Hervé Bocherens
Institut des Sciences de l'Evolution, Université Montpellier 2

Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna

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The ecological structure of the mammoth steppe fauna remains quite unclear. Stable isotope biogeochemistry of fossil collagen can help determining the discrimination in food resources among different herbivorous species, due to differences in carbon and nitrogen isotopic signatures in plants. Especially differences in nitrogen sources for different plants, such as grass, bushes and heather, lead to distinct isotopic signatures. Mammoths present more carbon-13-depleted and nitrogen-15-enriched collagen when compared to other herbivorous species, in all studied sites in Europe, Siberia and Alaska. One interpretation is that these isotopic differences reflect different dietary choices by herbivores, reindeer browsing on lichens, horse, woolly rhinoceros and bison grazing fresh grass, and mammoth consuming dry grass, with higher nitrogen-15 content than other plant resources. The low carbon-13 amounts of mammoth collagen might be due to fat utilisation in this species. This distinction between different herbivorous species leads to the potential to identify prey species of predators, including humans.

Correspondence: Hervé Bocherens, Institut des Sciences de l'Evolution, Université Montpellier 2, France; e-mail: bocheren@isem.univ-montp2.fr

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INTRODUCTION

The so-called mammoth steppe is a well-defined paleoecological unit covering middle and southern Europe, northern Asia and Alaska during the Upper Pleistocene cold phases. It was boarded to the north-west and to the east by icecaps, and was characterised by a rather homogeneous faunal assemblage dominated by *Mammuthus*, *Bison* and *Equus* (Guthrie 1982). How this cold and apparently poor ecosystem could sustain such a large diversity of species with many gigantic elements has been the subject of abundant speculation. Especially the plant cover has been either considered similar to present-day arctic tundra (e.g. Cwynar & Ritchie 1980; Elias *et al.* 1996) whereas some data suggest a much richer 'steppe-tundra' environment with no modern equivalent (e.g. Anderson *et al.* 1994; Guthrie 1982). It is the goal of this work to use isotopic biogeochemistry in order to further investigate the structure of this ecosystem.

PRINCIPLES

Carbon-13

Carbon isotopic compositions (expressed as ^{13}C values *) in ecosystems reflect primarily the photosynthetic pathways and environmental parameters of the plants at the basis of the food webs. In terrestrial plants, the two major photosynthetic pathways, i.e. the so-called 'C3' and 'C4' pathways, lead to clearly diffe-

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* Isotopic abundances are expressed as δ (delta) values, as follows: $\delta^{E}X = (R_{sample}/R_{standard} - 1).1000$ (‰), where X stands for C or N, E stands for 13 or 15 respectively, and R stands for the isotopic ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$ respectively.

rent isotopic discriminations. Both types of plants are ^{13}C-depleted relative to their source of inorganic carbon, atmospheric CO_2 with a $\delta^{13}C$ value around -8 ‰, but C4-plants are much less depleted than C3-plants ($\delta^{13}C$ = -27.1 ± 2.0 ‰ and $\delta^{13}C$ = -13.1 ± 1.2 ‰ for C3 and C4-plants respectively: O'Leary 1981). On a world-wide scale, most C4-plants are grasses from warm areas, and they are distributed in regions where the growing season is the warm one (monsoon system), whereas C3-plants are all the trees under any climatic conditions, as well as herbaceous plants from temperate and cold areas, where the growing season is cool. In the Euro-Siberian region, C4-plants are extremely scarce today (Mateu Andrès 1993). Thus the carbon isotopic variations observed in arctic and temperate areas are mainly due to isotopic variations in C3-plants. Less important in biomass but locally significant in the steppic areas are some C4 species, which are halophytes adapted to saline environments (Winter 1981; Frey & Kürschner 1983). Among C3-plants, some environmental conditions lead to different carbon isotopic compositions (Tieszen 1991; Heaton 1999; Fig. 1). The main environmental causes for ^{13}C-depleted plant biomass are linked to dense forests. Indeed, in closed forested environments where the CO2 available to understorey plants is ^{13}C-depleted relative to the general atmosphere due to the contribution of CO_2 generated by respiration and organic matter decomposition and where light intensity is low, plants exhibit $\delta^{13}C$ values lower than -28 ‰ (e.g. Medina & Minchin 1980; Van der Merwe & Medina 1991; Balesdent *et al.* 1993). Increase in CO_2 partial pressure, decrease of temperature and depletion in nutrients also lead to low $\delta^{13}C$ values in C3-plants (Tieszen 1991) but such factors are more difficult to link unequivocally to a given environment. On the other hand, the main environmental causes for high $\delta^{13}C$ values in plants are water and saline stress, which lead to less isotopic fractionation of carbon in C3-plants, presenting $\delta^{13}C$ values up to -20 ‰ (Guy *et al.* 1986). Decrease in CO_2 partial pressure also lead to higher $\delta^{13}C$

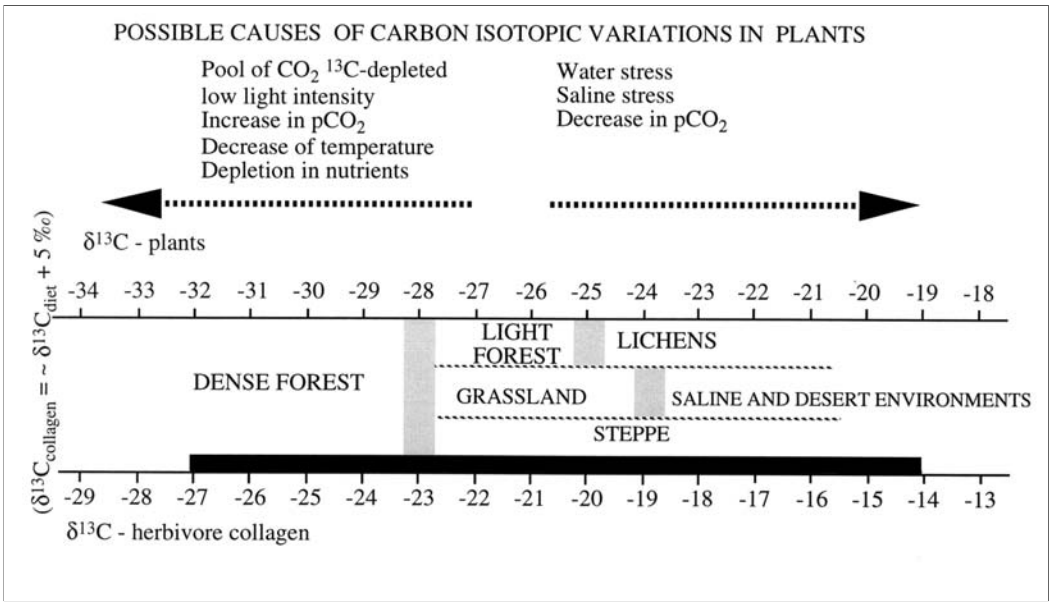

Figure 1 Range of herbivore collagen $\delta^{13}C$ values measured in modern arctic, temperate and steppic areas, with possible causes of carbon isotopic variations in plants and herbivores. Values are compiled from Nelson *et al.* (1986), Bocherens *et al.* (1994, 1996, 2000), Rodière *et al.* (1996).

values in C3-plants. Variations in atmospheric CO_2 partial pressure have been documented during the glacial/interglacial cycles (Neftel *et al*. 1982; Leuenberger *et al.* 1992) and may have influenced the $\delta^{13}C$ values of C3-plants (Leavitt & Danzer 1992). A type of plants important in tundra environments is lichen (Bliss & Richards 1982), and lichens are usually $\delta^{13}C$-enriched relative to co-eval vascular C3-plants (Fizet *et al.* 1995; Maguas & Brugnoli 1996; Heaton 1999). It is noteworthy that the carbon isotopic composition of atmospheric CO_2 has changed significantly since the industrial revolution, about 150 years ago. The addition of CO_2 evolved from fossil fuel combustion and deforestation with low $\delta^{13}C$ values led the $\delta^{13}C$ values of atmospheric CO_2 to decrease from around -6.5 ‰ in 1850 to -8 ‰ nowadays (Marino & McElroy 1991). This isotopic shift will have to be considered when comparison will be attempted between $\delta^{13}C$ values measured on fossil and modern specimens.

