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Tracking possible decline of woolly mammoth during the Gravettian in Dordogne (France) and the Ach Valley (Germany) using multi-isotope tracking (^{13}C , ^{14}C , ^{15}N , ^{34}S , ^{18}O)



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ABSTRACT

The woolly mammoth (*Mammuthus primigenius*) was an emblematic and key species of the so-called mammoth steppe ecosystem between ca. 110,000 and 12,000 years ago. Its contribution to human subsistence during the Gravettian period as source of raw material was documented in southwestern France and southwestern Germany, with some evidence of active hunting in the latter region. However, decreasing genetic diversity and increasing indications of nutritional stress point to a likely decline of this megaherbivore. The specificity of the ecological niche occupied by the woolly mammoth is clearly reflected by their collagen ^{13}C and ^{15}N abundances ($\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$), measured on skeletal remains of the typical mammoth steppe. The abundances of carbon-13 in mammoth collagen are comparable to those of other grazers like horse (*Equus* sp.), while the nitrogen-15 abundances are significantly higher (about 3‰) than in the other herbivores, either horse or reindeer (*Rangifer tarandus*). During the Aurignacian and Gravettian occupation at Geißenklösterle in the Ach Valley (Germany), the mammoths had the expected stable isotope signature, but the nitrogen-15 of horses showed an unexpected overlap with those of the mammoth. This unusual pattern was already occurring during the Aurignacian, while the oxygen-18 abundances in bone phosphate ($\delta^{18}\text{O}_{\text{bp}}$) of horse and reindeer were unchanged between Aurignacian and Gravettian periods, which rules out significant change in environmental and climatic conditions. Thus, we hypothesize that during the Aurignacian and Gravettian, the ecological niche of mammoth was intact but not occupied intensively by mammoths due to a decline in their population. This decline could be tentatively explained by human pressure through hunting. In Dordogne (France), decreasing horse and reindeer $\delta^{15}\text{N}_{\text{coll}}$ values coeval to decreasing horse $\delta^{18}\text{O}_{\text{bp}}$ values between the Aurignacian and the Early Gravettian periods reflected a clear change in the environment, while no contrast in $\delta^{15}\text{N}_{\text{coll}}$ values was observed between the Early and Final Gravettian at the Abri Pataud. The

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mammoth of Dordogne yielded slightly higher $\delta^{15}\text{N}_{\text{coll}}$ values than expected, probably as a consequence of the nursing effect since all the analyzed samples were ivory instead of bone. The direct dating and sulphur-34 measurement on the ivory of the Early Gravettian at Pataud showed that almost all of them were of contemporaneous and local origin. Significant contrasts in $\delta^{34}\text{S}_{\text{coll}}$ values were found between the Dordogne and the Ach Valley for the same herbivores species, which confirms the potential of sulphur-34 in collagen as a mobility tracker.

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1. Introduction

The woolly mammoth (*Mammuthus primigenius*) was a key species during the Late Quaternary and lent its name to the so-called mammoth steppe ecosystem between ca. 110,000 and 12,000 years ago. This period was characterized by generally cold and arid climatic landscapes, dominated by graminoids and forbs. Despite this seemingly unfavourable climate, it sustained a high diversity of large mammal species (e.g. Guthrie, 1968). This apparent paradox of high productivity despite the dominating cold conditions has been interpreted as the consequence of intense light exposure (Guthrie, 2001) and the impact of the high density of the herbivores themselves (Zimov et al., 1995). In modern African savannahs, the only modern ecosystem equivalent to the mammoth steppe in terms of density and diversity of mammal biomass, the impact of the proboscideans on the landscape through their mechanical (feeding, trampling, digging) and biological actions (incomplete digestion, dung rejection) shapes the landscape and enhances ecosystem productivity (e.g. Haynes, 2012). Similarly, Zimov et al. (2012) have hypothesized that, in the middle and high latitudes during the cold phases of the Late Pleistocene, the mammal species themselves contributed to the productivity of their environment, especially large herbivores such as the mammoth, while the climate would have acted as a secondary controlling factor. In such a scenario (Ecosystem Hypothesis), the ecosystem itself plays a key role in the functioning and the sustainability of the mammoth steppe, in contrast with the scenario that puts the emphasis on the climatic conditions of the Late Pleistocene (Climate Hypothesis). Even if the proponents of the Ecosystem Hypothesis versus the Climatic Hypothesis are still debating which scenario better explains the high productivity of the mammoth steppe ecosystem (e.g. Sher et al., 2005; Willerslev et al., 2014), all authors agree on the occurrence of a significant degree of competition among the large herbivores for food resources that led to some niche partitioning.

During the period of the mammoth steppe in Europe, the mammoth was not only an engineer species but also an important source of meat and raw material for human populations (e.g. Haynes, 1989; Gaudzinski et al., 2005; Velichko and Zelikson, 2005; Germonpré et al., 2014). The archeological sites of the Gravettian techno-complex have provided spectacular examples of the use of mammoth skeletal remains not only for artefacts but also for the construction of structures in the Danube corridor (e.g. Svoboda et al., 2005; Wojtal and Sobczyk, 2005; Brugère et al., 2009; Musil, 2010; Bosch, 2012). Moreover, the procurement of mammoth through direct hunting has been documented in some cases such as in the early Upper Paleolithic of the Swabian Jura (Münzel, 2001, 2005).

The issue of the extinction of the mammoth, beginning around 14,000 years ago in Western and Central Europe, has been extensively investigated (e.g. Stuart and Lister, 2007; Kuzmin, 2010). In this context, a recent study based on mitochondrial DNA points to a significant decline reflected by a genetic replacement of local

mammoth populations in Western Europe starting around 34,000 cal BP, long before the Lateglacial (Palkopoulou et al., 2013). Moreover, indicators of nutritional stress have been documented on mammoth remains of Central Europe at ca. 28,000 cal BP (Wojtal, 2001; Krzemińska, 2008; Leshchinskiy, 2012). A cryptic decline in mammoth local population in Europe could thus be suspected during a period of time corresponding to the Gravettian human culture.

Stable isotopes are now routinely used as paleoecological tracers since their abundances in animal tissues depend on those found in diet and can be preserved in fossil tissues (e.g. Rubenstein and Hobson, 2004; Koch, 2007; Bocherens and Drucker, 2013). As far as herbivores are concerned, the carbon-13 abundance ($\delta^{13}\text{C}$) in tissues, such as bone, reflect those of plants, which themselves depend on the source of carbon (e.g. recycled CO_2) and the photosynthetic process (reviews in Tieszen, 1991; Heaton, 1999). During the Late Pleistocene in Europe, plants exhibited a C_3 photosynthesis pathway and their $\delta^{13}\text{C}$ values vary according to the environmental conditions. The nitrogen isotopic composition of bone collagen ($\delta^{15}\text{N}$) from herbivores depends on dietary, physiological and climatic parameters. Bone collagen reflects the long-term isotopic trend as bone is continuously remodelled with a turnover of several years over life (review in Koch, 2007). In the mammoth steppe, the distinct stable isotopes signatures of bone collagen of large herbivores reflect their specialisation in the consumption of different types of plants (e.g. Bocherens, 2003; Fox-Dobbs et al., 2008). Indeed, reindeer (*Rangifer tarandus*) and mammoth can be clearly distinguished from the other large herbivores, by less depleted $\delta^{13}\text{C}$ values for reindeer and enriched $\delta^{15}\text{N}$ values for mammoth. The systematic enrichment in $\delta^{13}\text{C}$ values of reindeer collagen compared to other herbivores, such as horse (*Equus* sp.) and mammoth, has been attributed to its specialisation in lichen consumption (e.g. Drucker et al., 2003). An enrichment in $\delta^{15}\text{N}$ values from 3 to 6‰ on average of woolly mammoth collagen compared to horse and reindeer collagen has been widely observed, especially in eastern Beringia before the Last Glacial Maximum (LGM) period, a context without significant human impact (Fox-Dobbs et al., 2008; Szapak et al., 2010; Fig. 1). Such high $\delta^{15}\text{N}$ values place the mammoth in the same range as those of predators like the wolf, which exhibits collagen $\delta^{15}\text{N}$ values 3‰–5‰ higher than horse and reindeer, on which it preys (e.g. Bocherens and Drucker, 2003). The cause of the ^{15}N enrichment in mammoth collagen is not yet fully understood and the most frequently invoked hypotheses are physiological adaptation to aridity (Ambrose and DeNiro, 1986, but see Kuitens et al., 2012), consumption of mature grasses from disturbed areas (Bocherens, 2003) and coprophagy (Clementz et al., 2009). To our knowledge, the only exception to this isotopic pattern was found in the Ukrainian site of Mezhyrich dated to the late Upper Paleolithic where the $\delta^{15}\text{N}$ values of mammoth are as low as those of horses (Drucker et al., 2014). Since this period of time corresponds to the decline of the mammoth steppe in central Ukraine in the context of climatic change, the unexpectedly low ^{15}N abundance in mammoth

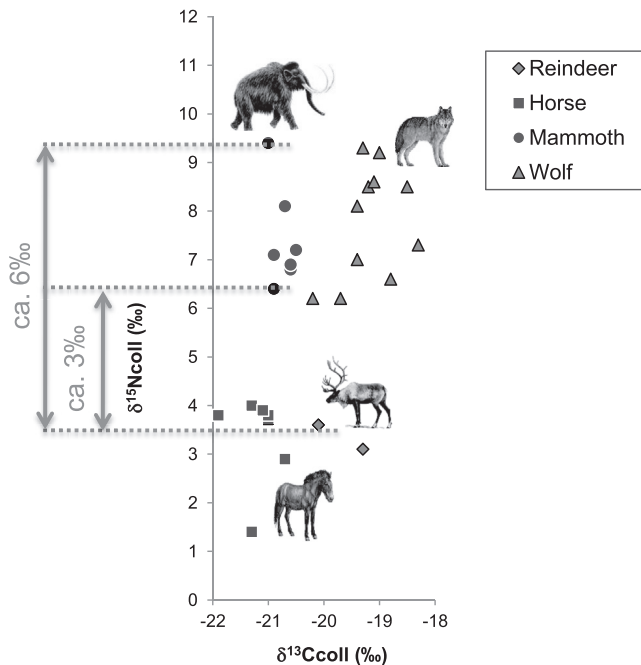


Fig. 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*), horse (*Equus* sp.) and wolf (*Canis lupus*) from eastern Beringia (Alaska and Yukon) during the pre-LGM (36.0–21.0 kyrs BP, ca. 42.0–25.0 kyrs cal BP; Fox-Dobbs et al., 2008; Szpach et al., 2010).

collagen was interpreted as the result of the loss of the ecological niche due to environmental change (Drucker et al., 2014). Thus, modification of the ecology of the woolly mammoth, most likely linked to its dietary specialization, could be tracked by stable isotope investigation on this species and the coeval large herbivorous species such as horse and reindeer.

