	11.14	−12.93475386	2.802351204	2.777443049
Equus caballus	Bocksteinhöhle, Stuttgart	3.78	−11.94	−10.25	20.29	−24.44	11.56	−15.54940807	−2.130958625	−1.928934
	Bocksteinhöhle, Stuttgart	4.72	−11.72	−8.66	21.93	−24.22	13.14	−13.32403893	2.067851083	2.076729933
	Bocksteinhöhle, Stuttgart	3.89	−11.59	−8.99	21.60	−24.09	12.82	−13.77918188	1.209090791	1.257472614
	Bocksteinhöhle, Stuttgart	4.72	−11.39	−9.39	21.18	−23.89	12.41	−14.34945303	0.133107494	0.230984549
Mammuthus primigenius	Bocksteinhöhle, Stuttgart	6.65	−11.53	−10.70	19.83	−24.03	11.11	−12.96582312	2.743729957	2.721518379
Megaloceros giganteus	Bocksteinhöhle, Stuttgart	5.70	−11.95	−8.92	21.66	−24.45	12.88	−11.21064493	6.055386924	5.880839125
Equus mosbachensis	Mauer, Karlsruhe	3.17	−13.91	−7.73	22.89	−26.41	14.07	−12.01367169	4.540242103	4.435390966
	Mauer, Karlsruhe	3.27	−13.10	−9.05	21.53	−25.60	12.75	−13.86674646	1.043874602	1.09985637
	Mauer, Karlsruhe	5.04	−12.83	−6.67	23.98	−25.33	15.12	−10.52866302	7.342145249	7.108406568
	Mauer, Karlsruhe	3.99	−12.72	−9.37	21.20	−25.22	12.43	−14.32292339	0.183163418	0.278737901
Palaeoloxodon antiquus	Mauer, Karlsruhe	3.21	−13.85	−8.77	21.82	−26.35	13.04	−10.91912894	6.605417102	6.405567915
	Mauer, Karlsruhe	6.70	−12.44	−8.14	22.47	−24.94	13.66	−10.2569374	7.854835088	7.597512674
	Mauer, Karlsruhe	5.83	−12.38	−10.20	20.34	−24.88	11.60	−12.44217189	3.731751143	3.66409059
Stephanorhinus etruscus or hundsheimensis	Mauer, Karlsruhe	3.14	−14.92	−7.68	22.94	−27.42	14.11	−9.772381931	8.769090695	8.469712523
	Mauer, Karlsruhe	3.39	−13.31	−7.81	22.81	−25.81	13.99	−9.905091485	8.518695312	8.230835328
	Mauer, Karlsruhe	3.63	−14.54	−8.40	22.20	−27.04	13.40	−10.5289008	7.34169661	7.107978566
	Mauer, Karlsruhe	3.01	−14.27	−7.26	23.38	−26.77	14.54	−9.318145159	9.62614121	9.287338714
	Mauer, Karlsruhe	3.43	−14.22	−8.41	22.19	−26.72	13.39	−10.54164551	7.317649986	7.085038086
	Mauer, Karlsruhe	4.02	−14.05	−7.47	23.16	−26.55	14.33	−9.544841209	9.198412813	8.879285824
	Mauer, Karlsruhe	3.54	−13.69	−7.54	23.09	−26.19	14.26	−9.619996653	9.056610088	8.744006024
Bos/Bison cf. *Bison*	Steinheim an der Murr, grube Sammet, Stuttgart	3.4	−11.5	−9.3	21.3	−23.99	12.50	−12.91220382	2.844898458	2.818033129
	Steinheim an der Murr, grube Sammet, Stuttgart	4.1	−11.4	−8.6	22.0	−23.86	13.19	−11.8913486	4.77104037	4.655572513
	Steinheim an der Murr, grube Sammet, Stuttgart	3.9	−11.3	−8.5	22.1	−23.82	13.32	−11.70308997	5.12624533	4.994438045
	Steinheim an der Murr, grube Sammet, Stuttgart	4.8	−11.1	−9.5	21.1	−23.58	12.29	−13.21518466	2.273236497	2.272667618
	Steinheim an der Murr, grube Sammet, Stuttgart	2.7	−12.0	−8.6	22.0	−24.51	13.25	−11.81569878	4.913775882	4.791742191
	Steinheim an der Murr, grube Sammet, Stuttgart	6.4	−11.7	−8.9	21.7	−24.16	12.91	−12.30227287	3.995711562	3.91590883
	Steinheim an der Murr, grube Sammet, Stuttgart	4.1	−10.6	−6.7	23.9	−23.07	15.05	−9.166894523	9.911519767	9.559589858
	Steinheim an der Murr, grube Sammet, Stuttgart	5.8	−10.6	−9.6	20.9	−23.07	12.17	−13.40152644	1.921648235	1.937252416
Cervus elaphus	Steinheim an der Murr, grube Sigrist, Stuttgart	4.5	−17.2	−7.7	23.0	−29.70	14.14	−10.10019983	8.150566358	7.879640305
	Steinheim an der Murr, grube Gruber, Stuttgart	3.1	−15.2	−4.8	25.9	−27.68	16.95	−7.614724082	12.84014324	12.35349665
	Steinheim an der Murr, grube Sigrist, Stuttgart	4.4	−13.3	−10.3	20.3	−25.81	11.55	−12.38590873	3.837908048	3.765364278
	Steinheim an der Murr, Stuttgart	4.3	−13.0	−10.9	19.6	−25.53	10.93	−12.94153457	2.789557417	2.765237775
	Steinheim an der Murr, Stuttgart	3.2	−12.9	−10.0	20.5	−25.44	11.80	−12.16826869	4.248549643	4.157116359
	Steinheim an der Murr, gruber Fritz, Stuttgart	3.6	−12.4	−10.1	20.5	−24.94	11.72	−12.24187607	4.109667797	4.024623078
	Steinheim an der Murr, grube Sammet, mammut shotter, Stuttgart	2.9	−12.4	−9.2	21.4	−24.89	12.60	−11.46257769	5.580042088	5.427360152
	Steinheim an der Murr, grube Bauer, antiquus schoter, Stuttgart	3.0	−12.2	−6.2	24.5	−24.70	15.58	−8.824583881	10.5573889	10.17574901
Coelodonta antiquitatis	Steinheim an der Murr, grube Müller, Stuttgart	4.33	−12.46	−9.16	21.42	−24.96	12.65	−11.33484174	5.821053312	5.657284859
	Steinheim an der Murr, grube Sammet, Stuttgart	5.15	−12.31	−7.98	22.63	−24.81	13.82	−10.08887213	8.171939384	7.900030172
	Steinheim an der Murr, grube Fritz and Kucher, Stuttgart	5.65	−11.92	−10.10	20.45	−24.42	11.71	−12.32933714	3.944646901	3.867193144
	Steinheim an der Murr, Stuttgart	5.46	−11.91	−7.68	22.94	−24.41	14.12	−9.770362578	8.772900796	8.473347359
	Steinheim an der Murr, grube Sammet, Stuttgart	4.28	−11.71	−7.68	22.94	−24.21	14.12	−9.765479337	8.782114458	8.482137193
	Steinheim an der Murr, grube Bauer, Stuttgart	2.51	−11.62	−10.53	20.01	−24.12	11.28	−12.78446251	3.085919798	3.047967487
Dama dama	Steinheim an der Murr, Stuttgart	3.3	−17.0	−4.9	25.8	−29.46	16.85	−7.698757621	12.68158939	12.20223628
	Steinheim an der Murr, gruber Fritz, Stuttgart	3.4	−15.2	−7.4	23.2	−27.68	14.39	−9.876385519	8.572857512	8.282506067
	Steinheim an der Murr, gruber Fritz, Stuttgart	3.6	−14.9	−8.5	22.1	−27.36	13.34	−10.80251978	6.82543438	6.615464399
	Steinheim an der Murr, grube Gruber,Stuttgart	3.7	−14.3	−7.3	23.3	−26.77	14.50	−9.778357743	8.757815579	8.458956062