The standard, internationally defined, is a marine carbonate (PDB) for carbon and atmospheric nitrogen (AIR) for nitrogen. Analytical error is 0.1 ‰ and 0.2 ‰ for $\delta^{13}C$ values and d15N values, respectively.
The carbon isotopic compositions of the plants are reflected in the tissues of their consumers, with an isotopic shift, which is mainly linked to the analysed tissue (DeNiro & Epstein 1978). The average $\delta^{13}C$ value of an organism's body is similar to that of the average diet, but its different biochemical fractions present consistently different carbon isotopic compositions, due to fractionation during the metabolic pathways (Deines 1980). For instance, carbohydrates present globally a $\delta^{13}C$ value similar as the whole body, whereas lipids are depleted (around 4 ‰) and proteins are enriched (around 2 ‰) relative to the whole body (DeNiro & Epstein 1978). The tissue of interest here is collagen in bone and dentine due to its potentials for long-term preservation. Soft tissues may also be exceptionally preserved in very dry or very cold environments, for instance in the form of mummies (e.g. Guthrie 1990; Ukraintseva 1993), and may be a support for carbon and nitrogen isotopic signatures (Bombin & Muehlenbachs 1985; Bocherens *et al*. 1996). The actual value of the isotopic shift between the carbon isotopic composition of diet and that of the analysed tissue, collagen, is crucial for interpreting the measured values. It has been investigated through laboratory experiments (e.g. DeNiro & Epstein 1978; Hare *et al*. 1991; Ambrose & Norr 1993; Tiezsen & Fagre 1993) as well as in the field (e.g. Vogel 1978; Van der Merwe 1982). Recently, some very well controlled dietary experiments on rodents have obtained key results regarding the relationship between dietary and measured carbon isotopic compositions (Ambrose & Norr 1993; Tieszen & Frage 1993). Both studies have clearly demonstrated that collagen presents $\delta^{13}C$ values directly linked to those of the protein fraction of the diet. In the case where all the biochemical fractions, i.e. lipids, carbohydrates and proteins, come from an isotopically homogeneous source, which is usually the case for herbivores, collagen is enriched around 5 ‰ relative to the average diet. In mummified soft tissues, the carbon isotopic composition depends on the relative proportions of the analysed biochemical fractions. Pure muscle proteins are around 3 ‰ enriched relative to the average diet (Bombin & Muehlenbachs 1985) whereas the presence of lipids will lead to lower $\delta^{13}C$ values, thus obscuring the interpretation of the dietary isotopic signal (Bocherens *et al*. 1996). For these reasons, it is recommended to work on pure biochemical fractions for ancient material.

Nitrogen-15

Contrary to carbon, a significant enrichment occurs between an organism's diet and its body, leading to $\delta^{15}N$ values around 3 to 4 ‰ higher in the body than in the average diet (Minagawa & Wada 1984). In a linear simple trophic chain, the collagen $\delta^{15}N$ values are directly linked to the trophic level. However,

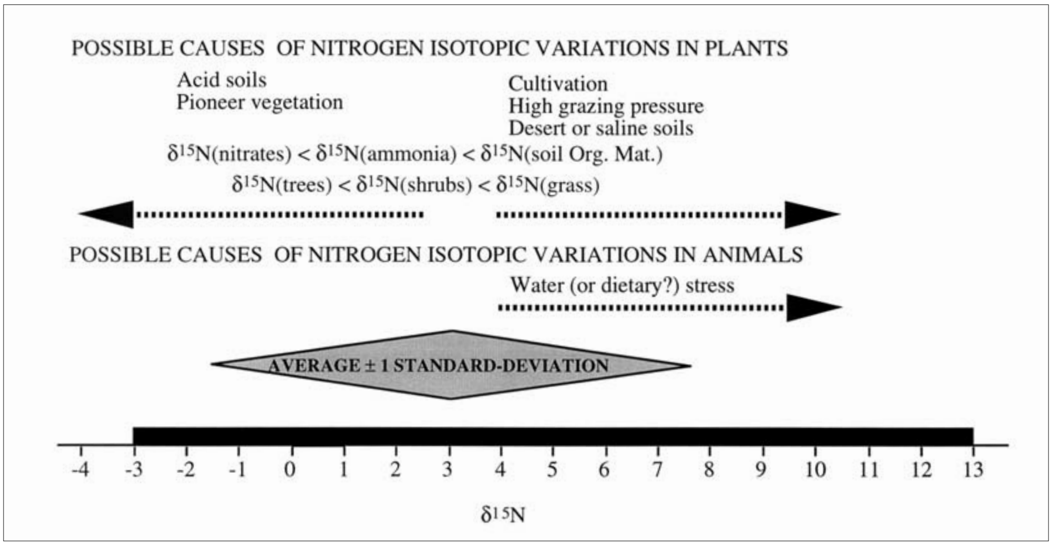

Figure 2 Range of herbivore collagen δ^{15}N values measured in modern arctic, temperate and steppic areas, with possible causes of nitrogen isotopic variations in plants and herbivores. Values are compiled from Nelson *et al.* (1986), Bocherens *et al.* (1994, 1996, 2000), Rodière *et al.* (1996).

when plant material with different δ^{15}N values coexist, the dietary choice of different herbivorous species will potentially lead to different nitrogen isotopic signatures, at a same trophic level. Several environmental factors are known to affect plant δ^{15}N values, but they are not as easy to categorise in ecosystems as for carbon (Fig. 2). The lowest δ^{15}N values are found on acid soils (e.g. Mariotti *et al*. 1980, Rodière *et al*. 1996) and for pioneer vegetation (e.g. Hobbie *et al*. 1998). On the contrary, factors such as cultivation (Riga *et al*. 1971), high grazing pressure (e.g. Schulze *et al.* 1998) and salinity (e.g. Page 1995) lead to high δ^{15}N values in plants.

A case where a relationship exists between ecological factors and plant δ^{15}N values is the arctic tundra and boreal forest (Fig. 3). In arctic plants, the use of various nitrogen resources by different ecological types of plants due to specific mycorrhizal associations leads to different isotopic compositions, allowing a clear isotopic discrimination between trees, shrubs and grass (Schulze *et al.* 1994; Michelsen *et al.* 1996). In an other study performed in northern Sweden, increasing δ^{15}N values were measured between shrub, tree and grass (Högberg *et al.* 1996).

Independently of dietary factors, a relationship has been found between herbivore d15N values and annual rainfall: collagen d15N values increase with aridity (Heaton *et al.* 1986, Sealy *et al*. 1987, Gröcke *et al.* 1997). Moreover, a complicating factor exists in mammals, in which the phase of suckling, with maternal milk as staple food, is isotopically distinct from the post-weaning phase, when the food is that of the adult. Since milk is one trophic level higher than adult diet, a significant enrichment in δ^{15}N will be recorded at this developmental stage, leading to δ^{15}N values in sucklings up to 4 ‰ higher than in adults for a given mammal species.

MATERIAL AND METHODS

The isotopic analyses discussed in this paper have been performed in the course of palaeoecological studies of Upper Pleistocene sites in Eurasia and Alaska during the last five years at the Laboratoire de Biogéochimie Isotopique (Paris, France) and at the Geophysical Laboratory of the Carnegie

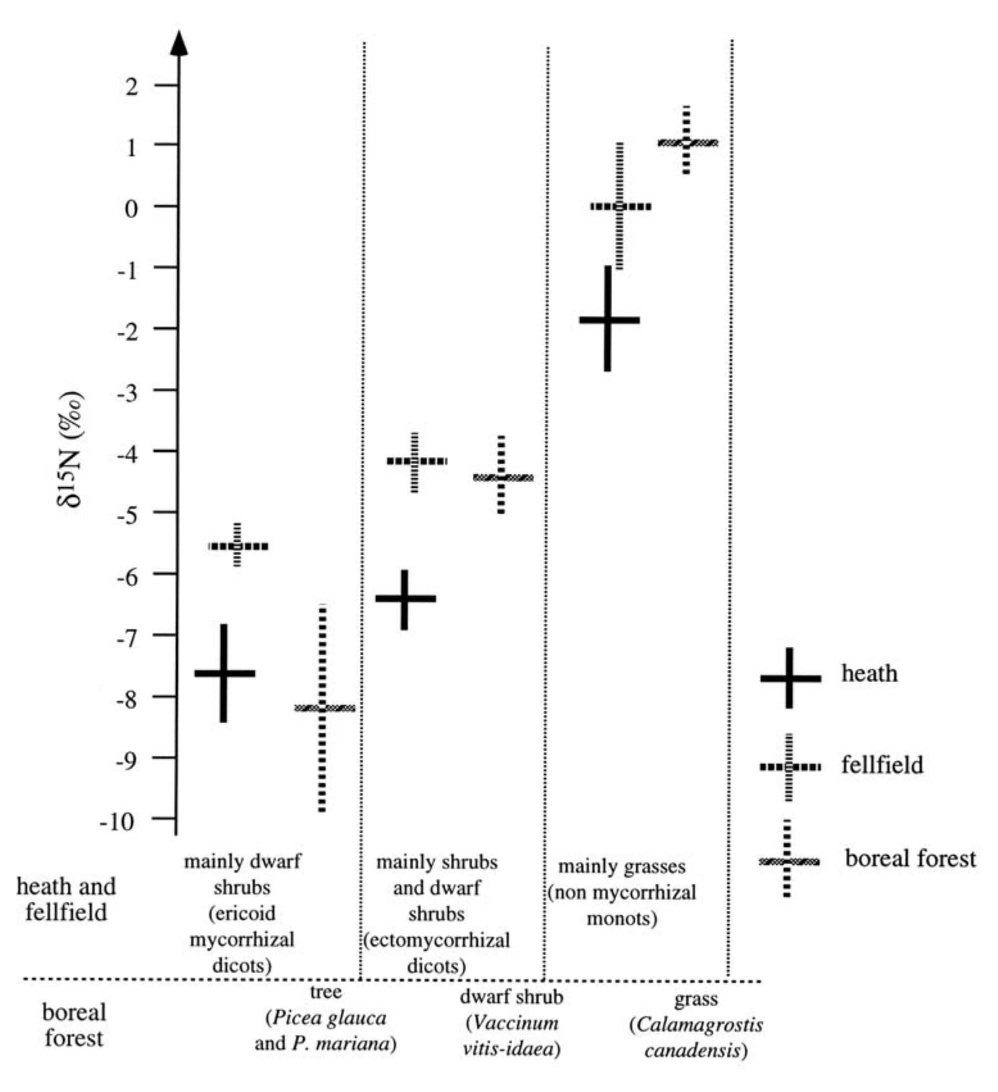

Figure 3 Nitrogen isotopic variations in plants from modern arctic and boreal ecosystems. Values are from Schulze et al. (1994), Michelsen *et al.* (1996) and Högberg *et al.* (1996).

