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Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model

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Abstract

The carbon and nitrogen isotopic abundances of the collagen extracted from the Saint-Césaire I Neanderthal have been used to infer the dietary behaviour of this specimen. A review of previously published Neanderthal collagen isotopic signatures with the addition of 3 new collagen isotopic signatures from specimens from Les Pradelles allows us to compare the dietary habits of 5 Neanderthal specimens from OIS 3 and one specimen from OIS 5c. This comparison points to a trophic position as top predator in an open environment, with little variation through time and space. In addition, a comparison of the Saint-Césaire I Neanderthal with contemporaneous hyaenas has been performed using a multi-source mixing model, modified from Phillips and Gregg (2003, Oecologia 127, 171). It appears that the isotopic differences between the Neanderthal specimen and hyaenas can be accounted for by much lower amounts of reindeer and much higher amounts of woolly rhinoceros and woolly mammoth in the dietary input of the Neanderthal specimen than in that of hyaenas, with relatively similar contributions of bovinae, large deer and horse for both predators,

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a conclusion consistent with the zooarchaeological data. The high proportion of very large herbivores, such as woolly rhinoceros and woolly mammoth, in Neanderthal's diet compare to that of the scavenging hyaenas suggests that Neanderthals could not acquire these prey through scavenging. They probably had to hunt for proboscideans and rhinoceros. Such a prey selection could result from a long lasting dietary tradition in Europe.

Keywords: Neanderthal; Saint-Césaire; Diet; Stable isotopes; Collagen; Hyaena; Hunting strategies; Western Europe

Introduction

Palaeodietary reconstruction using stable carbon and nitrogen isotopic signatures of collagen of European Pleistocene Hominids was first evaluated with Neanderthals of Marillac Cave (Charentes, France; today referred as "Les Pradelles") (Bocherens et al., 1991; Fizet et al., 1995). Since this pioneering research, the palaeodiet of further Neanderthal specimens has been investigated using isotopic approaches, for specimens from Belgium (Bocherens et al., 1999, 2001), Slovenia (Richards et al., 2000), and more recently the Neanderthal I specimen from Saint-Césaire (Bocherens and Drucker, 2003a; Drucker and Bocherens, 2004). An attempt to extend this approach to a Middle Eastern Neanderthal failed due to poor collagen preservation (Ambrose, 1998). All of these investigations have suggested that isotopic signatures of Neanderthal were similar to those of contemporary animal predators indicating that the diet of Neanderthals was dominated by the meat of large herbivores. Such a conclusion is consistent with the results of other archaeological approaches aimed at reconstructing Neanderthal's diet (e.g. zooarchaeology in Gaudzinski, 1996 and tooth wear patterns in Lalueza Fox and Pérez-Pérez, 1993).

However, other questions related to Neanderthal's dietary behaviour are crucial for palaeoanthropologists. For instance, it is still debated whether Neanderthals hunted actively or merely acquired ungulate meat through scavenging (e.g. Binford, 1988; Mellars, 1989; Patou, 1989; Marean, 1998), whether the hunting strategies of Neanderthals were different from those of early modern Humans (e.g. Chase, 1987; Stiner, 1994; Marean and Assefa, 1999; Pike-Tay et al., 1999; Hardy et al., 2001; Speth and Tchernov, 2001), and whether diet and health differences can account for the transition between Middle and Upper Palaeolithic and for the extinction of Neanderthals (e.g. Skinner, 1996; Cachel, 1997). The isotopic approach is destructive, and since Neanderthal specimens are very rare and precious, bringing insights into these important questions should now be the goal of future applications of isotopic investigations. Some limitations of the isotopic approach will remain, such as the limited number of Neanderthal samples available for analyses. However, certain limitations can be overcome to provide more detailed information about Neanderthal dietary habits, hunting strategies, and the possible role of dietary changes in the process of their extinction.

The Neanderthal specimen Saint-Césaire I is very useful for the purpose of inferring the influence of dietary habits and hunting strategies in the modalities of extinction of these hominids because it has been excavated from a rich archaeological layer with numerous faunal remains. Moreover, it is located in a region rich in archaeological and palaeontological sites of similar age, as well as with older and younger sites. Finally, it is dated from the transition between Middle and Upper Palaeolithic, and thus it represents one of the youngest Neanderthal specimens in Western Europe, possibly contemporaneous with early modern Humans in Europe.

This paper aims at addressing two key questions:

(1) Is there any isotopic evidence indicating a change in dietary strategies for Neanderthals between Middle-Upper Palaeolithic transition and Middle Palaeolithic Neanderthals? If a change is documented, this could indicate a dietary shift linked to increasing competition with other predators, such as anatomically modern humans for instance.

(2) Did the Saint-Césaire Neanderthal have a similar prey selection as animal predators such as hyaena? Hyaena being a scavenger, a different prey selection for this Neanderthal could indicate a different strategy for prey acquisition, i.e. hunting rather than scavenging.

Finally, the implications for the extinction of Neanderthals of our findings on dietary habits and the hunting strategies of these hominids will be considered.

Material and Methods

Bone and tooth material were selected from the Chatelperonian layers Ejop and Ejop sup from Saint-Césaire, which yielded the Neanderthal remains. Prior to collagen extraction, nitrogen amount in bones has been measured to screen out specimens devoid of organic matter. Only specimens with nitrogen content higher than 0.4 % have been chosen for collagen extraction (Drucker et al., 1999). In this last study, only four bones out of 28 yielded acceptable collagen. Although four additional bones from the Chatelperonian layers yielded reliable collagen, the number of faunal remains occuring with the human skeleton and useful for stable isotope analyses is still limited.

The scarcity of well preserved bones in the Chatelperonian layers of Saint-Césaire led us to look for additional faunal material from other sites from the same region of similar age. Two sites were selected: Camiac and La Berbie. These two sites are located about 120 to 150 km south-east of Saint-Césaire (Fig. 1). Both sites are natural accumulations that have yielded rich faunal assemblages dated around 35,000 years BP (Guadelli, 1987; Madelaine, 1999). The proportion of bones and teeth still containing well preserved collagen is high, with only one specimen from La Berbie not yielding collagen. Material from the main ungulate species possibly consumed by Neanderthals and animal predators has been selected: large bovids (bovinae), i.e. *Bison priscus* and *Bos primigenius*, both species being present and difficult to distinguish from fragmentary skeletal material; large deer, i.e. giant deer *Megaloceros giganteus* and red deer *Cervus elaphus*, whose isotopic signatures are very similar; reindeer *Rangifer tarandus*; horse *Equus caballus*; woolly rhinoceros *Ceolodonta antiquitatis*; and woolly mammoth *Mammuthus primigenius*. In order to complete the trophic reconstruction of an animal predator, we have selected bone material from cave hyaena *Crocuta spelaea*, a hunter and scavenger of ungulates (e.g. Baryshnikov, 1999).

