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Ecological and physiological variability of Sr/Ca and Ba/Ca in mammals of West European mid-Würmian food webs

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Abstract

The Middle to Upper Paleolithic transition in Western Europe is characterized, from an ecological point of view, by large-ungulate communities adapted to cold climatic conditions. The aim of this study is to reconstruct the trophic relationships prevailing in these paleoecosystems which have no equivalent in the modern world. Bone and dentine remains representing five mammalian assemblages dated around 35 ka BP, one of which included a Neandertal specimen, are investigated for Sr/Ca and Ba/Ca of bioapatites. Examination of the N content and U+REE luminescence of bulk material, Ca/P ratios, and Mn and Ca contents of purified samples demonstrates that the Sr/Ca and the Ba/Ca ratios of bone and dentine samples are not significantly altered by diagenesis. As a consequence of the biological discrimination of Sr and Ba in relation to Ca, Sr/Ca and Ba/Ca values are impoverished with increasing trophic position and are strongly correlated within a trophic web. The slopes of the linear regressions between Sr/Ca and Ba/Ca are consistent with modern variability. Furthermore, a statistical difference was found between Ba/Ca of foregut and hindgut herbivores. When coexisting collagen is preserved, the Sr+Ba/Ca and $\delta^{15}N$ are strongly correlated. The distribution of values suggests that the $\delta^{15}N$ range is mainly controlled by the variability of soil conditions whereas the $\delta^{13}C$ range may be related to resource availability.

Keywords: ungulates; bone; Sr/Ca; Ba/Ca; $^{15}N/^{14}N$; $^{13}C/^{12}C$; Europe; Pleistocene

1. Introduction

The goal of this study is to determine, after assessing the preservation of biogenic strontium/calcium and barium/calcium ratios (Sr/Ca and Ba/Ca respectively), the physiological, trophic and ecological constants resulting from the comparison of Sr/Ca and Ba/Ca of bioapatites and stable nitrogen and carbon isotopes ($\delta^{15}N$ and $\delta^{13}C$ re-

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spectively) of preserved collagen in bone and dentine remains of extinct (around 35 ka BP) West European mammals. West European continental environments coeval with marine oxygen isotopic stage 3 were characterized by steppic landscapes, cold climate with arid and humid oscillations and populated by large-mammalian communities (Guthrie, 1990). It is in this ecological setting, the so-called mammoth steppe, that Neandertal populations disappeared around 30 ka BP (Wolpoff, 1996). $\delta^{13}C$ and $\delta^{15}N$ of preserved bone and dentine collagen have been used to reconstruct the paleotrophic relationships of some Neandertals and coexisting fauna (e.g. Bocherens et al., 1997). However, this approach is limited by frequently poor collagen preservation. In addition, collagen stable isotopic composition is only a proxy for the source of the consumed proteins (Ambrose and Norr, 1993). Measurement of Sr/Ca and Ba/Ca of bioapatite may solve these problems.

The process of biological discrimination of Sr and Ba relative to Ca (biopurification of Ca) expresses the positive factor by which Sr and Ba decrease in transferring Ca through physiological reactions (e.g. Comar et al., 1957; French, 1961). Elias et al. (1982) demonstrate that Sr/Ca and Ba/Ca decrease in bone of animals with ascending trophic position. This phenomenon was extensively used to reconstruct paleodiet (e.g. Sillen, 1992; Sillen and Lee-Thorp, 1994; Gilbert et al., 1994; Ezzo et al., 1995). More recently, Burton et al. (1999) have shown that the relative decrease of Sr/Ca and Ba/Ca seems constant in a mammalian food web. For this studied case (i.e. a food web at the Michigan/Wisconsin frontier), the concomitant decrease of Sr/Ca and Ba/Ca could be illustrated by the following relationship: $\log(Sr/Ca) = -1.316 + 0.57 \times \log(Ba/Ca)$ (Burton et al., 1999). However, this relationship could be compared with other available Sr/Ca and Ba/Ca data (Gilbert et al., 1994; Elias et al., 1982). Fig. 1 shows that the biological discrimination of Sr and Ba relative to Ca seems constant and is independent of the ecological setting as indicated by the parallel slopes of regression lines. This led to a new equation, obtained by averaging regression lines A, B and C: $\log(Sr/Ca) = -0.98(\pm 0.3) + 0.55(\pm 0.05) \times \log(Ba/Ca)$, illustrating the current known variability.

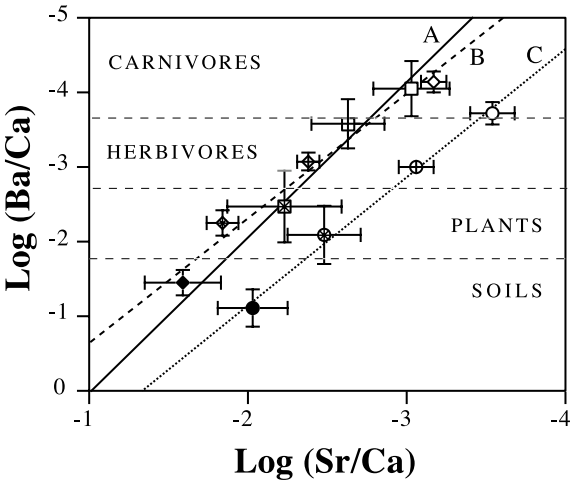

Fig. 1. Compilation of log(Sr/Ca) and log(Ba/Ca) in ecosystems located in Southwestern Cape (South Africa; A; squares; Gilbert et al., 1994), Yosemite Park (USA; B; diamonds; Elias et al., 1982) and the Michigan/Wisconsin frontier (USA; C; circles; Burton et al., 1999). Coefficients x and y of equation $\log(Ba/Ca) = x\log(Sr/Ca) + y$ are estimated to be 1.97 (A), 1.62 (B) and 1.71 (C), and 1.8 (A), 0.9 (B) and 2.3 (C), respectively. Omnivores and fish taxa were removed from the survey of Burton and co-workers. A shift towards negative values of log(Sr/Ca), probably due to higher Sr content in the soils, characterizes ecosystem C. As a consequence, it appears that the mean plant Sr/Ca of Wisconsin (C) overlaps the mean herbivore Sr/Ca of California (B) and South Africa (A). Ba values seem to be more constant and each trophic level may be characterized by a specific range of Ba/Ca ratios and log(Ba/Ca) of carnivorous species are lower than an average value of −3.6, which gives a threshold value of 95–100 ppm of Ba considering a mean value of 38% of Ca in bone.

In paleontological studies, original Sr/Ca and Ba/Ca are often altered by diagenesis. Despite the variability and the non-predictability of diagenetic histories, the chemical state of fossil tooth and bone is affected by precipitation of secondary minerals and chemical alteration of biogenic apatite (Kohn et al., 1999). The former is thought to be significantly eliminated by adapted chemical pretreatment (Sillen and Legeros, 1991; Price et al., 1992; Balter et al., 2001), while the latter definitively overprints the original chemistry. Because of the very low uranium and rare earth

elements (REE) contents in living phosphatic organisms (Hinners et al., 1998; Buseth et al., 1998), U+REE content evaluation has been proposed as a proxy of the chemical alteration of the Ca site (Kohn et al., 1999). REE could also be adsorbed onto the surface of the bioapatite crystals (Gaft et al., 1996; Reynard et al., 1999). As an alternative of wet process determination of U+REE, one convenient technique to assess the REE patterns in bioapatite (semi-quantitative determination and mechanisms of mineral trapping) is achieved by cathodoluminescence (Gaft et al., 1996). Despite the fact that each REE possesses an intrinsic sensitivity to luminescence which could be enhanced or diminished by the crystal-chemical environment (Blanc et al., 2000), typical concentrations at the ppm level could be detected for Sm^{3+}, Gd^{3+} and Dy^{3+} by cathodoluminescence (Barbarand and Pagel, 2001). Samples that have passed the U+REE test must be pre-treated by cleaning methods, in order to diminish the diagenetic effects (see 3. Methods for discussion). Subsequently, comparisons of Sr and Ba contents with diagenetic proxies were performed.

2. Material

Bone is usually studied because of its constant turnover (Sillen and Lee-Thorp, 1994). However, teeth, composed of enamel and dentine, represent the most abundant remains in fossil deposits. Dentine is known to be affected by remodelling that takes place in the pulp chamber and root canals (Hillson, 1986).