Institution (Washington D.C., USA) (Bocherens *et al.* 1994, 1995a, 1995b, 1996, 1997; Fizet *et al.* 1995; Drucker *et al.* 1999). These values have been published in other papers, where the extraction methods and collagen integrity have been fully discussed, but they were never considered together, which is the objective of the present work.

The studied sites are located at the western and eastern ends of the mammoth steppe (Fig. 4). Sites from western Europe are Marillac (Charentes, France, around 40-45,000 yBP: Fizet *et al.* 1995), Saint-Césaire (Charente-Maritime, France, around 30-36,000 yBP: Lévêque *et al.* 1993), Kent's Cavern (Great-Britain, around 28-40,000

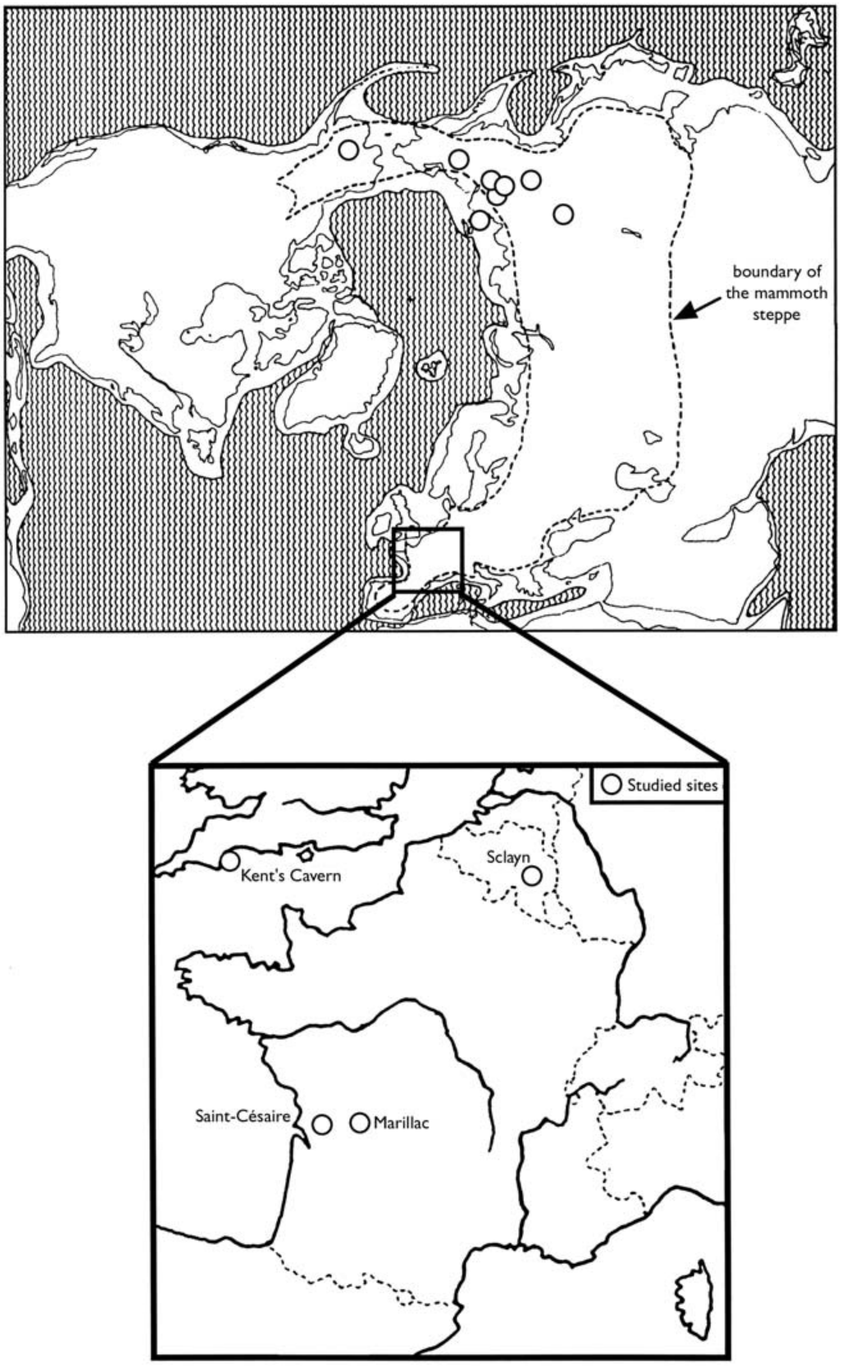

Figure 4 Location map of the studied sites.

yBP: Bocherens *et al.* 1995b) and Scladina Cave (Belgium, around 40,000 yBP for layer 1A: Bocherens *et al.* 1997). Samples from eastern Siberia and Alaska come from different areas in Yakutia (Bocherens *et al.* 1996) and from the Fairbanks area (Alaska; Bocherens *et al.* 1995a). The dates are given in the Appendix for some samples, but some other samples have unknown exact dates. However, the mammoth faunal complex is evenly distributed through time between at least 50,000 yBP and 10,000 yBP in northern Eurasia (Vasil'Chuk *et al.* 1997) and in Alaska (Guthrie 1990), thus the studied undated samples belong to this time interval. It is noteworthy that the great majority of the dated samples come from oxygen isotope stage (OIS) 3 (Fig. 5), which is an interstade during the last glacial period. Although the conditions were less extremely cold than during OIS 2 (glacial maximum) and OIS 4, the true glacial periods before and after OIS 3, the permanence of the mammoth steppe fauna has been demonstrated in Europe, Siberia and Alaska during this time interval (Guthrie 1990; Ukraintseva 1993).

The studied specimens belong to mammalian herbivore taxa, i.e. horse (*Equus* sp.), reindeer (*Rangifer tarandus*), bovine (*Bos* or *Bison*), moose (*Alces* sp.), woolly rhinoceros (*Coelodonta antiquitatis*) and woolly mammoth (*Mammuthus primigenius*). The taxonomy of equids in the mammoth steppe is quite unclear. In western Europe, caballine horses from the last glacial period are considered either as a subspecies from the modern *Equus caballus* or as a true species, such as *E. germanicus* and *E. gallicus* (Guérin 1996). In eastern Siberia and Alaska, horse taxonomy is also unclear between *E. caballus* and *E. lenensis* (Guthrie 1982) and no attempt was made to determine the exact species for the analysed specimens. However, none of the studied sample belongs to hemionine or hydruntine equids. The genera *Bos* and *Bison* are impossible to discriminate on most skeletal parts and therefore they are referred to here as bovine. The only specimen cetainly belonging to *Bison* is the sample from Yakutia. The samples from Marillac most probably belong to *Bison* as well (Fizet et *al*. 1995). Moose is either the extant *Alces alces*, or may belong to *Cervalces (Alces) latifrons*, an extinct taxon present in Alaska during OIS 3 (Guthrie 1995). Both taxa are comparable in morphological adaptations and thus most probably in habits (Guthrie 1995).

Due to the possible interference of suckling in the interpretation of nitrogen isotopic compositions as reflecting the average adult diet in herbivores discussed earlier in this paper, a choice of the analysed tissue, bone or dentine, had to be made. Indeed, tissues synthetised during the suckling phase and not totally remodelled afterwards, such as dentine, retain a higher $\delta^{15}N$ value relative to tissues formed or totally remodelled after weaning, such as bones, in a fully adult individual (Bocherens & Mariotti 1997). Thus, isotopic measurements performed for a palaeoecological purpose need to be done on adult bone. Dentine can be used only for species with teeth growing long after weaning, such as horses, bovine third molars, or mammoth molars and tusks. Dentine isotopic compositions from cervids will not be considered here due to the retention of collagen partially $\delta^{15}N$-enriched relative to the adult diet, which has been demonstrated for modern specimens of reindeer and roe deer (Bocherens *et al.* 1997) and also found on Upper Pleistocene cervid specimens (Bocherens et al. 1995b; Fizet *et al*. 1995; Drucker *et al.*1999). For woolly rhinoceros, the issue is not as clear since no test has yet been performed on collagen from dentine and bone from a same individual, modern or Pleistocene. The comparison of average bone and dentine collagen isotopic values from woolly rhinoceros suggests higher $\delta^{15}N$ values in dentine than in bone, although the difference is not statistically significant (Bocherens *et al.* 1995b). Thus only bone collagen isotopic values have been used for woolly rhinoceros in the present study.