Taxon	Location									
Equus ferus	Steinheim an der Murr, grube Bauer, Stuttgart	4.2	−14.2	−8.9	21.7	−26.72	12.88	−13.68979782	1.377739967	1.418363929
	Steinheim an der Murr, grube Sammet, Stuttgart	5.04	−13.56	−7.91	22.71	−26.06	13.89	−12.26849165	4.059449711	3.976715025
	Steinheim an der Murr, grube Sammet, Stuttgart	3.33	−13.43	−6.91	23.74	−25.93	14.89	−10.86033701	6.716345273	6.51139339
	Steinheim an der Murr, grube Sammet, Stuttgart	4.46	−13.33	−9.39	21.18	−25.83	12.42	−14.34124765	0.148589333	0.245754223
	Steinheim an der Murr, grube Sammet, Stuttgart	2.99	−13.29	−8.94	21.64	−25.79	12.86	−13.71207714	1.335703501	1.37826114
	Steinheim an der Murr, grube Sammet, Stuttgart	4.15	−13.03	−9.31	21.26	−25.53	12.49	−14.23793512	0.343518642	0.431716785
	Steinheim an der Murr, grube Sammet, Stuttgart	4.64	−12.53	−8.97	21.62	−25.03	12.84	−13.75084593	1.262554857	1.308477333
	Steinheim an der Murr, grube Sammet, Stuttgart	3.58	−12.45	−7.97	22.64	−24.95	13.83	−12.3522818	3.90135509	3.825892756
Equus ferus 32803.49 average	Steinheim an der Murr, grube Sammet, Stuttgart	4.2	−13.6	−7.6	23.0	−26.10	14.17	−11.86772811	4.815607344	4.698089406
Equus ferus 32803.67 avergae	Steinheim an der Murr, grube Sammet, Stuttgart	3.8	−12.8	−8.3	22.3	−25.30	13.50	−12.82030346	3.018295352	2.983453766
Equus hydruntinus	Steinheim an der Murr, grube Sammet, Stuttgart	4.6	−12.7	−7.9	22.7	−25.16	13.89	−12.26624991	4.063679421	3.980750168
	Steinheim an der Murr, grube Sigrist, Stuttgart	3.5	−12.3	−7.0	23.7	−24.84	14.81	−10.97661423	6.49695429	6.302094392
	Steinheim an der Murr, grube Gruber, Stuttgart	5.2	−12.2	−7.4	23.3	−24.70	14.43	−11.50152218	5.506561923	5.357260074
	Steinheim an der Murr, grube Fritz and Kucher, Stuttgart	3.8	−12.0	−9.1	21.5	−24.49	12.72	−13.91739832	0.948305058	1.008683026
Equus sp. *(ferus)*	Steinheim an der Murr, Stuttgart	5.3	−13.8	−7.4	23.2	−26.30	14.36	−11.61078456	5.300406483	5.160587785
	Steinheim an der Murr, grube Sigrist, Stuttgart	4.4	−12.7	−7.2	23.4	−25.17	14.56	−11.32997925	5.830227838	5.666037357
	Steinheim an der Murr, grube Gruber,Stuttgart grube Sigrist, Stuttgart	5.4	−12.5	−7.5	23.2	−25.00	14.34	−11.63298911	5.258511118	5.120619607
Equus sp. *(ferus) germanicus*	Steinheim an der Murr, grube Fritz, Stuttgart	4.8	−13.1	−7.3	23.3	−25.58	14.50	−11.4060235	5.686748115	5.529157701
Mammuthus primigenius fraasi	Steinheim an der Murr, Stuttgart	6.60	−13.10	−10.05	20.50	−25.60	11.75	−12.28295296	4.032164222	3.950684667
	Steinheim an der Murr, Stuttgart	8.03	−13.04	−9.14	21.43	−25.54	12.66	−11.31864195	5.851618955	5.686444483
	Steinheim an der Murr, Stuttgart	4.71	−12.97	−8.10	22.51	−25.47	13.70	−10.21015362	7.943106373	7.68172348
	Steinheim an der Murr, Stuttgart	6.74	−12.75	−8.61	21.99	−25.25	13.20	−10.74739861	6.929436592	6.714682509
	Steinheim an der Murr, Stuttgart	8.04	−12.56	−9.50	21.07	−25.06	12.31	−11.69182307	5.147503646	5.014718478
Megaloceros giganteus	Steinheim an der Murr, grube Fritz, Stuttgart	2.9	−16.2	−8.2	22.4	−28.70	13.58	−10.58895775	7.228381606	6.999876053
	Steinheim an der Murr, Stuttgart	4.76	−15.07	−2.90	27.87	−27.57	18.88	−5.899960694	16.07554586	15.44007075
	Steinheim an der Murr, grube Bauer, Stuttgart	3.3	−14.9	−2.1	28.7	−27.39	19.66	−5.213679684	17.37041569	16.67537657
	Steinheim an der Murr, Stuttgart	4.51	−12.84	−9.39	21.18	−25.34	12.41	−11.62652897	5.270700054	5.132247851
	Steinheim an der Murr, Stuttgart	3.97	−12.83	−8.80	21.79	−25.33	13.00	−11.10502544	6.254668984	6.070954211
	Steinheim an der Murr, grube Müller, Stuttgart	4.22	−12.68	−6.71	23.94	−25.18	15.08	−9.263616414	9.729025634	9.385490454
Palaeoloxodon antiquus	Steinheim an der Murr, Stuttgart	5.99	−13.22	−10.06	20.49	−25.72	11.75	−12.28449439	4.029255861	3.947910091
Palaeoloxodon antiquus	Steinheim an der Murr, Stuttgart	4.53	−13.13	−8.93	21.66	−25.63	12.88	−11.08754126	6.287658007	6.102425739
	Steinheim an der Murr, Stuttgart	8.20	−13.03	−9.49	21.08	−25.53	12.32	−11.68407758	5.162117772	5.028660354
	Steinheim an der Murr, Stuttgart	6.75	−12.89	−8.69	21.91	−25.39	13.12	−10.83217579	6.769479637	6.562083574
	Steinheim an der Murr, Stuttgart	8.98	−12.58	−9.16	21.42	−25.08	12.64	−11.33698208	5.817014947	5.65343226
Stephanorhinus cf. *hemitoechus*	Steinheim an der Murr, grube Sigrist, Stuttgart	4.9	−15.2	−7.4	23.2	−27.67	14.37	−9.503527289	9.276363605	8.953650879
	Steinheim an der Murr, grube Sigrist, Stuttgart	4.1	−11.9	−8.3	22.3	−24.38	13.49	−10.43394118	7.520865689	7.278905867
	Steinheim an der Murr, grube Fritz, Stuttgart	2.74	−14.98	−7.51	23.12	−27.48	14.29	−9.5883338	9.11635132	8.800999159
Stephanorhinus kirchbergensis	Steinheim an der Murr, Stuttgart	5.18	−14.24	−7.08	23.56	−26.74	14.72	−9.130922316	9.979391857	9.624339832
	Steinheim an der Murr, Stuttgart	3.78	−13.60	−8.35	22.26	−26.10	13.46	−10.47214529	7.448782473	7.21013848
	Steinheim an der Murr, Stuttgart	2.72	−13.22	−8.13	22.47	−25.72	13.67	−10.24871155	7.870355574	7.612319217
	Steinheim an der Murr, Stuttgart	2.15	−13.16	−8.32	22.28	−25.66	13.48	−10.44635418	7.497444947	7.256562479
	Steinheim an der Murr, Stuttgart	1.93	−13.05	−7.87	22.74	−25.55	13.93	−9.971640566	8.393131008	8.111046982
	Steinheim an der Murr, Stuttgart	2.77	−13.04	−8.99	21.59	−25.54	12.81	−11.15854535	6.153688023	5.974618374
Stephanorhinus sp. *(kircbergensis/hemitoechus)*	Steinheim an der Murr, grube Bauer, Stuttgart	2.5	−12.9	−8.9	21.7	−25.44	12.94	−11.02407709	6.407401714	6.216661235

Table 2 (*continued*)

Taxon	Site	CO_3 (%$CaCO_3$)	$\delta^{13}C$ carb (‰ VPDB)	$\delta^{18}O$ (‰ VPDB)	$\delta^{18}O$ (‰ SMOW)	Ecosystem	dOph (after Lecyuer et al., 2010)	Owat (after Lecyuer et al., 2010)	Temperature (after Skrzipek et al., 2011), northern areas	Temperature (after Skrzipek et al., 2011), central Europe
Coelodonta antiquitatis	Vogelherdhöhle, Stuttgart	3.66	−11.12	−9.72	20.84	−23.62	12.08	−11.93363893	4.691247299	4.579449923
	Vogelherdhöhle, Stuttgart	2.67	−10.99	−9.03	21.55	−23.49	12.77	−11.20225983	6.071207864	5.895932302
Equus caballus	Vogelherdhöhle, Stuttgart	4.45	−12.17	−9.49	21.08	−24.67	12.32	−14.48580873	−0.124167413	−0.014455712
Mammuthus primigenius	Vogelherdhöhle, Stuttgart	5.09	−12.23	−10.79	19.73	−24.73	11.02	−13.0652156	2.55619698	2.542611919
	Vogelherdhöhle, Stuttgart	2.74	−11.72	−11.45	19.06	−24.22	10.37	−13.75722236	1.250523842	1.296999745

In brachydont and mesodont or low- and medium-crowned teeth, respectively, we sampled the lower part of the tooth close to the bottom of approximately 0.5−1 cm length. In a high-crowned herbivore, for example, a tooth can represent up to 1.5 years of growth or more, with different portions of the crown representing different seasons. Because incremental lines in hypsodont or high-crowned ungulates' teeth (bovids, equids) are difficult to determine, we sampled the longer portion of the tooth also closer to the bottom, however, we could not sample more than 1 cm. In horses, the average growth rate ranges between 3 and 4 vertical cm/year, and, thus, one year of growth sample should be collected from approximately 3−4 vertical cm (Hoppe et al., 2004). Nevertheless, we sampled the whole length of teeth in two horses from Steinheim (specimens Horse 32803.49 and Horse 32803.67) for the reference of the whole year growth period and possible seasonal changes by drilling horizontal lines on a tooth.

Enamel samples were either mechanically separated and ground to a finer condition in an agate mortar or drilled with a diamond-impregnated rotary tool. The uppermost surface of the tooth was removed before sampling usually by drilling with a dremel© borer. Samples of approximately 20 mg were analysed. Both fossil and modern samples of the enamel powders were pre-treated following the method described by Bocherens et al. (1996), but using the Continuous Flow (CF) for collecting carbon dioxide (Jacques et al., 2008; Bocherens et al., 2009). Some authors have reported possible side effects or insufficient efficiency of pretreatment protocols used for carbonate in tooth enamel (e.g. Zazzo et al., 2004; Chenery et al., 2012). These works deal with more extreme conditions and/or fossil material preserved in different taphonomic context. Our experience with fossil material from limestone cave has shown that the pretreatment used here is strong enough to remove exogenous carbonates, but we are aware of possible slight changes of the oxygen isotopic composition of tooth enamel carbonate. Enamel powders for carbon and oxygen isotope analyses of structural carbonate within biogenic apatite were first reacted with 2.5% sodium hypochlorite (NaOCl) for 24 h at 20 °C to oxidise organic residues, and rinsed with distilled water. This procedure was repeated twice. Then the remaining powder was treated with 0.1 M buffer acetic acid−calcium acetate (pH = 4.75) for 24 h at 20 °C to remove exogenous carbonate (Bocherens et al., 1996; Koch et al., 1997; Ecker et al., 2013), and finally washed with distilled water and dried at 45 °C. Then the treated powders were reacted with 100% phosphoric (=orthophosphoric) acid H_3PO_4 at 70 °C for 5 h to produce CO_2.