Another isotopic tracker, oxygen-18 is even more directly related to environmental factors, namely temperature and humidity (e.g. Koch, 2007; Bocherens and Drucker, 2013). Oxygen isotopic ($\delta^{18}\text{O}$) values in the phosphate fraction of bone relate to those of ingested water for large mammals (e.g. Longinelli, 1984; Iacumin et al., 1996; Kohn et al., 1996). Studies on woolly mammoth teeth and bone confirmed the correlation between the $\delta^{18}\text{O}$ values of carbonate or phosphate and the $\delta^{18}\text{O}$ values of meteoric water, which are themselves a function of temperature and aridity (e.g. Tütken et al., 2007; Arppe and Karhu, 2010; Iacumin et al., 2010). Sequential measurements of oxygen-18 within single tusks have demonstrated seasonal signals (e.g. Koch et al., 1989; Fox et al., 2007). The analysis of the apatite phosphate of bone on the other hand delivers an averaged record over several years due to the constant remodeling of bone. Hence, large-scale changes in temperature and/or aridity over time or space are apparent in the phosphate fraction of bulk bone (e.g. Arppe and Karhu, 2010; Iacumin et al., 2010).

A possible decline in mammoth population during the Gravettian could be suspected in Dordogne in southwestern France and in the Ach Valley in southwestern Germany. In southwestern France, few mammoth remains have been reported (e.g. Delpech, 1983; Clot and Duranthon, 1990; Álvarez-Lao and García, 2012). Moreover, most of them are ivory pieces, which led some authors to suggest that they were imported either from another location or were recovered from subfossil accumulations rather than from animals living locally (e.g. Goutas, 2004; White, 2006; Heckel, 2009). In all cases, mammoth ivory was a raw material often used

to manufacture body ornaments, statuettes, hunting weapons and enigmatic objects that are neither numerous, nor frequent (e.g. Goutas, 2013). In contrast, the mammoth remains in the Ach Valley are more frequent and associated with evidence of active acquisition through hunting (Münzel, 2001, 2005). Mammoth ivory and bones seem to be relatively common raw materials used to make a range of tools, weapons, body ornaments and art objects. While ivory was an important raw material during the Aurignacian for all kinds of everyday tools, such as chisels, retouchers, and projectile points, as well as for personal ornaments, figurative art and flutes, the Gravettian people rarely used any ivory other than that chosen for the production of personal ornaments. A change in the availability of the mammoth could be invoked to explain such cultural changes (e.g. Barth et al., 2009).

In this paper, the aim is to examine the possible decline in mammoth populations during the Gravettian in Dordogne and in the Ach Valley using stable isotope measurements of bone and ivory collagen (carbon-13, nitrogen-15, sulphur-34) and apatite phosphate (oxygen-18), combined with direct radiocarbon dating. Significant modifications in the ecology of the large herbivores of the mammoth steppe should be reflected by unusual isotopic patterns among the main species, which are the woolly mammoth, horse and reindeer. If a climatic impact was the driving factor behind such changes, we should expect variability in oxygen-18 as well. If a change in the ecology of some species happened independently of climate change, we expect to see changes in the carbon and nitrogen isotopic composition only. If bone and ivory materials have a different origin, some differences among the sulphur isotopes of their collagen should be observed. Indeed, the potential of sulphur isotope analyses as a tracker of geographical origin was suggested in studies of human remains from archaeological sites as a result of local geology contrast and proximity of the sea (e.g. Vika, 2009). Recent works on mammal remains in continental context confirmed the possibility to track mobility using collagen sulphur-34 (Drucker et al., 2011; Towers et al., 2011).

2. Material and methods

Recent radiocarbon dating investigations have provided a significant set of data from early Upper Paleolithic occupations at the sites of Geißenklösterle in the Ach Valley in southwestern Germany and the Abri Pataud in Dordogne in southwestern France (Fig. 2; Higham et al., 2011, 2012; Henry-Gambier et al., 2013). The results allowed a thorough revision of the chronology of the Gravettian and preceding Aurignacian occupations of these two key sites. Based on calibrated dates and Bayesian modeling at 1 sigma, level AH I (subdivided in Ir, Is, It and Ia) at Geißenklösterle ranges between 30.5 and 33.5 ka cal BP; there are few dates from these phases and so precision is not particularly good. For level 5 at Abri Pataud, however, the precision is better and ranges between 32 and 33 ka cal BP (Bayesian modeled calibrations at 1 sigma). Taken together, it is tempting to conclude that there is some overlap in the two sites in terms of dating, perhaps over the period 30–34 ka cal BP, even if more dating is needed from Geißenklösterle. Levels AH IIa and IIb at Geißenklösterle date between 40.5 and 37 ka cal BP, whilst levels 10 to 13 at Abri Pataud cover the range 40–38 ka cal BP during the Aurignacian. In other words, these levels at the two Aurignacian sites are quite contemporaneous.

The collagen extracted from the dated animal bones offers the opportunity to investigate the diet and environment of large ungulates, more specifically mammoth (*M. primigenius*), reindeer (*R. tarandus*) and horse (*Equus* sp.) using stable isotopes of carbon (^{13}C), nitrogen (^{15}N) and sulphur (^{34}S). In this study, we measured the ^{13}C abundances on six samples of directly dated collagen and

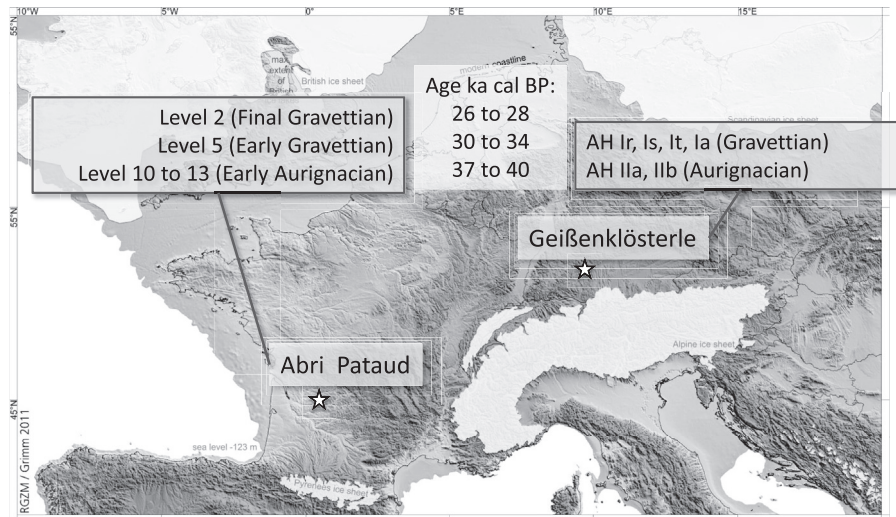


Fig. 2. Location of the sites of Geißenklösterle in the Ach Valley (southwestern Germany) and the Abri Pataud in Dordogne (southwestern France). Map with the Last Glacial Maximum shoreline and ice sheet extension from ©RGZM/Grimm 2011.

two new samples as well as the ^{34}S abundances on five dated samples and four other collagen, in addition to the dataset published in Bocherens et al. (2011) for Geißenklösterle (Tables 1 and 2). From the Abri Pataud, the previously studied stable isotopes of reindeer and horse specimens (Vercoutère et al., 2014) were augmented by the analysis of 12 collagen samples that were previously radiocarbon dated (Tables 1 and 3). The Early Aurignacian and Early Gravettian occupation in the region of Dordogne benefited from previous isotopic analysis on horse and reindeer by Drucker et al. (2003) and Bocherens et al. (2014). Data from Combe Saunière 1 and Le Flageolet I were used to complement the results found at Pataud for the Gravettian and Aurignacian periods. The ages of these sites are not as well constrained as in the case of the other sites, particularly Pataud and further dating is needed (Table 1). Despite their poorer precision, however, the Gravettian

dates of level VI at Combe Saunière 1 fit with the range found for level 5 at Abri Pataud. The dating available so far for the Gravettian levels V and VII at le Flageolet I are more recent than the well-established dating of the level 5 at Pataud. Nevertheless, the striking similarity in the industry, especially in the unique succession of Noaillian and Rayssian techno-complexes, makes a close comparison of the two groups reasonable. Two new samples of mammoth ivory from Abri Castanet were also included. The Early Aurignacian layer at Abri Castanet ranges between 35.8 and 37.9 ka cal BP (White et al., 2012), which is slightly younger than the more recent Early Aurignacian layer of Abri Pataud. However, Abri Castanet is one of the major sites in southwestern France that has yielded ivory remains from Aurignacian contexts, and could thus provide us with the mammoth isotopic signature for this period of time.