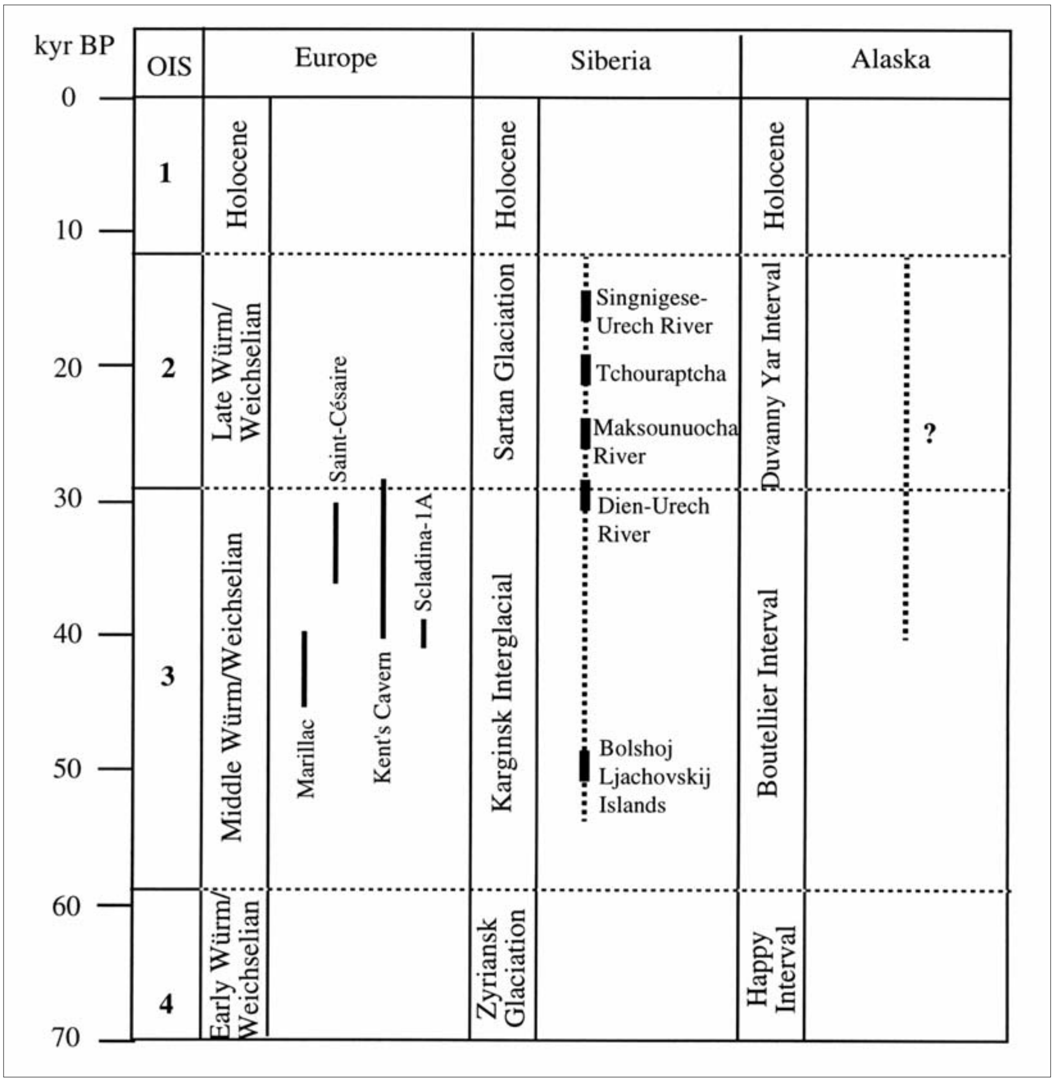

Figure 5 Chronological framework of the studied sites.

RESULTS

In sites with mammoths

Three sets of sites have yielded mammoths associated with other herbivores and carnivores all together: Yakutia, Alaska and Scladina (Belgium). The isotopic data from the three areas show that although herbivores (except mammoth) and carnivores present the expected relationship for a trophic chain as compared with modern equivalents, mammoths exhibit slightly lower $\delta^{13}C$ values and much higher $\delta^{15}N$ values than those of other herbivores (Fig. 6). The $\delta^{15}N$ values of mammoths are close to those of coeval carnivores.

For reason of such isotopic differences between mammoths and other herbivores, as well as the isotopic differences previously noticed between some herbivore species such as horse and reindeer (Fizet *et al.* 1995; Drucker *et al.* 1999), a large scale comparison of collagen isotopic compositions in mam-

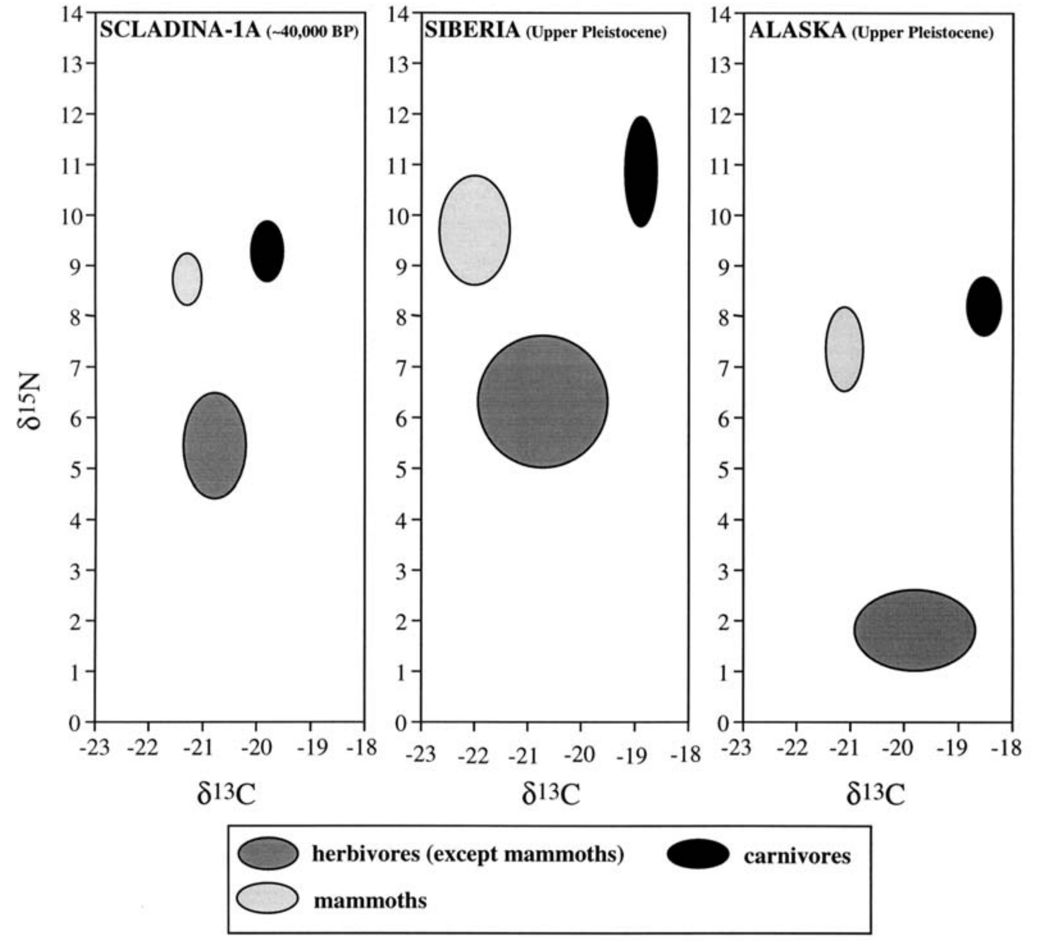

Figure 6 Carbon and nitrogen isotopic variations in Upper Pleistocene mammal collagen from Siberia, Alaska and Scladina (average ± one standard-deviation). Values used to calculate averages and standard-deviations are from Bocherens *et al.* (1994, 1996, 1997).

moth steppe herbivores has been performed. At this stage of research, none of the studied sites could provide the whole range of herbivore species with a sufficient number of individuals to allow statistical analysis of the isotopic variations, thus a clustering of data from a number of sites has been performed. Some geographical variations have been shown to exist in plant and herbivore collagen $\delta^{13}C$ values in Europe for Holocene samples (van Klinken *et al.* 1994), and comparable variations have been evidenced for Upper Pleistocene western European herbivore collagen samples (Bocherens *et al.* 1997). Such variations have been roughly quantified for Europe based on wood $\delta^{13}C$ value variations (van Klinken *et al.* 1994). But no such calibration has been attempted yet for the whole area covered in the present study. Thus it was preferred to mix all the available isotopic values for the different specimens of a given taxon. Using this approach and remaining aware of its limitations, it was possible to make comparisons between average and standard deviations for the different taxa.

Table 1 Average and standard-deviation of carbon and isotopic compositions for the different studied taxa.

Taxon	n	$\delta^{13}C$	$\delta^{15}N$
Horse	44	-21.0 ± 0.7	5.6 ± 1.5
Reinder	21	-19.5 ± 0.4	4.1 ± 1.3
Bovine	13	-20.2 ± 0.3	6.0 ± 1.2
Moose	2	-20.5 ± 0.6	1.4 ± 0.6
woolly rhinoceros	5	-21.0 ± 0.8	5.8 ± 1.7
woolly mammoth	19	-21.4 ± 0.6	8.5 ± 1.4

Differences between herbivore species

The average and standard deviations are well defined for each herbivore species (Table 1; Fig. 7). Moose is excluded from the following comparisons since only two specimens have been analysed so far. For the other taxa, the standard deviation values range from 0.3 to 0.7 for $\delta^{13}C$ values and from 1.2 to 1.5 ‰ for $\delta^{15}N$ values. This reflects rather homogenous isotopic values within a taxon despite the large temporal and geographic areas of sampling for each species. It is noteworthy that the standard deviation values for all the studied specimens of a given species are very similar to those of the same species within a given site, illustrating the fact the geographical variations have little effect on the approach used here. Statistical tests (Student's t-test) show that reindeer presents carbon and nitrogen isotopic compositions significantly different from all the other species. Among the other species, horse $\delta^{13}C$ values are significantly different from those of bovine, but not from those of rhinoceros and mammoth. The $\delta^{15}N$ values are not significantly different in horse, rhinoceros and bovine, whereas mammoth's $\delta^{15}N$ values are significantly higher than those of any other herbivore species (Table 2). Thus the global isotopic differences reflect those observed on a more local basis in the three sites with mammoths; it seems thus legitimate to consider that these isotopic variations reflect biological differences between the studied species.