The carbon and oxygen isotopic ratios were measured with a Finnigan Mat 252 mass spectrometer with an attached Gasbench II at the Geochemistry Laboratory, University of Tübingen. This system is particularly well suited for fossil enamel carbonate isotopic analysis because it has an integrated chromatographic column and allows for the analysis of the gas evolved from the reaction with orthophosphoric acid 10 times instead of one as with the Multiflow system from Micromass (e.g., Tütken et al., 2007). Therefore, it removes the contaminants better and produces purer CO_2.

Isotopic ratios, expressed as the delta value, are calculated as follows: $\delta^E X = [(R \text{ sample}/R \text{ standard}) - 1] \times 1000$, where $^E X$ is $\delta^{13}C$ or $\delta^{18}O$, and R is $^{13}C/^{12}C$ or $^{18}O/^{16}O$, respectively. The standards are the marine carbonate VPDB for carbon and SMOW for oxygen. For fossil samples the analytical error is 0.1−0.2‰ for $\delta^{13}C$ and $\delta^{18}O$, based on multiple isotopic analysis of modern tooth enamel of camel and hippopotamus prepared and analysed at the same time as the fossil samples.

2.3. Statistical analysis

We used both parametric and nonparametric tests with $\alpha = 0.05$ level of significance. As ANOVA is robust enough to handle
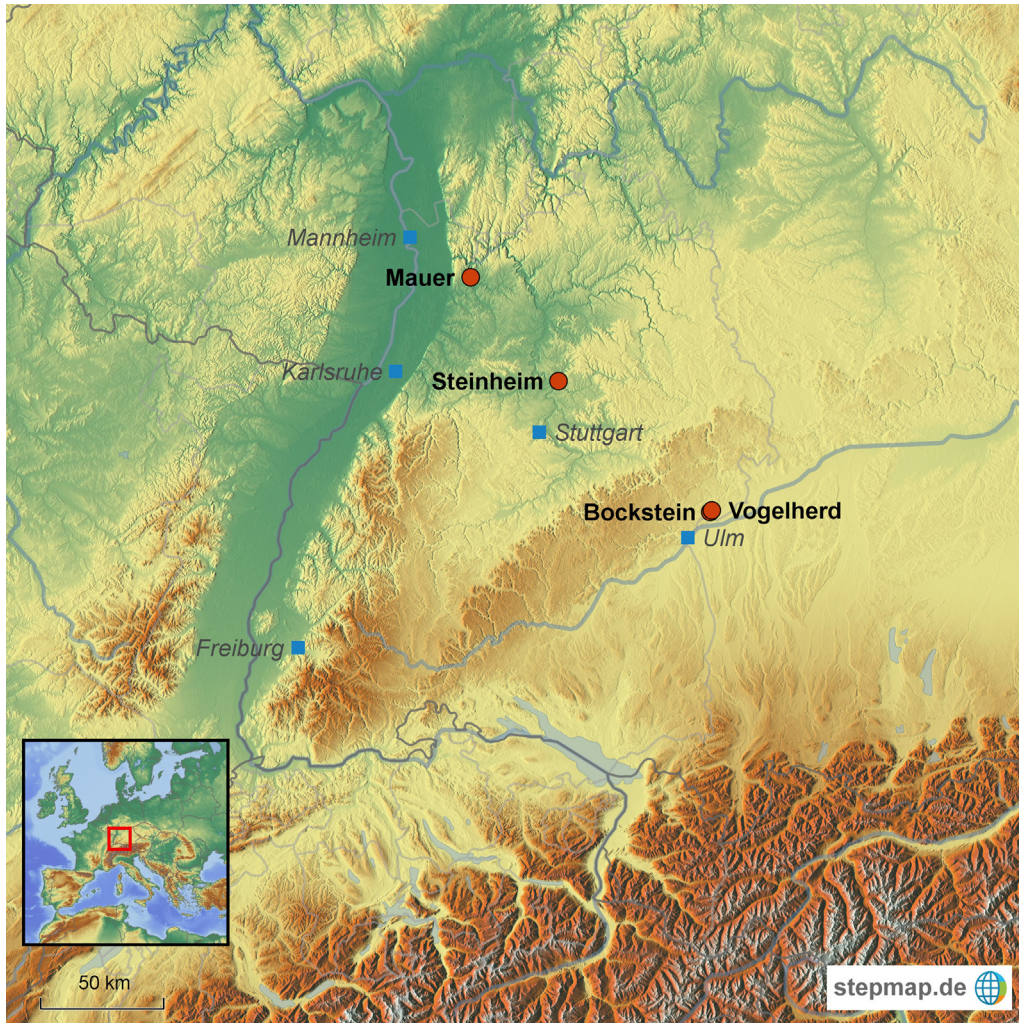
Fig. 2. Map of studied sites.

departures from normality and unequal variances, and the distribution in our samples did not significantly depart from normal to affect t-test statistics, we incorporated it to see the differences in means among the sites. To identify the sources of significant differences in these multiple comparisons, we used post hoc Tukey tests. However, we also confirmed all results using nonparametric tests of Mann–Whitney and Kruskal–Wallis (analogous to ANOVA) among species because they make no assumptions about the sample distributions (normality).

3. Results

3.1. Variation among sites (Table 3)

Carbon isotopic (δ^{13}C) ratios of carbonate tooth enamel and, thus, these of the ecosystem of the glacial caves Bockstein and Vogelherd, are significantly higher than those of the interglacial sites Steinheim and Mauer (ANOVA $F_{3,94} = 7.32$, $p < 0.001$, $r^2 = 0.19$; Kruskal–Wallis $H(3) = 26.91$, $p < 0.001$). Post hoc differences are significant between Mauer and Bockstein ($p = 0.001$), Mauer and Vogelherd ($p = 0.01$), between Steinheim and Bockstein ($p = 0.006$), and Vogelherd ($p = 0.05$). Oxygen isotope (δ^{18}O) ratios are significantly lower in the glacial caves (δ^{18}O ANOVA $F_{3,94} = 4.83$, $p = 0.004$, $r^2 = 0.133$; Kruskal–Wallis $H(3) = 16.522$, $p = 0.001$), especially δ^{18}O between Mauer and Vogelherd (post hoc $p = 0.05$), Steinheim and Bockstein ($p = 0.05$) and Steinheim and Vogelherd ($p = 0.024$). Both carbon and oxygen isotopic ratios' deviation is lower than or equal to 3‰ in the glacial caves Bockstein and Vogelherd. In Bockstein the lowest δ^{13}C were found in *M. giganteus* and *E. caballus* and the highest δ^{13}C in *C. antiquitatis* and *E. caballus*, the lowest δ^{18}O values were observed in the late mammoth and the highest δ^{18}O values in *E. caballus*. In Vogelherd, the late mammoth had the lowest δ^{13}C and δ^{18}O, and the woolly rhinoceros the highest δ^{13}C and δ^{18}O.

Table 3
Ecosystem based on carbon of species per site.

Site	Mauer	Steinheim, all	Vogelherd	Bockstein
Ecosystem based on δ^{13}C (mean and the ranges)	Woodland – shrubland −26.09 (−27.42 to −24.88)	From dense forest and woodland to shrubland, grassland and tundra: −25.56 (−29.7 to −23.07) Pit Sammet – shrubland and grassland: −24.74 (−26.10 to −23.07) Pits Fritz, Sigrist, Gruber, Müller, Bauer: −26.04 (−29.7 to −24.12) Unidentified Steinheim pits: −25.79 (−29.46 to −24.41)	Open tundra – grassland −24.15 (−24.73 to −23.49)	Open tundra – grassland −24.16 (−24.45 to −23.88)

Within identified Steinheim pits, all isotopic signatures of the species from the pit Sammet represented the most open landscape and a rather cold environment with little variation in $\delta^{13}C$ and $\delta^{18}O$ (less than 3‰). The species' isotopic signatures from the pits Fritz, Bauer, Sigrist, Gruber and Müller as well as from other unidentified Steinheim pits demonstrated similar more closed environments and much greater variation in both $\delta^{13}C$ and $\delta^{18}O$ than in Sammet, and probably represented more temperate and rather forested habitats. In the Steinheim sites, the lowest $\delta^{13}C$ and $\delta^{18}O$ values were found in *Cervus elaphus* and the highest $\delta^{13}C$ in *Bison/Bos*, and the highest $\delta^{18}O$ in *M. giganteus*. In Mauer, the lowest $\delta^{13}C$ were shown by *Stephanorhinus etruscus/hundsheimensis*, and the highest by *P. antiquus*, and the lowest $\delta^{18}O$ were shown by *P. antiquus*, and the highest by *Equus mosbachensis*.

3.2. Variation within and among species

Given the background dissimilarity of the cold and warm localities from warm and cold periods, it is clear that overall $\delta^{13}C$ and ecosystem, as well as $\delta^{18}O$ differed significantly among species ($\delta^{13}C$ Kruskal−Wallis $H(11) = 57.13$, $p < 0.001$; ANOVA $F_{11,86} = 9.56$, $p < 0.001$, $r^2 = 0.5 \times 5$; $\delta^{18}O$ Kruskal−Wallis $H(11) = 28.06$, $p = 0.003$; ANOVA $F_{11,86} = 3.07$, $p = 0.001$, $r^2 = 0.28$). Within the most variable Steinheim locality, due to the mixture of specimens from glacial and interglacial layers, both isotope ratios are significantly different among the species ($\delta^{13}C$ Kruskal−Wallis $H(10) = 42.94$, $p < 0.001$, $\delta^{18}O$ $H(10) = 17.52$, $p = 0.064$; $\delta13C$ ANOVA $F_{10,59} = 7.63$, $p < 0.001$, $r^2 = 0.56$; $\delta^{18}O$ ANOVA $F_{10,59} = 2.07$, $p = 0.041$, $r^2 = 0.26$). Below, we discuss $\delta^{13}C$ and $\delta^{18}O$ in each family, comparing the species among the sites and to other species (Figs. 3 and 4; Table 2).

3.3. Proboscideans: P. antiquus, M. primigenius, M. p. fraasi

The early mammoth *M. p. fraasi* from Steinheim showed significantly lower $\delta^{13}C$ (Mann−Whitney $U = 0.000$, $p = 0.025$, Chi-square approximation $\chi^2(1) = 5$), and significantly higher $\delta^{18}O$ (Mann−Whitney $U = 15$, $p = 0.025$, $\chi^2(1) = 5$) than the late mammoth from Vogelherd and Bockstein glacial caves. Unexpectedly, *P. antiquus* and *M. p. fraasi* had similar carbon and oxygen isotopic signatures, indicating similar ecosystems and temperatures or/and drinking regime and place preferences, at both sites Mauer and Steinheim. The late mammoth *Mammuthus primigenius primigenius* had the lowest of all species $\delta^{18}O$ values in both glacial caves (Kruskal−Wallis $H(3) = 7.697$, $p = 0.053$).

3.4. Rhinoceroses: C. antiquitatis, S. kirchbergensis, S. hemitoechus, S. etruscus/hundsheimensis

C. antiquitatis demonstrated lower $\delta^{13}C$ values in Steinheim than in the glacial caves (Mann−Whitney $U = 0.000$, $p = 0.046$, Chi-square approximation $\chi^2(1) = 4$). In Vogelherd, the woolly rhinoceros had higher $\delta^{13}C$ than in Bockstein (Mann−Whitney $U = 0.0$, $p = 0.083$, Chi-square approximation $\chi^2(1) = 3$). In Steinheim, the woolly rhinoceros had significantly higher $\delta^{13}C$ than the narrow-nosed *S. hemitoechus* (Mann−Whitney $U = 20$, $p = 0.088$, Chi-square approximation $\chi^2(1) = 2.91$), and Merck's rhino *S. kirchbergensis* (Mann−Whitney $U = 0.000$, $p = 0.004$, Chi-square approximation $\chi^2(1) = 8.31$). *S. hemitoechus* showed wider ranges in $\delta^{13}C$ than both *S. kirchbergensis* and *Coelodonta* ($\delta^{13}C$ among rhinoceroses Kruskal−Wallis $H(2) = 8.059$, $p = 0.018$), with two individuals with values lower than *S. kirchbergensis* and two with values similar to *Coelodonta*.

C. antiquitatis demonstrated wider $\delta^{18}O$ variation (both lower and higher) in Steinheim than in Vogelherd and Bockstein, and

slightly wider $\delta^{18}O$ ranges than *S. kirchbergensis* and *S. hemitoechus*, because of the 2 individuals with higher $\delta^{18}O$ in the warmer range, but generally not significantly lower $\delta^{18}O$ ranges. In the glacial caves, the woolly rhinoceros had significantly lower $\delta^{18}O$ than Steinheim than *S. kirchbergensis* and *S. hemitoechus*, although *Coelodonta's* M1 was sampled and should produce higher $\delta^{18}O$ than in M3 of the Merck's rhino.

Compared to other species, the woolly rhino from both Vogelherd and Bockstein exhibited the highest $\delta^{13}C$ values (Kruskal−Wallis $H(2) = 6.727$, $p = 0.035$), significantly higher $\delta^{13}C$ values than the late mammoth (Mann−Whitney $U = 0.0$, $p = 0.006$, Chi-square approximation $\chi^2(1) = 7.5$), than the early mammoth and forest elephant in Steinheim (Kruskal−Wallis $H(2) = 10.8$, $p = 0.005$), and $\delta^{18}O$ values significantly higher than the late mammoth (Mann−Whitney $U = 0.0$, $p = 0.025$, $\chi^2(1) = 5$), but not different from *Mammuthus* or *Palaeoloxodon* in Steinheim, only wider $\delta^{18}O$ ranges than the early mammoth. However, taking into account that *Coelodonta* M1 was sampled, compared to M3 in Proboscidae, $\delta^{18}O$ values can be significantly different from *Mammuthus* or *Palaeoloxodon* in Steinheim and not from the late mammoth, because M1 produces higher $\delta^{18}O$ than M3.

3.5. Equids: Equus ferus, E. hydruntinus, E. mosbachensis

E. ferus demonstrated a significant variation in $\delta^{13}C$ from the highest values in Bockstein and Vogelherd to the lowest in Steinheim (Kruskal−Wallis $H(3) = 11.366$, $p = 0.010$ or Mann−Whitney $U = 0.000$, $p = 0.003$, $\chi^2(1) = 8.842$), and lower $\delta^{18}O$ in Bockstein and Vogelherd compared to Steinheim (Mann−Whitney $U = 49.000$, $p = 0.026$, $\chi^2(1) = 4.974$). Both Steinheim horses evaluated for seasonal changes demonstrated variation of less than 1‰ in $\delta^{13}C$ (from -13.9‰ to -13.3‰ for Horse 1, and from -13‰ to -12.4‰ for Horse 2), and in $\delta^{18}O$ less than 2 and 3‰ (respectively, -8.4 to -6.6‰ and -9.5 to -6.8‰). Both of the horses showed lower carbon isotopic values at the tip of the teeth or earlier in life than at the bottom of the teeth. In oxygen isotopic values, they demonstrated diverse values at the tip of the teeth or during the early life stage than at the bottom, where the values were quite similar. Other horse species had $\delta^{13}C$ variation less than 1.5‰, and $\delta^{18}O$ less than 2‰ and less than 3‰ in *E. mosbachensis* from Mauer. *E. mosbachensis* was similar to *E. ferus* from Steinheim, and together had significantly lower $\delta^{13}C$ (Kruskal−Wallis $H(3) = 26.91$, $p < 0.001$), and higher $\delta^{18}O$ values (Kruskal−Wallis $H(3) = 16.48$, $p = 0.001$) than *E. caballus* from Bockstein and Vogelherd. In Steinheim, *E. ferus* had significantly lower $\delta^{13}C$ values than *E. hydruntinus* (Mann−Whitney $U = 3$, $p = 0.008$, Chi-square approximation $\chi^2(1) = 7.049$), which might be ambiguous, since horse M1 and M2 can produce slightly ^{13}C depleted values compared to donkey's P3 and P4. The horse $\delta^{18}O$ were not different from the donkey in Steinheim, which probably will hold true even with the offset and horse's M1 and M2 elevated $\delta^{18}O$ values compared to donkey's P3 and P4.

Overall, compared in all sites, the horses demonstrated higher $\delta^{18}O$ than the mammoths and straight-tusked elephants (Kruskal−Wallis $H(2) = 8.28$, $p = 0.016$; only mammoths (Mann−Whitney $U = 33.000$, $p = 0.008$, Chi-square approximation $\chi^2(1) = 7.094$)). In both Bockstein and Vogelherd, there was no significant difference between the horse and other species in $\delta^{13}C$ but a variation in $\delta^{18}O$ from the lowest in the late mammoth and the highest in the horse and giant deer (Kruskal−Wallis $H(3) = 7.697$, $p = 0.053$; horses – late mammoth difference in $\delta^{18}O$ (Mann−Whitney $U = 0.000$, $p = 0.025$, Chi-square approximation $\chi^2(1) = 5$)). One P3 horse sample value occurred in the midst of M1−M2 $\delta^{13}C$ values, which was also higher than the late mammoth M3.

In Steinheim, horses showed wider and slightly lower δ^{13}C ranges and significantly higher δ^{18}O than *C. antiquitatis*, *Palaeoloxodon* and *Mammuthus* (Kruskal−Wallis $H(2) = 7.353$, $p = 0.025$), only elephant (Mann−Whitney $U = 11$, $p = 0.026$, Chi-square approximation $\chi^2(1) = 4.937$), only mammoth (Mann−Whitney $U = 13$, $p = 0.042$, $\chi^2(1) = 4.149$). The proboscidean results, however, might not indicate significant differences after considering possible ^{18}O enrichment in M1−M2.

3.6. Bovids: Bison/Bos

Bovids were only present in Steinheim as unidentified genus *Bison/Bos*, and we compare them to the rest of the species. In Steinheim and compared to all localities, bovids demonstrated the highest significantly δ^{13}C values, opposite to the lowest values observed in cervids (the red deer *C. elaphus*, fallow deer *D. dama*, giant deer *M. giganteus*) (Kruskal−Wallis $H(3) = 17.2$, $p = 0.001$; Mann−Whitney $U = 1.000$, $p = 0.002$, Chi-square approximation $\chi^2(1) = 9.763$), higher δ^{13}C than *Cervus* (Mann−Whitney $U = 0.0$, $p = 0.001$, Chi-square approximation $\chi^2(1) = 11.294$), higher δ^{13}C and lower δ^{18}O than *Dama* (δ^{13}C Mann−Whitney $U = 0.000$, $p = 0.007$, Chi-square approximation $\chi^2(1) = 7.385$; δ^{18}O Mann−Whitney $U = 29.000$, $p = 0.027$, Chi-square approximation $\chi^2(1) = 4.875$). Overall, differences among bovids and cervids in δ^{18}O appeared nonsignificant.

Bovids showed significantly higher δ^{13}C values than all rhinos δ^{13}C (Kruskal−Wallis $H(3) = 17.1$, $p = 0.001$), higher than *Coelodonta* (Mann−Whitney $U = 5$, $p = 0.014$, $\chi^2(1) = 6.017$), *S. kirchbergensis* (Mann−Whitney $U = 0.000$, $p = 0.002$, $\chi^2(1) = 9.6$) even with the M1−M3 offset, *S. hemitoechus* (Mann−Whitney $U = 1$, $p = 0.011$, $\chi^2(1) = 6.49$). δ^{18}O was not significantly different between bovids and the woolly rhino. Bovids demonstrated nonsignificantly lower δ^{18}O than both warm-adapted *S. kirchbergensis* and *S. hemitoechus*, which can be significant, considering ^{18}O enrichment in M1 bovid teeth in comparison with Merck's rhinos M3.

Bovids had significantly higher δ^{13}C values than both *E. hydruntinus* and *E. ferus* (Kruskal−Wallis $H(2) = 19.21$, $p < 0.001$), only *E. hydruntinus* (Mann−Whitney $U = 1.0$, $p = 0.011$, Chi-square approximation $\chi^2(1) = 6.49$), only *E. ferus* (Mann−Whitney $U = 0.0$, $p < 0.001$, Chi-square approximation $\chi^2(1) = 14.61$) but not different in δ^{18}O.

3.7. Cervids: M. giganteus, C. elaphus, D. dama

The red deer *C. elaphus* and the fallow deer *D. dama* were only present in Steinheim, and the giant deer was also present in Bockstein. As mentioned in the Section 3.6, in Steinheim the giant deer demonstrated the lowest δ^{13}C values of all species. The red deer demonstrated the widest ranges in δ^{13}C and δ^{18}O of all other species, even considering possible M1−M3 offset.

M. giganteus in Bockstein had the lowest of all species δ^{13}C and lower δ^{13}C than in Steinheim. Steinheim giant deer showed much lower δ^{13}C values (also in M3) than *Palaeoloxodon*'s (Wilcoxon test $Z = 2.934$, $p = 0.003$) and the early mammoth, and much wider in ranges than both proboscideans.

Overall, *Megaloceros* showed significantly higher δ^{18}O values than *Paleoloxodon* (ANOVA post hocs δ^{18}O $p = 0.028$), *Mammuthus* (δ^{18}O $p = 0.001$), and *Coelodonta* (δ^{18}O $p = 0.015$), and significantly higher than *Palaeoloxodon* in Steinheim (δ^{18}O Mann−Whitney $U = 4$, $p = 0.045$, Chi-square approximation $\chi^2(1) = 4.033$) but these results may be insignificant, considering the offset between M3 of proboscideans and ^{18}O enriched M1/M2 of the giant deer.

The giant deer did not differ in δ^{13}C and δ^{18}O from horses, *S. kirchbergensis* and *S. hemitoechus*, except for the two giant deer individuals with very low δ^{13}C and high δ^{18}O, and showed similar δ^{13}C values to *C. elaphus*, except for two samples with very low δ^{13}C (Mann−Whitney $U = 56.0$, $p = 0.003$, Chi-square approximation $\chi^2(1) = 8.842$).

The fallow deer showed slightly lower δ^{13}C and higher δ^{18}O than *C. elaphus*, and quite similar to *Megaloceros*, *S. kirchbergensis*, *S. hemitoechus*. Overall, the fallow deer had lower δ^{13}C and higher δ^{18}O than the early mammoth (δ^{13}C ANOVA post hocs $p = 0.045$, $p = 0.054$; Mann−Whitney $U = 20$, $p = 0.014$, Chi-square approximation $\chi^2(1) = 6$); (δ^{18}O ANOVA post hocs $p < 0.001$; Mann−Whitney $U = 1$, $p = 0.027$, Chi-square approximation $\chi^2(1) = 4.86$).

D. dama had significantly lower δ^{13}C than both *E. ferus* and *E. hydruntinus* (Kruskal−Wallis $H(2) = 14.16$, $p = 0.001$), and significantly lower than the horse alone in Steinheim (Mann−Whitney $U = 56$, $p = 0.003$, Chi-square approximation $\chi^2(1) = 8.842$) and the donkey (Mann−Whitney $U = 0.0$, $p = 0.021$, Chi-square approximation $\chi^2(1) = 5.333$). Differences in δ^{18}O were not significantly different between the fallow deer and the horse.

4. Discussion

4.1. Locality differences

Clear environmental, temperature and habitat differences were indicated among the 4 sites, with Mauer representing the warmest and most densely wooded habitat or woodland, whereas Vogelherd and Bockstein represent the coldest and most open landscape or steppe and steppe-tundra, with the highest δ^{13}C and lowest δ^{18}O. Steinheim, the site with interglacial and glacial components or deposits mixed, demonstrated the greatest temperature and habitat variation, suggesting that its environments were most distinct. Based on the sedimentology, Steinheim is suggested to belong to the Rissian (Saalian) glacial period, succeeding the Holsteinian interglacial sands/gravels (Bloos, 1994) (Fig. 1). The majority of large mammal spectrum of Steinheim species derives from Sammet and indicates the steppe environment by species status, "Steppenelefanten-Kiese", corresponding to a glacial phase. However, the interglacial species, which supposedly also belong to the preceding Holsteinian interglacial, are present in Steinheim as well. The water buffalo *B. murrensis* and *B. primigenius* were both discovered in Steinheim for the first time in central Europe, suggesting a strong maritime effect, mild winters and warm temperature (Von Koenigswald, 2007). We have not analysed all Steinheim species, but isotopic results of the fossils collected from several identified pits belong to ecologically different habitats that existed either during the Holsteinian interglacial or Saalian interstadials. For example, the pit Sammet with its majority of species quite uniformly represented the most open and coldest habitat in Steinheim as has been previously suggested, with δ^{13}C values very close to those of the glacial caves. However, the other pits (Fritz, Baur, Sigrist, Gruber, and Muller) demonstrated more closed forested environments than Sammet, with variations in water or temperature, suggesting a more closed-canopy or humid (or aquatic) habitats, as well as both colder and much warmer habitats than Sammet. Even considering the mixed nature of Steinheim, the isotopic variation in the identified pits suggested more variation in temperate environments.

It is possible that the "forest" temperate fauna lived alongside the cold-adapted species. Mammals could have also been migrating from nearby territories, similar to Siberia today with discontinuous permafrost and boreal forest situated on the borderline. The Holsteinian was longer and warmer than the Eemian interglacial, and the temperate fauna could have spread further northward to coexist with cold-adapted species that could have also had more ecological flexibility, persisting further southward of their original habitat (Pushkina, 2007).
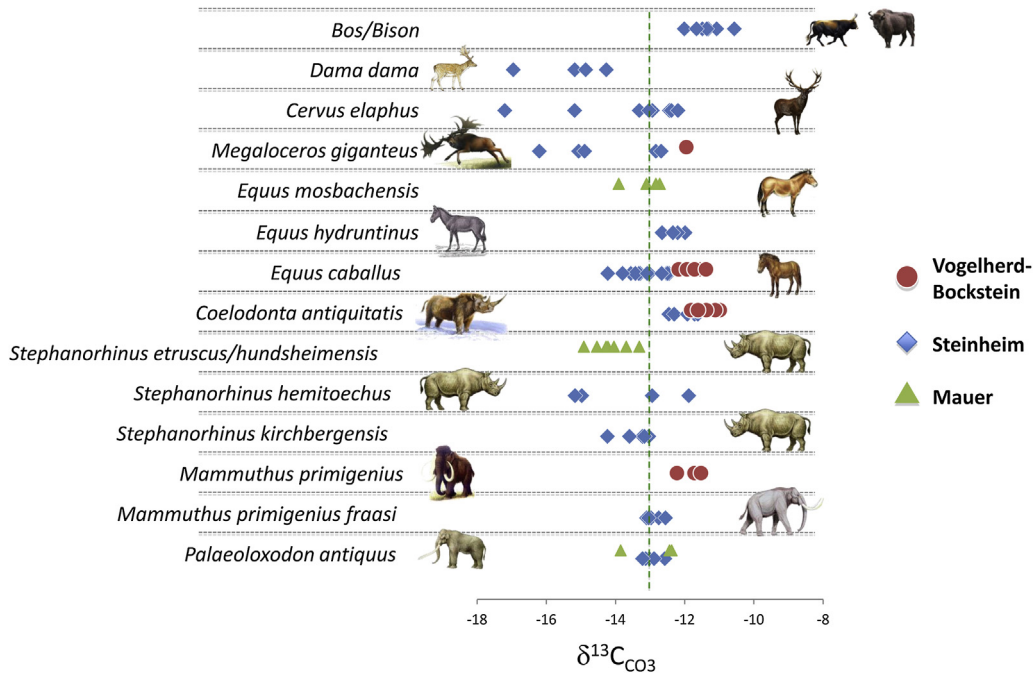
Fig. 3. δ^{13}C values of the studied species.

4.2. Species ecological flexibility

Remarkably, the early mammoth *M. p. fraasi* and *P. antiquus* shared similar habitats in temperature and openness, shrubland, suggested by the Steinheim data, which were not as open and cold as for the late woolly mammoth, highly specialized for grazing in cold habitats. Similarity between the early *Mammuthus* and *Palaoloxodon* in Europe has also been observed in microwear teeth patterns (Rivals et al., 2012). *M. p. fraasi* is considered the early *M. primigenius* or late *M. trogontherii*, with a lesser number of and wider spaced enamel plates (Lister and Sher, 2001), more similar to the forest elephant than to the late mammoth. *Palaeoloxodon* from Mauer appeared similar in temperature and ecosystem preferences to the one from Steinheim. In contrast, the late *M. p. primigenius* from Vogelherd and Bockstein evolved to occupy the coldest and more open environments, known as the mammoth steppe.

C. antiquitatis, on the other hand, appeared to have occupied more open territories than the late woolly mammoth and the early mammoth, even considering a possible M1-M3 offset, showing an ecological specialization to open habitats already in the early forms.
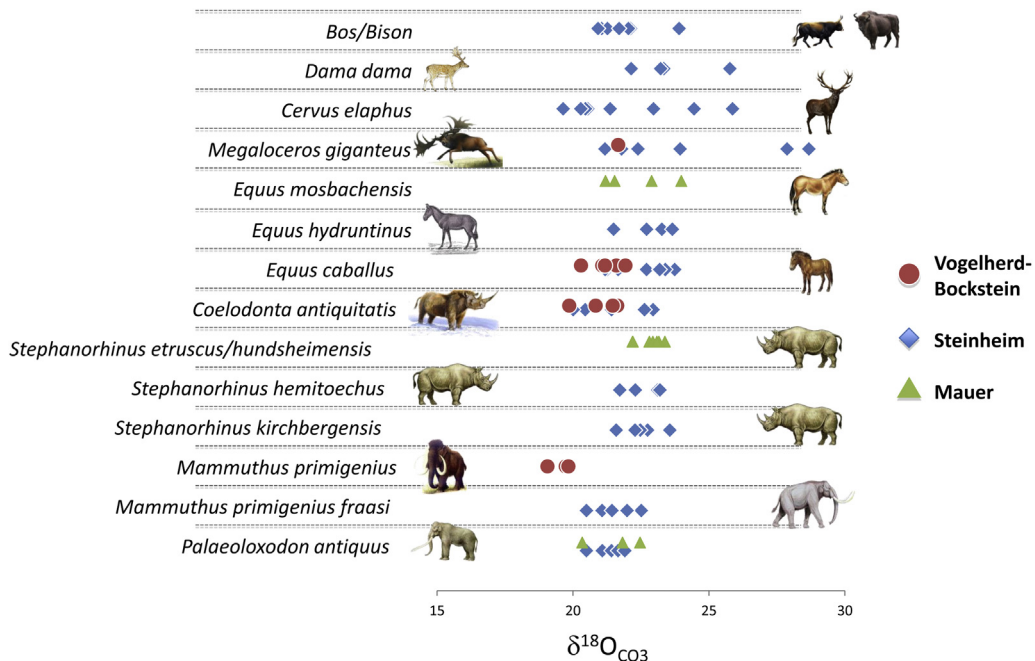

Fig. 4. δ^{18}O values of the studied species.

It appeared in grasslands in Steinheim and Bockstein, and even tundra in Vogelherd (very high δ^{13}C and low δ^{18}O). *Coelodonta* appeared to have persisted in slightly wider δ^{18}O ranges than the early woolly mammoth and in wider temperature conditions in Steinheim compared to Vogelherd and Bockstein, although always in open conditions and never in closed-canopy forest. Interestingly, it was suggested that the woolly rhinoceros along with several Siberian species of beetles and plants never crossed the Bering bridge to Northern America because of the existence of a biological filter between the continents (Elias and Crocker, 2008), whereas some American species were not able to conquer Eurasian territories. It is possible that a combination of colder harsher conditions and the loss of flexibility in enduring a wider range of temperature conditions along with moister and more forested habitat were involved in the failure to conquer the Americas. In general, the species during the glacial periods demonstrated narrower ranges δ^{13}C and δ^{18}O than during the interglacial periods, during which more variation in habitats has been discovered.

Compared to *Coelodonta*, *S. hemitoechus* and *S. kirchbergensis* similarly appeared in a more closed habitat of shrubland and woodland, although *S. hemitoechus* appears to have been able to persist in a wider range of habitats, in woodlands as *S. kirchbergensis* and grasslands as *Coelodonta*, but apparently more sensitive to temperature. In Steinheim, *S. hemitoechus* appeared to have shared an ecological niche between *S. kirchbergensis* and *Coelodonta*, less in the forest than *S. kirchbergensis* and less in the open habitat than *Coelodonta*.

Intriguingly, bovids in Steinheim occupied more extreme, open territories than the early mammoth, horses, and even *Coelodonta*. Only later, during the middle and late Weichselian, did *Coelodonta* and the late mammoth appear in grasslands in Bockstein, similar in openness to the lowest range of the bovids already in Steinheim. In Vogelherd, the woolly rhino is associated with tundra with high δ^{13}C and low δ^{18}O, the highest bovid ranges in δ^{13}C, and an ecosystem that existed in Steinheim.

Equids are a variable group because of the existence of many variants of horses that partially were different species or subspecies, and, therefore, probably could have endured different ecological and climatic variations. In our study, horses also seemed ecologically diverse, but not as much as the red deer. In Bockstein and Steinheim, the horses appeared in less open environments than the grassland and tundra of *Coelodonta*, and in Steinheim and Mauer also in apparently more humid habitats with denser vegetation, sharing woodland and shrubland habitat with *S. kirchbergensis* and possibly, *S. hemitoechus*. The concept of woodland as horse habitat is also consistent with the studies by Van Asperen (2010) on the late Middle Pleistocene horses from German sites (e.g. Steinheim), and our unpublished isotopic and mesowear analyses (Pushkina et al. in preparation).

We were not able to discern clear seasonal patterns from Steinheim horses 1 and 2, sampled in more detail. However, both appeared to have spent the first stages of life (and possibly been born) in more closed environments than later in "sampled" life. Oxygen isotopic signatures were different at the early stage of life for each of these horses and within similar ranges during later stage, where they could have joined groups of horses, occupying similar landscapes. The variation in δ^{18}O was higher than in δ^{13}C, suggesting that some horses must have occupied a range of ecological niches, from warmer and more temperate habitats to colder, drier and more open habitats or/and environments, reflecting different rainfall with drinking water obtained from the rivers from higher altitudes. *E. hydruntinus*, the Pleistocene donkey in Steinheim, appeared in the ecological niche between the horses in the shrubland and bovids in the grassland, similar to the woolly rhino, although slightly higher in temperature and more closed in habitat.

It must have been competition that differentiated the species along the ecosystem humidity, temperature and habitat closeness gradients that alternated during the end of Pleistocene and Holocene. Several Middle and Late Pleistocene and Early Holocene horses (tarpan, the forest horse) appeared to have had a preference to a more closed habitat than do the modern wild horse (Przewalski) and donkeys (Forsten, 1988). Bovids, on the other hand, appeared as a more grassland species during the Pleistocene than nowadays, given that two large bovid species (bison *Bison priscus* and aurochs *Bos primigenius*) were present in Steinheim. The aurochs during the Holocene was a forest species (Bunzel-Drüke, 2001). The Pleistocene bison gave rise to two species of modern bison (American and European), one of which, the American bison, has become an open prairie large herd migratory species, and another, European bison, a forest species that does not migrate much (Julien et al., 2012) and lives in small groups. A similar case could have been prevalent for the Pleistocene "forest" horses.

Cervids in our study appear to have occupied the densest environments of all species. *C. elaphus* and *D. dama* maintained their characteristics as temperate and forest species, the fallow deer having been more sensitive to cold and habitat openness compared to the red deer that demonstrated the most variation in habitat preferences. *D. dama* appears in denser forest and, possibly, warmer habitat than the early mammoth and the horse in Steinheim. The red deer appears to have occupied shrubland and woodland habitats similar to horses in Steinheim, but also deeper forests. *M. giganteus* occupied shrubland to woodland habitats and wider ranges of more forested habitat than did mammoth or forest elephant in Steinheim, although probably avoiding dense forests, and grassland in Bockstein, which is consistent with its large size and broad antlers. The giant deer appeared either in the warmest temperature ranges in Steinheim or obtained its drinking water from high canopy browsing.

The isotopic results confirm that despite having a "species status" as cold or warm-adapted and post-mortem mixture due to time averaging, the species must have coexisted to a certain extent, sharing resources, during the interglacial or interstadial periods. As climatic variability during both interglacial and glacial could have been extensive, species ecological variability can be attributed to this. Many supposedly glacial or open habitat species apparently persisted in much milder temperate and closed environments (early mammoth, woolly rhinoceros, horses, giant deer, *S. hemitoechus*). Most were glacial assemblage representatives, evolving during the Elsterian and Saalian glaciations that still could have had flexibility to endure milder conditions or were not fully adapted to or specialized for glacial conditions. Certainly, evaluations of exact teeth mineralization times and their extrapolation on ecological preferences are complex, but we demonstrated the general trends.

It appears that towards the Holocene, some evolutionary trends selected for the loss of ecological flexibility or more specialization in species, and non-analogous assemblages were less and less common. Species assemblages became more and more common or similar to the present communities. Intriguingly, the species of both more ancient interglacial and more recent glacial assemblages survived into the Holocene by tracking their habitats through space as long as possible, which has become increasingly difficult due to human-induced fragmentation and climatic changes.

5. Conclusions

This study is a good example of the direct detection of habitat independently of the estimated age and climate or species associations. We revealed important and striking individual variations in species, considered as having been adapted either to cold or warm

environments. The same species are shown to have existed during different temperature and ecosystem regimes, obtaining water from different sources. Stable isotopic differences and similarities suggested that large mammals were rather flexible in their ecological preferences or not fully specialized, especially at the beginning of the process of their origination, and must have shared resources during the Pleistocene.

Remarkable findings are: sharing of similar habitats in temperature and openness by *P. antiquus* and the early *M. p. fraasi* in Steinheim; a much more open habitat for the large bovines (*Bos* or *Bison*) compared to other glacial open environment species; the presence of the "steppe rhinoceros" *S. hemitoechus* in the forested habitat in Steinheim; the appearance of horses in slightly warmer and denser habitat than the woolly rhinoceros; the existence of the woolly mammoth and woolly rhinoceros in milder conditions and, possibly, temperate species, such as deer, in colder and drier habitats. The species showed less variation in $\delta^{13}C$ and $\delta^{18}O$ and less ecological flexibility during the glacial periods and appeared to have been more ecologically flexible at their dawn.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2013.12.033.

References

Aaris-Sørensen, K., 2009. Diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial-interglacial cycle, 115-0 kyr BP. Fossils and Strata 57, 1–59.

Alcocks, J.P.H., 1988. Veld Types of South Africa. In: Memoirs of the Botanical Survey of South Africa, vol. 57, pp. 1–146 (An update of the first edition published in 1953).

Alexeeva, L.I., 1980. Characteristics of the theriocomplex of the last interglacial period of the Russian PlainMammals of Eastern Europe during the Anthropogene. Proceedings of the Zoological Institute 93, 68–74 (in Russian).

Ancrenaz, M., Delhomme, A., 1997. Teeth eruption as a means of age determination in captive Arabian oryx, Oryx leucoryx (Bovidae, Hippotraginae). Mammalia 61 (1), 135–138.

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. Quaternary Science Reviews 29, 1263–1275.

Arppe, L., Aaris-Sыrensen, K., Daugnora, L., Lõugas, L., Wojtal, P., Zupiņ, I., 2011. The palaeoenvironmental $\delta^{13}C$ record in European woolly mammoth tooth enamel. Quaternary International 245, 285–290.

Bibi, F., Souron, A., Bocherens, H., Uno, K., Boisserie, J.R., 2013. Ecological change in the lower Omo Valley around 2.8 Ma. Biology Letters 9 (1), 20120890. http://dx.doi.org/10.1098/rsbl.2012.0890. Print 2013 Feb 23.

Bloos, G., 1994. 3.4.1.2. Flussablagerungen; 3.4.1.3. Quartäre Krustenbewegungen bei Stein-heim an der Murr; 3.4.1.5. Löß und Lößlehm (lö). In: Brunner, H. (Ed.), Geologische Karte von Baden-Württemberg. Erläuterungen zu Blatt 7021 Marbach am Neckar (Stuttgart 1994), pp. 51–101.

Bocherens, H., 2009. Neanderthal dietary habits: review of the isotopic evidence. In: Hublin, J.-J., Richards, M.P. (Eds.), The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence, Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, pp. 241–250.

Bocherens, H., 2011. Diet and ecology of Neanderthals: insights from bone and tooth biogeochemistry. In: Conard, N.J., Richter, J. (Eds.), Neanderthal Lifeways, Subsistence and Technology. In: Delson, E., MacPhee, R. (Eds.), Vertebrate Paleobiology and Paleoanthropology. Springer, Heidelberg, New York, pp. 73–85.

Bocherens, H., Rousseau, L., 2008. Le cadre environnemental des occupations humaines. Isotopes sur grands mammifères et plancher stalagmitique. In: Moncel, M.-H. (Ed.), Le site de Payre, Mémoire de la Société préhistorique française, vol. 46, pp. 113–122.

Bocherens, H., Fizet, M., Mariotti, A., Billiou, D., Bellon, G., Borel, J.-P., Simone, S., 1991. Biogéochimie isotopique (13C, 15N, 18O) et Paléoécologie des ours pléistocènes de la grotte d'Aldène (Cesseras, Hérault). Bulletin du Musée d'Anthropologie et de Préhistoire, Monaco 31, 29–49.

Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred by stable carbon and nitrogen isotopes biogeochemistry: implications for Pleistocene bears. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 213–225.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.-J., 1996. Isotopic biogeochemistry (13C, 18O) of mammal enamel from African Pleistocene hominid sites: implications for the preservation of paleoclimatic isotopic signals. Palaios 11, 306–318.

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 Scladina Cave (Belgium). Journal of Archaeological Science 26, 599–607.

Bocherens, H., Drucker, D., Billiou, D., 2005. Paléoenvironnements et Hominidés: Approches biogéochimiques. In: Tuffreau, A. (Ed.), Peuplements humains et variations environnementales au Quaternaire, British Archaeological Reports, International Series, vol. S1352, pp. 55–68.

Bocherens, H., Jacques, L., Ogle, N., Moussa, I., Kalin, R., Vignaud, P., Brunet, M., 2009. Reply to the comment by A. Zazzo, W.P Patterson and T.C. Prokopiuk on "Implications of diagenesis for the isotopic analysis of Upper Miocene large mammalian herbivore tooth enamel from Chad" by Jacques et al. (2008). Palaeogeography, Palaeoclimatology, Palaeoecology 266, 200–210. Palaeogeography, Palaeoclimatology, Palaeoecology 277, 269–271.

Bocherens, H., Sandrock, O., Kullmer, O., Schrenk, F., 2011. Hominin palaeoecology in Late Pliocene Malawi: insights from isotopes (13C, 18O) in mammal teeth. South African Journal of Science 107 (3/4), 95–100.

Bosinski, G., 2001. L'industrie lithique de Bockstein (Württemberg): le niveau Bockstein III. In: Cliquet, D. (Ed.), Les industries à outils bifaciaux du Paléolithique moyen d'Europe occidentale. Actes de la table-ronde internationale organisee à Caen (Basse-Normandie, France) — 14 et 15 octobre 1999, Liège, ERAUL, vol. 98, pp. 193–194.

Bradshaw, R.H.W., Hannon, G.E., Lister, A.M., 2003. A long-term perspective on ungulate–vegetation interactions. Forest Ecology and Management 181, 267–280.

Britton, K., Gaudzinski-Windheuser, S., Roebroeks, W., Kindler, L., Richards, M.P., 2012. Stable isotope analysis of well-preserved 120,000-year-old herbivore bone collagen from the Middle Palaeolithic site of Neumark-Nord 2, Germany reveals niche separation between bovids and equids. Palaeogeography, Palaeoclimatology, Palaeoecology 333–334, 168–177.

Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica 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. Geochimica et Cosmochimica Acta 60, 5145–5148.

Bunzel-Drüke, M., 2001. Ecological substitutes for wild horse (Equus Ferus Boddaert, 1785 = E. Przewalskii Poljakov, 1881) and Aurochs (Bos Primigenius Bojanus, 1827). In: Natur- und Kulturlandschaft, Höxter/Jena, Band 4. AFKP (WWF Large Herbivore Initiative), p. 10.

Calvin, M., Benson, A.A., 1948. The path of carbon in photosynthesis. Science 107, 476–480.

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.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene–Pliocene boundary. Nature 389, 153–158.

Cerling, T.E., Harris, J.M., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120, 364–374.

Champion, T., Gamble, C., Shennan, S., Whittle, A., 2009. Prehistoric Europe. Left Coast Press Inc., Walnut Creek.

Chenery, C.A., Pashley, V., Lamb, A.L., Sloane, H.J., Evans, J.A., 2012. The oxygen isotope relationship between the phosphate and structural carbonate fractions of human bioapatite. Rapid Communications in Mass Spectrometry 26, 309–319.

Currant, A., Jacobi, R., 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. Quaternary Science Reviews 20, 1707–1716.

Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

DeNiro, M.J., Epstein, S., 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197, 261–263.

DeSantis, L.R.G., Feranec, R.S., MacFadden, B.J., 2009. Effects of global warming on ancient mammalian communities and their environments. PLoS ONE 4 (6), 5750. http://dx.doi.org/10.1371/journal.pone.0005750.

Drucker, D.G., Bocherens, H., 2009. Carbon stable isotopes of mammal bones as tracers of canopy development and habitat use in temperate and boreal contexts. In: Creighton, J.D., Roney, P.J. (Eds.), Forest Canopies: Forest Production, Ecosystem Health, and Climate Conditions. Nova Science Publishers, Inc, ISBN 978-1-60741-457-5, pp. 103–109.

Drucker, D.G., Bocherens, H., Billiou, D., 2003. Evidence for shifting environmental conditions in Southwestern France from 33 000 to 15 000 years ago derived from carbon-13 and nitrogen-15 natural abundances in collagen of large herbivores. Earth and Planetary Science Letters 216, 163–173.

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. Palaeogeography, Palaeoclimatology, Palaeoecology 266, 69–82.

Ecker, M., Bocherens, H., Julien, M.-A., Rivals, F., Raynal, J.-P., Moncel, M.-H., 2013. Middle Pleistocene ecology and Neanderthal subsistence: insights from stable

isotope analyses in Payre (Ardèche, France). Journal of Human Evolution 65, 363–373.

Elias, S.A., Crocker, B., 2008. The Bering Land Bridge: a moisture barrier to the dispersal of steppe tundra biota? Quaternary Science Reviews 27, 2473–2483.

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 (2), 191–205.

Feranec, R.S., Hadly, E.A., Paytan, A., 2009. Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 153–160.

Feranec, R.S., GarcÃa, N., D'ez, J.C., Arsuaga, J.L., 2010. Understanding the ecology of mammalian carnivorans and herbivores from Valdegoba cave (Burgos, northern Spain) through stable isotope analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 263–272.

Forsten, A., 1988. Middle Pleistocene replacement of stenonid horses by caballoid horses - ecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 65, 23–33.

García García, N., Feranecc, R.S., Arsuagaa, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleistocene deposits of the Sierra De Atapuerca, northern Spain. Journal of Archaeological Science 36, 1142–1151.

Guthrie, R.D., 1984. Mosaics, allelochemicals and nutrients: an ecological theory of Late Pleistocene megafaunal extinctions. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, AZ, pp. 259–298.

Hatch, M.D., Slack, C.R., Johnson, H.S., 1967. Further studies on a new pathway of photosynthetic carbon dioxide fixation in sugarcane, and its occurrence in other species. The Biochemical Journal 102, 417–422.

Hobson, K.A., Sease, J.L., 1998. Stable carbon isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lions. Marine Mammal Science 114, 116–129.

Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. Palaeogeography, Palaeoclimatology, Palaeoecology 206, 355–365.

Jacques, L., Ogle, N., Moussa, I., Kalin, R., Vignaud, P., Brunet, M., Bocherens, H., 2008. Implications of diagenesis for the isotopic analysis of upper Miocene large mammalian herbivore tooth enamel from Chad. Palaeogeography, Palaeoclimatology, Palaeoecology 266, 200–210.

Jenkins, S.G., Partridge, S.T., Stephensin, T.R., Farley, S.D., Robbins, C.T., 2001. Nitrogen and carbon isotope fractionation between neonates, and nursing offspring. Oecologia 129, 336–341.

Jones, A.M., O'Connell, T.C., Young, E.D., Scott, K., Buckingham, C.M., Iacumin, P., Brasier, M.D., 2001. Biogeochemical data from well preserved 200 ka collagen and skeletal remains. Earth and Planetary Science Letters 193, 143–149.

Julien, M.-A., Bocherens, H., Burke, A., Drucker, D.G., Patou-Mathis, M., Krotova, O., Péan, S., 2012. Were European steppe bison migratory? 18O, 13C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. Quaternary International 271, 106–119.

Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-coelodonta Faunal Complex in Eurasia (Large Mammals). The Mammoth Site of Hot Springs, Fenske Companies, Rapid City, SD, USA.

Kaiser, T.M., Franz-Odendaal, T.Q., 2004. A mixed-feeding *Equus* species from the Middle Pleistocene of South Africa. Quaternary Research 62, 316–323.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 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. Journal of Archaeological Science 24, 417–429.

Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America. Part 1. Florida. Chemical Geology 152, 119–138.

Kohn, M.J., 1996. Predicting animal d^{18}O: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60 (23), 4811–4829.

Kowalski, K., 1980. Origin of mammals of the Arctic tundra. Folia Quaternaria 51, 3–16.

Kovács, J., Moravcavá, M., Újvári, G., Pinter, 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. Quaternary International 276–277, 145–154.

Kronneck, P., Niven, L., Uerpmann, H.-P., 2004. Middle Palaeolithic subsistence in the Lone Valley (Swabian Alb, southern Germany). International Journal of Osteoarchaeology 14, 212–224.

Kuitems, M., van der Plicht, J., van Kolfschoten, T., Serangeli, J., Bocherens, H., 2012. Stable isotope analysis of well-preserved 300-400 ka year old bone collagen from Schöningen. In: Abstracts of the 77th SAA Annual Meeting, p. 204.

Lecuyer, C., Balter, V., Martineau, F., Fourel, F., Bernard, A., Amiot, R., Gardien, V., Otero, O., Legendre, S., Panczer, G., Simon, L., Martini, R., 2010. Oxygen isotope fractionation between apatite-bound carbonate and water determined from controlled experiments with synthetic apatites precipitated at 10–37 degrees C. Geochimica et Cosmochimica Acta 74, 2072–2081.

Lee-Thorp, J.A., van der Merwe, N.J., 1987. Carbon isotope analysis of fossil bone apatite. South African Journal of Science 83, 71–74.

Lee-Thorp, J., Sponheimer, M., 2003. Three case studies used to reassess the reliability of fossil bone and enamel isotope signals for paleodietary studies. Journal of Anthropological Archaeology 22, 208–216.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences 103, 11201–11205.

Lister, A.M., Sher, A.V., 2001. The origin and evolution of the woolly mammoth. Science 294, 1094–1097.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta 48, 385–390.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta 48, 1689–1693.

MacFadden, B.J., Higgins, P., 2004. Ancient ecology of 15-million-year old browsing mammals within C3 plant communities from Panama. Oecologia 140, 169–182.

Markova, A., 2000. The Mikulino (=Eemian) mammal faunas of the Russian plain and Crimea. Geologie en Mijnbouw/Netherlands Journal of Geosciences 79, 293–301.

Mounier, A., Marchal, F., Condemi, S., 2009. Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. Journal of Human Evolution 56 (3), 219–246.

Münzel, S.C., Stiller, M., Hofreiter, M., Mittnik, A., Conard, N.J., Bocherens, H., 2011. Pleistocene bears in the Swabian Jura (Germany): genetic replacement, ecological displacement, extinctions and survival. Quaternary International 245, 225–237.

Palmqvist, P., Gröcke, D.R., Arribas, A., Fariña, R.A., 2003. Paleoecological reconstruction of a lower Pleistocene large mammals community using biogeochemical (δ13C, δ15N, δ18O, Sr:Zn) and ecomorphological approaches. Paleobiology 29, 204–228.

Pushkina, D., 2007. The Pleistocene easternmost Eurasian distribution of the species associated with the Eemian *Palaeoloxodon antiquus* assemblage. Mammal Review 37, 224–245.

Pushkina, D., Bocherens, H., Chaimanee, Y., Jaeger, J.-J., 2010. Stable carbon isotope reconstructions of diet and paleoenvironment from the late Middle Pleistocene Snake Cave in Northeastern Thailand. Naturwissenschaften 97 (3), 299–309.

Quade, J., Cerling, T.E., Andrews, P., Alpagut, B., 1995. Paleodietary reconstruction of Miocene faunas from Pasalar, Turkey using stable carbon and oxygen isotopes of fossiltooth enamel. Journal of Human Evolution 28, 373–384.

Rivals, F., Schulz, E., Kaiser, T.M., 2008. Climate-related dietary diversity of the ungulate faunas from the middle Pleistocene succession (OIS 14-12) at the Caune de l'Arago (France). Paleobiology 34, 117–127.

Rivals, F., Semprebon, G., Lister, A., 2012. An examination of dietary diversity patterns in Pleistocene proboscideans (*Mammuthus*, *Palaeoloxodonta*, and *Mammut*) from Europe and North America as revealed by dental microwear. Quaternary International 255, 188–195.

Rodière, É., Bocherens, H., Angibault, J.-M., Mariotti, A., 1996. Particularités isotopiques chez le chevreuil (*Capreolus capreolus* L.): Implications pour les reconstitutions paléoenvironnementales. Comptes Rendus de l'Académie des Sciences, Série II, Paris 323, 179–185.

Sher, A.V., 1992. Beringian fauna and early Quaternary mammalian dispersal in Eurasia: ecological aspects. Courier Forschungs-Institute Senckenberg 153, 125–133.

Sher, A.V., 1997. Late Quaternary extinction of large mammals in northern Eurasia: a new look at the Siberian contribution. In: Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota. NATO ASI Series, vol. 147, pp. 319–339.

Skrzypek, G., Wiśniewski, A., Grierson, P.F., 2011. How cold was it for Neanderthals moving to Central Europe during warm phases of the last glaciation? Quaternary Science Reviews 30, 481–487.

Smith, B.N., Epstein, S., 1971. Two categories of ^{13}C/^{12}C ratios for higher plants. Plant Physiology 47, 380–384.

Sponheimer, M., Lee-Thorp, J.A., 1999. The ecological significance of oxygen isotopes in enamel carbonate. Journal of Archaeological Science 26, 723–728.

Sponheimer, M., Lee-Thorp, J.A., 2001. The oxygen isotope composition of mammalian enamel carbonate from Morea Estate, South Africa. Oecologia 126, 153–157.

Stafford Jr., T., Semken Jr., H., Graham, R., Klippel, W., Markova, A., Smirov, N., Southon, J., 1999. First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities. Geology 27, 903–906.

Stewart, J.R., 2008. The progressive effect of the individualistic response of species to Quaternary climate change: an analysis of British mammalian faunas. Quaternary Science Reviews 27, 2499–2508.

Stuart, A.J., 1986. Pleistocene occurrence of hippopotamus in Britain. Quartärpaläontologie 6, 209–218.

Stuart, A.J., 1991. Mammalian extinctions in the late Pleistocene of Northern Eurasia and North America. Biological Review 66, 453–562.

Tütken, T., Furrer, H., Vennemann, T.W., 2007. Stable isotope compositions of mammoth teeth teeth from Niederweningen, Switzerland: implications for the Late Pleistocene climate, environment, and diet. Quaternary International 164–165, 139–150.

Van Asperen, E.N., 2010. Ecomorphology and migratory behaviour of Late Middle Pleistocene horses in northwest Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 584–596.

Van der Merwe, N.J., Medina, E., 1989. Photosynthesis and ^{13}C/^{12}C ratios in Amazonian rain forests. Geochimica et Cosmochimica Acta 53, 1091–1094.

Van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. Journal of Archaeological Science 18 (3), 249—259.

Van Kolfschoten, T., 2000. The Eemian mammal fauna of Central Europe. Geologie en Mijnbouw/Netherlands Journal of Geosciences 79 (2/3), 269—281.

Vereshchagin, N.K., Baryshnikov, G.F., 1980. Areas of ungulates in the fauna of the USSR in the anthropogeneMammals of Eastern Europe during the Anthropogene. Proceedings of the Zoological Institute 93, 3—20 (in Russian).

Vereshchagin, N.K., Baryshnikov, G.F., 1985. Extinction of mammals during Quaternary in Northern EurasiaMammals of Northern Eurasia during the Quaternary. Proceedings of the Zoological Institute 131, 3—38 (in Russian).

Vogel, J.C., Fuls, A., Ellis, R.P., 1978. The geographic distribution of kranz grasses in southern Africa. South African Journal of Science 75, 209—215.

Von Koenigswald, W., 1999. Migration and extinction in the Quaternary faunas of Central and Western Europe. Annales Geologiques des pays Helleniques (1e serie) 39A, 327.

Von Koenigswald, W., 2002. Lebendige Eiszeit. Klima und Tierwelt im Wandel, p. 190. Theiss.

Von Koenigswald, W., 2003. Mode and causes for the Pleistocene turnovers in the mammalian fauna of Central Europe. Deinsea 10, 305—312.

Von Koenigswald, W., 2007. Mammalian faunas from the interglacial periods in Central Europe and their stratigraphic correlation. Developments in Quaternary Sciences 7, 445—454.

Wahl, J., König, H.G., Ziegler, R., 2009. Die Defekt- und Verformungsspuren am Schädel des Urmenschen von Steinheim an der Murr. Fundberichte aus Baden-Wiirttemberg 30, 7—28 (Stuttgart 2009).

Wright, L.E., Schwarcz, H.P., 1998. Stable carbon and oxygen isotopes in human tooth enamel: identifying breastfeeding and weaning in prehistory. American Journal of Physical Anthropology 106, 1—18.

Yeakel, J.D., Guimaraes, P.R., Bocherens, H., Koch, P.L., 2013. 2013 the impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. Proceedings of the Royal Society B: Biological Sciences 280 (1762), 20130239. http://dx.doi.org/10.1098/rspb.2013.0239.

Zazzo, A., Lécuyer, C., Mariotti, A., 2004. Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions. Geochimica et Cosmochimica Acta 68, 1—12.