All discussed sites are shown in Fig. 2. Caves of Camiac (Camiac-et-Saint Denis, Gironde, France), Scladina (Sclayn, Namur, Belgium), Unikoté (Iholdy, Pyrénées-Atlantiques, France) were frequently used as denning area by hyenas *Crocuta crocuta* (Guadelli, 1987; Simonet, 1992; Michel, 1994). La Berbie (Castels, Dordogne, France) is a swallow hole where the assemblage of bone is considered to be the result of accidentally fallen animals (Madelaine, personal communication). La Roche à Pierrot (Saint-Césaire, Charente-Maritime, France) is a rock shelter where bones were accumulated by *Homo sapiens*

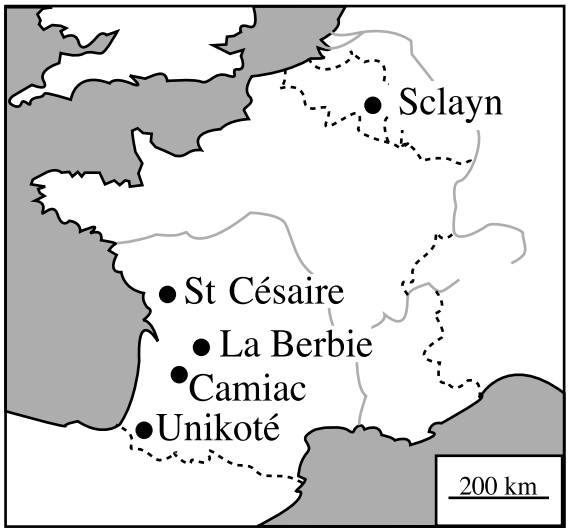

Fig. 2. Geographic location of the sites discussed in the text.

neanderthalensis (Lévêque and Vandermeersch, 1980; Patou-Mathis, 1993). Bone and dentine remains were collected in layers corresponding to an average age of 35 ka BP. Calibrated ^{14}C on collagen yield: Camiac layer D, 35.1 ± 2 kyr BP (Guadelli, 1987); Scladina layer 1A, > 36.2 and 38.7 ± 1.5 kyr BP (Gilot, 1992); La Berbie, 35.8 ± 5, 33.5 ± 2.5, 33.2 ± 2.7 kyr BP (Madelaine, unpublished report). Thermoluminescence values of six burnt flints give an average age of 36.3 ± 2.7 kyr BP for layer EJOPsup. of Saint-Césaire (Mercier et al., 1993). Overlying bones at Unikoté give an age of calibrated ^{14}C 30 ± 1.6 kyr BP (Michel, unpublished report). In summary, these ages support the interpretation that these communities were contemporaneous. In addition, faunal compositions are homogeneous, with the exception of the additional presence of wild boar at Unikoté and Saint-Césaire, and reindeer at Saint-Césaire and La Berbie (Guadelli, 1987; Simonet, 1992; Patou-Mathis, 1993; Michel, 1994). One hundred and forty samples have been collected, representing 14 taxa. Description of the samples is listed in the Appendix. Samples of soils were collected in the field at Scladina and Unikoté. For Camiac and Saint-Césaire, they were separated from adjoining bones.

3. Methods

3.1. Luminescence of U+REE

Because luminescence of U occurs in the form of free UO_2^{2+}, and REE promote luminescence when they are located in the Ca site of apatite (Gaft et al., 1996), luminescence spectra were performed on raw and heated samples (1100 K during 2 h). Cathodoluminescence spectra were recorded with a Jobin-Yvon H10 UV spectrometer attached to a JEOL JSM 840A scanning electron microscope. Operating conditions are given in Perseil et al. (2000).

3.2. Cleaning method and elemental measurements

The diagenetic occurrence of Sr and Ba is mainly linked to the precipitation of secondary carbonates and Mn–Fe oxyhydroxydes respectively (Kohn et al., 1999). Efficiency of removing secondary minerals on trace element chemistry by cleaning methods has been discussed by several authors (e.g. Tuross et al., 1989; Price et al.,

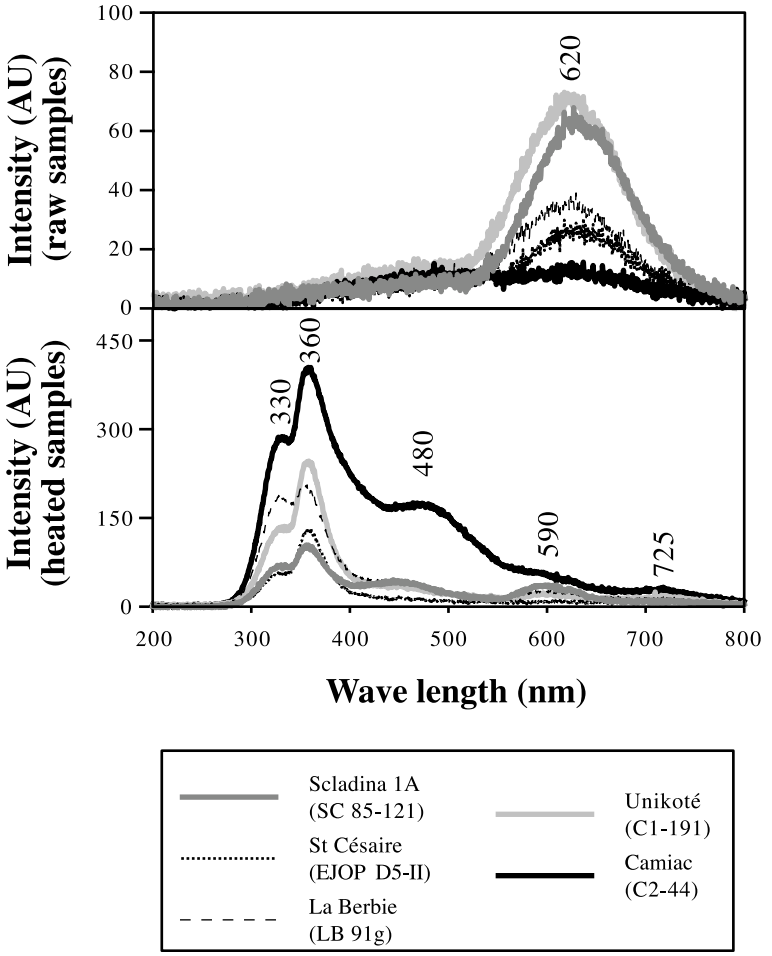

Fig. 3. Cathodoluminescence spectra from samples corresponding to a given locality. Intensity of luminescence of raw sample is very low, displays no UO_2^{2+} luminescence pattern (Gaft et al., 1996), but is characteristic of Mn activation in calcite (de Rafélis et al., 2000). Heated samples display more intense luminescent peaks whose wavelength does not correspond to a REE activation in phosphates. Heating sample promotes organic matter destruction and diffusion of REE in the apatite lattice. Heated samples show a systematic set of broad peaks at 330, 360, 480, 590 and 725 nm, which are not characteristic of REE luminescence.

1992). Recently, Nielsen-Marsch and Hedges (2000) have demonstrated that commonly used acetic acid pretreatment is efficient for removing secondary carbonates for histologically well preserved material, i.e. with high protein content (%N). This is due to the fact that remaining collagen, protecting pristine bioapatite (Person et al., 1996), is not dissolved by acetic acid. For samples with low protein content, Nielsen-Marsch and Hedges (2000) found that acetic acid pretreatment results in hypermineralized remaining bioapatite. In order to isolate the less altered bioapatite, the solubility profile procedure was developed by Sillen and Legeros (1991). However, this method is time-consuming and as a first approach the same cleaning procedure was applied to samples with high and low nitrogen content (Balter et al., 2001). Methods and analytical conditions for Ca, P, Sr, Ba and Mn determination in washed powders were according to Balter et al. (2001). Soluble fractions of soil samples were analyzed according to the Shirahata et al. (1980) procedure after extensive rinsing to remove modern water fraction. All results are expressed in log for Sr/Ca and Ba/Ca. For quality control, the standard NIST SRM 1400 'Bone ash' was used for all elements and results are presented in the Appendix.

3.3. Collagen quantity and extraction and isotopic analysis

Collagen quantity was measured by means of a CHN elemental analyzer. Procedures for collagen extraction and $\delta^{13}C$ and $\delta^{15}N$ analyses are given in Bocherens et al. (1997). The isotope ratios are expressed for carbon as $\delta^{13}C$ vs. PDB and for nitrogen vs. atmospheric N_2: $\delta = [(R_{sample} - R_{standard}) - 1] \times 1000$ where R stands for $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

4. Results

4.1. Diagenetic proxies

About 50 samples (10 for each site) were studied for their luminescence spectra. All raw samples were poorly luminescent and displayed a single broad peak at 620 nm (Fig. 3). According to Blanc et al. (2000) and Roeder et al. (1987), REE in apatite promote sharp intense luminescent