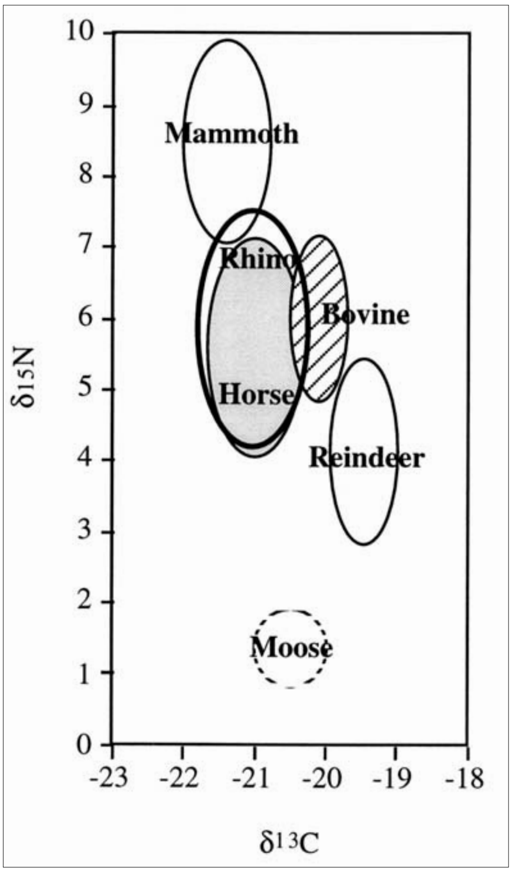

Figure 7 Average and standard-deviation of $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen of mammoth steppe herbivores. Values used to calculate averages and standard-deviations are given in the Appendix.

Table 2 Results of Student's t-tests for the different herbivorous taxa of the mammoth steppe. S = significant; NS = not significant ($\alpha = 0.01$)

$\delta^{13}C$, $\delta^{15}N$	horse	reindeer	bovine	rhinoceros	mammoth
horse		S, S	S, NS	NS, NS	NS, S
reindeer	S, S		S, S	S, S	S, S
bovine	S, NS	S, S		S, NS	S, S
rhinoceros	NS, NS	S, S	S, NS		S, S
mammoth	NS, S	S, S	S, S	S, S	

DISCUSSION

Differences in diet and physiology

Two species appear very similar isotopically, horse and woolly rhinoceros. This result is not really surprising since both species have been recognised as essentially grazers in the mammoth steppe context, based on stomach content from frozen mummies and on tooth morphology (Guthrie 1990; Ukraintseva 1993). Both species have a similar digestive system, being both caecalid monogastrics, this type of digestion being better adapted to deal with a diet of low to modest nutrient levels (Guthrie 1990). The average isotopic values of the bovine samples present a significant difference with horse and woolly rhinoceros as far as carbon is concerned. Steppe bison is considered a grazer, based on stomach contents and dental characters (Guthrie 1982, 1990; Vereschagin & Baryshnikov 1982). Not all the analysed specimens belong to *Bison* with certainty, since aurochs (*Bos primigenius*) may be also present among the samples from western Europe. However, this species is also considered to be mainly a grazer (Degerbøl & Ferdskild 1970), and the isotopic compositions are rather well clustered for all the bovine samples. Unlike horse, bison is a grazer that cannot live on low-protein grass alone and need to complement its diet with higher nutrient food, such as short grass and leaves (Guthrie 1982). Also bovines are ruminants, such in contrast to horse and woolly rhinoceros. These dietary and physiological differences between bovines on the one side, and horse and woolly rhinoceros on the other side, probably explain the isotopic differences between these two groups of herbivores within the mammoth steppe herbivores.

Reindeer presents significantly different mean isotopic compositions compared to other species, both horse and woolly rhinoceros, or bovine. The diet of reindeer is different from the other species, notably with an important proportion of lichens consumed in winter, and a variety of plants consumed all year round, such as shrub leaves and grasses (Guthrie 1982; Russell 1998). As seen earlier in this paper, these different plants present different isotopic compositions in modern arctic ecosystems, especially lichens present higher $\delta^{13}C$ values than vascular plants. Such an isotopic characteristic is suggested when modern reindeer collagen carbon isotopic

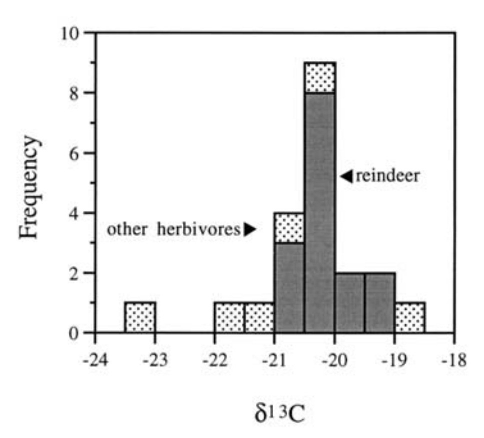

Figure 8 Comparison of modern reindeer collagen carbon isotopic compositions with those of other arctic herbivores (bison, muskox, wild sheep, moose). Values are from Nelson *et al.* (1986), Bocherens *et al.* (1994, 1996).

compositions are compared to those of other arctic herbivores (Fig. 8), although more systematic isotopic studies of modern herbivores including reindeer in arctic environments will be necessary to document this point more fully. Moreover, shrubs are ^{15}N-depleted relative to grass. Such isotopic differences in modern arctic plants are coherent with those observed in Upper Pleistocene herbivore collagen. Moose seems to exhibit much lower δ^{15}N values than the other studied herbivores. Such a difference is coherent with a diet based on leaves (Guthrie 1982), although the interpretation of these data remains to be confirmed by more analyses on this taxon. Finally, woolly mammoth exhibits a strong difference in δ^{15}N and a slight difference in δ^{13}C compared to horse and woolly rhinoceros, although this species is considered to be globally similar to both perissodactyles as far as diet (grass) and physiology (monogastric) are concerned. Similar isotopic differences between woolly mammoths and other coeval herbivores have been found for Eastern European mammoths (Ambrose 1998), as well as for North American mammoths south of the Ice cap (Koch 1991; Bocherens *et al.* 1994). Thus such an isotopic pattern is probably linked to dietary and/or physiological differences. The higher δ^{15}N values of the mammoth might be due to a difference in the diet quality compared to the other herbivores, such as older plant parts, or plants from more disturbed environments. Some physiological factors such as a larger amount of nitrogen recycling in mammoths than in other herbivores might also partly explain these high δ^{15}N values. As far as the rather low δ^{13}C values are concerned, it is difficult to consider forest plants as a cause for this particularity. Indeed, morphological features and stomach contents discovered in mammoth frozen carcasses clearly show that they were grazing animals feeding in open environments (Kubiak 1982, Ukraintseva 1993), although tree bark and twigs constituted a small part of their winter diet (Olivier 1982; Vereshchagin & Baryshnikov 1982). A possible physiological factor, which could have led to lower δ^{13}C values, is fat deposition and use as a way to survive winter food shortage (Kubiak 1982, Olivier 1982), since fat is ^{13}C-depleted relative to other nutrients.

Implications for plant cover and ecology

None of the measured isotopic compositions point out clearly to significant closed canopy environments, contrarily to the situation during the last interglacial, where such environments are evidenced through herbivore collagen isotopic compositions (Fig. 9). Also there is no isotopic evidence of C4-plants, thus confirming the conclusion of Bombin & Muehlenbachs (1985) on a much wider geographical basis. Yurtsev (1996) had also already noticed the lack of C4-plants in the Beringian steppe plants on the basis of relict plant communities in the Beringian territories

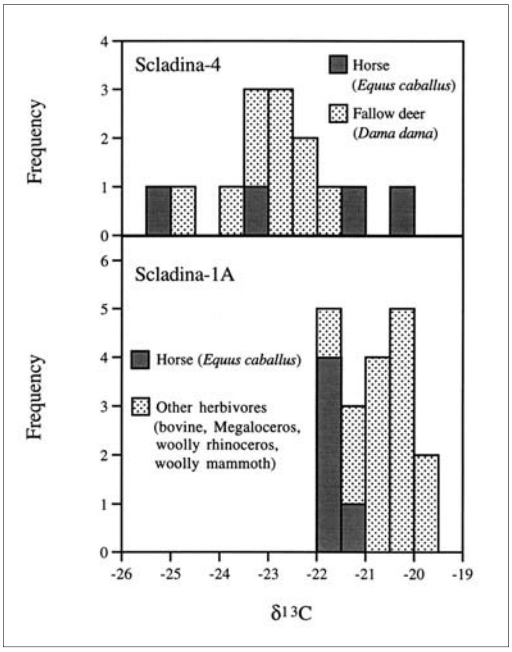

Figure 9 Comparison of horse collagen carbon isotopic compositions with those of other herbivores in two different layers of Scladina. Scladina-1A is around 40,000 BP and correspond to a steppic episode whereas Scladina-4 is around 120,000 BP and corresponds to an interglacial (Eemian) forested episode. Values are from Bocherens *et al.* (1997, 1999).

of Asia and North America. Such an absence is worth noting since, on the basis of a decrease in atmospheric CO2 partial pressure, C4-plants might have increased their distribution towards northern latitudes during glacial episodes despite lower temperatures (Collatz *et al.* 1998). Apparently, if such a northward extension of C4-plants occurred, it was not recorded in the studied specimens, perhaps because they come from sites located too far north. Finally, an attempt of interpretation of nitrogen isotopic variations in terms of plant food selection by the different herbivore species is presented on Figure 10. This graph shows that the average differences in $\delta^{15}N$ values between the major herbivore species of the mammoth steppe fauna can be interpreted as reflecting differences in terms of preferred plant food.