In large mammals, bone collagen is considered to reflect several years of the lifetime of the studied individual prior to its death (e.g. Klepinger, 1984; Parfitt, 2002; Price et al., 2002). Tooth dentine from cervids and carnivores has not been sampled since this tissue has been shown to yield nitrogen isotopic signatures different from bone from the same individuals, possibly due to the influence of ^{15}N–enriched collagen incorporated in dentine during the nursing period (Bocherens et al., 1994; Bocherens and Mariotti, 1997).

Collagen was extracted from bones with more than 0.4 % nitrogen, which corresponds to a maximum collagen loss of 90 % (Bocherens et al., in press). The protocol routinely used for Pleistocene samples has been used to extract collagen (Bocherens et al., 1997). Carbon and nitrogen were evolved from the extracted collagen as CO_2 and N_2, respectively, via flash combustion followed by gas chromatography in an Elemental Analyser (Carlo Erba NA 1500) connected to an Isotopic Ratio Mass Spectrometer (VG Optima) in the department of Earth Sciences, University P. & M. Curie (Paris, France). This allows the measurement of the percentage of carbon and nitrogen and the isotopic ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in the analysed collagen. Isotopic ratios 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. The standard is the marine carbonate VPDB for carbon and atmospheric nitrogen (AIR) for nitrogen. Analytical error is 0.1 ‰ and 0.2 ‰ for $\delta^{13}C$ values and $\delta^{15}N$ values, respectively.

A mathematical mixing model based on isotopic data from western France can be used to

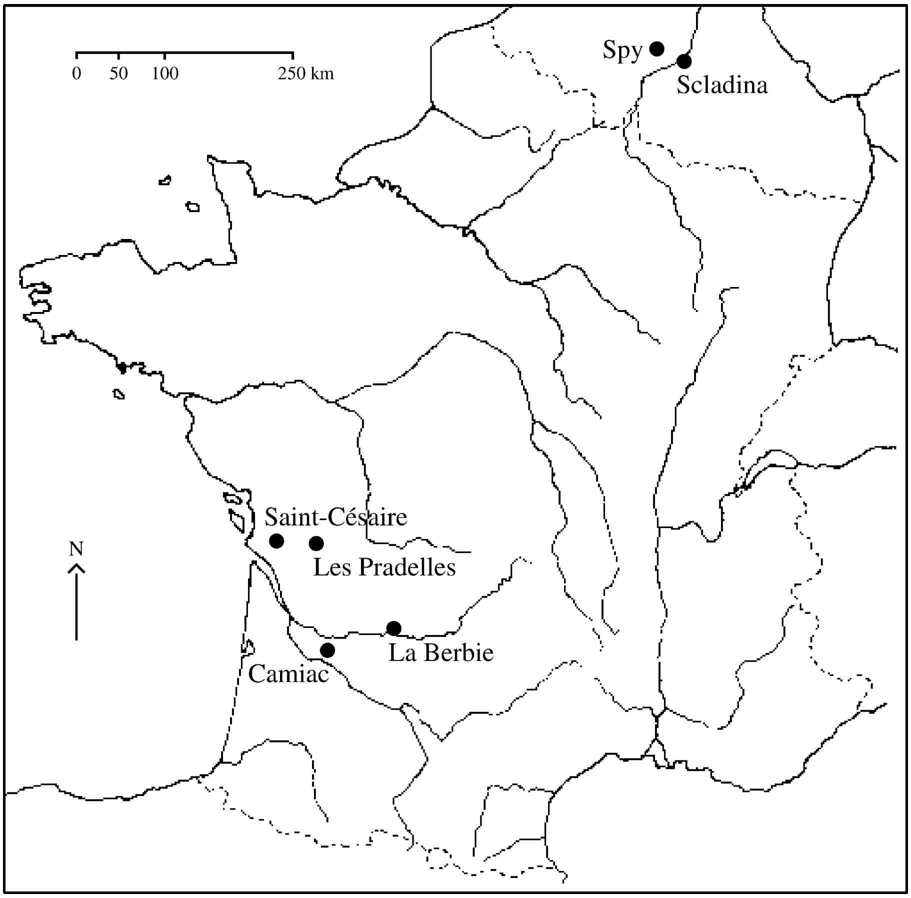

Fig. 1. Map depicting the location of the sites discussed in the text.

determine the likely composition of the diet of Neanderthals and that of an animal predator such as hyaena. Until recently, mixing models have been developed in order to cope with a situation with two isotopic pairs, such as $^{13}C/^{12}C$ and $^{15}N/^{14}N$, and no more than 3 possible dietary sources (e.g., Phillips, 2001; Phillips and Gregg, 2001; Phillips and Koch, 2002). A preliminary attempt to quantitatively estimate reindeer, mammoth, and large ungulates (horse and bovinae) in the Saint-Césaire Neanderthal's diet using the model published by Phillips and Koch (2002) has been presented previously (Drucker and Bocherens, 2004). The recent publication of an upgraded mixing model that can cope with a situation with two isotopic pairs and more than 3 dietary sources (Phillips and Gregg, 2003; Newsome et al., 2004) allows us to consider in the present study all the different possible prey available to Saint-Césaire Neanderthal.

Two modifications have been performed relative to the original approach developed by Phillips and Gregg (2003). Firstly, we subtracted the fractionation factors from the consumer signatures rather than adding it to the prey signatures. The aim of this modification was to enable the use of the isotopic signatures measured on the fossil material. Secondly, we used for these calculations a range of carbon and nitrogen isotopic fractionations between prey and predator collagen instead of a constant value for these fractionation factors. Previous work has shown that the $\delta^{13}C$ values of predator collagen is 0.8 to 1.3 ‰ more positive than that of its average prey, whereas the $\delta^{15}N$ values of predator collagen is 3 to 5 ‰ more positive than that of its $\delta^{15}N$ of its average prey (Bocherens and Drucker, 2003b; Drucker and Bocherens, 2004). This calculation yields four extreme carbon and nitrogen isotopic signatures for the prey collagen of each predator, which can be graphically depicted as a rectangle that includes all the possible isotopic signatures for the collagen of prey.

Using this approach, we obtain average carbon and nitrogen isotopic signatures of the collagen of six potential prey (i.e. Bovinae, large deer, reindeer, horse, woolly rhinoceros, and woolly mammoth). These six isotopic signatures were compared with two rectangles of carbon and nitrogen isotopic signatures representing the average isotopic signatures possible for the prey of Neanderthal and for those of Hyaena (Fig. 2). Following Phillips and Gregg (2003), the isotopic values of the collagen of the six prey delineated a four-sided surface delimited by the average isotopic signature of woolly mammoth, horse, reindeer, and woolly rhinoceros, with the isotopic values of bovinae and large deer being enclosed inside this surface (Fig. 2). Both rectangles of the isotopic signatures of the collagen of the possible prey collagen intersect this surface at two points for Hyaena and at four points for Neanderthal (Fig. 2). The possible percentage of each prey in the predator's diet for these intersection points as well as for the extreme predator isotopic signature (rectangle corner) that are also enclosed in surface delimited by the average isotopic signature of potential prey have been calculated using the computer program IsoSource, available at http://www.epa.gov/wed/pages/models.htm (Fig. 2). For each chosen pair of carbon and nitrogen isotopic signatures, this program calculates the statistical distribution of the possible percentage of each prey that is compatible with the measured isotopic values. The calculation takes into account a tolerance value and a source increment, set at 0.05 and 2 %, respectively. For each chosen point, results are presented as the average percent values with their standard-deviation for each prey, as well as the possible range of percentage for each prey. Finally, we combined the results obtained for the extreme points chosen to estimate the most likely range of possible percentage for each prey, with standard-deviation and extreme possible ranges.

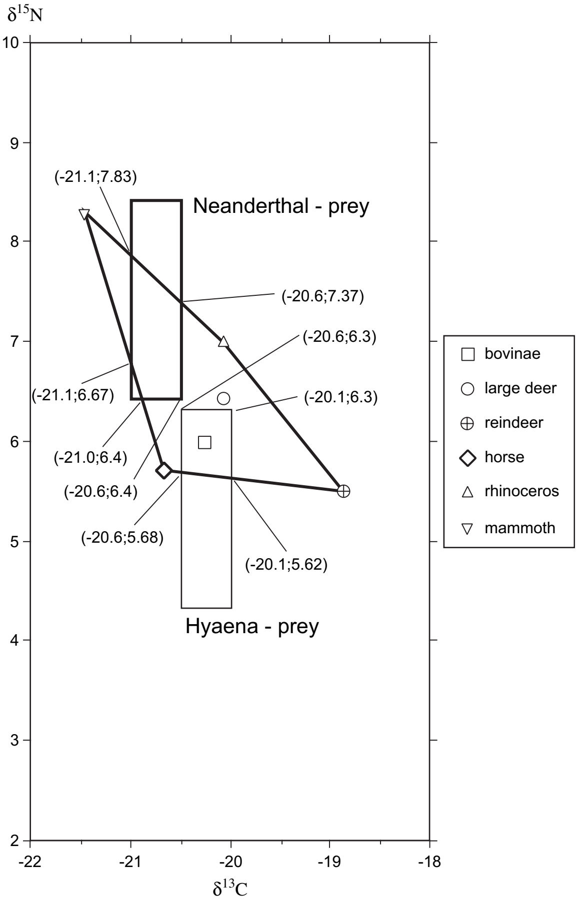

Fig. 2. Summary of the average isotopic signature of prey species in Saint-Césaire, La Berbie and Camiac, compared with the possible range of prey collagen isotopic signatures for Hyaena and the Saint-Césaire Neanderthal. Fractionation factors have been subtracted from the consumer signatures. $\delta^{13}C$ and $\delta^{15}N$ values are given for the points of intersection between the surface delimited by the average isotopic signature of potential prey (see Appendix) and the rectangles of the possible prey collagen isotopic signatures, as well as for the extreme values of the rectangles of the possible prey collagen isotopic signatures enclosed into this surface. The percentage calculations have been performed for these points.

Results and Discussion

Isotopic evidence for possible changes in dietary strategy between Middle Palaeolithic and Middle-Upper Palaeolithic transition Neanderthals

The first question that we address is whether isotopic evidence points to a change in dietary strategy for a Neanderthal specimen from the Middle-Upper Palaeolithic transition, Saint-Césaire I, relative to Middle Palaeolithic Neanderthals. In order to accomplish this goal, we first review the published isotopic signatures of other Neanderthal specimens, and then compare the suitable isotopic data to the isotopic signatures of Saint-Césaire I specimen.

Review of the isotopic signatures of Neanderthal specimens usable for palaeodietary reconstruction

So far, twelve Neanderthal specimens were analysed for the carbon and nitrogen isotopic signature of their bone collagen. Ten adults and two children (Table 1), including three new isotopic analyses performed on specimens from Les Pradelles (formerly know as "Marillac") are presented in this paper. However, isotopic signatures of prehistoric human collagen need to follow a number of requirements in order to be usable for palaeodietary reconstruction. The first requirement is to assess the chemical reliability of the extracted collagen. The second requirement has to do with the period of life reflected in the extracted collagen, especially with respect to nursing. The third requirement is to have a reasonably good set of isotopic data on contemporaneous herbivorous and carnivorous mammals in order to reconstruct the trophic structure of the foodweb.

The first aspect to consider is the reliability of the isotopic data obtained on Neanderthals. Reliability of the isotopic signatures of ancient collagen is addressed through its chemical composition, most notably percent carbon (%C) and nitrogen (%N), and C:N ratio (DeNiro, 1985; Ambrose, 1990). Only collagen extracts with C:N ratios ranging from 2.9 to 3.6 and %N $>$ 5 % are considered uncontaminated and not significantly altered. Among the isotopic results obtained on Neanderthals, two from Les Pradelles have been measured on collagen extracts that had ambiguous chemical compositions. The first one was originally published by Bocherens et al. (1991) at a time when carbon and nitrogen percent determinations on collagen were not performed routinely. This specimen had its amino acid composition determined instead, and the resulting pattern was close but not identical to that of fresh collagen (Bocherens et al., 1991). The measured isotopic signatures are probably close to the original ones, but they may have been slightly shifted due to chemical degradation. It is thus preferable to discard this result from further discussion. Two of the three new isotopic measurements (M300 and M400) exhibit chemical compositions well within the range of fresh collagen chemical compositions. In contrast, M100 exhibits carbon and nitrogen concentrations lower than those of fresh collagen, although its C:N ratio is within the range of that of fresh collagen (Table 1). Using the criteria proposed by Ambrose (1990), this extract can be considered at the lower limit of reliability, and therefore we prefer to be conservative and discard this specimen also from palaeodietary interpretations. It is noteworthy that this last specimen has been sampled from an occipital bone exhibiting cut marks (Le Mort, 1987). This specimen might then correspond to an individual who was submitted to a particular treatment. This raises questions about the possible causes of the isotopic particularity of this specimen relative to other Neanderthals. For example this individual was perhaps linked to a different state of preservation or a specific status of this individual during his lifetime reflected in his diet, or both. With the recent reactivation of excavation in Les Pradelles, additional human remains have been unearthed (Beauval et al., 2002; Maureille, 2003), and further isotopic work will most likely clarify some of these uncertainties.

The second aspect to consider is the individual age of the Neanderthal specimens, in order to take into account the possible nursing effects on $\delta^{15}N$ values of children. Indeed, nursing mammals, including humans, are enriched in ^{15}N relative to their mother because milk presents $\delta^{15}N$ values similar to those of the mother's tissues (e.g. Fogel et al., 1989; Katzenberg and Pfeiffer, 1995).

Table 1
Summary of the Neanderthal specimens which collagen has been analysed for $\delta^{13}C$ and $\delta^{15}N$ values

No analysis	Site	Age	Piece	No excavation	Yield (mg g^{-1})	%C	%N	C/N	$\delta^{13}C$	$\delta^{15}N$	Reference
27801	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	skull fragment		7.0	n.d.	n.d.	n.d.	−20.2*	9.3*	Bocherens et al. (1991)
64801	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	skull fragment		82.4	38.8	13.7	3.3	−19.1	11.6	Fizet et al. (1995)
M300	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	skull fragment	M70 c10 F10-41	107.4	41.1	14.7	3.3	−19.1	11.5	this paper
M400	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	mandible	H1	41.5	37.6	13.1	3.3	−19.5	11.4	this paper
M100	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	skull fragment°	H2	13.4	18.9	7.0	3.2	−21.8**	8.4**	this paper
RPB7000	La Roche-à-Pierrot (Saint-Césaire, Charentes-Maritimes, France)	OIS3	fibula		26.0	40.8	14.2	3.3	−19.8	11.4	Bocherens and Drucker (2003a)
MT500	Scladina Cave (Sclayn, Belgium)	OIS5b?§	phalanx	SCLA 1B 4	n.d.	39.9	14.7	3.2	−21.2	11.8	Bocherens et al. (2001)
SC18800	Scladina Cave (Sclayn, Belgium)	OIS5c	skull fragment	SCLA 4A 2	62.0	38.7	14.1	3.2	−19.9	10.9	Bocherens et al. (1999)
MT100	Awirs Cave (Belgium)	OIS3	skull fragment	Engis 2	176.4	41.7	14.4	3.4	−19.6#	12.6#	Bocherens et al. (2001)
MT200	Spy (Betche-al-Roche) Cave (Belgium)	OIS3	scapula	SPY OMO 1	123.9	41.5	14.4	3.4	−19.8	11.0	Bocherens et al. (2001)
VI-207	Vindija Cave (Croatia)	OIS3	mandible		65	37.1	13.5	3.2	−19.5	10.1	Smith et al. (1999)
VI-208	Vindija Cave (Croatia)	OIS3	parietal		42	36.1	11.7	3.6	−20.5	10.8	Smith et al. (1999)

§ this specimen has been relocated since the initial publication (Bocherens et al., 2001) and belongs to layer 3 (OIS 5b) instead of layer 1B (OIS 3)

* at the time of the original study, no measurement of %C and %N were performed, and amino acid analysis showed a pattern close to collagen but not identical; the isotopic reliability of this collagen cannot be proven

° this specimen exhibits cut-marks

** this specimen exhibits chemical characteristics acceptable for well preserved collagen, but not identical to fresh collagen

this specimen is juvenile and may present an extra-^{15}N-enrichment due to milk consumption

Therefore, a nursing infant behaves similar to a predator, one trophic level higher than adult individuals of his population, as far as $\delta^{15}N$ values are concerned. The Engis Neanderthal child is only 5-6 years old based on the dental eruption pattern (Tillier, 1983), and a child this age may still be affected by such an effect if weaning occurred later than for most modern human populations (Bocherens et al., 2001). Therefore, due to the uncertainty regarding his nursing status, this specimen will not be discussed in palaeodietary terms. Another Neanderthal child is the specimen from layer 4A in Scladina Cave. This specimen has been aged at approximately 11 years (Otte et al., 1993). Consequently, this specimen was old enough to have erased the nursing isotopic signal and thus, it is acceptable for palaeodietary reconstruction.

A final aspect to consider is the chronological distribution of the studied Neanderthals and the availability of isotopic data on contemporary faunal material. Indeed, considering pertinent coeval fauna is crucial before drawing palaeodietary conclusions. For instance, significant variations occurred in herbivorous large mammals from Western Europe between 33,000 and 15,000 years ago (Drucker et al., 2003), and comparing the isotopic signatures of prehistoric humans with those of faunal specimens from a different age can be misleading (e.g. Drucker and Bocherens, 2004). A prerequisite is thus to compare the isotopic signatures of ancient humans with those of herbivores and carnivores from the same site and age, or at least from sites relatively close geographically and with a reasonable chronological similarity.

The two Neanderthals from Vindija do not meet this prerequisite, since there is only one deer from the same layer (G_1) than the human specimens for which isotopic signatures have been measured (Richards et al., 2000). The few other members of the fauna from the same site are from an older stratum, layer G_3 (Richards et al., 2000). Since this layer is more than 12,000 years older than the one that yielded the Neanderthal specimens (Ahern et al., 2004), they cannot be directly compared to the Neanderthal specimens. A palaeodietary reconstruction of Vindija Neanderthals' diet is thus pending isotopic data on contemporary herbivorous and carnivorous fauna.

In Belgium, the Neanderthal from Spy was found during the 19th century and no faunal remains clearly associated with the human could be selected. However, in this case, a comparison can be performed with the isotopic data evolved from the rich contemporary mammal fauna of layer 1A from Scladina Cave, both dated around 40,000 years ago and only a few kilometres apart (Bocherens et al., 2001). The Neanderthal specimen from Scladina Cave called "SCLA-1B" was originally attributed to layer 1B and thus compared to the mammal fauna from layers 1A and 1B from Scladina Cave (Bocherens et al., 2001). However, a recent revision of Scladina Cave material reassessed this specimen to layer 3 (D. Bonjean, pers. comm. 2003). Therefore, this specimen is contemporary with Oxygen Isotopic Stage (OIS) 5b, around 90,000 years BP (Ellwood et al., 2004). This indicates that the specimen is approximately 50,000 years older than previously thought. As a result, an isotopic study of the mammal fauna of layer 3 of Scladina Cave is currently under way in order to determine the trophic position of this specimen. In sum, it is still premature to attempt a palaeodietary reconstruction for this Neanderthal. The oldest Neanderthal specimen from Scladina Cave comes from layer 4A, and is contemporary to OIS 5c, around 100,000 years BP. This specimen was compared with the isotopic data obtained on the fauna from the same layer (Bocherens et al., 1999).

In France, the three Neanderthal specimens with chemically reliable collagen from Les Pradelles can be compared with the isotopic data obtained on the fauna from the same site, dating from OIS 3 (Fizet et al., 1995). The Saint-Césaire I Neanderthal meets the prerequisite presented above since we have gathered isotopic data on herbivorous and carnivorous mammals from the same region and the same age, around 35,000 years ago (this paper).

In conclusion, among the 12 Neanderthal specimens with isotopic signatures, only 5 specimens from OIS 3 and one specimen from OIS 5c can be considered so far for palaeodietary reconstruction after considering the prerequisite for chemical, physiological and stratigraphical characteristics.

Isotopic palaeodietary comparison of the Saint-Césaire Neanderthal with other Neanderthal specimens

The Saint-Césaire I Neanderthal will first be compared with the Neanderthals from Les Pradelles since these sites are separated by only a few dozen kilometres. Les Pradelles yielded a Mousterian lithic assemblage together with human Neanderthal osteological material during excavations directed by B. Vandermeersch (1976). A rich faunal assemblage was recovered during this excavation (Fizet et al., 1995). Isotopic results obtained on faunal specimens from layer 7 have been discarded due to a general increase in $\delta^{15}N$ values for all the components of the food web during this period (Fizet et al., 1995) and since none of the Neanderthal specimens originate from this particular layer. The age of the Neanderthals is considered to be contemporary to Oxygen Isotopic Stage 3, between 40,000 and 45,000 years BP (Fizet et al., 1995). As discussed in the previous paragraph, only three of the five Neanderthal specimens from Les Pradelles for which isotopic measurements have been performed are considered to be totally reliable and will be discussed further. These three specimens exhibit very similar isotopic signatures (Table 1, Fig. 3). Although the diversity of the species for which isotopic data are available in Les Pradelles is not as high as for Saint-Césaire, it is possible to compare the relative position of the isotopic signatures of Les Pradelles Neanderthal specimens with the same ungulate species, i.e. reindeer, bovinae and horse, and with the predatory hyaena (Fig. 3). It appears that Les Pradelles Neanderthal specimens present $\delta^{13}C$ values similar to those of animal predators, such as hyaena and wolf, in a similar way than the Saint-Césaire Neanderthal specimen presents similar $\delta^{13}C$ values to hyaena. In both cases, Neanderthals exhibit $\delta^{15}N$ values significantly more positive than those of animal predators (Fig. 3). Although the chronological and cultural contexts are different for Les Pradelles and Saint-Césaire Neanderthals, their trophic position seems to be similar in both cases.

The Neanderthal from Spy together with the rich mammal fauna from layer 1A from Scladina Cave offers the possibility of a thorough comparison with the Saint-Césaire Neanderthal. Both sites present a similar pattern (Fig. 3). Among herbivores, woolly mammoth and woolly rhinoceros exhibit the highest $\delta^{15}N$ values, whereas reindeer exhibit the most positive $\delta^{13}C$ values. In both cases, hyaenas present the highest $\delta^{15}N$ values measured on faunal samples which is expected for carnivores, and Neanderthals present $\delta^{15}N$ values about 2 ‰ higher than those of hyaenas (Fig. 3). The similarity of the patterns of isotopic variations in both cases strongly suggest that Neanderthals from Saint-Césaire and Spy had a similar trophic ecology. However, both sites are several hundreds of kilometres away, and Spy Neanderthal is several thousand years older than the Chatelperronian individual from Saint-Césaire.

A final comparison can be made between the Saint-Césaire Neanderthal and the Neanderthal from layer 4A in Scladina Cave (Scladina-4A). In this case, not only are the sites well separated spatially, but also chronologically and ecologically, since the Belgian specimen is about 65,000 years older than the French one and the environment during OIS 5c was more temperate and forested than during OIS 3 (Cordy and Bastin, 1992). These ecological differences are clearly reflected in the $\delta^{13}C$ values of herbivorous mammals. The samples from Scladina-4A have more negative $\delta^{13}C$ values than those from western France, which is likely due to a more pronounced canopy effect under a forested vegetation than would be under steppe vegetation (Bocherens et al., 1999). Hence, the Neanderthal from Scladina-4A relied on prey from an open environment rather than on prey from the forest. Despite dramatic environmental differences, the isotopic signature of the Neanderthal from Scladina-4A is very similar to that of the other Neanderthals including the specimen from Saint-Césaire, implying a stable trophic position through time and ecological variations in Western Europe.

The comparison of the isotopic signatures of these Western European Neanderthals points to a trophic position as top predator in an open environment, with little variation through time and space. It is worth noting that in each case, the $\delta^{15}N$ values of Neanderthals appear more positive than those of animal predators such as hyaena or wolf. A detailed quantitative study of

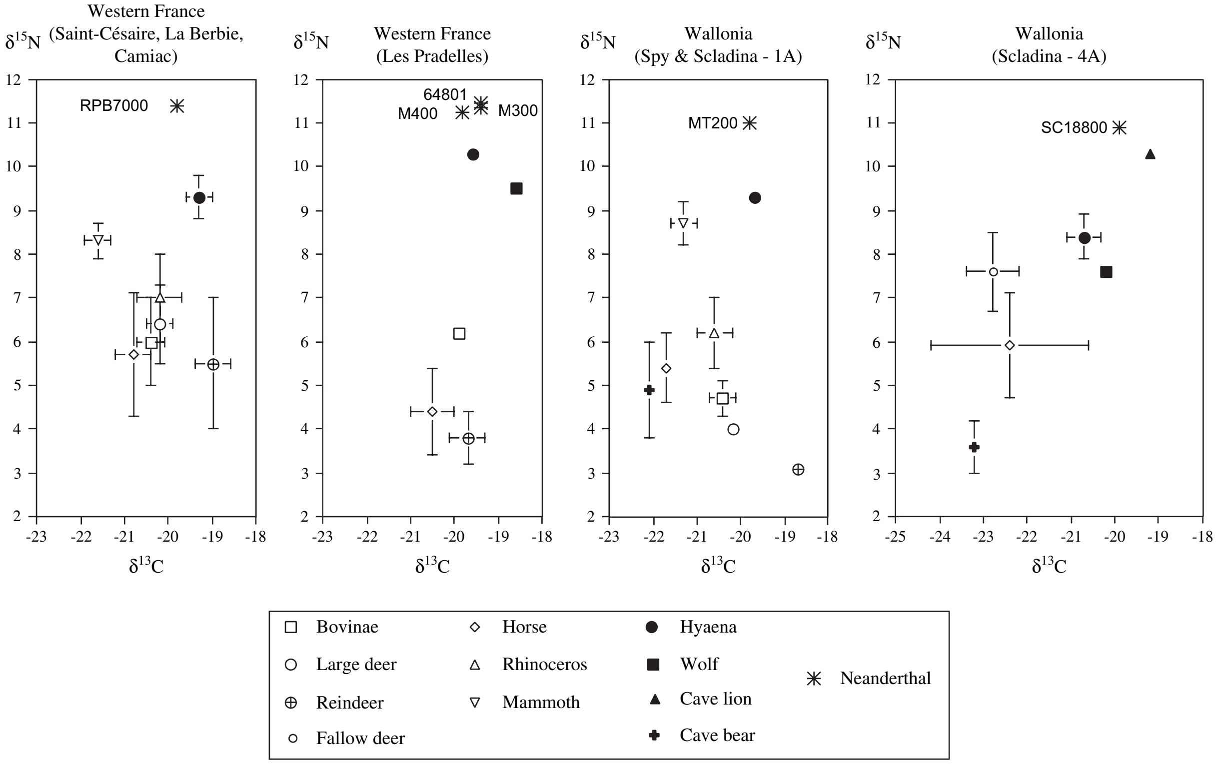

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of Neanderthal collagen from southwestern France (Saint-Césaire, Camiac, La Berbie), Les Pradelles, Wallonia (Spy and Scladina – 1A), and Scladina – 4A, compared to those of their respective contemporary mammal fauna (average ± standard-deviation for different herbivorous and carnivorous species).

the situation in Western France, using isotopic data from Saint-Césaire, La Berbie and Camiac provides insights into such an intriguing pattern.

Comparison of Saint-Césaire Neanderthal with contemporaneous hyaenas using a multi-source mixing model

The results of the multi-source mixing model are presented on Fig. 4. The range of extreme percent represents the entire range of mathematically feasible solutions, whereas the range of mean percent does give some idea of how the central tendency of the distribution of feasible results shifts between Neanderthal and hyaena. The following discussion is based on the range of mean percent since, although extreme percents are mathematically feasible, they would require fractionation values to be at the extreme opposites of their possible end values for each predator. Thus the results presented below are indicative, but not definitive.

The obtained patterns are similar for both predators – Neanderthal and hyaena – for Bovinae, large deer and horse, but they are different for reindeer, woolly rhinoceros and woolly mammoth (Fig. 4). Both predators exhibit a similar pattern of consumption of Bovinae and large deer, with a range of most likely contribution from approximately 0 to 25 %. For both predators, horse exhibits a large interval of possible contribution, ranging from a few percent to approximately 70 to 85 %, for Neanderthal and hyaena, respectively. The patterns are very different for reindeer, with a contribution to dietary input lower than approximately 5 % for Neanderthal whereas hyaena could have consumed from approximately 5 % to 40 % reindeer. Woolly

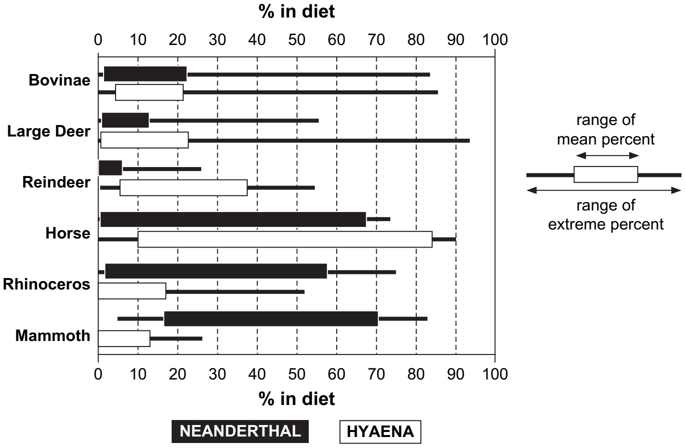

Fig. 4. Summary of the mean and extreme possible ranges of prey percentage for Neanderthal and Hyaena in southwestern France around 36,000 years BP. The solid black bar takes the means from the distributions of solutions from IsoSource for the 4 or 5 key data points in Fig. 2 (corners of rectangles and intersections of rectangles with the mixing polygon) and shows the range of those means.

rhinoceros and woolly mammoth are apparently preyed upon much more by Neanderthals than by hyaenas. Woolly rhinoceros contribution range from a few to as much as approximately 60 % in the diet of Neanderthals, whereas it composes less than approximately 20 % of the diet of hyaenas. The contrast is even greater in the case of woolly mammoth since its contribution ranges from approximately 15 to 70 % in Neanderthal's diet, whereas it is not higher than approximately 15 % in hyaena's diet. In conclusion, the isotopic differences between Neanderthals and hyaenas reflect essentially much lower amounts of reindeer and much higher amounts of woolly rhinoceros and woolly mammoth in the dietary input of Neanderthal than in that of hyaena, with relatively similar contributions of bovinae, large deer and horse for both predators.

The dietary analysis presented above does not take plant food into account. Collagen isotopic signatures reflect principally the isotopic signatures of the protein fraction of the diet (e.g. Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Since it is much poorer in proteins than meat, plant food proteins would be almost invisible in a mixed diet containing few plants and a lot of meat, as it was probably the case of periarctic dwellers like Neanderthals during OIS 3. Moreover, plant foods are ^{15}N-depleted relatively to herbivore meat. Therefore, the inclusion of plant food in significant proportion in Neanderthal diet would require the inclusion of even more ^{15}N-enriched food resource to account for the observed collagen isotopic values, meaning that the contribution of mammoth and rhinoceros meat would need to be even higher than calculated by the mixing model. Neglecting plant food in this discussion does not change the general picture of dietary resources consumed by Neanderthal.

A comparison with the conclusions based on the zooarchaeological remains from layer Ejop sup in Saint-Césaire yields a similar picture. The identified remains of large mammals from this layer are diverse. Considering the MNI (Minimal Number of Individuals), Bovinae (Aurochs and Bison) are dominant relative to reindeer and horse (Patou-Mathis, 1993). When the meat weight is estimated for each species, Bovinae remain the most important potential meat providers, but mammoth and woolly rhinoceros yielded more meat than cervids (Patou-Mathis, 1993).

Finally, the Neanderthals that led to the deposit of layer Ejop sup in Saint-Césaire consumed more meat from large herbivore species than meat from middle size and small species. This contrasts with hyaena, which consumed relatively more middle size and small herbivore species than large ones.

Implications for the Saint-Césaire I Neanderthal dietary habits and hunting strategy

The differences observed between the amount of different prey consumed by Neanderthal and hyaena provide insights about hunting strategies of Chatelperronian Neanderthals in Saint-Césaire. Spotted hyaena is an opportunistic predator and scavenger with dietary preference for large and medium size ungulates (e.g. Cooper et al., 1999; di Silvestre et al., 2000). The isotopic signatures of spotted hyaenas in southwestern France around 36,000 years ago indicate that horse was the most abundant prey species, whereas bison, aurochs, red deer, giant deer, and reindeer were relatively abundant, woolly rhinoceros were less consumed, and mammoth were the least consumed of large herbivores. Spotted hyaenas from Belgium and Great-Britain of the same age exhibit similar isotopic signatures (Bocherens et al., 1995, 1997), suggesting that this dietary pattern probably holds for north western Europe. Among these available prey, Neanderthals consumed much less reindeer and much more rhinoceros and mammoth than hyaenas. The low proportions of mammoth and rhinoceros in the diet of hyaena, a famed scavenger, indicates that available carcasses of these large herbivores were relatively rare in the landscape. Thus, the high proportions of these animals in the diet of Neanderthals indicate that they were obtained through another strategy than simply scavenging. Active hunting of these large herbivores by Saint-Césaire Neanderthals is thus strongly suggested by the isotopic evidence. There is some zooarchaeological evidence of proboscideans and rhinoceros hunting by Neanderthals (e.g. Scott, 1980; Auguste, 1995; Auguste et al., 1998; Locht and Patou-Mathis, 1998; Bratlund, 2000; Patou-Mathis, 2000, 1999; Conard and Niven, 2001; Moncel, 2001). However, mammoth and rhinoceros remains do not dominate Neanderthal faunal assemblages even if they are usually present in small numbers (e.g. Patou-Mathis, 2000). This discrepancy between significant consumption of very large herbivores by Neanderthals and the remains of very large herbivores being scarce in Neanderthal sites might be due to transport decisions: filleted meat could have been transported to the occupation sites, leading to an underrepresentation of the role of large-bodied animals in Middle Paleolithic diet (Rabinovitch and Hovers, 2004).

The available isotopic data indicate that there was limited dietary competition between Neanderthal and hyaena during the Chatelperronian in southwestern France. Similarly Middle Palaeolithic Neanderthals of western Europe are systematically more ^{15}N–enriched than hyaenas. It is conceivable that the systematic enrichment in Neanderthal relative to animal predators such as hyaena and wolf could be linked to greater consumption of mammoth meat by Neanderthals compared to animal predators (hyaenas). Moreover, evidence for proboscidean meat consumption in Europe reaches back into the Early Palaeolithic (e.g. Thieme and Veil, 1985; Fosse, 1998; Piperno and Tagliacozzo, 2001). Mammoth consumption in the Middle Palaeolithic could result from a long-lasting dietary tradition in Europe.

Summary and Conclusion

Isotopic data show that the Saint-Césaire I Neanderthal relied primarily on herbivore meat as a dietary resource, in a similar way as older Neanderthals from western Europe during OIS 3. The present study provides an estimation of the range of proportions of different prey species in his diet, thanks to the favourable context accompanying this specimen. Very large species such as woolly rhinoceros and especially woolly mammoth were high in proportion in the consumed meat for the Saint-Césaire I Neanderthal. On the contrary, smaller herbivore species such as reindeer were in low proportions in this specimen's diet.

Zooarchaeological approaches provided a similar result, with large size herbivores being more abundantly consumed than small and middle size herbivores. These zooarchaeological approaches reflect a biased average of the dietary refuse of a human group (e.g. Rakham, 1994). In contrast, the isotopic approach is based on the very bones of a given individual and reflects an average diet of several years for the studied individual. The fact that both approaches lead to similar conclusions was not obvious, since dietary habits can differ among individuals in a given group. The similarity of the results obtained independently with both approaches indicates that a similar subsistence strategy is reflected at different demographic, spatial, and chronological scales. Such consistency reinforces the contribution of large-sized herbivore species in Chatelperronian Neanderthals' diet.

The comparison of prey selection by animal predators such as hyaenas and by Neanderthals does not support scavenging as the principal subsistence pattern of these humans. This result is in keeping with recent reviews of archaeological evidence that indicate an active hunting for Neanderthals as opposed to scavenging (e.g. Marean and Kim, 1998). Isotopic data reinforce the picture of western European Neanderthals as accomplished hunters, capable of taking down prey species as large as woolly mammoth on a regular basis. Such a hunting strategy involving effective large-mammal exploitation qualifies for modern behaviour and should be taken into account in the current debate about the origin of modern human behaviour (e.g. Henshilwood and Marean, 2003).

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Appendix. List of collagen chemical compositions and carbon and nitrogen isotopic signatures for skeletal material from Saint-Césaire, La Berbie and Camiac.

Analysis number	Species	Sample	Site	Yield (mg g^{-1})	$\%C_{coll}$	$\%N_{coll}$	C/N_{coll}	$\delta^{13}C$	$\delta^{15}N$
RPB8000	Bovine (Bos or Bison)	metapodium	Saint-Césaire	3.0	30.1	11.3	3.1	−20.9	6.1
LBR100	Bison (*Bison priscus*)	metatarsus	La Berbie	31.9	39.5	14.5	3.2	−20.3	6.1
LBR200	Bison (*Bison priscus*)	metatarsus	La Berbie	14.8	37.8	14.0	3.2	−20.1	5.6
LBR300	Bison (*Bison priscus*)	metatarsus	La Berbie	27.6	35.3	13.1	3.1	−20.8	4.7
LBR400	Bison (*Bison priscus*)	metatarsus	La Berbie	12.5	36.9	13.7	3.1	−20.3	5.6
LBR500	Bison (*Bison priscus*)	metatarsus	La Berbie	26.1	40.3	14.8	3.2	−20.2	6.1
LBR600	Bison (*Bison priscus*)	metatarsus	La Berbie	18.2	29.0	11.1	3.0	−20.2	6.0
LBR700	Bison (*Bison priscus*)	metatarsus	La Berbie	41.0	38.4	14.3	3.1	−20.9	4.6
LBR3100	Bison (*Bison priscus*)	radius	La Berbie	36.3	39.0	14.9	3.0	−20.5	5.3
CAM100	Aurochs? (cf. *Bos primigenius*)	femur or tibia	Camiac	66.9	40.8	14.7	3.2	−20.0	6.1
CAM200	Aurochs? (cf. *Bos primigenius*)	femur or tibia	Camiac	58.7	42.0	15.1	3.2	−20.7	6.2
CAM300	Aurochs? (cf. *Bos primigenius*)	femur or tibia	Camiac	52.3	41.6	14.9	3.3	−20.4	7.4
CAM400	Aurochs? (cf. *Bos primigenius*)	tibia	Camiac	23.4	39.5	14.3	3.2	−20.1	8.6
CAM500	Aurochs? (cf. *Bos primigenius*)	tibia	Camiac	14.4	39.1	14.0	3.3	−20.0	6.0
CAM600	Aurochs? (cf. *Bos primigenius*)	femur or tibia	Camiac	35.9	41.0	14.7	3.3	−20.4	5.3
							av.	−20.4	6.0
							s.d.	0.3	1.0
							n	15	15
RPB650	Giant deer (*Megaloceros giganteus*)	maxillary bone	Saint-Césaire	28.9	34.1	12.7	3.1	−20.5	5.0
CAM900	Giant deer (*Megaloceros giganteus*)	femur	Camiac	10.0	33.2	11.9	3.2	−20.0	6.4
CAM1000	Giant deer (*Megaloceros giganteus*)	long bone	Camiac	36.8	26.7	9.6	3.3	−20.1	7.7

(*continued on next page*)

Appendix (*continued*)

Analysis number	Species	Sample	Site	Yield (mg g^{-1})	%C$_{coll}$	%N$_{coll}$	C/N$_{coll}$	δ^{13}C	δ^{15}N
CAM1100	Red deer (*Cervus elaphus*)	long bone	Camiac	24.4	37.5	13.4	3.3	−20.0	6.9
CAM1200	Red deer (*Cervus elaphus*)	long bone	Camiac	8.7	35.4	13.4	3.1	−20.6	6.2
							av.	−20.2	6.4
							s.d.	0.3	0.9
							n	5	5
RPB1200	Reindeer (*Rangifer tarandus*)	jawbone	Saint-Césaire	9.5	23.6	8.6	3.2	−18.8	4.9
RPB7200	Reindeer (*Rangifer tarandus*)	metapodium	Saint-Césaire	31.7	41.5	15.0	3.2	−18.3	7.3
LBR900	Reindeer (*Rangifer tarandus*)	humerus	La Berbie	18.7	40.4	14.7	3.2	−19.2	3.7
LBR1000	Reindeer (*Rangifer tarandus*)	humerus	La Berbie	20.1	38.3	14.0	3.2	−19.4	3.9
LBR1100	Reindeer (*Rangifer tarandus*)	jawbone	La Berbie	14.6	39.9	14.4	3.2	−19.1	7.6
LBR3400	Reindeer (*Rangifer tarandus*)	femur	La Berbie	16.8	39.4	13.9	3.3	−19.4	5.8
							av.	−19.0	5.5
							s.d.	0.4	1.5
							n	6	6
RPB2300	Horse (*Equus caballus*)	upper 2nd premolar	Saint-Césaire	14.1	17.7	6.5	3.1	−20.5	7.3
RPB2400	Horse (*Equus caballus*)	lower tooth	Saint-Césaire	6.2	34.7	13.1	3.1	−21.7	5.7
LBR1600	Horse (*Equus caballus*)	metacarpus 2 or 4	La Berbie	22.4	40.3	14.7	3.2	−20.4	7.5
LBR1700	Horse (*Equus caballus*)	femur	La Berbie	36.5	41.9	15.3	3.2	−20.9	3.5
CAM1600	Horse (*Equus caballus*)	tibia	Camiac	56.1	41.9	14.7	3.2	−20.7	5.2
CAM1700	Horse (*Equus caballus*)	tibia	Camiac	34.6	40.6	14.6	3.2	−20.5	5.2
							av.	−20.8	5.7
							s.d.	0.4	1.4
							n	6	6
RPB1400	Rhinoceros (*Coelodonta antiquitatis*)	lower tooth	Saint-Césaire	7.8	31.4	12.6	2.9	−20.9	5.4
LBR2200	Rhinoceros (*Coelodonta antiquitatis*)	skull	La Berbie	27.6	39.1	14.4	3.2	−19.6	7.2
CAM1300	Rhinoceros (*Coelodonta antiquitatis*)	humerus	Camiac	22.6	38.1	13.7	3.2	−19.9	8.4
CAM1400	Rhinoceros (*Coelodonta antiquitatis*)	humerus	Camiac	27.0	39.3	14.3	3.2	−20.1	7.1
CAM1500	Rhinoceros (*Coelodonta antiquitatis*)	humerus	Camiac	78.1	40.3	14.7	3.2	−20.6	7.1
							av.	−20.2	7.0
							s.d.	0.5	1.0
							n	5	5
LBR1900	Mammoth (*Mammuthus primigenius*)	femur	La Berbie	11.9	37.2	13.4	3.2	−21.8	8.5
CAM700	Mammoth (*Mammuthus primigenius*)	femur	Camiac	57.2	39.1	14.1	3.2	−21.2	8.7
CAM800	Mammoth (*Mammuthus primigenius*)	femur	Camiac	32.3	40.6	14.7	3.2	−21.8	7.7
							av.	−21.6	8.3
							s.d.	0.3	0.4
							n	3	3
LBR1300	Hyaena (*Crocuta crocuta*)	humerus	La Berbie	41.0	40.6	14.8	3.2	−19.9	9.5
LBR1400	Hyaena (*Crocuta crocuta*)	humerus	La Berbie	26.4	39.9	14.7	3.2	−19.1	8.5
LBR3300	Hyaena (*Crocuta crocuta*)	neck vertebra	La Berbie	14.7	34.5	12.0	3.3	−19.1	9.8
CAM1800	Hyaena (*Crocuta crocuta*)	long bone	Camiac	72.3	41.6	14.9	3.3	−19.3	9.8
CAM1900	Hyaena (*Crocuta crocuta*)	long bone	Camiac	53.1	40.6	14.6	3.2	−19.0	9.1
							av.	−19.3	9.3
							s.d.	0.3	0.5
							n	5	5
RPB7000	Neandertal (*Homo neandertalensis*)	fibula	Saint-Césaire	26.0	40.8	14.2	3.3	−19.8	11.4

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