Table 1

Directly dated samples of bone and ivory remains at Geißenklösterle in the Ach Valley (SW Germany), the Abri Pataud, Le Flageolet I, and Combe-Saunière 1 in Dordogne (SW France). 1 = Evin et al. (1985); 2 = Gowlett et al. (1986); 3 = Mellars et al. (1987); 4 = Drucker et al. (2003); 5 = Higham et al. (2011); 6 = Higham et al. (2012); 7 = Henry-Gambier et al. (2013).

Site	Lab-nr.	Species	Part	Excavation nr-	Level	Culture	Conv. ^{14}C date BP (lab code)	Source	Comment
Geißenklösterle	21814	Mammoth	Rib	Quadr 130 Fund 328	It	Gravettian	27,960 ± 290 (OxA-21660)	6	Cut-marks
Geißenklösterle	22981	Mammoth	Rib	Quadr 26 Fund 18	Ia	Gravettian	28,600 ± 290 (OxA-21739)	6	Cut- and impact marks
Geißenklösterle	22976	Mammoth	Rib	Quadr 58 Fund 246	IIb	Aurignacian	33,950 ± 550 (OxA-21724)	6	Retoucheur, impact marks
Geißenklösterle	21815	Reindeer	Metacarpal	Quadr 86 Fund 122	Ic	Gravettian	32,900 ± 450 (OxA-21661)	6	Bite marks
Geißenklösterle	P-21810	Horse	Scapula	Quadr 0 Fund 131	IIa	Aurignacian	33,000 ± 500 (OxA-21656)	6	Cut- and impact marks
Geißenklösterle	P-22980	Horse	Humerus	Quadr 0 Fund 143	IIb	Aurignacian	34,900 ± 600 (OxA-21738)	6	Retoucheur
Geißenklösterle	GK16/TUB-78	Horse	Humerus	Quadr 67 Fund 931	IIb	Aurignacian	34,800 ± 600 (OxA-21742)	6	Cut- and impact marks
Abri Pataud	PATi-4	Mammoth	Ivory	sac976	5	Early Gravettian	27,610 ± 170 (GrA-56410)	This work	Ochred
Abri Pataud	PATi-8	Mammoth	Ivory	AP 5 FR35205 sac512	5	Early Gravettian	28,050 ± 170 (GrA-56409)	This work	Ochred
Abri Pataud	PAT-4	Reindeer	Metacarpal L	AP58 B64-2	2	Final Gravettian	21,800 ± 90 (GrA-45013)	7	Found near human humerus
Abri Pataud	PAT-5	Reindeer	Tibia, dia	AP58 B64-1	2	Final Gravettian	21,910 ± 90 (GrA-45133)	7	Found near human humerus
Abri Pataud	PAT-7	Reindeer	Metacarpal L	AP58 B59-5	2	Final Gravettian	22,360 ± 90 (GrA-45132)	7	Found near human skull
Abri Pataud	P-19930	Reindeer	Radius	AP 5 FR22683/EIV	5	Early Gravettian	28,230 ± 290 (OxA-21586)	5	Cutmarks

(continued on next page)

Table 1 (continued)

Site	Lab-nr.	Species	Part	Excavation nr-	Level	Culture	Conv. ¹⁴ C date BP (lab code)	Source	Comment
Abri Pataud	P-19931	Reindeer	Metacarpal	AP 5 F3600/BIII	5	Early Gravettian	28,150 ± 290 (OxA-21587)	5	Cutmarks
Abri Pataud	P-19932	Reindeer	Tarsal	AP 5 FR24897/AIV(E)	5	Early Gravettian	28,250 ± 280 (OxA-21588)	5	Cutmarks
Abri Pataud	P-19918	Reindeer	Tibia	AP 11 F1861/BIII	11	Early Aurignacian	33,550 ± 550 (OxA-21581)	5	Cutmarks
Abri Pataud	P-21953	Reindeer	Bone	AP 12 F6340/BII	12	Early Aurignacian	33,450 ± 500 (OxA-21670)	5	Cutmarks
Abri Pataud	P-21954	Reindeer	Bone	AP 12 F6290/BII/III	12	Early Aurignacian	34,300 ± 600 (OxA-21671)	5	Retoucheur
Abri Pataud	P-19912	Reindeer	Tibia	AP 13 F6011/BIII	13	Early Aurignacian	34,850 ± 600 (OxA-21599)	5	Cutmarks
Abri Pataud	P-19913	Reindeer	Metatarsal III-I	AP 13 F6030/BIV	13	Early Aurignacian	34,200 ± 550 (OxA-21600)	5	Cutmarks
Abri Pataud	P-21960	Horse	Tooth	AP 10/11 F6416/DIII	10	Early Aurignacian	33,650 ± 500 (OxA-21679)	5	Impact marks
Abri Pataud	P-19916	Horse	Metatarsal III	AP 11 F1768/CIV	11	Early Aurignacian	33,500 ± 500 (OxA-21602)	5	Retoucheur
Abri Pataud	P-19917	Horse	Metapodial III	AP 11 F1813/BIII	11	Early Aurignacian	33,550 ± 550 (OxA-21580)	5	Retoucheur
Abri Pataud	P-21956	Horse	Metacarpal III	AP 12 F6334/BII	12	Early Aurignacian	34,050 ± 550 (OxA-21672)	5	
Le Flageolet I	FLA-1	Red deer	Right tibia	FLAG I D10, V 134	V	Gravettian	25,700 ± 700 (OxA-447)	2,3	
Le Flageolet I	—	Horse	Mandible	FLAG I AØ CVII 667	VII	Gravettian	26,150 ± 600 (Ly-2723)	1	
Le Flageolet I	—	Horse	Tibia	FLAG I D7 CXI 2464	XI	Early Aurignacian	33,800 ± 1800 (OxA-598)	2,3	
Combe Saunière 1	—	bone	bone		VI	Gravettian	26,620 ± 340 (OxA-6876)	4	
Combe Saunière 1	—	bone	bone		VI	Gravettian	27,880 ± 440 (OxA-6514)	4	

Table 2

Results of stable isotope analyses of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and bone phosphate ($\delta^{18}\text{O}_{\text{bp}}$) of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) at Geißenklösterle in the Ach Valley (SW Germany). The carbon, nitrogen and sulphur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). 1 = Bocherens et al. (2011); 2 = Stephan (1999).

Lab-nr.	Quadr-nr	Fund-nr	Species	Part	AH	C_{coll}	N_{coll}	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$	$\delta^{15}\text{N}_{\text{coll}}$	S_{coll}	$\delta^{34}\text{S}_{\text{coll}}$	$\text{C}/\text{S}_{\text{coll}}$	$\text{N}/\text{S}_{\text{coll}}$	$\delta^{18}\text{O}_{\text{bp}}$	$^{13}\text{C}/^{15}\text{N}$ source	^{34}S source	^{18}O source	
						(%)	(%)		(‰)	(‰)	(%)	(‰)	(%)	(%)					
21814	130	328	Mammoth	Rib	It	43.4	15.0	3.4	-21.0	8.9	0.17	-1.8	665	197		This work	This work	This work	
22981	26	18	Mammoth	Rib	Ia	44.1	15.3	3.4	-21.3	8.1	0.13	-2.2	885	263		This work	This work	This work	
22976	58	246	Mammoth	Rib	IIB	44.4	15.4	3.4	-21.5	8.0	0.14	1.9	874	259		This work	This work	This work	
RA-GK 294	79	501	Reindeer	Metatarsus	It	43.4	15.5	3.2	-19.0	4.2					15.0	1		2	
RA-GK 295	99	331	Reindeer	Tibia	It	43.6	16.0	3.2	-19.3	3.7	0.19	-1.4	626	197	15.5	1		This work	2
RA-GK 296	130	336	Reindeer	Tibia	It	44.0	15.5	3.3	-19.0	4.2					15.7	1		2	
RA-GK 298	88	620	Reindeer	Left tibia	Ib	42.0	14.6	3.3	-19.3	1.0	0.20	11.9	559	167	17.8	1		This work	2
21815	86	122	Reindeer	Metacarpal	Ic	44.2	16.4	3.1	-18.9	4.6						This work			
RA-GK 299	76	392	Reindeer	Talus	Ila	41.7	14.5	3.3	-19.2	3.8					16.0	1		2	
RA-GK 300	110	415	Reindeer	Humerus	Ila	40.6	14.3	3.3	-18.6	3.8					17.1	1		2	
RA-GK 302	59	195	Reindeer	Metatarsus	Ila	39.6	14.8	3.1	-19.1	4.6					16.7	1		2	
RA-GK 304	57	628	Reindeer	Humerus	IIB	36.2	12.9	3.2	-19.5	4.4					16.3	1		2	
RA-GK 306	68	376	Reindeer	Talus	IIB	43.1	14.9	3.3	-19.4	4.7					15.8	1		2	
GK15	55	36	Horse	Radius	Is	39.3	14.0	3.3	-20.4	7.1					16.6	This work		This work	
GK13/ EQ-GK314	99	557	Horse	Tibia	It	43.2	15.7	3.2	-20.7	8.7					13.7	1		2	
GK14	24	225	Horse	Radius	Ib	41.1	14.6	3.3	-20.6	6.3					14.0	This work		This work	
EQ-GK 316	88	644	Horse	Humerus	Ib	41.5	14.6	3.3	-20.6	7.3					15.6	1		2	
EQ-GK 317	56	364	Horse	Femur	Ib	36.3	13.5	3.1	-20.7	5.5					14.2	1		2	
EQ-GK 318	57	508	Horse	Tibia	Ib	42.8	14.3	3.5	-21.8	3.4					16.4	1		2	
P-21810	0	131	Horse	Scapula	Ila	45.2	15.7	3.4	-20.8	8.9	0.14	0.8	870	259		This work	This work		
GK18/ EQ-GK319	56	495	Horse	Humerus	Ila	42.2	14.8	3.3	-21.4	4.2					15.6	1		2	
EQ-GK 321	58	170	Horse	Tibia	Ila	37.8	13.9	3.1	-20.1	8.5					14.9	1		2	
EQ-GK 322	45	60	Horse	Tibia	Ila	36.3	13.7	3.1	-20.8	6.3	0.17	3.6	567	183	15.6	1		This work	2
EQ-GK 323	36	138	Horse	Tibia	Ila	36.1	13.6	3.1	-20.7	6.1					15.0	1		2	
EQ-GK 325	76	435	Horse	Tibia	Ila	41.6	14.4	3.3	-20.8	7.1					14.8	1		2	
P-22980	0	143	Horse	Humerus	IIB	44.4	15.5	3.3	-20.9	6.3	0.14	-0.4	861	258		This work	This work		
GK16/TUB-78	67	931	Horse	Humerus	IIB	39.7	14.2	3.3	-21.2	8.5	0.14	1.4	740	226		1		This work	
EQ-GK 326	36	188	Horse	Humerus	IIB	42.9	15.3	3.2	-21.0	6.1					15.4	1		2	
EQ-GK 327	57	650	Horse	Tibia	IIB	41.6	15.0	3.2	-20.9	5.9					16.4	1		2	
EQ-GK 329	46	523	Horse	Tibia	IIB	40.7	15.5	3.0	-20.8	6.9					14.5	1		2	
EQ-GK 330	67	1111	Horse	Tibia	IIB	28.6	10.9	3.0	-21.6	6.9					15.3	1		2	

Table 3
 Results of stable isotope analyses of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and phosphate ($\delta^{18}\text{O}_{\text{bp}}$) of bone and ivory of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) at the Abri Pataud (AP), the Abri Castanet (CST), Le Flageolet I (FLG), Combe-Saunière 1 (CS) in Dordogne (SW France). The carbon, nitrogen and sulphur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). 1 = Drucker et al. (2003); 2 = Bocherens et al. (2014a); 3 = Vercoutère et al. (2014).

Site	Lab-nr.	Species	Part	Excavation nr	Level	C_{coll} (%)	N_{coll} (%)	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$ (‰)	$\delta^{15}\text{N}_{\text{coll}}$ (‰)	S_{coll} (%)	$\delta^{34}\text{S}_{\text{coll}}$ (‰)	$\text{C}/\text{S}_{\text{coll}}$ (%)	$\text{N}/\text{S}_{\text{coll}}$ (%)	$\delta^{18}\text{O}_{\text{bp}}$	$^{13}\text{C}/^{15}\text{N}$ source	^{34}S source	^{18}O source
AP	PATi-1	Mammoth	Ivory	AP/58-2-37799 sac115/Tr.IV Lens2b	2										17.5			This work
AP	PATi-2	Mammoth	Ivory	AP/58-2-309/FIV Lens1	2										20.4			This work
AP	PATi-3	Mammoth	Ivory	AP/58-2-37795/Tr.III Lens2	2										18.6			This work
AP	PATi-4	Mammoth	Ivory	sac976	5	39.8	13.8	3.4	-20.5	10.8	0.18	11.9	595	177	16.1	This work	This work	This work
AP	PATi-6	Mammoth	Ivory	AP 5 FR9847 sac1072	5	37.4	13.0	3.4	-20.3	10.6	0.20	12.2	504	150	16.1	This work	This work	This work
AP	PATi-7	Mammoth	Ivory	AP 5 F8674/1131	5	38.4	13.2	3.4	-20.5	10.2	0.14	11.5	708	208	16.9	This work	This work	This work
AP	PATi-8	Mammoth	Ivory	AP 5 FR35205 sac512	5	35.9	12.4	3.4	-21.0	10.0	0.20	13.6	477	142	17.8	This work	This work	This work
AP	PATi-10	Mammoth	Ivory	AP 5 FF71579 sac739	5	25.9	9.0	3.4	-20.9	10.9					15.9	This work		This work
AP	PATi-12	Mammoth	Ivory	AP 5 FR30444	5	40.9	14.0	3.4	-20.6	10.6						This work		
AP	PATi-13	Mammoth	Ivory	couche 5, Upper sac955	5	37.1	12.8	3.4	-21.2	10.1	0.23	12.7	422	125	15.5	This work	This work	This work
AP	PATi-14	Mammoth	Ivory	AP 5 FF45463	5	32.7	11.4	3.4	-20.5	11.1	0.26	7.1	339	101	15.4	This work	This work	This work
AP	PATi-15	Mammoth	Ivory	AP 5 FF45817	5	40.6	14.0	3.4	-20.7	10.7	0.16	11.1	673	199	16.9	This work	This work	This work
AP	PATi-16	Mammoth	Ivory	AP 5 FF45816	5	40.3	14.1	3.3	-20.8	10.7	0.18	2.6	584	175	16.8	This work	This work	This work
CST	CST-A7	Mammoth	Ivory			35.2	12.8	3.2	-20.8	11.6						This work		
CST	CST-A9	Mammoth	Ivory			24.2	8.3	3.4	-21.1	10.9						This work		
AP	PAT-4	Reindeer	Metacarpal I	AP58 B64-2	2	45.7	16.2	3.3	-19.3	4.7	0.15	7.8	794	241	3		This work	
AP	PAT-5	Reindeer	Tibia	AP58 B64-1	2	45.9	16.3	3.3	-19.2	3.8	0.15	15.2	812	248	3		This work	
AP	PAT-6	Reindeer	Long bone	AP58 B64-3	2	43.3	14.9	3.4	-19.5	4.4	0.17	8.8	690	203	3		This work	
AP	PAT-7	Reindeer	Metacarpal I	AP58 B59-5	2	44.7	15.5	3.4	-19.1	4.9	0.14	8.8	843	250	3		This work	
AP	PAT-8	Reindeer	Long bone	AP58 B59-6	2	43.7	14.7	3.5	-18.7	4.3	0.15	6.2	776	223	3		This work	
AP	P-19930	Reindeer	Radius	AP 5 FR22683/EIV	5	43.3	15.3	3.3	-18.9	4.1						This work		
AP	P-19931	Reindeer	Metacarpal III-I	AP 5 F3600/BIII	5	44.0	15.5	3.3	-19.2	6.0						This work		
AP	P-19932	Reindeer	Central + fourth t	AP 5 FR24897/AIV(E)	5	43.3	15.3	3.3	-19.2	6.0						This work		
CS	CS900	Reindeer	Long bone	G22D 14	VI	40.8	15.2	3.1	-19.0	4.6					1			
CS	CS1000	Reindeer	Long bone	G22D 14	VI	40.4	14.9	3.2	-19.0	4.4					1			
AP	P-19918	Reindeer	Tibia	AP 11 F1861/BIII	11	44.1	15.5	3.3	-19.3	7.5						This work		
AP	P-21953	Reindeer	Bone	AP 12 F6340/BII	12	46.0	15.9	3.4	-19.2	7.2						This work		
AP	P-21954	Reindeer	Bone	AP 12 F6290/BII/III	12	44.6	15.7	3.3	-19.1	7.5						This work		
AP	P-19912	Reindeer	Tibia	AP 13 F6011/BIII	13	44.1	15.6	3.3	-18.6	6.6						This work		
AP	P-19913	Reindeer	Metatarsal III-I	AP 13 F6030/BIV	13	44.2	15.6	3.3	-19.2	7.4						This work		
AP	PAT-26	Horse	Tibia L	AP/06-2-T75C-176/UA F	2	40.0	14.2	3.3	-20.4	2.6	0.14	11.7	759	230	18.0	3	This work	This work
AP	PAT-28	Horse	Tooth root R	AP/06-2-S75C-193/UA E	2	40.0	14.3	3.3	-21.0	4.3					16.9	3		This work
AP	PAT-29	Horse	Tooth root R	AP/06-2-S75D-156/UA E	2	40.3	14.3	3.3	-20.7	3.8	0.16	12.7	692	210	16.9	3	This work	This work
FLG	FLA-4	Horse	Rib	FLAG I C4 115	V	42.0	15.2	3.2	-20.6	3.0					17.2	2		This work
FLG	FLA-5	Horse	Tibia L	FLAG I C10 CV 480	V	39.6	14.5	3.2	-20.7	5.9					18.1	2		This work
FLG	FLA-6	Horse	Tibia L	FLAG I C8 CV 735	V	41.7	15.2	3.2	-20.3	3.9					16.0	2		This work
FLG	FLA-8	Horse	M ² (sup)	FLAG I A0 CVII 668	VII	39.8	14.4	3.2	-20.5	3.8					16.3	2		This work
FLG	FLA-9	Horse	M ¹ (sup)	FLAG I A0 CVII 669	VII	41.1	14.9	3.2	-20.5	3.9					17.2	2		This work
FLG	FLA-10	Horse	P3-4 (inf) R	293 D5	VII	41.9	15.3	3.2	-20.5	3.7					17.5	2		This work
CS	CS300	Horse	Phalanx	G21C 0	VI	43.8	16.0	3.2	-20.0	5.5					1			
CS	CS400	Horse	Radius-ulna	H21C 27	VI	42.2	15.4	3.2	-21.0	5.1					1			
CS	CS600	Horse	Metapodial	G22C 11	VI	41.6	15.3	3.2	-20.4	3.7					1			
CS	CS700	Horse	Femur	G22C 9	VI	41.7	15.3	3.2	-20.5	4.5					1			
CS	CS800	Horse	Radius-ulna	H22C 27	VI	40.4	15.1	3.1	-20.1	4.7					1			
AP	P-21960	Horse	Tooth	AP 10/11 F6416/DIII	10	44.6	15.9	3.3	-20.8	8.5						This work		
AP	P-19916	Horse	Metatarsal III	AP 11 F1768/CIV	11	43.7	15.6	3.3	-20.6	8.0						This work		
AP	P-19917	Horse	Metapodial III	AP 11 F1813/BIII	11	45.1	15.9	3.3	-20.0	8.6						This work		
AP	P-21956	Horse	Metacarpal III	AP 12 F6334/BII	12	45.7	16.2	3.3	-21.0	5.7						This work		
FLG	FLA-18	Horse	Tibia, r	FLAG I D7 CXI 2464	XI	40.4	14.7	3.2	-19.9	7.4					18.2	2		This work
FLG	FLA-19	Horse	Metapodial	FLAG I D6 CXI 2128 Map a	XI	37.9	13.9	3.2	-20.5	7.1					17.5	2		This work
FLG	FLA-22	Horse	Tibia	FLAG I CII CXI(10) 2451	XI	40.6	14.8	3.2	-20.5	7.4					19.1	2		This work
FLG	FLA-23	Horse	Tibia	FLAG I D10 CXI 2751(7)	XI	42.0	15.0	3.3	-20.9	4.9					17.5	2		This work
AP	PAT-30	Wolf	Metatarsal IV R	AP/08-2-U77C-123/UA G	2	35.8	12.9	3.2	-19.2	9.0					3			
AP	PAT-33	Wolf	Tibia R	AP/08-2-U77D-72/UA L	2	29.0	9.4	3.6	-19.4	9.0						This work		

Collagen was extracted following a protocol based on Longin (1971) and modified by Bocherens et al. (1997). The extraction process includes a step of soaking in 0.125 M NaOH between the demineralization and solubilization steps to achieve the elimination of lipids and humic substances. Elemental analysis (C_{coll} , N_{coll} , S_{coll}) and isotopic analysis ($\delta^{13}C_{\text{coll}}$, $\delta^{15}N_{\text{coll}}$, $\delta^{34}S_{\text{coll}}$) was conducted at the Department of Geosciences of Tübingen University using a NC2500 CHN-elemental analyzer coupled to a Thermo Quest Delta + XL mass spectrometer. The international standards are a marine carbonate (V-PDB) for $\delta^{13}C$, atmospheric nitrogen (AIR) for $\delta^{15}N$ and Canyon Diablo Troilite (V-CDT) for $\delta^{34}S$. Measurements were normalized to $\delta^{13}C$ values of USGS24 ($\delta^{13}C = -16.00\text{‰}$) and to $\delta^{15}N$ values of IAEA 305A ($\delta^{15}N = 39.80\text{‰}$). Analytical error, based on within-run replicate measurement of laboratory standards (albumen, modern collagen, USGS 24, IAEA 305A), was $\pm 0.1\text{‰}$ for $\delta^{13}C$ values and $\pm 0.2\text{‰}$ for $\delta^{15}N$ values. Samples were calibrated to $\delta^{34}S$ values relative to CDT of NBS 123 ($\delta^{34}S = 17.10\text{‰}$), NBS 127 ($\delta^{34}S = 20.31\text{‰}$), IAEA-S-1 ($\delta^{34}S = -0.30\text{‰}$) and IAEA-S-3 ($\delta^{34}S = 21.70\text{‰}$). The reproducibility is $\pm 0.4\text{‰}$ for $\delta^{34}S$ measurements, and the error on amount of S measurement is 5%. Reliability of the $\delta^{13}C_{\text{coll}}$ and $\delta^{15}N_{\text{coll}}$ values can be established by measuring its chemical composition, with C/N_{coll} atomic ratio ranging from 2.9 to 3.6 (DeNiro, 1985), percentage of C_{coll} and N_{coll} above 8% and 3%, respectively (Ambrose, 1990). We retained $\delta^{34}S$ values of samples whose atomic C/S_{coll} and N/S_{coll} ratios were included in the range of 300–900 and 100–300, respectively (Nehlich and Richards, 2009).

The $\delta^{18}O$ analyses of phosphate were performed at the Department of Geosciences (University Tübingen, Germany). Prior to these analyses of the bone phosphate fraction, bone powders were chemically pre-treated with 2% NaOCl solution, followed by a 1 M Ca-acetate from acetic acid buffer solution (Bocherens et al., 1996). Oxygen isotope composition of phosphate ($\delta^{18}O_p$) was measured on silver phosphate (Ag_3PO_4). About 4 mg of pre-treated powder were dissolved in 2 M HF, neutralized with NH_4OH and the PO_4 in solution was rapidly precipitated as Ag_3PO_4 by adding 2 M $AgNO_3$ according to the method described in Tütken et al. (2006). Ag_3PO_4 of each sample and standard was analyzed in triplicate ($\sim 500 \mu\text{g}$ for a single measurement) for $\delta^{18}O_p$. The $\delta^{18}O_p$ measurements were performed using a Finnigan TC-EA at $1450 \text{ }^\circ\text{C}$ linked via a Finnigan Conflow III to a ThermoFinnigan Delta Plus XL CFIRMS at the

University of Tübingen with a reproducibility of $\pm 0.3\text{‰}$ based on standard replicates. Samples are calibrated to $\delta^{18}O$ values of TU-1 ($\delta^{18}O = 21.11\text{‰}$, relatively to VSMOW); TU-2 ($\delta^{18}O = 5.35\text{‰}$, relatively to VSMOW); 130-0.5-1 ($\delta^{18}O = -1.13\text{‰}$, relatively to VSMOW) and 130-0.5-9 ($\delta^{18}O = 8.42\text{‰}$, relatively to VSMOW).

3. Results and discussion

3.1. The Gravettian at Geißenklösterle (Ach Valley, Germany)

The $\delta^{13}C_{\text{coll}}$ values of the horses of the Gravettian layers of Geißenklösterle varied from -21.8 to -20.4‰ , which encompassed the values found for the two mammoth bones of the same period (-21.3 and -21.0‰ ; Fig. 3B). The reindeer delivered higher $\delta^{13}C_{\text{coll}}$ values ranging from -19.3 to -18.9‰ , as a consequence of their specific consumption of lichen that provided them with high ^{13}C amounts forage (e.g. Fizet et al., 1995; Drucker et al., 2003, 2010; Bocherens et al., 2011). The $\delta^{15}N_{\text{coll}}$ values of the three species of large mammals ranged from 1.0 to 8.9‰ with typically higher values for the mammoths (8.1 and 8.9‰) than for the reindeer (1.0–4.6‰). However, the horses showed a surprisingly large range of variation, from 3.4 to 8.7‰, leading to some overlap with the $\delta^{15}N_{\text{coll}}$ values of the mammoths. A difference of ca. 5‰ between the extreme values of the horse could be compared to the difference between two trophic levels and reflected an impressive variability possibly of the ^{15}N amounts of the consumed plants. Except for one specimen that had a $\delta^{15}N_{\text{coll}}$ value of 3.4‰, the horses of Geißenklösterle showed higher ^{15}N abundances in their collagen than those expected based on the reindeer of the site. The highest horse $\delta^{15}N_{\text{coll}}$ value was even comparable to those of the mammoths. For this last case, the consumption of the same plants as those foraged by the mammoths seems to be a plausible hypothesis and the intermediate values found for the other horses would reflect a mixed-diet between the mammoth-like forage and the expected horse diet represented by the lowest ^{15}N horse. An alternative explanation is that there is a different environmental origin of the plants and thus habitat of the high ^{15}N horses compared to the low ^{15}N one. The results of bone phosphate $\delta^{18}O$ values (Fig. 4) did not support such an environmental contrast, however, since there was no obvious correlation between the

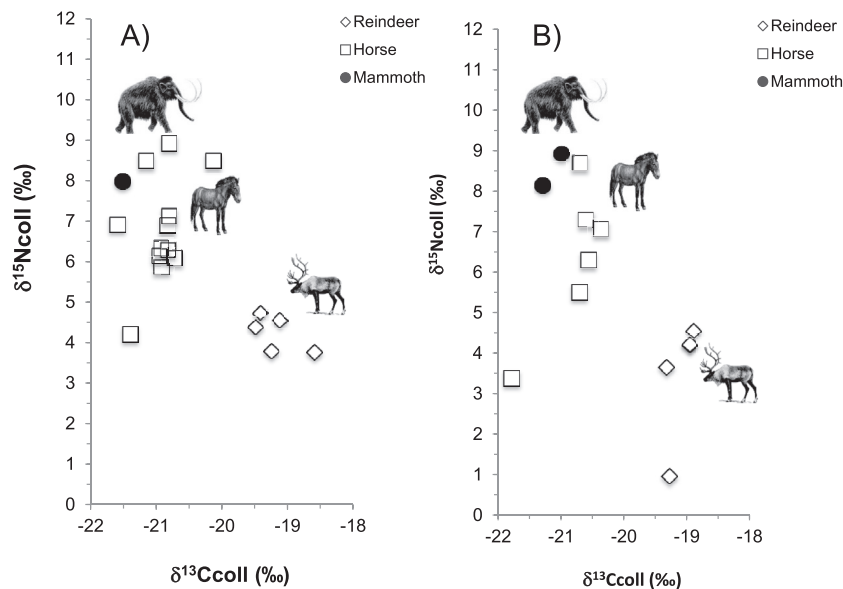


Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from Geißenklösterle in the Ach Valley during A) the Aurignacian and B) the Gravettian.

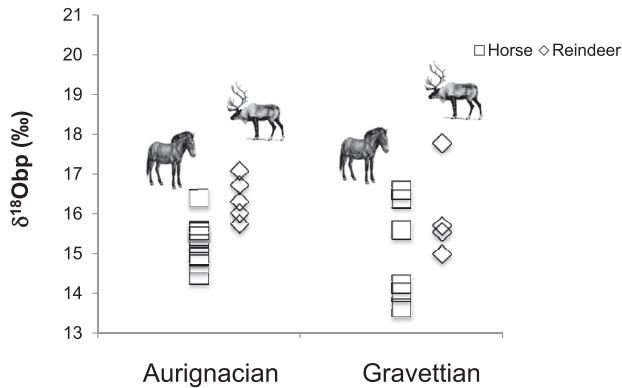


Fig. 4. $\delta^{18}\text{O}$ values of bone phosphate of reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from Geißenklösterle during the Aurignacian and Gravettian.

$\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{18}\text{O}_{\text{bp}}$ measured on the same individuals. Interestingly, the reindeer delivering the lowest $\delta^{15}\text{N}$ values (1‰ against 3.7–4.2‰ for its counterparts) also provided the highest $\delta^{18}\text{O}_{\text{bp}}$ value (17.8‰; Stephan, 1999) compared to the other reindeer (15.0–15.7‰; Stephan, 1999) and the horses (13.7–16.6‰). In this case, the specific ^{15}N signature of this reindeer could be interpreted as the consequence of a difference in habitat origin.

The isotopic analysis performed in Geißenklösterle on the Aurignacian occupation delivered results (Fig. 3A) that were quite comparable to those of the Gravettian occupation (Fig. 3B). The reindeer had $\delta^{13}\text{C}_{\text{coll}}$ values ranging from -19.5 to -18.6 ‰, while the horse $\delta^{13}\text{C}_{\text{coll}}$ values varied from -21.6 to -21.1 ‰. The measured mammoth bone yielded $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values of -21.5 and 8.0 ‰, respectively. These results were close to those of the horse samples showing a range of 5.9 – 8.9 ‰ in $\delta^{15}\text{N}_{\text{coll}}$ values. As in the Gravettian, only one Aurignacian horse produced a $\delta^{15}\text{N}_{\text{coll}}$ value (4.2‰) comparable to those of the coeval reindeer (3.8–4.7‰). The $\delta^{18}\text{O}_{\text{bp}}$ values of the horse varied from 14.5 to 16.4‰, with the lowest values overlapping those of the reindeer $\delta^{18}\text{O}_{\text{bp}}$ (15.8–17.1‰; Stephan, 1999). We could thus consider that the factor responsible for the high ^{15}N amounts in horse to be a long-term one, already at work during the Aurignacian.

Taken together, the $\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{18}\text{O}_{\text{bp}}$ values of the remains of mammoth, horse and reindeer were similar between the Gravettian layers and the preceding Aurignacian occupations. This similarity implies that the same environmental and climatic conditions prevailed over this duration. The reindeer tibia from layer Ib was the only exception with a significantly lower $\delta^{15}\text{N}_{\text{coll}}$ and higher $\delta^{18}\text{O}_{\text{bp}}$ values than those of all the other ungulate specimens, including reindeer. Interestingly, Barth et al. (2009) have identified an antler adze found in the Gravettian layer of the neighboring site of Hohle Fels that derives from a male reindeer. Bulls shed their antlers during fall, a season for which there is no indication of human occupation in the Early Paleolithic in the Ach Valley. It was therefore concluded that this artifact was of a non-local origin (Barth et al., 2009), a conclusion that we could also invoke for the layer Ib reindeer tibia.

3.2. The Gravettian at the Abri Pataud (Dordogne, France)

As far as the early phases of Gravettian are concerned, the isotopic signatures of the horse (Le Flageolet I, level V and VII and Combe-Saunière 1, level VI) and reindeer (Abri Pataud, level 5) fitted the expected distribution in $\delta^{13}\text{C}_{\text{coll}}$ values (-21.0 to -20.0 ‰ and -19.2 to -18.9 ‰, respectively) and expected equivalent range in $\delta^{15}\text{N}_{\text{coll}}$ values (3.0–5.9‰ and 4.1–6.0‰, respectively). The mammoth of level 5 of the Abri Pataud had $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values ranging from -21.2 to -20.3 ‰ and 10.0 to 11.1 ‰, respectively (Fig. 5B). On average, the difference in ^{15}N abundances between the mammoth and other ungulates is slightly higher than 5‰. However, enrichment in ^{15}N can be observed in dentine compared to bone as an effect of the milk consumption in the first months of the life of the individual (Bocherens et al., 1994). A review of the literature confirmed generally higher $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values in samples of ivory compared to bone of mammoth associated in the same archaeological site, with averaged values ranging from 0.1 to 0.7‰ in $\delta^{13}\text{C}$ and 1.3 to 1.6‰ in $\delta^{15}\text{N}$ (Appendix A; data from Jacobi et al., 2010; Richards et al., 2012). Thus, a ca. 1‰ shift to higher $\delta^{15}\text{N}_{\text{coll}}$ values could be expected between ivory and bone originating from the same mammoth group. Altogether, the isotopic results of the Early Gravettian occupation of Dordogne comply with those of a classical mammoth steppe ecosystem.

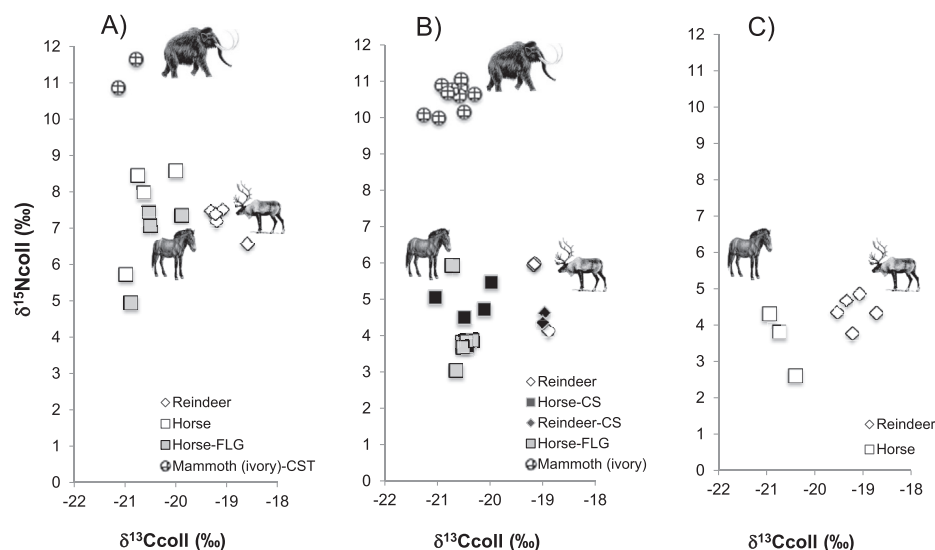


Fig. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from the Abri Pataud in Dordogne during A) the Aurignacian, B) the Early Gravettian, C) the Final Gravettian.

The horse and reindeer of the Early Aurignacian at Pataud (layer 10–13) and Le Flageolet I (layer XI) gave also the same range of $\delta^{13}\text{C}_{\text{coll}}$ values as their Gravettian counterpart from the same region (-21.1 to -19.9‰ for horse, -19.3 to -18.6‰ for reindeer; Fig. 5A). However, their $\delta^{15}\text{N}_{\text{coll}}$ values were significantly higher with the horse ranging from 4.9 to 8.6‰ and the reindeer from 6.6 to 7.5‰ . Except for the two horses with the lowest ^{15}N levels (4.9 and 5.7‰ for $\delta^{15}\text{N}_{\text{coll}}$), there is no overlap in the ^{15}N abundances for the same species between the two periods. Such high $\delta^{15}\text{N}_{\text{coll}}$ values in the Aurignacian were already demonstrated in Bocherens et al. (2014) in the Dordogne region. Among other hypotheses, a peak of aridity during the Aurignacian period was evoked to explain the high ^{15}N amounts observed at that time on the collagen of reindeer, red deer, large bovine and horse (Bocherens et al., 2014). Indeed, horse from the Aurignacian of Le Flageolet I showed rather higher $\delta^{18}\text{O}_{\text{bp}}$ values than those of the Gravettian of the same site and the

except for one sample in layer 2 which exhibited the highest value found for this proboscidean (20.4‰ against 15.4 – 18.6‰ ; Fig. 6). Since the tusk grows by accretion of successive layers of dentine, a limited portion of it could correspond to a short period of time during which the water source was different. As for the nitrogen, the oxygen could be obtained from milk derived from the mother's body water, which were enriched compared to the meteoric water (Wright and Schwarcz, 1998). Unfortunately, the mammoth ivory samples of layer 2 of the Abri Pataud contained no collagen and a comparison between the $\delta^{18}\text{O}_{\text{bp}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values, which should be positively correlated in the case of the nursing effect, was not possible. The sequential analysis of $^{18}\text{O}_{\text{bp}}$ along the section of the tip of a juvenile mammoth from the site of Předmostí revealed values up to 4‰ higher in the earlier formed layer than in the later formed ones (Table 4, Appendix B). Thus, the nursing effect could account for the higher ^{18}O ivory in layer 2 compared to layer 5.

Table 4
Results of stable isotope analyses of collagen ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$, $\delta^{34}\text{S}_{\text{coll}}$) and bone phosphate ($\delta^{18}\text{O}_{\text{bp}}$) of a mammoth (*Mammuthus primigenius*) tusk at Předmostí I in Moravia (Czech Republic). The carbon, nitrogen and sulphur composition of the collagen is given through elemental composition (C_{coll} , N_{coll} , S_{coll}) and atomic ratio ($\text{C}/\text{N}_{\text{coll}}$, $\text{C}/\text{S}_{\text{coll}}$, $\text{N}/\text{S}_{\text{coll}}$). 1=Bocherens et al. (2015).

Lab-nr.	Species	Part	C_{coll} (%)	N_{coll} (%)	$\text{C}/\text{N}_{\text{coll}}$	$\delta^{13}\text{C}_{\text{coll}}$ (‰)	$\delta^{15}\text{N}_{\text{coll}}$ (‰)	S_{coll} (%)	$\delta^{34}\text{S}_{\text{coll}}$ (‰)	$\text{C}/\text{S}_{\text{coll}}$ (%)	$\text{N}/\text{S}_{\text{coll}}$ (%)	$\delta^{18}\text{O}_{\text{bp}}$	$^{13}\text{C}/^{15}\text{N}$	^{34}S	^{18}O
TSK II-1	Mammoth	Tusk	23.3	7.6	3.6	-20.9	9.6					12.8	1		This work
TSK II-2	Mammoth	Tusk										15.1			This work
TSK II-3	Mammoth	Tusk	38.6	13.9	3.2	-20.7	9.8	0.16	3.5	627	194	13.1	1	1	This work
TSK II-4	Mammoth	Tusk										13.9			This work
TSK II-5	Mammoth	Tusk										11.2			This work
TSK II-6	Mammoth	Tusk										13.0			This work
TSK II-7	Mammoth	Tusk	25.2	8.4	3.5	-21.8	8.2					14.1	1		This work

Abri Pataud. This suggests that the climate was more arid during the Aurignacian than later in time.

The mammoth ivory of the Early Aurignacian occupation of the Abri Castanet also showed $\delta^{15}\text{N}_{\text{coll}}$ values higher than those of the Gravettian ivory of Pataud, perhaps to a lesser extent than the difference measured on the other ungulates (Fig. 5A and B). In any case, a change in the environmental conditions of the ecosystem is the most likely explanation for such a general shift toward lower ^{15}N abundances during the Gravettian. The $\delta^{18}\text{O}_{\text{bp}}$ values of the mammoth of Pataud were similar to those of horses of the same layer,

Abri Pataud offered the opportunity to investigate further the evolution of the isotopic signature through the recent excavations of layer 2 corresponding to a Final Gravettian occupation (Fig. 5C). Compared to the Early Gravettian, the horse and reindeer $\delta^{13}\text{C}_{\text{coll}}$ (-21.0 to -20.4‰ for horse, -19.5 to -18.7‰ for reindeer) and $\delta^{15}\text{N}_{\text{coll}}$ values (2.6 – 4.3‰ for horse, 3.8 – 4.9‰ for reindeer) were similar. The layer 2 of the Abri Pataud has been attributed to the Final Gravettian (previously named Protomagdalenian) techno-complex, an industry also found in a few sites such as Les Peyrugues in Lot and Le Blot in the Massif Central. Here too stable isotope investigations have been conducted (Drucker et al., 2003 and Appendix D). Compared with the data of the layer 2 at Abri Pataud, the reindeer from Les Peyrugues yielded a very similar isotopic range (-19.5 to -18.7‰ for $\delta^{13}\text{C}_{\text{coll}}$, 3.3 – 5.6‰ for $\delta^{15}\text{N}_{\text{coll}}$). At Le Blot, most of the $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values varied between -19.3 and -18.9‰ and 3.6 – 4.3‰ , respectively, which fits the range described above. Only one specimen of reindeer showed higher $\delta^{13}\text{C}_{\text{coll}}$ and lower $\delta^{15}\text{N}_{\text{coll}}$ values (-18.5 and 2.9‰ , respectively), which could reflect the colder temperature and higher lichen availability in the mountainous context of the Massif Central. The Final Gravettian horses of Le Blot yielded also some slightly higher $\delta^{13}\text{C}_{\text{coll}}$ (-21.3 to -20.0‰) and lower $\delta^{15}\text{N}_{\text{coll}}$ (1.8 – 3.7‰) values compared to Abri Pataud, but, as for reindeer, the values are still close between the two sites. The large herbivores analyzed so far for the Final Gravettian occupation at Pataud do not reflect significantly different environmental setting compared with the Early Gravettian at the same place or to other coeval occupations at other regions in southern France.

3.3. The Early Gravettian at Geißenklösterle and the Abri Pataud

When considering the Early Gravettian period over space, the isotopic signatures of horse, reindeer and mammoth appeared to

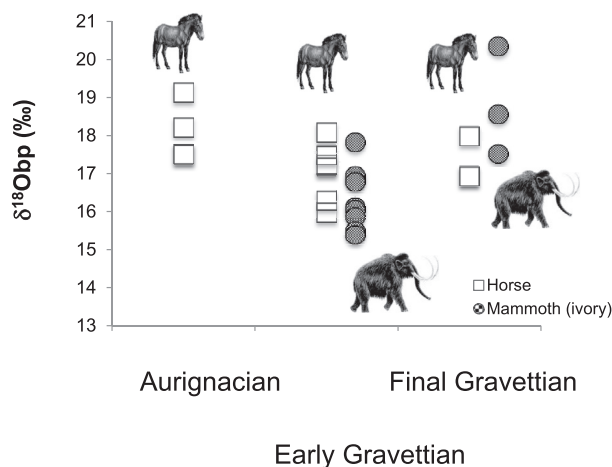


Fig. 6. $\delta^{18}\text{O}$ values of bone phosphate of horse (*Equus* sp.) and mammoth (*Mammuthus primigenius*) from the Abri Pataud during the Aurignacian, the Early Gravettian, and the Final Gravettian.

reflect the ecosystem specificities of the Ach and Dordogne regions. First of all, the reindeer from both regions showed a significant overlap in their $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values, while those of horse displayed a high variability within each region, as well as between the different areas. The low inter-individual variability in the isotopic values of the reindeer could be explained not only by the low number of analyzed data, but also by the migratory behavior of this species. This allowed them to average the isotopic signature of their forage on a large scale among large numbers of individuals. Higher ^{15}N abundances were found in the mammoth of the Abri Pataud compared to their counterparts from Geißenklösterle, but this could be due to the difference in the measured tissues, ivory in the first case and bone in the second. Mean $\delta^{18}\text{O}_{\text{bp}}$ values of the horse were about 2‰ higher in the Dordogne than in the Ach Valley. The continental effect corresponding to the isotopic depletion of the water vapor moving inland probably accounts for the ^{18}O shift between the two regions, and the difference in the $\delta^{18}\text{O}$ values of the underground water is indeed of the same range (Arppe and Karhu, 2010).

The significant difference in the horse $\delta^{15}\text{N}_{\text{coll}}$ values between the Ach Valley and Dordogne was due to the unusually high values of the species in the site of Geißenklösterle. This isotopic anomaly was already occurring during the Aurignacian and could tentatively be explained by a specificity of the available forage. Some of the plants consumed by the horse may have high ^{15}N abundances either because of special local environmental conditions similar to those of the usual foraging of the mammoths or because they corresponded to the plants usually foraged by the mammoths. Interestingly, Bocherens (2003) hypothesized that the ^{15}N amounts of mammoth reflect their specialization in the consumption of mature grasses from disturbed areas. In parallel, Zimov et al. (2012) insisted on the positive feedback role of the mammoth on the forage quantity and quality, more particularly, on the key role of animal density on the soils and vegetation. A higher animal density leads to higher soil and vegetation productivity through the input of animal carcasses, urine and feces, trampling action and accelerated decomposition in the animal's stomachs (Hobbs, 2006). Zimov et al. (2012) postulated that only a part of the forage was consumed during summer and the rest was eaten during winter, giving the opportunity for some plants to reach very mature states. The niche partitioning, reflected by specific isotopic signatures of herbivores, would have been a way to avoid direct diet competition among the high diversity of large ungulates of the mammoth steppe. Reindeer, for instance, were able to sustain themselves on high amounts of lichen, as confirmed by the high ^{13}C abundances of their collagen, while this plant was avoided by other herbivores due to its toxicity (e.g. Fizet et al., 1995; Drucker et al., 2003, 2010; Bocherens et al., 2011). In contrast, the high ^{15}N abundances of the horse of Geißenklösterle suggest a possible direct competition with mammoth for the same forage and/or forage growth conditions. It could well be that the mammoths were not fully occupying their niche, although this niche was still available as confirmed by their unchanged isotopic signatures. Environmental impact would thus not be a convincing cause for such a pattern and we favor instead the hypothesis of a declining mammoth population, probably due to human pressure. Reduced numbers of mammoth after repeated spring hunting on juvenile animals, as evidenced by cut marks on calves (Münzel, 2001, 2014; Barth et al., 2009), would have left the opportunity open for horse to access forage resources normally consumed by mammoth during the rest of the year, or from year to year, depending on the recovery of the mammoth population. According to this scenario, the interspecific competition between horse and mammoth would be replaced by an intra-specific competition among horse individuals, some of them occupying the niche partially vacated by the mammoths.

The ecology of the mammoth in the Early Gravettian seems to be mainly undisturbed in Dordogne. The interpretation of the isotopic data of mammoths in Dordogne could be complicated by the nature of the analyzed tissue, however, this being ivory instead of bone. Some questions could be raised about the geographical and chronological origin of the pieces of ivory brought to the site of Pataud. In a region where the mammoth bone remains are not common (e.g. Heckel, 2009; Álvarez-Lao and García, 2012), might the material have come from another area or even older period of time? To test this last possibility, direct radiocarbon dating was conducted on two ivory samples from layer 5 that were formerly analyzed for stable isotopes. The results were $27,610 \pm 170$ BP (GrA-56410), $31,700\text{--}31,100$ cal BP (95.5% probability) and $28,050 \pm 170$ BP (GrA-56409), $32,490\text{--}31,380$ cal BP (95.4% probability). The results are in excellent agreement with determinations obtained on bone collagen for the same layer (Higham et al., 2011).

Even if the possibility of subfossil ivory use can be excluded, the local origin of the ivory remains to be investigated. Unfortunately, the isotopic analysis of strontium, a classic tracker of mobility, is not recommended on bone and dentine, because it is more sensitive to diagenetic alteration of the biogenic strontium than the highly crystalline and compact tooth enamel (Budd et al., 2000; Hoppe et al., 2003). Instead, we analyzed sulphur-34 because the ^{34}S abundance in plants consumed by animals should be primarily controlled by the geochemical composition of the underlying bedrock. The $\delta^{34}\text{S}_{\text{coll}}$ values of the Gravettian reindeer from the Abri Pataud varied from 6.2 to 15.2‰ and encompassed the values of the coeval horses (11.7 and 12.7‰; Fig. 7). These values are likely to reflect results for animals dwelling in the surroundings of the site. Most of the $\delta^{34}\text{S}$ values of the mammoths of the layer 5 at Pataud ranged from 11.1 to 13.6‰, fitting the range of the horse and reindeer. Two samples of ivory exhibited lower values: one still compatible with a local signature (7.1‰), while the other (2.6‰) was clearly out of the range observed on the hunted ungulates of the Abri Pataud. On another hand, this last $\delta^{34}\text{S}$ value is very comparable to those found at Geißenklösterle, which range from -2.2 to 3.6 ‰ with a significant overlap among reindeer, horses and mammoths. The reindeer from Geißenklösterle exhibiting outlier $\delta^{15}\text{N}_{\text{coll}}$ and $\delta^{18}\text{O}_{\text{bp}}$ values yielded an outlier $\delta^{34}\text{S}_{\text{coll}}$ value of 11.9‰ that is suggestive of a foreign origin. Interestingly enough, the $\delta^{34}\text{S}_{\text{coll}}$ measured on a mammoth tusk from the site of Předmostí yielded a similar value to those of the Ach Valley (3.5‰). In addition, the reindeer $\delta^{34}\text{S}_{\text{coll}}$ values (-0.4 and 0.8 ‰) of Předmostí were similar to those of Geißenklösterle (Bocherens et al., 2015). Hence, the low ^{34}S mammoth of Pataud is close to the values observed in the more eastern Gravettian sites, which are significantly different from those of the Abri Pataud. Of course, we cannot state on this evidence a link between these various locations in western and central Europe. Most of the ivory of layer 5 at the Abri Pataud is probably derived from the close surroundings of the site, but a small proportion appears to have come from distance.

It is difficult, based on limited evidence, to posit a precise location from which this material could have originated. There are many other Gravettian sites, of course, and only some have been investigated isotopically. In Belgium, for instance, at Maisières-Canal, there is an important site that has some stable isotope evidence (Jacobi et al., 2010). The dates published for Maisières-Canal (Jacobi et al., 2010) place it in the same chronological range. However, the $\delta^{15}\text{N}_{\text{coll}}$ values of the mammoths, either bone or ivory, the horse and the reindeer were lower than in the Ach Valley and Dordogne, and the reindeer values were somewhat higher in $\delta^{13}\text{C}_{\text{coll}}$ values (Fig. 8). The latter results suggest perhaps a higher availability of lichen in the ecosystem of Maisières-Canal, which is consistent with the more accentuated periglacial conditions reflected by the low ^{15}N abundances. From an isotopic point of view,

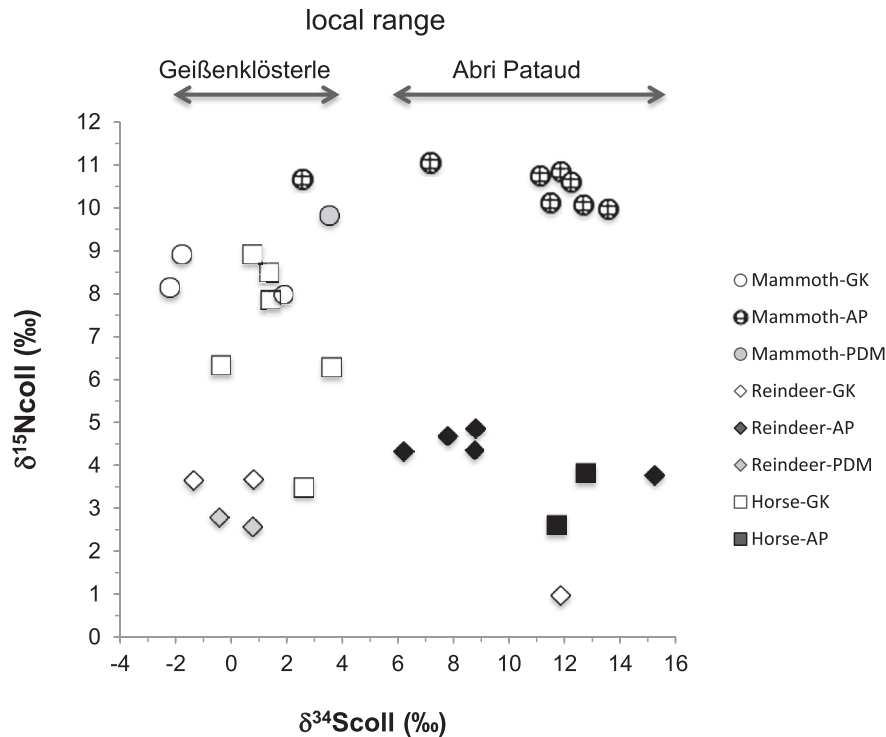


Fig. 7. $\delta^{34}\text{S}$ values of bone collagen of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from Geißenklösterle (GK), the Abri Pataud (AP) and Předmostí (PDM).

Maisières-Canal resembles the classic mammoth steppe from higher latitudes, where the three main encountered ungulates mammoth, horse and reindeer, show a clear separation and specialization in their diet and habitat. To the east of Pataud, in the Massif Central at La Vigne-Brun, a lithic industry similar to that of

Pataud level 5 and the Gravettian layers of Geißenklösterle has been observed (Digan et al., 2008). Unfortunately, attempts to isolate collagen from the horse teeth at the site led to negative results due to the high rate of organic matter loss (Appendix C). The very poor condition of the collagen preservation precludes further radiocarbon dating sadly. Hence, the limited isotopic data available so far do not indicate any exchange of ivory between Belgium and either Dordogne or the Ach Valley.

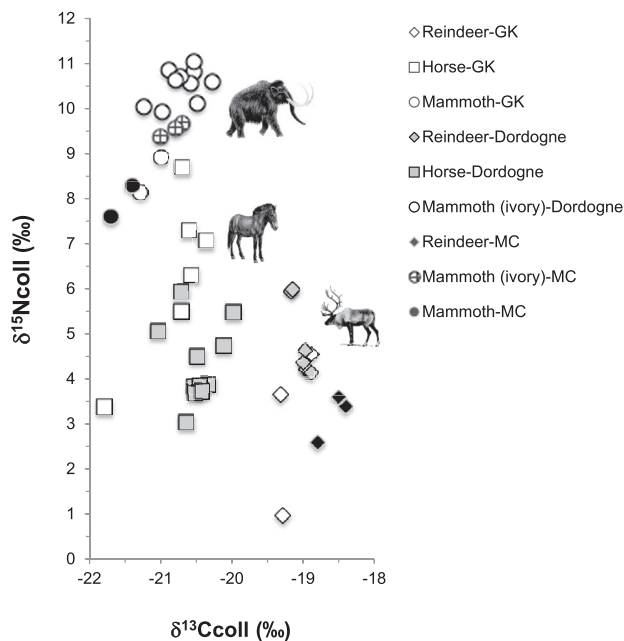


Fig. 8. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen of mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) and horse (*Equus* sp.) from Geißenklösterle, Dordogne and Maisières-Canal (Jacobi et al., 2010).

4. Conclusions

The Gravettian occupations of the Ach Valley have yielded assemblages that show that the mammoth occupied a major position in the procurement patterns of raw material and sometimes for dietary subsistence. Mammoth, even if rare in the number of bone remains, was also a source of ivory artefacts for the Gravettian populations of Dordogne. The result of multi-isotopic ecological tracking methods, based on ^{18}O amounts in bone phosphate and ^{13}C , ^{15}N and ^{34}S abundances in bone collagen, points to some interesting changes in the ecology of this key species of mega-herbivore. The impact of climatic change, considered as a major trigger in the decline of the mammoth in western Europe (e.g. Palkopoulou et al., 2013), is reflected in the chronological variation in ^{15}N and ^{18}O of associated ungulates in the Dordogne between the Aurignacian and the Early Gravettian. A different pattern is observed in the Ach Valley through the fauna of Geißenklösterle, where an apparent niche overlap between horse and mammoth is documented by the unusual ^{15}N abundances in horse collagen as high as those found in mammoth collagen. The decline of the mammoth in the Ach Valley is not explained by clear environmental factors, since the ecological niche reflected by stable isotopes abundances remains unchanged. Instead, it is hypothesized that the “mammoth niche” was partially vacant, a situation that benefited the horse. This apparent depletion of mammoth

populations in the absence of environmental change in general and of the niche of the mammoth in particular, together with the evidence of hunting of juvenile mammoths in the Ach Valley, invites us to consider the possibility that humans have played an important role in the demise of the mammoth, at least on the local scale of Swabian Jura. Finally, the ^{34}S measurements revealed a significant contrast between Dordogne and the Ach Valley. Sulphur-34 may offer the unprecedented opportunity to pinpoint the import of artefacts or raw material, and thus improve our knowledge of the bone and ivory procurement system of the Gravettian populations. Such a multi-isotopic approach appears to be a singularly useful tool in attempting to disentangle the impact of natural *versus* human variables in the context of the Gravettian mammoth steppe.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2014.11.028>.

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