Implications for trophic webs reconstructions

This study shows that the mammoth steppe food web is not isotopically simple and that ecological interpretations of isotopic data needs to be performed in a global manner, not just with a linear food chain pattern in mind, where nitrogen isotopic composition reflects the amount of meat consumed by a given species with unknown diet, with average ‘herbivore’ and ‘carnivore’ ^{15}N values as end values. The recognition of isotopic differences between different herbivore species in the mammoth steppe fauna provides a potential way to test hypotheses concerning prey preference among predators, such as wolves, lions and hyenas, as well as humans.

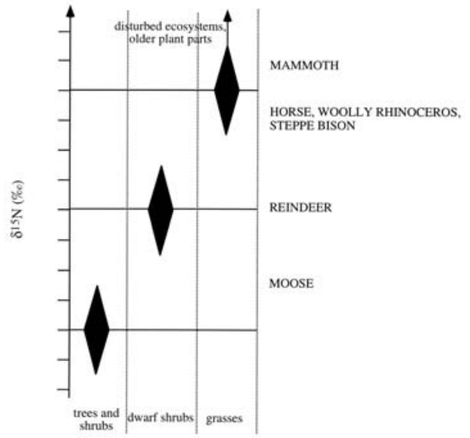

Figure 10 Attempt of interpretation of nitrogen isotopic variations between herbivore species in terms of plant food selection by the different species. The vertical scale is left blank since the absolute nitrogen isotopic values of the different plants may change with local conditions but the differences between the different plant categories are maintained at a given location.

CONCLUSION

A food segregation for the different herbivore species of the mammoth steppe fauna is strongly suggested by the preliminary isotopic data presented in this paper. These results seem to confirm the ‘mosaic’ pattern proposed by Guthrie (1982, 1990). Also apparent in this paper is the seemingly coherent pattern observed between both ends of the mammoth steppe ecosystem, although local variations may exist. The accumulation of additional isotopic data for the different herbivore species from sites presenting a large geographical and chronological distribution will allow documenting such variations through space and time. This novel approach opens the possibility to study ecological variations on a very fine scale, notably during climatic oscillations. It also provides a way to test hypotheses upon the past ecological flexibility of species, which are nowadays restricted to narrow ecological conditions. Moreover, additional work is needed for less abundant Late Pleistocene herbivore species in the mammoth steppe fauna, such as moose, saiga antelope and muskox. The isotopic results presented here are in agreement with the concept of faunal coherence of the mammoth steppe fauna and of its continuity from western Europe to Alaska, as suggested by Guthrie (1990). Mammoth appears an isotopically unique herbivore in the mammoth steppe fauna, due to its dietary and/or physiological adaptations. This species thus seems particularly appropriate as a symbol for this Late Pleistocene northern Eurasian ecosystem.

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REFERENCES

Ambrose, S.H., 1998 - Prospects for stable isotopic analysis of later Pleistocene hominid diets in West Asia and Europe - In: Akazawa, T., Aoki, K. & Bar-Yosef, O. (ed.) - Origin of Neandertals and Humans in West Asia - pp. 277-289, Plenum Press, New York

Ambrose, S.H. & Norr, L., 1993 - Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone colla gen and carbonate - In: Lambert, J. & Grupe, G. (eds.) - Prehistoric Human Bone, Archaeology at the Molecular Level - pp. 1-37, Springer, Berlin

Anderson, P.M., Bartlein, P.J. & Brubaker, L.B., 1994 - Late Quaternary history of tundra vegetation in Northwestern Alaska - Quaternary Research 41: 306-315

Balesdent, J., Girardin, C. & Mariotti, A. 1993 - Site-related ^{13}C of tree leaves and soil organic matter in a temperate forest - Ecology 74 (6): 1713-1721

Bliss, L.C. & Richards, J.H., 1982 - Present-day arctic vegetation and ecosystems as a predictive tool for the arctic-steppe mammoth biome - In: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds.) - Paleoecology of Beringia - pp. 241-257, Academic Press

Bocherens, H. & Mariotti, A., 1997 - Comments on: Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope bio chemistry: Implications for Pleistocene bears by Bocherens *et al*. - Reply - Palaeogeography, Palaeoclimatology, Palaeoecology 128 (1/4): 362-364

Bocherens, H., Fizet, M., Mariotti, A., Gangloff, R.A. & Burns, J.A., 1994 - Contribution of isotopic biogeo chemistry (^{13}C, ^{15}N, ^{18}O) to the paleoecology of mammoths (*Mammuthus primigenius*) - Historical Biology 7: 187-202

Bocherens, H., Emslie, S.D., Billiou, D. & Mariotti, A., 1995a - Stable isotopes (^{13}C, ^{15}N) and paleodiet of the giant short-faced bear (*Arctodus simus*) - Comptes Rendus de l'Académie des Sciences, Paris 320: 779-784

Bocherens, H., Fogel, M.L., Tuross, N., & Zeder, M., 1995b - Trophic structure and climatic information from isotopic signatures in a Pleistocene cave fauna of Southern England - Journal of Archaeological Science 22: 327-340

Bocherens, H., Pacaud, G., Lazarev, P. & Mariotti, A., 1996 - Stable isotope abundances (^{13}C, ^{15}N) in collagen and soft tissues from Pleistocene mammals from Yakutia. Implications for the paleobiology of the mammoth steppe - Palaeogeography, Palaeoclimatology, Palaeoecology 126 (1/2): 31-44

Bocherens, H., Billiou, D., Patou-Mathis, M., Bonjean, D., Otte, M. & Mariotti, A., 1997 - Isotopic biogeochemistry (13C, 15N) of fossil mammal collagen from Scladina cave (Sclayn, Belgium) - Quaternary Research 48: 370-380

Bocherens H., Billiou D., Charpentier V. & Mashkour M., 2000 - Palaeoenvironmental and archaeological implications of bone and tooth isotopic biogeochemistry (^{13}C, ^{15}N) in Southwestern Asia. In : Archaeozoology of the Near East IV, H. Buitenhuis, M. Mashkour & F. Poplin (Eds), Proc. 4th int. Symp. Archaeozoology of Southwestern Asia and adjacent areas (ASWA, Paris, june 1998) - Groningen: Archaeological Research and Consultancy, Vol. B: 104-115

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 (6): 599-607

Bombin, M. & Muehlenbachs, K., 1985 - ^{13}C/^{12}C ratios of Pleistocene mummified remains from Beringia - Quaternary Research 23: 123-129

Collatz, G.J., Berry, J.A. & Clark, J.S., 1998 - Effect of climate and atmospheric CO_2 partial pressure on the global distribution of C4 grasses: present, past, and future - Oecologia 114: 441-454

Cwynar, L.C. & Ritchie, J.C., 1980 - Arctic steppe-tund ra: A Yukon perspective - Science 208: 1375-1377

Degerbøl, M. & Ferdskild, B., 1970 - The Urus (*Bos primigenius* Bojanus) and neolithic domesticated cattle (*Bos taurus domesticus* Linné) in Denmark with a revision of *Bos* remains from the kitchen middens - Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 17, 1

Deines, P., 1980 - The isotopic composition of reduced organic carbon - In: Fritz, P. & Fontes, J.Ch. (eds.) - Handbook of environmental isotope geochemistry, Vol.1: The terrestrial environment - pp. 329-406, Elsevier

DeNiro, M.J. & Epstein, S., 1978 - Influence of diet on the distribution of carbon isotopes in animals - Geochimica et Cosmochimica Acta 42: 495-506

Drucker, D., Bocherens H., Mariotti A., Lévêque F., Vandermeersch B. & Guadelli J.L.,1999 - Conservation des signatures isotopiques du collagène d'os et de dents du Pléistocène upérieur (Saint-Césaire, France): implications pour les reconstitutions des régimes alimentaires des Néandertaliens - Bulletins et Mémoires de la Société d'Anthropologie de Paris 11 (3/4): 289-305

Elias, S.A., Short, S.K., Nelson, H. & Birks, H.H., 1996 - Life and times of the Bering land bridge - Nature 382: 60-63

Fizet, M., Mariotti, A., Bocherens, H., Lange-Badré, B., Vandermeersch, B., Borel, J.P. & Bellon, G., 1995 - Effect of diet, physiology and climate on carbon and nitrogen isotopes of collagen in a late Pleistocene anthropic paleoecosystem (France, Charente, Marillac) - Journal of Archaeological Science 22: 67-79

Frey, W. & Kürschner, H., 1983 - Photosyntheseweg und Zonierung von Halophyten an Salzseen in der Türkey, in Jordanien und im Iran - Flora 173: 293-310