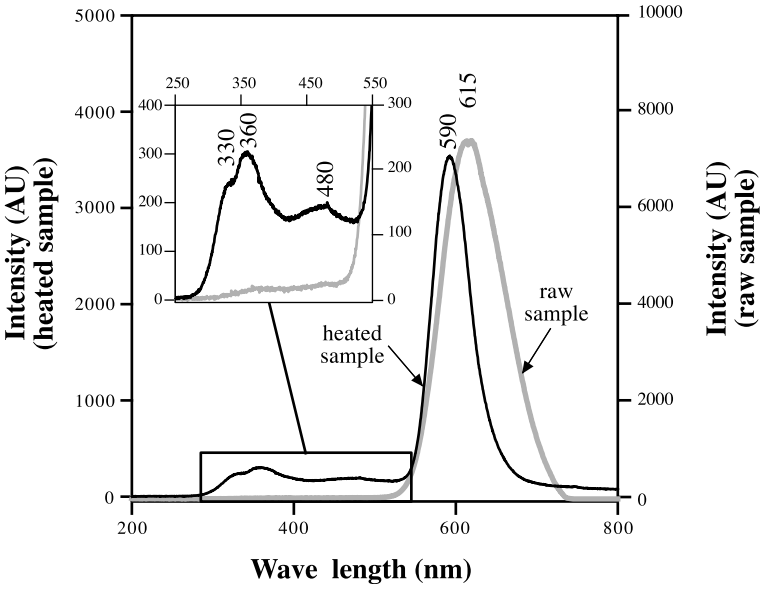

Fig. 4. Cathodoluminescence spectra of a micrite containing 500 μg/g of Mn characterized by a luminescence peak at 615 nm. Corresponding lime exhibits a set of luminescent peaks whose wavelengths match those of heated fossil bone samples.

peaks whose wavelength does not correspond to those observed in the case of heated samples, which are due to Mn in lime (Fig. 4). Since detection limits of REE luminescence activation are poorly defined and luminescence efficiency varies for each element and can be either enhanced or suppressed by impurities, precise measurement of REE cannot be direct. However, absence of REE-activated luminescence allows an estimation of the magnitude range of the possible REE contents below the ppm level (Roeder et al., 1987). Table 1 summarizes Fisher test results performed between Ca, Sr, Ba and Mn of bioapatite powders after chemical pretreatments for each locality. Mn content is not correlated with Ba content, indicating that possible Fe–Mn-bearing oxyhydroxydes etched by nitric acid contain no additional Ba. Values of Ca seem to be not correlated with Sr, attesting to a lack of significant amount of Sr-bearing carbonates. The fact that no remnant diagenetic Ca exists is strengthened by the bioapatitic Ca/P ratio (Fig. 5), whose lower and upper boundaries of 1.57 and 1.8 (molar ratio), given by Legeros and Legeros (1984), correspond to 1.99 and 2.33 (weight ratio). Organic content (%N) is not correlated with either Sr or Ba content ($r = -0.136$ and $r = -0.122$ respectively). None of these diagenetic proxies shows a clear relationship with Sr and Ba contents: thus, it could be a posteriori inferred that diagenesis has not significantly altered paleobiological Sr/Ca and Ba/Ca ratios.

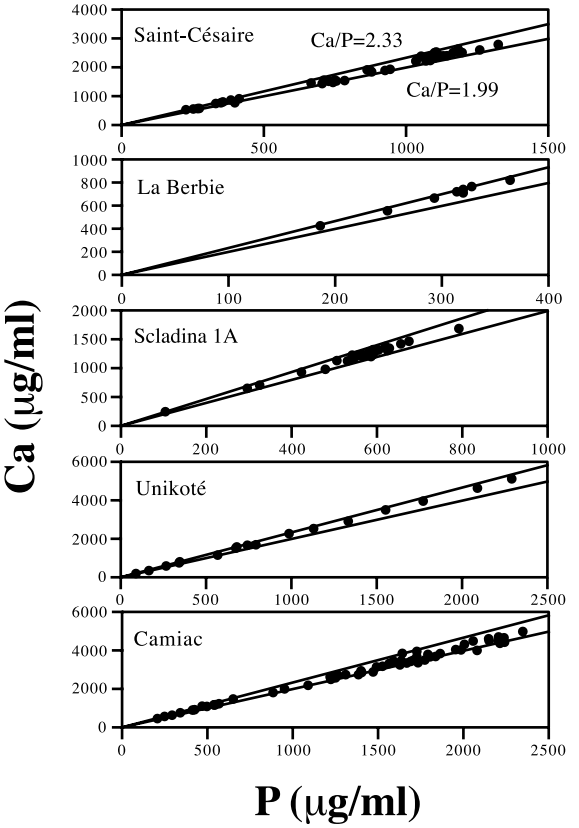

Fig. 5. Ca/P ratios of the analyzed samples, plotted in relation to modern variability. Values of the lower and upper boundaries are given by Legeros and Legeros (1984), table 4, p. 377.

4.2. Sr and Ba in bone and dentine

Concomitant analyses of bone and dentine of a given individual show that Sr contents vary slightly among tissues, but that the Ba difference is null whatever the Ba contents may be (Fig. 6). Systematic shifts are observed in $\delta^{15}N$ in collagen of bone and dentine (Bocherens and Mariotti, 1997). Similarities in Sr and Ba contents of bone and dentine suggest that those shifts are probably due to metabolic processes involving isotopic fractionation rather than diachronic steps of bone and dentine mineralization with different dietary intakes. Clearly, more work is needed to find out which factors determine these $\delta^{15}N$ variations between bone and dentine in different mammals species. At this stage, it seems justified to consider both tissues as equivalent as far as trace element control is concerned.

Table 1
Results for r and P of Fisher tests between Sr and Ca, and Ba and Mn performed for each locality

Site	r		P	
	Sr,Ca	Ba,Mn	Sr,Ca	Ba,Mn
Camiac	0.267	0.115	0.2584	0.6346
La Berbie	0.284	−0.318	0.5137	0.4609
Saint Césaire	0.226	0.293	0.1006	0.0312
Scladina 1A	0.293	−0.106	0.1310	0.5952
Unikoté	0.112		0.6739	

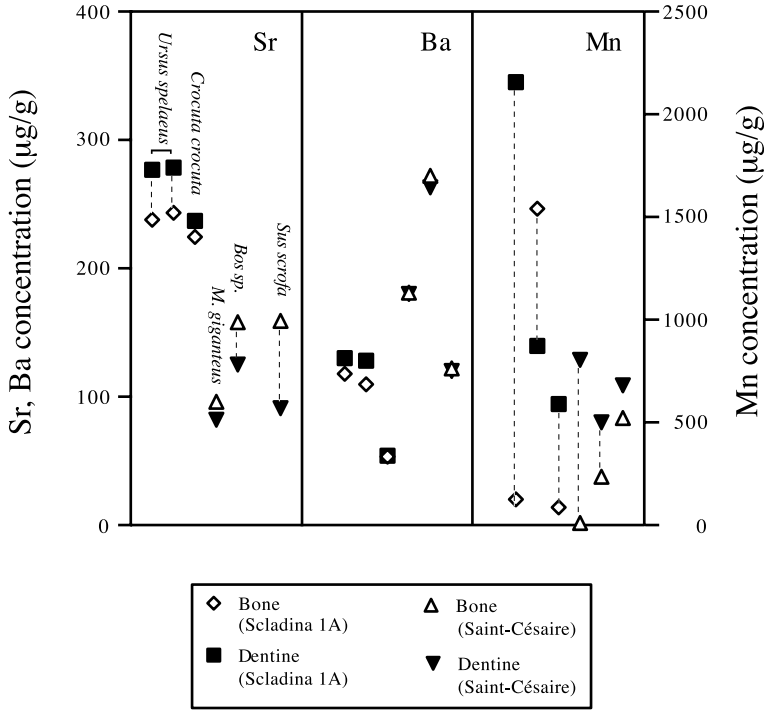

Fig. 6. Comparison of dentine and bone Sr, Ba and Mn. For one specimen, values of Sr of bone mimic those of dentine with a mean difference of 23 µg/g, except in the wild boar (70 µg/g) which may be due to its omnivorous diet. Congruence of Ba in these two tissues is very pronounced. Values of Mn are plotted as well to show that the correlation of Sr and Ba in bone and dentine is not related to diagenesis.

4.3. Sr/Ca, Ba/Ca, $\delta^{13}C$ and $\delta^{15}N$

At all sites, values of log(Sr/Ca) and log(Ba/Ca) are lower for carnivorous than for herbivorous species (Fig. 7). Omnivorous species when they are present have intermediate log(Sr/Ca) and log (Ba/Ca) values (Sr/Ca: $P = 0.0185$, Camiac; $P = 0.0061$, Saint-Césaire; $P = 0.0003$, Scladina 1A; $P = 0.0019$, Unikoté; Ba/Ca: $P = 0.0023$, Camiac; $P < 0.0001$, Saint-Césaire; $P = 0.2124$, Scladina 1A; $P = 0.0283$, Unikoté). Despite the non-significant difference in Ba/Ca at Scladina 1A, these results are in agreement with predicted trophic position (see Appendix). Log(Sr/Ca) ranges and absolute values are highly variable and distinctive of each food web. Nitrogen content (%N) below 0.4% does not allow collagen extraction (Bocherens et al., 1997): for instance, %N at Saint-Césaire was extremely low, and only few samples yield isotopic values (Drucker et al., 1999; Appendix). C/N values (Appendix) of all extracted residues are characteristic of fresh collagen, comprised between 2.9 and 3.6 (DeNiro, 1985). Collagen $\delta^{13}C$ and $\delta^{15}N$ values for Scladina 1A have been presented and discussed previously (Bocherens et al., 1997), as well as for Saint-Césaire (Drucker et al., 1999). The distribution of carbon and nitrogen isotopic compositions at Camiac and la Berbie is consistent for upper Pleistocene mammals from Western Europe. The range of $\delta^{13}C$ values ($\Delta\delta^{13}C$) is 2.8‰, 2.8‰ and 3.9‰ at Camiac, La Berbie and Scladina 1A respectively, whereas $\Delta\delta^{15}N$ is 4.6‰, 4.8‰ and 7.8‰ at Camiac, La Berbie and Scladina 1A respectively. $\Delta\delta^{15}N$ at Camiac reflects an unexpectedly low ^{15}N enrichment from herbivores to carnivores. The high $\delta^{15}N$ value (9.4‰) of the *Ursus spelaeus* specimen at Camiac is surprising, considering the omnivorous diet of these animals (Bocherens and Mariotti, 1997).

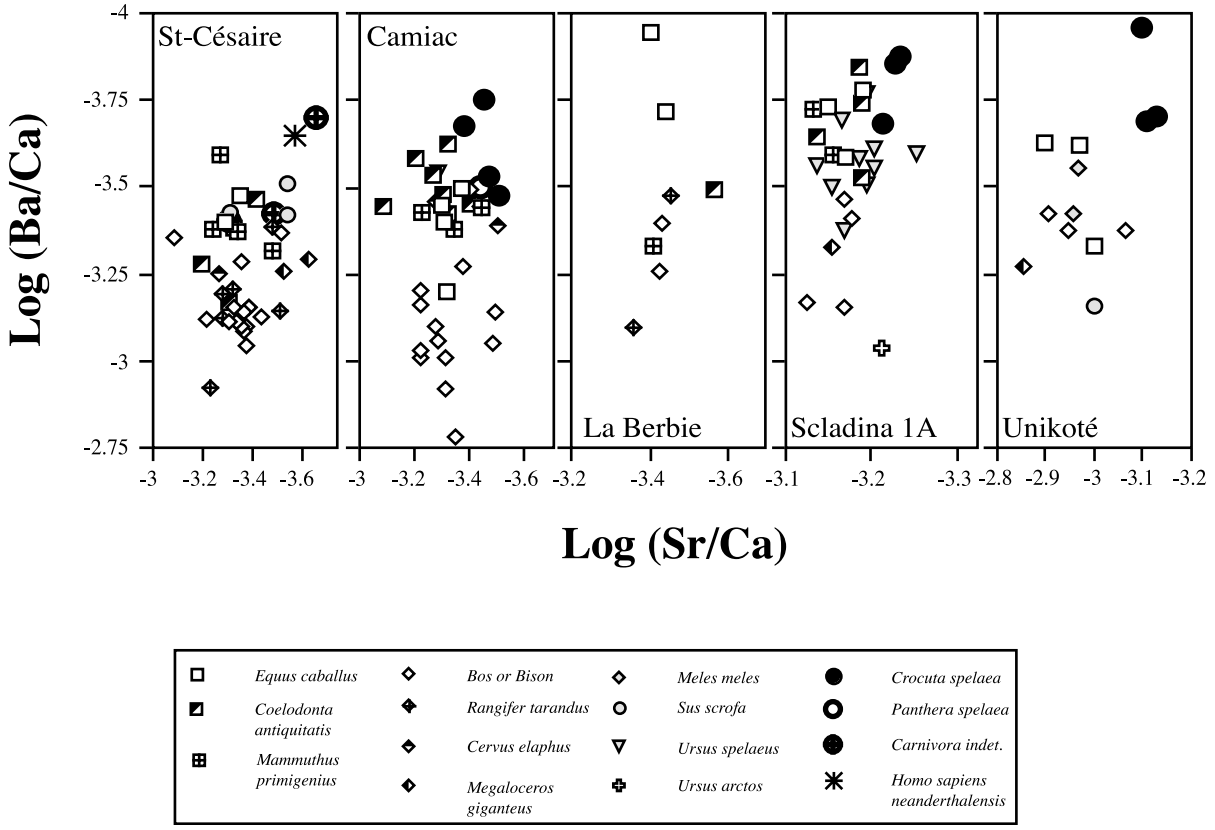

Fig. 7. Relation of log(Ba/Ca) and log(Sr/Ca) in each site, representing all samples. Omnivorous taxa are represented by gray filling. They are statistically different in log(Ba/Ca) ($P < 0.0001$) and log(Sr/Ca) ($P < 0.0001$) from herbivorous and carnivorous taxa. Distribution of all samples seems to be constrained by log(Ba/Ca) and log(Sr/Ca).

5. Discussion

5.1. Sr/Ca and Ba/Ca distribution

We will discuss Sr/Ca and Ba/Ca results of soils, within animals, and their covariation along trophic webs in comparison to modern data. Soils containing calcite are unsuitable for the determination of their Sr/Ca and Ba/Ca ratios. This is especially the case for sediments surrounding bones (see the Appendix for Camiac and Saint-Césaire). Thus, providing original Sr/Ca and Ba/Ca ratios of soils remains feasible but extreme care in the sampling must be taken. Herbivore distributions (Fig. 7) reveal that bovines and reindeer are enriched in Ba by comparison to horses, rhinoceros and mammoths ($P = 0.0005$, Camiac; $P = 0.0002$, Saint-Césaire; $P = 0.0027$, Sclayn; $P = 0.833$, La Berbie; $P = 0.28$, Unikoté). Bovines and reindeer are ruminants with foregut microbial fermentation, whereas horses, rhinoceros and mammoths are monogastric herbivores. It is thus proposed that the distinction in Ba/Ca between the two groups is due to the difference in gastrointestinal tracts. Examination of Ba/Ca values of Gilbert et al. (1994) reveals that in antelope these are significantly ($P = 0.09$) higher than in other herbivores, and the same trend is observed for deer in the study of Burton et al. (1999). The enrichment of Ba in bovines and reindeer is possibly related to the long-lasting retention of digesta (Uden et al., 1982) in addition to the more efficient cellulose degradation. Consequently, trace element release could be more important in foregut herbivores compared to hindgut herbivores. However, no direct evidence supports this

assumption, and the Ba enrichment observed in ruminants might also be linked to diet. This must be confirmed by further studies.

The coefficient of variation (CV) of Sr/Ca and Ba/Ca within herbivore taxa are low. The mean CV, calculated within herbivore taxa for each locality, gives for Sr/Ca and Ba/Ca respectively: 9 ± 6% and 18 ± 12% with $n = 8$ at Unikoté; 5 ± 1% and 23 ± 6% with $n = 23$ at Scladina 1A; 15 ± 9% and 16 ± 10% with $n = 32$ at Camiac; 19 ± 7% and 17 ± 10% with $n = 36$ at Saint-Césaire. Low CV at Unikoté might be due to the small number of samples analyzed. Except for the very low CV of Sr/Ca at Scladina 1A, other values are compatible with the so-called biological threshold value of 20% (Sillen, 1992). However, it is not clear whether diagenesis involves a reduction of CVs by an equilibration process of bones with soil matrices (Sillen, 1992), or an increase of CVs due to the presence of heterogeneous amounts of Sr and Ba in secondary minerals (Burton et al., 1999). The strong statistical differences in Ba/Ca between foregut and hindgut herbivores, and in Sr/Ca and Ba/Ca between herbivores, omnivores and carnivores suggest that biological rather than diagenetic phenomena (which would imply a 'taxa-selective' diagenesis) account for the observed distribution in Sr/Ca and Ba/Ca ratios.

Calculated slopes of linear regressions between log(Sr/Ca) and log(Ba/Ca) of present paleoecosystems are similar to the modern ones (Fig. 8), supporting the fact that the fossil Sr/Ca and Ba/Ca ratios are biologically constrained (Burton et al., 1999). However, detailed observations of modern ecosystems reveal that concomitant transfer of Sr and Ba is not constant. For instance, Gilbert et al. (1994) claimed that leopards and hyraxes have predator–prey relationships. Using the definition of the observed ratio (OR) for Sr (given by $(Sr/Ca)_{bone}/(Sr/Ca)_{precursor}$ or $(Sr/Ca)_{predator}/(Sr/Ca)_{prey}$; Comar et al., 1957) we obtain a value of 0.36 for OR_{Sr} and 0.46 for OR_{Ba}. These results do not support the fact that leopards and hyraxes have predator–prey relationships because Ba is less segregated in comparison to Sr as was demonstrated by Elias et al. (1982), with martens and voles ($OR_{Sr} = 0.16$ and $OR_{Ba} = 0.09$) and Burton et al. (1999) with the pair bobcat/hare ($OR_{Sr} = 0.3$ and $OR_{Ba} = 0.12$). To evaluate the proportion by which Sr is segregated in relation to Ba, one can divide the OR_{Ba} used between carnivores and herbivores by the equivalent OR_{Sr} ($K_{Ba/Sr}$). This gives $K_{Ba/Sr}$ values of 0.55 for ecosystems B and C, and 0.85 for ecosystem A, meaning that, in comparison to ecosystems B and C, Ca is less biopurified in Ba in relation to Sr. This leads to the evidence that concomitant biosegregation of Sr and Ba is more complex than the so-called relative reduction of 10:5:1 (French, 1961), which should theoretically yield a $K_{Ba/Sr}$ ratio of 0.2. In paleoecosystems D, E, F and G, $K_{Ba/Sr}$ is evaluated to be 0.64, 0.64, 0.69 and 0.65 respectively, which is in intermediate position with the variability of available modern data. Differential transfer of Sr and Ba at the level of one organism needs to be evaluated more accurately to progress in the understanding of their trophic behavior.

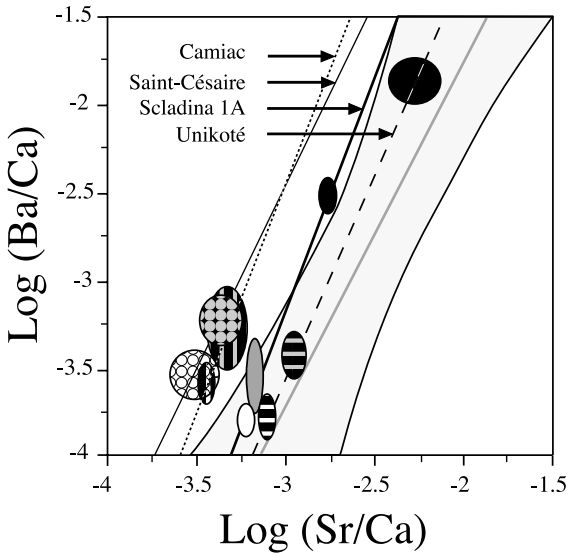

Fig. 8. Comparison of average ± 1 S.D. for herbivores and carnivores from Camiac (vertical bars), Saint-Césaire (circles), Scladina 1A (no design) and Unikoté (horizontal bars). For each site, herbivores are represented by open symbols, carnivores by gray filled symbols and soils by black filled symbols. Modern variability is illustrated by the gray area, representing average ± 2 S.D.

5.2. Elemental and isotopic variations

Trophic positions of different species are very

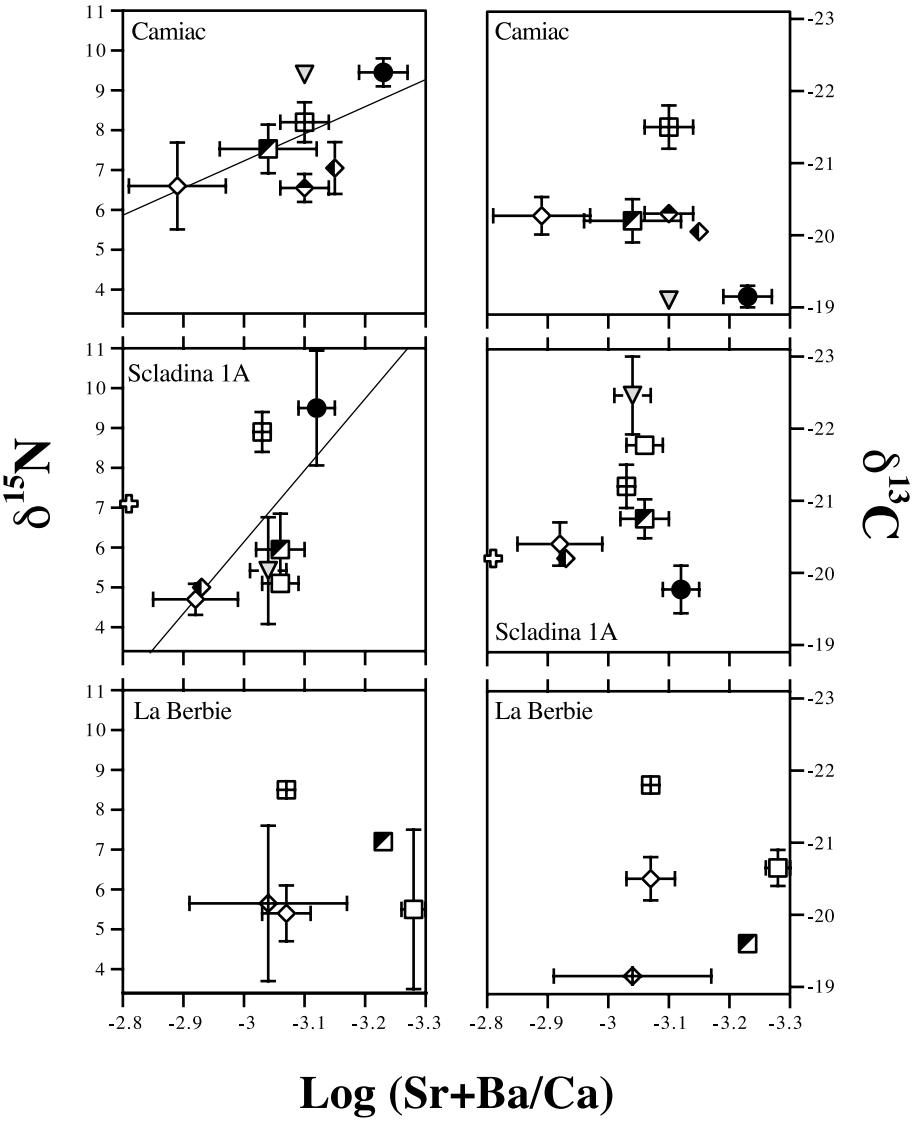

Fig. 9. Distribution of log(Sr+Ba/Ca) in relation of $\delta^{15}N$ (on the left) and $\delta^{13}C$ (on the right) averaging (±1 S.D.) by taxon. Isotopic values were obtained from collagen extracted from the same aliquot on which trace element contents were determined (see Fig. 7 for symbol description).

well illustrated using log(Sr+Ba/Ca) and $\delta^{15}N$ variations, especially because Sr and Ba are added to promote a higher ranking effect (Fig. 9). The Camiac and La Berbie communities are characterized by a higher range of log(Sr+Ba/Ca) (−3.27 to −2.67 and −3.29 to −2.91 respectively) and a lower range of $\delta^{15}N$ (5.2–9.8 and 3.7–8.5 respectively) in comparison to Scladina 1A (−3.14 to −2.81 and 4.3–11.5). This may be explained by a higher diversity of geological substrates, and therefore of soil conditions of living areas of herbivores at Camiac and La Berbie in comparison to Scladina 1A. This is supported by the results of Schoeninger (1985), who observed that scattering of Sr and $\delta^{15}N$ increases with sampling area in a modern food web. This hypothesis is strengthened

by the low $\delta^{15}N$ increase (2.5–3‰) from herbivores to carnivores at Camiac. Reported values of fossil reindeer and mammoth $\delta^{15}N$ (Iacumin et al., 2000), interpreted in terms of variation of aridity in Eurasia during the Pleistocene–Holocene period, may also be explained by different soil characteristics leading to various $\delta^{15}N$ in plants (Mariotti et al., 1980). Ranges of $\delta^{13}C$ at Camiac and La Berbie are lower than at Scladina 1A. These features, in addition to the lower range of log(Sr+Ba/Ca) at Scladina 1A in comparison to Camiac and La Berbie, are possibly related to a higher availability of resources (leading to an averaging of $\delta^{13}C$) at Camiac and La Berbie in comparison to Scladina 1A (Feranec and MacFadden, 2000).

Preliminary results concerning the Neandertal of Saint-Césaire reveal that this human specimen was quasi-strictly carnivorous (Balter et al., 2001). A quantification of the proportions of meat vs. plants was possible through tests of different foodstuffs containing known amounts of Sr and Ca with the model proposed by Burton and Wright (1995). It was shown that while there is a wide variability in Sr/Ca of the plants used in the model, the Sr/Ca of the bone of the Neandertal is only predicted with a quasi-totality of meat in the diet (97 wt%) and a plant or fish supplementation. In addition, the association of plant and fish is impossible in any proportion. The collagen extracted from the same sample of the Neandertal gives $\delta^{13}C$ and $\delta^{15}N$ values of −19.8‰ and 11.4‰ respectively (Bocherens and Drucker, 2002), which indicate a diet predominantly based upon meat consumption. As the single use of the trace elements or stable isotopes in many cases gives conflicting dietary interpretations (Sillen and Lee-Thorp, 1994; Schoeninger, 1985), we suggest that these methods should be applied together in further studies of paleodiet in order to better constrain possible dietary sources and their relative proportions.

6. Conclusion

The absence of relationship between different physico-chemical proxies of diagenesis and Sr and Ba content of bone and dentine indicates that diagenesis effects on Sr/Ca and Ba/Ca ratios are not significant. Slopes of log(Sr/Ca) and log (Ba/Ca) regression lines calculated for past ecosystems differ slightly from modern ones due to the variability of the amplitude of biopurification of Ca in relation to Sr and Ba. Rough extrapolation of experimental surveys does not reflect ecological reality and the degree by which an element is segregated in comparison to the other must be further investigated. An unexpected enrichment of Ba in ruminants in comparison to monogastric taxa is observed and must be confirmed with modern data. We suggest that by comparing the range of log(Sr+Ba/Ca), $\delta^{15}N$ and $\delta^{13}C$, paleoecological interpretations are possible in terms of habitat area and resource availability. Further investigations at 30–40 ka BP West European prehistoric sites will probably shed light upon paleoenvironments coeval to the Neandertalian replacement by Modern humans.

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Appendix

Results of bone and dentine Ca/P, Sr, Ba, log(Sr/Ca), log(Ba/Ca), Mn, N and corresponding collagen $\delta^{13}C$ and $\delta^{15}N$ for all fossil samples, and results of international standard NIST SRM 1400 'Bone ash'. Numbers in parentheses and in brackets indicate number of analyses and variation coefficient (%) respectively. n.m.: not measured; n.e.c.: no extractable collagen.

Analysis number L.G.B.S.	Analysis number L.B.I.	Excavation number	Species	Predicted diet	Sample	Bioapatite					Collagen				Bulk	
						Ca/P	Sr (μg/g)	Ba (μg/g)	Log (Sr/Ca)	Log (Ba/Ca)	Yield (mg/g)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Mn (μg/g)	N (%)
La Berbie																
P11-031	LBR 300	LB98 M9a 349	*Bison priscus*	herbivorous	metatarsus r.	2.3	130	142	−3.44	−3.4	27.6	3.1	−20.8	4.7	< 10	1
P11-032	LBR 500	LB96 L10a 44	*Bison priscus*	herbivorous	metatarsus l.	2.22	131	197	−3.43	−3.25	26.1	3.2	−20.2	6.1	40	0.8
P11-033	LBR 900	LB96 AV M7bc	*Rangifer tarandus*	herbivorous	humerus r.	2.32	154	282	−3.36	−3.09	18.7	3.2	−19.2	3.7	< 10	0.8
P11-034	LBR 1100	LB91 grotte puits	*Rangifer tarandus*	herbivorous	mandible	2.25	126	120	−3.45	−3.48	14.6	3.2	−19.1	7.6	< 10	0.4
P11-035	LBR 1600	LB91 grotte	*Equus caballus*	herbivorous	metacarpus	2.33	130	70	−3.44	−3.72	22.4	3.2	−20.4	7.5	213	0.6
P11-036	LBR 1700	LB95 K10 AB	*Equus caballus*	herbivorous	femur	2.28	132	38	−3.4	−3.94	36.5	3.2	−20.9	3.5	< 10	1.1
P11-037	LBR 1900	grotte	*Mammuthus primigenius*	herbivorous	femur	2.23	134	161	−3.41	−3.33	11.9	3.2	−21.8	8.5	81	0.3
P11-038	LBR 2200	grotte	*Coelodonta antiquitatis*	herbivorous	cranium	2.27	92	110	−3.57	−3.49	27.6	3.2	−19.6	7.2	343	0.8
Camiac																
P202		C2-02	*Bos* sp.	herbivorous	long bone shaft	2.12	231	247	−3.23	−3.2	n.m.					0.8
P203		C2-44	*Bos* sp.	herbivorous	tibia	2.04	171	643	−3.35	−2.78	n.m.					0.4
P204		C2-47	*Bos* sp.	herbivorous	long bone shaft	2.06	225	375	−3.23	−3.01	n.m.					1.4
P205		D2	*Bos* sp.	herbivorous	long bone shaft	2.08	225	263	−3.23	−3.16	n.m.					1.2
P206		D3-22	*Bos* sp.	herbivorous	tibia	2.01	120	331	−3.49	−3.05	n.m.					0.5
P207	CAM600	D4-8	*Bos* sp.	herbivorous	femur or tibia	1.94	185	310	−3.29	−3.06	35.9	3.3	−20.4	5.3	n.m.	1.1
P209	CAM100	E1-7	*Bos* sp.	herbivorous	femur or tibia	2.01	160	206	−3.38	−3.27	66.9	3.2	−20	6.1	n.m.	2.1
P210	CAM200	E2-14	*Bos* sp.	herbivorous	femur or tibia	2.09	190	476	−3.32	−2.92	58.7	3.2	−20.7	6.2	n.m.	2.1
P211	CAM300	E2-64	*Bos* sp.	herbivorous	femur or tibia	2.03	199	299	−3.28	−3.1	52.3	3.3	−20.4	7.4	n.m.	1.7
P213		F1-14	*Bos* sp.	herbivorous	long bone shaft	2.04	220	353	−3.23	−3.03	n.m.					1.7
P308	CAM400	E2-40	*Bos* sp.	herbivorous	tibia	2.18	171	350	−3.32	−3.01	23.4	3.2	−20.1	8.6	n.m.	1.9
P309	CAM500	E2-82	*Bos* sp.	herbivorous	tibia	2.16	123	281	−3.5	−3.14	14.4	3.3	−20	6	n.m.	1.2
P214		B2-64 (A)	*Mammuthus primigenius*	herbivorous	femur	2.17	209	134	−3.23	−3.43	n.m.				132	0.6
P215	CAM700	D6	*Mammuthus primigenius*	herbivorous	humerus	2.06	167	155	−3.34	−3.38	57.2	3.2	−21.2	8.7	57	1.6
P216	CAM800	D7	*Mammuthus primigenius*	herbivorous	femur	2.05	136	135	−3.44	−3.44	32.3	3.2	−21.8	7.7	< 10	0.8
P218	CAM900	C2-51	*Megaloceros giganteus*	herbivorous	femur	2.18	144	143	−3.44	−3.44	10	3.2	−20	6.4	62	1.4
P306	CAM1000	D2-30	*Megaloceros giganteus*	herbivorous	long bone shaft	2.17	153	128	−3.41	−3.49	36.8	3.3	−20.1	7.7	129	1
P305	CAM1100	C2-55	*Cervus elaphus*	herbivorous	long bone shaft	2.26	213	138	−3.28	−3.46	24.4	3.3	−20	6.9	116	0.9
P307	CAM1200	D8-30	*Cervus elaphus*	herbivorous	long bone shaft	2.16	120	160	−3.51	−3.39	8.7	3.1	−20.6	6.2	< 10	0.5
P222	CAM1400	B2-52	*Coelodonta antiquitatis*	herbivorous	humerus	2.01	234	98	−3.21	−3.58	27	3.2	−20.1	7.1	< 10	0.8
P223	CAM1300	B2-68	*Coelodonta antiquitatis*	herbivorous	humerus	2.09	309	137	−3.09	−3.44	22.6	3.2	−19.9	8.4	< 10	0.8
P244	CAM1500	D6-2	*Coelodonta antiquitatis*	herbivorous	long bone shaft	1.94	134	120	−3.41	−3.45	78.1	3.2	−20.6	7.1	< 10	2.1
P240		E3-90	*Coelodonta antiquitatis*	herbivorous	long bone shaft	2.11	184	150	−3.33	−3.42	n.m.				n.m.	1.3
P226		E6-6	*Coelodonta antiquitatis*	herbivorous	long bone shaft	1.97	183	94	−3.33	−3.62	n.m.				10	1.3
P241		E2-12	*Coelodonta antiquitatis*	herbivorous	long bone shaft	2.03	156	65	−3.38	−3.76	n.e.c.				57	0.1
P227		Ra-1	*Coelodonta antiquitatis*	herbivorous	long bone shaft	2.1	186	127	−3.31	−3.48	n.m.				70	n.m.
P228		Rb-1	*Coelodonta antiquitatis*	herbivorous	long bone shaft	2.13	206	113	−3.27	−3.53	n.m.				34	n.m.
P229		B2-29	*Equus caballus*	herbivorous	tibia-fibula	2.02	194	136	−3.3	−3.45	n.e.c.				147	0.2
P231		C3	*Equus caballus*	herbivorous	tibia-fibula	2.14	164	122	−3.37	−3.5	n.m.				< 10	1.6
P234		E2-32	*Equus caballus*	herbivorous	tibia-fibula	2.25	195	254	−3.32	−3.2	n.m.				n.m.	1.6
P235		E3-103	*Equus caballus*	herbivorous	tibia-fibula	2.03	176	143	−3.31	−3.4	n.m.				< 10	1.3
	CAM1600	D6-3	*Equus caballus*	herbivorous	tibia-fibula	n.m.	n.m.	n.m.	n.m.	n.m.	56.1	3.2	−20.7	5.2	n.m.	n.m.
	CAM1700	D7-24	*Equus caballus*	herbivorous	tibia-fibula	n.m.	n.m.	n.m.	n.m.	n.m.	40.6	3.2	−20.5	5.2	n.m.	n.m.
P242	CAM1900	C6-18	*Crocuta crocuta*	carnivorous	long bone shaft	2.19	124	131	−3.51	−3.48	53.1	3.2	−19	9.1	n.m.	2.4
P243	CAM1800	D51	*Crocuta crocuta*	carnivorous	long bone shaft	2.1	137	69	−3.45	−3.75	72.3	3.3	−19.3	9.8	n.m.	2.6

Appendix (*Continued*).

Analysis number L.G.B.S.	Analysis number L.B.I.	Excavation number	Species	Predicted diet	Sample	Bioapatite					Collagen				Bulk	
						Ca/P	Sr (μg/g)	Ba (μg/g)	Log (Sr/Ca)	Log (Ba/Ca)	Yield (mg/g)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Mn (μg/g)	N (%)
P301		B2	*Crocuta crocuta*	carnivorous	long bone shaft	2.28	122	105	−3.47	−3.53	n.m.				61	1.2
P315		B2-72	*Crocuta crocuta*	carnivorous	long bone shaft	2.16	170	84	−3.38	−3.68	n.m.				42	2.1
P244	CAM2000	C2-35 (A)	*Ursus spelaeus*	omnivorous	cubitus r.	2.07	218	82	−3.24	−3.66	57.5	3.2	−19.1	9.4	n.m.	1
P317		C2-35 (B)	*Ursus spelaeus*	omnivorous	long bone shaft	2.18	213	121	−3.29	−3.54	n.m.				n.m.	n.m.
P245		B3-2	*Panthera spelaea*	carnivorous	tibia r.	2.13	143	123	−3.44	−3.5	n.m.				n.m.	1.9
G713		SED_C2	Soil		bone sediment	–	98	139	−3.6	−3.45						–
G716		SED_D2	Soil		bone sediment	–	105	n.m.	−3.57	n.m.						–
G719		SED_D4-4	Soil		bone sediment	–	74	131	−3.71	−3.47						–
Saint Césaire																
P732	RPB 2100	EJOPsup. I4(IV) 25s-26s	*Equus* sp.	herbivorous	tooth (E+D)	2.15	169	133	−3.3	−3.4	n.e.c.				111	0.1
P736	RPB 300	EJOPsup. E5(IV) 27i	*Equus* sp.	herbivorous	C (E+D)	2.21	152	116	−3.36	−3.47	n.e.c.				608	0.1
P706		EJOPsup. E5	*Rangifer tarandus*	herbivorous	mandible	2.19	162	210	−3.32	−3.21	n.m.				n.m.	n.m.
P722		EJOPsup. E5	*Rangifer tarandus*	herbivorous	mandible	2.18	173	247	−3.28	−3.12	n.m.				167	n.m.
P723		EJOPsup. I4(I) 22i	*Rangifer tarandus*	herbivorous	metapod	2.07	160	194	−3.28	−3.2	n.m.				1150	n.m.
P730	RPB 1100	EJOPsup. G5(II) 23s	*Rangifer tarandus*	herbivorous	Mi (E+D)	2.25	190	385	−3.23	−2.93	n.e.c.				166	0.1
P746	RPB 1200	EJOP E7(III) 32s	*Rangifer tarandus*	herbivorous	mandible	2.34	97	230	−3.52	−3.14	9.5	3.2	−18.8	4.9	801	0.4
P738	RPB 600	EJOPsup. G4(II) 23	*Megaloceros giganteus*	herbivorous	maxillary	2.08	96	181	−3.53	−3.26	21.7	3.2	−19.8	3.2	10	0.7
P739	RPB 700	EJOPsup. G4(II) 24	*Megaloceros giganteus*	herbivorous	M2s (E+D)	2.12	82	180	−3.63	−3.29	n.e.c.				804	0.1
P757		EJOPsup. F6(II) 25s	*Cervus elaphus*	herbivorous	M1-2i (D)	2.25	215	223	−3.27	−3.25	n.m.				677	n.m.
P708		EJOPsup. I5 22s	*Bos* sp.	herbivorous	metapod	2.1	139	242	−3.39	−3.15	n.m.				918	n.m.
P709		EJOPsup. I5 22s	*Bos* sp.	herbivorous	metapod	2.11	143	246	−3.39	−3.15	n.m.				984	n.m.
P718		EJOPsup. F6(II) 26i	*Bos* sp.	herbivorous	M3id (D)	2.14	125	263	−3.44	−3.12	n.m.				500	n.m.
P724		EJOPsup. H6(I) 25	*Bos* sp.	herbivorous	mandible	2.11	138	271	−3.39	−3.09	n.m.				688	n.m.
P725		EJOPsup. I5(IV) 24i	*Bos* sp.	herbivorous	metapod	2.1	143	314	−3.38	−3.04	n.m.				734	n.m.
P733	RPB 2500	EJOPsup. D6(II) 28i	*Bos* sp.	herbivorous	bone (ind.)	2.09	159	257	−3.32	−3.11	n.e.c.				524	0.2
P734	RPB 2600	EJOPsup. H6(I) 25i	*Bos* sp.	herbivorous	bone (ind.)	2.02	135	265	−3.37	−3.08	n.e.c.				445	0.1
P748	RPB 1500	EJOP E7(I) 32s	*Bos* sp.	herbivorous	Ps (E+D)	2.21	140	242	−3.38	−3.14	n.e.c.				518	0.3
P749	RPB 1600	EJOP D5(II) 27s	*Bos* sp.	herbivorous	tooth (E+D)	2.28	208	265	−3.22	−3.12	n.e.c.				177	0.2
P750	RPB 1800	EJOP G2(IV) 32i	*Bos* sp.	herbivorous	tooth (E+D)	2.26	145	265	−3.36	−3.1	n.e.c.				485	0.3
P751	RPB 1900	EJOP E7(I) 31i	*Bos* sp.	herbivorous	tooth (E+D)	2.29	159	238	−3.33	−3.15	n.e.c.				361	0.2
P752	RPB 2000	EJOP G5(IV) 24s	*Bos* sp.	herbivorous	tooth (E+D)	2.21	149	177	−3.36	−3.29	n.e.c.				439	0.1
P753	RPB 2200	EJOP D5(II) 26	*Bos* sp.	herbivorous	tooth (E+D)	2.19	279	153	−3.09	−3.35	n.e.c.				518	0.1
P711		EJOPsol E8(I)	*Mammuthus primigenius*	herbivorous	M (D)	2.04	104	152	−3.48	−3.32	n.m.				421	n.m.
P713		EJOPsol E8(I)	*Mammuthus primigenius*	herbivorous	M (D)	2.06	193	141	−3.24	−3.38	n.m.				372	n.m.
P721		EJOPsup. H4(II) 22s	*Mammuthus primigenius*	herbivorous	M (D)	2.13	179	85	−3.27	−3.6	n.m.				197	n.m.
P729	RPB 800	EJOPsup. H5(III) 24i	*Mammuthus primigenius*	herbivorous	M (E+D)	2.05	150	140	−3.34	−3.37	n.e.c.				532	0.1
P714		EJOPsup. (III–IV) 29s	*Coelodonta antiquitatis*	herbivorous	M1-2i (D)	1.94	154	217	−3.32	−3.17	n.m.				353	n.m.
P715		EJOPsup. F5(IV)	*Coelodonta antiquitatis*	herbivorous	P2sd (D)	2.08	201	171	−3.21	−3.27	n.m.				432	n.m.
P731	RPB 1700	EJOPsup. G5(III) 23i	*Coelodonta antiquitatis*	herbivorous	tooth (E+D)	2.14	158	142	−3.33	−3.38	n.e.c.				501	0.1
P747	RPB 1300	EJOP G5(IV) 24s	*Coelodonta antiquitatis*	herbivorous	humerus	2.2	124	114	−3.43	−3.46	n.e.c.				360	0.1
P728	RPB 550	EJOPsup. E6(II) 24i–26i	*Sus scrofa*	omnivorous	maxillary	1.99	159	122	−3.31	−3.43	n.e.c.				521	0.1
P737	RPB 500	EJOPsup. E6(II) 24i–26i	*Sus scrofa*	omnivorous	Ms (D)	1.86	91	120	−3.54	−3.42	n.e.c.				680	0.1
P755		EJOPsup. H4(IV) 23s	*Sus scrofa*	omnivorous	M3i (D)	2.22	109	118	−3.55	−3.51	n.m.				443	n.m.
P754		EJOPsup. G7(III) 30s	*Vulpes vulpes*	omnivorous	M (D)	2.2	127	149	−3.49	−3.42	n.m.				508	n.m.
P740	RPB 200	EJOP F3(IV) 23s	Carnivore	carnivorous	C (D)	2.04	76	70	−3.66	−3.7	n.e.c.				117	0.1
P741	RPB 400	EJOP E6(II) 27s	Carnivore	carnivorous	tibia	2.25	177	144	−3.31	−3.4	n.e.c.				247	0.1
P743	RPB 7000	EJOPsup.	*Homo sapiens neanderthalensis*		fibula	2.13	86	73	−3.57	−3.65	26		−19.8	11.4	801	0.6
G714		SED_RPB H6–G6			bone sediment	–	88	85	−3.61	−3.63						–

Appendix (*Continued*).

Analysis number L.G.B.S.	Analysis number L.B.I.	Excavation number	Species	Predicted diet	Sample	Bioapatite					Collagen				Bulk	
						Ca/P	Sr (μg/g)	Ba (μg/g)	Log (Sr/Ca)	Log (Ba/Ca)	Yield (mg/g)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Mn (μg/g)	N (%)
G722		SED_RPB H5(IV) 24			bone sediment	–	98	82	−3.59	−3.66						–
Sclayn																
P800	SC3900	SC 87-140	*Equus caballus*	herbivorous	upper tooth (D)	2.16	259	99	−3.17	−3.59	18.9	3.2	−21.7	5.2	450	1.4
P801	SC4100	SC 89-135	*Equus caballus*	herbivorous	upper tooth (D)	2.21	255	66	−3.19	−3.78	51.7	3.1	−21.7	5.1	175	1.7
P803	SC4200	SC 83-304	*Equus caballus*	herbivorous	upper tooth (D)	2.22	275	72	−3.15	−3.73	43.9	3.2	−21.9	5	198	1.7
P808	SC2500	SC 86-131	*Megalocerus giganteus*	herbivorous	upper tooth (D)	2.18	278	190	−3.16	−3.32	48	3.2	−20.2	5	378	2
P804	SC4500	SC 89-94	*Bos* sp.	herbivorous	Pi (D)	2.14	259	132	−3.17	−3.46	35.5	3.2	−20.5	4.8	385	1.3
P805	SC4700	SC 86-21	*Bos* sp.	herbivorous	P3i (D)	2.18	266	277	−3.17	−3.15	32.4	3.2	−20.5	4.3	354	1.2
P806	SC4800	SC 83-282	*Bos* sp.	herbivorous	M1i (D)	2.18	249	148	−3.18	−3.41	28.6	3.1	−19.9	5.3	584	1.7
P807	SC4900	SC85-158	*Bos* sp.	herbivorous	P3i (D)	2.13	284	261	−3.13	−3.16	29.7	3.2	−20.7	4.4	857	1.7
P812	SC600	SC 83-285	*Mammuthus primigenius*	herbivorous	tooth (E+D)	2.17	267	98	−3.16	−3.59	45.1	3.2	−20.9	8.4	509	1.4
P813	SC700	SC 85-121	*Mammuthus primigenius*	herbivorous	tooth (E+D)	2.17	284	73	−3.13	−3.72	31.7	3.2	−21.5	9.4	365	1.2
P802	SC1200	SC 87-126	*Coelodonta antiquitatis*	herbivorous	P2i (D)	2.23	290	91	−3.14	−3.64	79.4	3.2	−21.1	5.3	937	2.5
P809	SC900	SC 82-210	*Coelodonta antiquitatis*	herbivorous	P2i (D)	2.19	255	118	−3.19	−3.52	86.7	3.2	−20.9	5.5	418	2.8
P810	SC1300	SC 87-129	*Coelodonta antiquitatis*	herbivorous	P2i (D)	2.05	242	53	−3.19	−3.84	44.9	3.2	−20.4	7.5	1302	1.8
P811	SC1400	SC 81-205	*Coelodonta antiquitatis*	herbivorous	P2i (D)	2.17	248	71	−3.19	−3.74	80.8	3.2	−20.6	5.5	280	2.6
P814	SC3100	SC 85-130	*Ursus spelaeus*	omnivorous	mandible	2.36	238	118	−3.2	−3.5	75.7	3.2	−22.5	3.7	1540	2.6
P815	SC3300	SC 87-171	*Ursus spelaeus*	omnivorous	mandible	2.12	243	110	−3.2	−3.55	60.1	3.2	−22.2	6	125	2.3
P816	SC3500	SC 87-103	*Ursus spelaeus*	omnivorous	phalanx II	2.19	217	100	−3.25	−3.59	80	3.2	−21.8	5.1	374	2.1
P817	SC3600	SC 82-131	*Ursus spelaeus*	omnivorous	phalanx II	2.21	282	107	−3.14	−3.56	73.4	3.2	−21.8	3	461	2.1
P818	SC3700	SC 86-136	*Ursus spelaeus*	omnivorous	phalanx II	2.09	261	79	−3.17	−3.69	55.3	3.2	−22	6.1	848	1.4
P819	SC3800	SC 83-291	*Ursus spelaeus*	omnivorous	phalanx II	2.13	239	95	−3.21	−3.61	119.7	3.2	−2.22	5	1283	2.8
P820	SC2700	SC 83-295	*Ursus spelaeus*	omnivorous	I3i (D)	2.14	247	66	−3.2	−3.77	44.1	3.2	−23	6.5	180	1.6
P822	SC3000	SC 83-63b	*Ursus spelaeus*	omnivorous	I3i (D)	2.12	254	102	−3.19	−3.58	95.1	3.2	−22.5	7	308	2.8
P823	SC3150	SC 85-130	*Ursus spelaeus*	omnivorous	P4i (D)	2.26	277	130	−3.19	−3.5	87	3.2	−23.3	4.5	2233	2.9
P824	SC3350	SC 87-171	*Ursus spelaeus*	omnivorous	P4i (D)	2.2	278	128	−3.16	−3.49	77.6	3.2	−23.3	7.3	872	2.4
P825	SC300	SC 85-94	*Ursus arctos*	omnivorous	I3i (D)	2.09	234	353	−3.21	−3.04	62.1	3.2	−20.2	7.1	0	2
P826	SC1800	SC 85-150	*Crocuta crocuta*	carnivorous	phalanx I	2.19	241	83	−3.22	−3.68	62.5	3.2	−20.2	8.8	1322	2.1
P827	SC2000	SC 83-93	*Crocuta crocuta*	carnivorous	phalanx I	2.05	224	53	−3.23	−3.85	110	3.2	−19.7	8.2	86	3.2
P828	SC1750	SC 83-93b	*Crocuta crocuta*	carnivorous	P3i (D)	2.23	237	54	−3.23	−3.88	60.4	3.2	−19.4	11.5	589	1.7
G11-001		Sclayn 1A G32	Soil		excavation sediment	–	285	413	−2.75	−2.59						–
G11-002		Sclayn 1A G33	Soil		excavation sediment	–	310	421	−2.73	−2.6						–
G11-003		Sclayn 1A G34	Soil		excavation sediment	–	285	473	−2.79	−2.57						–
G11-004		Sclayn 1A G35	Soil		excavation sediment	–	327	805	−2.78	−2.38						–
Unikoté																
P249	Z2-20	*Equus caballus*		humerus l.	2.21	388	181	−3.00	−3.33	n.m.				n.m.	0.5	
P325		C8-36	*Equus caballus*		tibia-fibula	2.03	486	91	−2.9	−3.63	n.e.c.				n.m.	0.3
P330		A1-46	*Megaloceros giganteus*	herbivorous	humerus	2.24	530	205	−2.86	−3.27						
P246		A1-5	*Bos* sp.	herbivorous	femur r.	2.16	430	163	−2.95	−3.37	n.m.				n.m.	0.7
P247		B1-43	*Bos* sp.	herbivorous	humerus r.	2.08	318	160	−3.07	−3.37	n.m.				n.m.	0.1
P248		HS 91	*Bos* sp.	herbivorous	humerus l.	2.07	447	141	−2.91	−3.42	n.m.				n.m.	0.4
P313		E2-49	*Sus scrofa*	omnivorous	cubitus	2.14	381	262	−3.00	−3.16	n.m.				n.m.	0.2
P321		21(4)	*Meles meles*	carnivorous	humerus	2.01	442	151	−2.96	−3.42	n.m.				n.m.	0.6
P322		B2-1	*Meles meles*	carnivorous	tibia	1.83	396	105	−2.97	−3.55	n.m.				n.m.	0.8

Appendix (*Continued*).

Analysis number L.G.B.S.	Analysis number L.B.I.	Excavation number	Species	Predicted diet	Sample	Bioapatite					Collagen				Bulk	
						Ca/P	Sr (μg/g)	Ba (μg/g)	Log (Sr/Ca)	Log (Ba/Ca)	Yield (mg/g)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Mn (μg/g)	N (%)
P251		C1-191	*Crocuta crocuta*	carnivorous	tibia l.	2.23	323	44	−3.1	−3.96	n.m.				n.m.	0.3
P252		D1-111	*Crocuta crocuta*	carnivorous	cubitus r.	2.23	309	80	−3.11	−3.69	n.m.				n.m.	0.3
P253		E1-2	*Crocuta crocuta*	carnivorous	humerus l.	2.27	292	79	−3.13	−3.7	n.m.				n.m.	1.1
G717		UNI. II Hz B	Soil		excavation	–	302	772	−2.39	−1.98						–
					sediment											
G720		UNI. II Hz C	Soil		excavation	–	284	767	−2.38	−1.95						–
					sediment											
G723		UNI. II Hz A	Soil		excavation	–	251	654	−2.24	−1.82						–
					sediment											
G724		UNI. I B4	Soil		excavation	–	320	709	−2.06	−1.71						–
					sediment											
							Sr	Ba	Ca	P						
NIST SRM 1400							(μg/g)	(μg/g)	(%)	(%)						
					Certified value		249	240	38.1	17.9						
					Measured value		246 (27) [5,7]	248 (11) [13,4]	38.9 (21) [6,1]	17.2 (25) [5]						

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