Gröcke, D.R., Bocherens, H. & Mariotti, A., 1997 - Annual rainfall and nitrogen-isotope correlation in Macropod collagen: Application as a paleoprecipita tion indicator - Earth and Planetary Science Letters 153: 279-285

Guérin, C., 1996 - IV. Famille des Equidae - In: Guérin, C. & Patou-Mathis, M. (eds.) - Les grands mammifères Plio-Pléistocènes d'Europe - pp. 121-136, Masson, Paris

Guthrie, R.D., 1982 - Mammals of the mammoth steppe as paleoenvironmental indicators - In: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds.) - Paleoecology of Beringia - pp. 307-326, Academic Press

Guthrie, R.D., 1990 - Frozen fauna of the mammoth steppe - The University of Chicago Press, Chicago and London

Guthrie, R.D., 1995 - Mammalian evolution in response to the Pleistocene-Holocene transition and the break-up of the mammoth steppe: two case studies - Acta Zoologica Cracoviensia 38 (1): 139-154

Guy, R.D., Reid, D.D.M. & Krouse, H.R. 1986 - Factors affecting $^{13}C/^{12}C$ ratios of inland halophytes. II. Ecophysiological interpretation in the field - Canadian Journal of Botany 64: 2700-2707

Hare, P.E., Fogel, M.L., Stafford, T.W. Jr., Mitchell, A.D. & Hoering, T.C., 1991 - The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins - Journal of Archaeological Science 18: 277-292

Heaton, T.H.E., 1999 - Spatial, species, and temporal variations in the $^{13}C/^{12}C$ of C3 plants:implications for paleodiet studies - Journal of Archaeological Science 26 (6): 637-650

Heaton, T.H.E., Vogel, J.C., Chevallerie, G.V.L. & Collett, G., 1986 - Climatic influence on the isotopic composition of bone nitrogen - Nature 322: 822-824

Hobbie, E.A., Macko, S.A. & Shugart, H.H., 1998 - Patterns of N dynamics and N isotopes during primary succession in Glacier Bay, Alaska - Chemical Geology 152: 3-11

Högberg, P., Högbom, L., Schinkel, H., Högberg, M., Johannisson, C. & Wallmark, H., 1996 - 15N abundance of surface soils, roots and mycorrhizas in profiles of European forest soils - Oecologia 108: 207-214

Koch, P.L., 1991 - The isotopic ecology of Pleistocene proboscideans - Journal of Vertebrate Paleontology 11 (3): 40A

Kubiak, H., 1982 - Morphological characters of the mammoth: An adaptation to the arctic-steppe environ ment - In: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds.) - Paleoecology of Beringia - pp. 281-289, Academic Press

Leavitt, S.W. & Danzer, S.R., 1992 - $\delta^{13}C$ variations in C3 plants over the past 50,000 years - Radiocarbon 34 (3): 783-791

Leuenberger, M., Siegenthaler, U. & Langway, C.C., 1992 - Carbon isotope composition of atmospheric CO_2 during the last ice age from an Antarctic ice core - Nature 357: 488-490

Lévêque, F., Backer, A.M. & Guilbaud, M., (eds.) 1993 - Context of a Late Neandertal. Implications of multi disciplinary research for the transition to Upper Paleolithic adaptations at Saint-Césaire, Charente-

Maritime, France - Monographs in World Archeology, 16, Prehistory Press, Madison, Wisconsin

Maguas, C. & Brugnoli, E., 1996 - Spatial variation in carbon isotope discrimination across the thalli of several lichen species - Plant, Cell and Environment 19: 437-446

Marino, B.D. & McElroy, M.B., 1991 - Isotopic composition of atmospheric CO2 inferred from carbon in C4 plant cellulose - Nature 349: 127-131

Mariotti, A., Pierre, D., Vedy, J. C., Bruckert, S. & Guillemot, J., 1980 - The abundance of natural nitrogen 15 in the organic matter of soils along an altitudinal gradient - Catena 7: 293-300

Mateu Andrès, I., 1993 - A revised list of the European C4 plants - Photosynthetica 26 (3): 323-331

Medina, E. & Minchin, P., 1980 - Stratification of δ^{13}C values of leaves in Amazonian Rain Forests - Oecologia (Berlin) 45: 377-378

Michelsen, A., Schmidt, I.K., Jonasson, S., Quarmby, C. & Sleep, D. 1996 - Leaf 15N abundance of subarctic plants provides field evidence that ericoid, ectomy corrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen - Oecologia 105 : 53-63

Minagawa, M. & Wada, E., 1984 - Stepwise enrichment of 15N along food chains : further evidence and the relation between 15N and animal age - Geochimica et Cosmochimica Acta 48: 1135-1140

Neftel, A., Oeschger, H., Schwander, J., Stauffer, B. & Zumbrunn, R., 1982 - Ice core sample measurements give atmospheric CO_2 content during the past 40,000 yr - Nature 295: 220-223

Nelson, B.K., DeNiro, M.J., Schoeninger, M J., De Paolo, D.J. & Hare, P.E., 1986 - Effects of diagenesis on strontium, carbon, nitrogen and oxygen concentra tion on isotopic composition of bone - Geochimica et Cosmochimica Acta 50: 1941-1949

O'Leary, M.H., 1981 - Carbon isotope fractionation in plants - Phytochemistry 20 (4): 553-567

Olivier, R.C.D., 1982 - Ecology and behavior of living elephants: Bases for assumptions concerning the extinct woolly mammoths - In: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds.) - Paleoecology of Beringia - pp. 291-305, Academic Press

Page, H.M., 1995 - Variation in the natural abundance of 15N in the halophyte, *Salicornia virginica*, associated with groundwater subsidies of nitrogen in a southern California salt-marsh - Oecologia 104: 181-188

Riga, A., Van Praag, H. J., & Brigode, N., 1971 - Rapport isotopic naturel de l'azote dans quelques sols forestiers et agricoles de Belgique soumis à divers traitements culturaux - Geoderma 6: 213-222

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, Paris 323: 179-185

Russell, H.J., 1998 - L'univers des caribous - Trécarré, Saint-Laurent, Québec

Schulze, E.-D., Chapin, III F. S. & Gebauer, G., 1994 - Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska - Oecologia 100: 406-412

Schulze, E.-D., Williams, R J., Farquhar, G.D., Schulze, W., Landgridge, J., Miller, J.M. & Walker, B.H., 1998 - Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia - Australian Journal of Plant Physiology 25: 413-425

Sealy, J.C, Van der Merwe, N.J, Lee-Thorp, J.A. & Lanham, J.L., 1987 - Nitrogen isotopic ecology in southern Africa : implications for environmental and dietary tracing -Geochimica et Cosmochimica Acta 51: 2707-2717

Tieszen, L.L., 1991 - Natural variations in the carbon isotope values of plants : implications for archaeolo gy, ecology, and paleoecology - Journal of Archaeological Science, 18: 227-248

Tieszen, L.L. & Fagre, T., 1993 - Effect of diet quality and composition on the isotopic composition of respiratory CO2, bone collagen, bioapatite, and soft tissues - In: Lambert, J. & Grupe, G. (eds.) - Prehistoric Human Bone, Archaeology at the Molecular Level - pp. 121-155, Springer, Berlin

Ukraintseva, V.V., 1993 - Vegetation cover and environment of the "Mammoth Epoch" in Siberia - The Mammoth Site of Hot Springs, Rapid City, South Dakota

Van der Merwe, N.J., 1982 - Carbon isotopes, photosynthesis and archaeology - American Scientist 70: 596-606

Van der Merwe, N.J., & Medina, E., 1991 - The canopy effect, carbon isotope ratios and foodwebs in Amazonia. Journal of Archaeological Science 18:

249-259

Van der Merwe, N.J., & Vogel, J.C., 1983 - Recent carbon isotope research and its implications for African archaeology - African Archaeology Review 1: 33-56

Van Klinken, G.J., van der Plicht, H. & Hedges, R.E.M., 1994 - Bone $^{13}C/^{12}C$ ratios reflect (palaeo-)climatic variations - Geophysical Research Letters 21 (6): 445-448

Vasil'Chuk, Y., Punning J.-M. & Vasil'Chuk, A., 1997 - Radiocarbon ages of mammoths in northern Eurasia: Implications for population development and late Quaternary environment - Radiocarbon 39 (1): 1-18

Vereshchagin, N.K. and Baryshnikov, G.F., 1982. Paleoecology of the mammoth fauna in the Eurasian arctic - In: Hopkins, D.M., Matthews, J.V., Schweger, C.E. & Young, S.B. (eds.) - Paleoecology of Beringia - pp. 267-279, Academic Press

Vogel, J.C., 1978 - Isotopic assessment of the dietary habits of ungulates - South African Journal of Science 74: 298-301

Winter, K., 1981 - C4 plants of high biomass in arid regions of Asia - Occurrence of C4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR -Oecologia 48: 100-106

Yurtsev, B.A., 1996 - The origin of some Beringian eco systems on evidence from phytogeography - Paleontological Journal 30 (6): 751-754

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APPENDIX Dates of study sites and occuring species

Area	Site (layer)	Age	δ¹³C	δ¹⁵N	Reference
	Horse				
France	Marillac (3)	~40-45,000 BP	-20.1	4.9	Fizet et al. (1995)
France	Marillac (3)	~40-45,000 BP	-20.7	4.8	Fizet et al. (1995)
France	Marillac (3)	~40-45,000 BP	-20.8	3.0	Fizet et al. (1995)
France	Marillac (3)	~40-45,000 BP	-20.5	3.0	Fizet et al. (1995)
France	Marillac (4)	~40-45,000 BP	-20.5	5.0	Fizet et al. (1995)
France	Marillac (4)	~40-45,000 BP	-21.0	5.1	Fizet et al. (1995)
France	Marillac (6)	~40-45,000 BP	-20.5	4.8	Fizet et al. (1995)
France	Marillac (6)	~40-45,000 BP	-20.8	4.8	Fizet et al. (1995)
France	Marillac (6)	~40-45,000 BP	-20.3	3.6	Fizet et al. (1995)
France	Marillac (6)	~40-45,000 BP	-20.3	4.6	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-21.9	7.9	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-20.7	6.8	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-20.4	5.5	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-20.7	5.9	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-22.2	6.4	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-20.4	7.4	Fizet et al. (1995)
France	Marillac (8)	~40-45,000 BP	-19.2	3.9	Fizet et al. (1995)
France	Marillac (8)	~40-45,000 BP	-20.6	5.3	Fizet et al. (1995)
France	Marillac (9)	~40-45,000 BP	-21.4	6.3	Fizet et al. (1995)
France	Marillac (10)	~40-45,000 BP	-20.4	2.3	Fizet et al. (1995)
France	Marillac (10)	~40-45,000 BP	-20.4	5.5	Fizet et al. (1995)
France	Marillac (11)	~40-45,000 BP	-20.1	4.2	Fizet et al. (1995)
France	Saint-Césaire (Ejj)	~30-32,000 BP	-20.6	5.6	Drucker et al. (1999)
France	Saint-Césaire (Ejm)	~30-32,000 BP	-21.2	6.5	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-20.3	8.5	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-21.2	6.2	Drucker et al. (1999)
France	Saint-Césaire (Ejop)	~36,000 BP	-21.7	5.7	Drucker et al. (1999)
Great-Britain	Kent's Cavern	~28-40,000 BP	-20.8	4.4	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.2	7.8	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.2	8.4	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.6	6.8	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.6	7.7	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.9	6.9	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.6	6.0	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.4	3.3	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.0	8.5	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-21.6	5.4	Bocherens et al. (1995b)
Belgium	Scladina (1A)	~40,000 BP-21.7		5.2	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP-21.7		5.1	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP-21.9		5.0	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP-21.5		4.8	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP-21.6		7.0	Bocherens et al. (1997)
Yakutia	Maksounuocha River	~25,000 BP-21.1		4.3	Bocherens et al. (1996)
Yakutia	?	Upper Pleistocene	-22.7	6.8	Bocherens et al. (1996)
	Average		**-21.0**	**5.6**	
	standard-deviation		**0.7**	**1.5**	

APPENDIX Dates of study sites and occuring species (continued)

	Reindeer		δ13C	δ15N	
France	Marillac (3)	~40-45,000 BP	-19.5	2.6	Fizet et al. (1995)
France	Marillac (4)	~40-45,000 BP	-19.7	3.1	Fizet et al. (1995)
France	Marillac (4)	~40-45,000 BP	-19.9	3.3	Fizet et al. (1995)
France	Marillac (5)	~40-45,000 BP	-20.4	4.4	Fizet et al. (1995)
France	Marillac (6)	~40-45,000 BP	-20.2	4.2	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-19.7	5.5	Fizet et al. (1995)
France	Marillac (8)	~40-45,000 BP	-19.2	3.8	Fizet et al. (1995)
France	Marillac (9)	~40-45,000 BP	-19.5	3.9	Fizet et al. (1995)
France	Marillac (10)	~40-45,000 BP	-19.6	4.6	Fizet et al. (1995)
France	Marillac (11)	~40-45,000 BP	-19.6	4.4	Fizet et al. (1995)
France	Marillac	~40-45,000 BP	-19.0	3.5	Fizet et al. (1995)
France	Marillac	~40-45,000 BP	-20.2	0.9	Fizet et al. (1995)
France	Saint-Césaire (Ejj)	~30-32,000 BP	-19.4	6.5	Drucker et al. (1999)
France	Saint-Césaire (Ejm)	~30-32,000 BP	-18.8	4.3	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-19.4	6.7	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-18.9	3.5	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-19.6	3.5	Drucker et al. (1999)
France	Saint-Césaire (Ejosup)	~32,000 BP	-19.4	4.6	Drucker et al. (1999)
France	Saint-Césaire (Ejosup)	~32,000 BP	-19.2	4.5	Drucker et al. (1999)
France	Saint-Césaire (Ejop)	~36,000 BP	-18.8	4.9	Drucker et al. (1999)
Alaska	Upper Cleary	~40-10,000 BP	-18.4	2.7	Bocherens et al. (1995a)
		Average	**-19.5**	**4.1**	
		standard-deviation	**0.4**	**1.3**	

	Bovine (*Bison* or *Bos*)		δ13C	δ15N	
France	Marillac (3)	~40-45,000 BP	-20.1	6.3	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-19.9	8.1	Fizet et al. (1995)
France	Marillac (7)	~40-45,000 BP	-19.9	7.5	Fizet et al. (1995)
France	Marillac (10)	~40-45,000 BP	-19.7	6.3	Fizet et al. (1995)
France	Marillac (10)	~40-45,000 BP	-19.8	5.9	Fizet et al. (1995)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-20.5	7.8	Drucker et al. (1999)
France	Saint-Césaire (Ejf)	~30-32,000 BP	-19.9	5.3	Drucker et al. (1999)
Great-Britain	Kent's Cavern	~28-40,000 BP	-20.6	5.6	Bocherens et al. (1995b)
Belgium	Scladina (1A)	~40,000 BP	-20.5	4.8	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP	-20.5	4.3	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP	-19.9	5.3	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP	-20.7	4.4	Bocherens et al. (1997)
Yakutia	?	Upper Pleistocene	-19.3	6.3	Bocherens et al. (1996)
		Average	**-20.2**	**6.0**	
		standard-deviation	**0.3**	**1.2**	

APPENDIX Dates of study sites and occuring species (continued)

	Moose		$\delta^{13}C$	$\delta^{15}N$	
Alaska	Ester Creek	~40-10,000 BP	-21.0	1.9	Bocherens et al. (1995a)
Alaska	Cripple Creek	~40-10,000 BP	-19.9	0.8	Bocherens et al. (1995a)
		Average	**-20.5**	**1.4**	
		standard-deviation	**0.6**	**0.6**	

	Woolly Rhinoceros		$\delta^{13}C$	$\delta^{15}N$	
Great-Britain	Kent's Cavern	~28-40,000 BP	-20.6	3.7	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-20.6	5.9	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-20.6	4.4	Bocherens et al. (1995b)
Great-Britain	Kent's Cavern	~28-40,000 BP	-22.5	6.7	Bocherens et al. (1995b)
Yakutia	Tchouraptcha	~20,000 BP	-20.6	8.4	Bocherens et al. (1996)
		Average	**-21.0**	**5.8**	
		standard-deviation	**0.8**	**1.7**	

	Mammoth		$\delta^{13}C$	$\delta^{15}N$	
Belgium	Scladina (1A)	~40,000 BP	-20.9	8.4	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP	-21.5	9.4	Bocherens et al. (1997)
Belgium	Scladina (1A)	~40,000 BP	-21.6	8.3	Bocherens et al. (1997)
Russia	Brianskaya Oblast	Upper Pleistocene	-20.7	7.2	Bocherens et al. (1994)
Russia	Novo-Petroskoye	Upper Pleistocene	-21.7	7.7	Bocherens et al. (1994)
Yakutia	Dien-Urech River	~30,000 BP	-22.4	9.1	Bocherens et al. (1996)
Yakutia	Singnigese-Urech River	~15,000 BP	-20.7	8.1	Bocherens et al. (1996)
Yakutia	Tchokourdakh	Upper Pleistocene	-21.8	10.8	Bocherens et al. (1996)
Yakutia	Kien-Ajaan River	Upper Pleistocene	-22.8	8.8	Bocherens et al. (1996)
Yakutia	Tchokourdakh	Upper Pleistocene	-21.5	10.4	Bocherens et al. (1996)
Yakutia	Bolshoj Ljachovskij Isl.	~50,000 BP	-22.3	10.2	Bocherens et al. (1996)
Yakutia	?	Upper Pleistocene	-21.6	11.4	Bocherens et al. (1996)
Yakutia	?	Upper Pleistocene	-21.3	7.2	Bocherens et al. (1996)
Alaska	Lost Chicken Creek	Upper Pleistocene	-20.8	6.8	Bocherens et al. (1994)
Alaska	Chatanika	Upper Pleistocene	-21.0	6.4	Bocherens et al. (1994)
Alaska	Fairbanks	Upper Pleistocene	-20.9	6.9	Bocherens et al. (1994)
Alaska	?	Upper Pleistocene	-21.7	6.8	Bocherens et al. (1994)
Alaska	Eielson AFB	Upper Pleistocene	-21.2	8.5	Bocherens et al. (1994)
Alaska	?	Upper Pleistocene	-21.1	8.3	Bocherens et al. (1994)
		Average	**-21.4**	**8.5**	
		standard-deviation	**0.6**	**1.4**	

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P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands