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Trophic Structure and Climatic Information From Isotopic Signatures in Pleistocene Cave Fauna of Southern England

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The preservation of trophic structure and climatic information in Kent's Cavern Upper Pleistocene mammal bones and teeth was assessed by comparing the isotopic composition of modern and fossil equivalents. Yields of collagen from both bone ($N=19$) and tooth ($N=49$) were extremely variable, with values relative to modern bone ranging from 0% to 100%. No evidence of preferential preservation of tooth collagen was detected. The carbon and nitrogen isotopic differences in the herbivore versus carnivore collagen from Kent's Cavern fauna were consistent with those observed in modern faunas. Moreover, an enrichment of 0·4–1·7‰ in ^{15}N was observed in tooth collagen of both deer and hyena as compared to bone collagen. This enrichment presumably reflects a trophic shift from the consumption of milk during infancy. Herbivores and carnivores had distinct differences in the carbon isotopic composition of enamel carbonate hydroxylapatite, similar to those measured in modern specimens from similar climatic environments. The spacing between the $\Delta^{13}C$ values (difference between isotopic composition in collagen and carbonate hydroxylapatite) of Kent's Cavern herbivores and carnivores is similar to that measured in modern mammals from a single locality. The preservation of primary oxygen isotopic composition of enamel carbonate hydroxylapatite was more difficult to assess, however. Oxygen isotopic compositions of Kent's Cavern enamel are systematically lower than those of contemporaneous faunas from Southern France, which is consistent with a latitudinal effect on rainfall oxygen isotopic compositions. Although the Kent's Cavern specimens have been subjected to extensive diagenetic alteration, the biological isotopic signals seem to have utility for paleoecological reconstructions.

Keywords: STABLE ISOTOPES, CARBON, NITROGEN, OXYGEN, TOOTH, BONE, COLLAGEN, APATITE, TROPHIC LEVEL, ISOTOPIC DIFFERENCES, KENT'S CAVERN, UPPER PLEISTOCENE.

Introduction

Kent's Cavern is a Pleistocene cave formed in Devonian limestone located near the town of Torquay, on the southern coast of Devonshire (Great Britain). The largest excavation of this cave took place from 1865 to 1880 under the direction of William Pengelly. The tens of thousands of objects that were removed during those 15 years have been dispersed to many museums world-wide, and the material analysed in this work came from the zooarchaeological collections of the Smithsonian Institution's National Museum of Natural History.

The samples discussed in this paper come from the stratigraphic layer called ''cave-earth'' that yielded an abundant fauna associated with Middle Paleolithic (Mousterian) and Early Upper Paleolithic (Aurignacian) artifacts (Garrod, 1926; Campbell, 1977). Four radiocarbon dates from the bone at the ''cave-earth'' layer (GrN6201, GrN6202, GrN6324 and GrN6325) span 28,000 to 38,000 years BP (Campbell, 1977) and are in agreement with a more recent date of $39{,}630 \pm 1420$ BP (OxA-3403) obtained from

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rhinoceros bone collagen. Spatial localization of the bone samples within 1 m^2 in the cave is possible due to the detailed numbering on each specimen, and the extensive records left by Pengelly. The majority of bone samples analysed for this work were excavated in the ''Smerdon's Passage'', an undervault close to the south entrance, linking the ''Passage of Urns'' to ''North Sally Port''. A few samples come from two other places also located near the entrances of the cave in the ''cave-earth'' layer, ''North Sally Port'' and ''Vestibule''.

The ''cave-earth'' layer contains a very abundant Devonsian fauna of large mammals (Garrod, 1926; Campbell, 1977). This fauna includes carnivores, such as hyena (*Crocuta crocuta*) in great abundance, and herbivores, such as woolly rhinoceros (*Coelodonta antiquitatis*), equid (*Equus* sp.), bison (*Bison* sp.) and wild ox (*Bos primigenius*), reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*) and giant elk (*Megaloceros giganteus*), mammoth (*Mammuthus primigenius*), as well as brown bear (*Ursus arctos*: Campbell (1977) has deleted the cave bear *Ursus spelaeus* from the last glacial faunal list because this species occurs *in situ* only in the earlier ''breccia'' layer). The samples analysed in this study are presented in Tables 1 & 2. The diet and paleoecology of these species are already well known from their morphology, in some cases frozen stomach contents. Some of these species are living today, often in different climatic conditions.

Based on stomach and intestine contents, it is known that horse and woolly rhinoceros were eating mostly grasses in the Eurasian arctic (Vereshchagin & Baryshnikov, 1982). The summer diet of mammoths, inferred from fossilized stomach contents found in frozen carcasses, was composed of herbaceous plants, mosses, bushes and tree twigs and bark (Vereshchagin & Baryshnikov, 1982, 1984; Sutcliffe, 1985). The red deer is very adaptable and exhibits a considerable variation in size. Further, the red deer was capable of living in forests as well as in open country (Chaplin, 1975; Guthrie, 1982). The giant deer was most probably an opportunistic browser that supplemented its diet with large amounts of grass (Barnosky, 1986). Wild ox lived in open country and open forest (Anderson, 1984). The spotted hyena was the top carnivore and scavenger of this ecosytem, by comparison with the living ones in Africa (Vereshchagin & Baryshnikov, 1984). Finally, brown bears were omnivorous and their diet may be mostly composed of plant material or meat according to the availability of these sources of food (Dendaletche, 1982).

Trophic structure and climatic information can be recorded in the isotopic composition of vertebrate bones and teeth, in bone and dentin organic matter (^{13}C, ^{15}N) and in enamel carbonate hydroxylapatite (^{13}C, ^{18}O). If preserved, this isotopic signature provides a way to retrieve the structure of ancient trophic webs and to reconstruct paleoclimates. One test of preservation of the isotopic signals is the comparison of some specific isotopic signatures in fossil samples with those in modern equivalents. The diet of a mammal is reflected in the isotopic composition of animal tissues based on the trophic level of the individual as an adult, and on the shift of diet from mother's milk to adult diet at weaning. The trophic level effect leads to a difference in bone collagen carbon and nitrogen isotopic abundances (Schoeninger & DeNiro, 1984; van der Merwe, 1989) and in enamel carbonate hydroxylapatite carbonate isotopic abundances between an animal and its diet (Krueger & Sullivan, 1984; Lee-Thorp *et al.*, 1989).

The shift of diet at weaning (i.e. the nursing effect) leads to a difference in nitrogen isotopic abundances (Fogel *et al.*, 1989, Tuross & Fogel, 1994) which is recorded as a difference between bone and dentin collagen of an individual in species where teeth stop their growth shortly after weaning time (Bocherens *et al.*, 1992, 1994). Individuals from species where teeth continue to grow after weaning contain ^{15}N abundances similar to those in bone, because collagen is synthesized from the adult diet in both teeth and bones (Bocherens *et al.*, 1992, 1994).

Climatic conditions also influence the isotopic signals in mammal mineralized tissues. The nitrogen isotopic composition of collagen can be influenced by water and food availability through a trophic system (Heaton *et al.*, 1986; Sealy *et al.*, 1987; Ambrose, 1991). Carbon isotopic composition of carbonate hydroxylapatite of herbivore enamel has been shown to depend on the climate: for similar collagen carbon isotopic compositions, the enamel carbon isotopic abundances in herbivores from cold areas are more enriched in ^{13}C relative to those of herbivores from South Africa (Bocherens & Mariotti, 1992). Finally, the oxygen isotopic composition of carbonate hydroxylapatite is linked to those of the drinking water, and thus to the temperature (Koch *et al.*, 1989).

Kent's Cavern ''cave-earth'' deposit provides a favorable setting to investigate the preservation of the isotopic signal of trophic structure in bone organic matter (^{13}C, ^{15}N) and enamel (^{13}C, ^{18}O), by comparing the isotopic values between herbivorous and carnivorous animals, isotopic values in bone and teeth of jawbones from deer and hyenas, and by comparing the isotopic values obtained in Kent's Cavern samples with those measured in French Upper Pleistocene localities already published (Bocherens *et al.*, 1991*a*,*b*, 1994; Fizet *et al.*, 1994). We tested the preservation of the isotopic composition in the organic matter extracted from bone and dentin, and in the carbonate hydroxylapatite of enamel. The carbonate hydroxylapatite of bone and dentin has been shown to be isotopically altered in the early diagenesis (Lee-Thorp, 1989; Koch *et al.*, 1990) and thus will not be considered here. In summary, the diverse fossil mammal fauna of the Upper Pleistocene of Kent's Cavern was used to test if the isotopic compositions are preserved by comparing the results with those obtained on modern and on fossil equivalents.

Table 1. Isotopic composition of collagen and of enamel carbonate hydroxylapatite of herbivores from Kent's Cavern

Sample no. 1	Sample no. 2	Layer	Taxon	Sample	Yield (mg g^{-1})	Collagen			Apatite		
						C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	$\Delta\delta^{13}C$ (‰)
214264		n.d.	*Equus*	M_3	112·2	3·4	− 20·8	4·4			
61351	12/3468	SP	*Equus*	tooth	172·8	3·5	− 21·2	7·8	− 10·2	26·3	11·0
61370	10/4849	NSP	*Equus*	upper tooth	92·4	3·9	*− 22·0*	2·2	− 11·6	26·9	10·4
61372	4/4871	NSP	*Equus*	metacarpal	2·7	3·5	− 21·2	8·4			
61375	9/5308	SP	*Equus*	tooth	9·3	n.d.	− 21·6	6·8	− 10·9	24·2	10·7
61376		SP	*Equus*	tooth	81·5	3·5	− 21·6	7·7			
61376	6/5315	SP	*Equus*	tooth	n.d.	3·7	*− 20·4*	7·2	− 11·5	24·9	9·9
61376	7/5315	SP	*Equus*	tooth	6·8	4·0	*− 21·4*	4·6			
61376	8/5315	SP	*Equus*	tooth					− 12·0	24·8	
61377	16/3389	SP	*Equus*	upper tooth	94·2	3·4	− 21·9	6·9			
61378	9/3400	SP	*Equus*	tooth	107·2	3·5	− 21·6	6·0	− 10·5	25·9	11·1
61381	2/3461	SP	*Equus*	tooth	4·5	3·5	− 21·4	3·3			
61386	8/3528	SP	*Equus*	lower tooth	171·5	3·6	− 21·0	8·5	− 11·5	26·7	9·5
61387	2/3536	SP	*Equus*	tooth	1				− 11·3	26·4	
	4/3536	SP	*Equus*	tooth	158·8	3·4	− 21·6	5·4	− 11·4	25·0	9·7
					Average		− 21·4	6·5	− 11·2	25·7	10·3
						s.d.	± 0·3	± 1·7	± 0·6	± 1·0	± 0·6
214255	ac38778-1	n.d.	*Coelodonta*	long bone	183·7	3·4	− 20·6	3·7			
61369	2/4809	NSP	*Coelodonta*	scapula	16·5	no N	b.p.	b.p.			
	4860	NSP	*Coelodonta*	bone	4·3	3·5	− 20·6	5·9			
61372	4871	NSP	*Coelodonta*	bone	32·9	no N	b.p.	b.p.			
61374	1/5297	SP	*Coelodonta*	astragalus	47·3	3·3	− 20·6	4·4			
61377	1/3389	SP	*Coelodonta*	metapodial	33·4	3·8	*− 21·2*	6·6			
61381	3461	SP	*Coelodonta*	bone	91·2	3·5	− 22·5	6·7			
61389	1/3643	SP	*Coelodonta*	bone	0						
61389	3643	SP	*Coelodonta*	bone	118·2	5·7	b.p.	b.p.			
					Average (bones)		− 21·1	5·2			
					s.d.		± 0·9	± 1·4			
61369		NSP	*Coelodonta*	tooth	168·1	3·3	− 20·2	8·3	− 8·9	26·0	11·3
61376	24/5315	SP	*Coelodonta*	tooth	142·1	3·5	− 20·7	6·4			
61377	11/3389	SP	*Coelodonta**	cement	161·8	3·4	− 20·8	4·7	− 11·0	26·0	9·8
61377	11/3389	SP	*Coelodonta**	dentin	151·1	3·4	− 20·2	4·3	− 11·0	26·0	
61378	21/3400	SP	*Coelodonta*	tooth	169·4	3·3	− 20·7	6·0			
61381	6/3461	SP	*Coelodonta*	tooth	164·3	3·4	− 21·0	4·4	− 10·8	23·2	10·2
	4/3470	SP	*Coelodonta**	dentin	179·8	3·5	− 20·2	8·0	− 10·2	24·0	10·0
	4/3470	SP	*Coelodonta**	cement	52·5	n.d.	− 20·7	8·2	− 10·2	24·0	10·5
61387	5/3536	SP	*Coelodonta*	tooth	n.d.	3·4	− 20·2	5·7	− 10·7	26·8	9·5
	60/2104	V	*Coelodonta*	tooth	25·7	n.d.	− 21·0	9·1	− 12·0	27·1	9·0
					Average (teeth)		− 20·6	6·5	− 10·6	25·5	10·0
					s.d.		± 0·3	± 1·8	± 1·0	± 1·6	± 0·7
214257		n.d.	cervid*	maxillary bone	15·1	n.d.	− 21·0	5·1			
61371	15/4860	NSP	cervid	radius	61·8	3·5	− 23·3	5·3			
61378	5/3400	SP	cervid	astragalus	16·2	3·6	− 23·4	5·5			
					Average (bones)		− 22·6	5·3			
					s.d.		± 1·4	± 0·2			
214257		n.d.	cervid*	M^2	103·7	3·4	− 20·1	6·7	− 11·1	25·7	9·0
214257		n.d.	cervid*	M^3	65·1	3·4	− 20·5	6·4	− 11·1	26·7	9·4
61369	4/4809	NSP	cervid	tooth	8·9				− 9·9	21·5	
61370	13/4849	NSP	cervid*	M_2	44·4	3·7	*− 21·0*	8·0	− 11·1	26·6	9·9
61370	13/4849	NSP	cervid*	M_3	68·6	3·5	− 20·3	7·4	− 10·9	24·9	9·4
61378	11/3400	SP	cervid	tooth	166·6	3·5	− 20·6	5·0			
61378	12/3400	SP	cervid	tooth	115·6	3·4	− 21·1	7·3			
					Average (teeth)		− 20·5	6·6	− 10·8	25·1	9·4
					s.d.		± 0·4	± 1·1	± 0·5	± 2·1	± 0·4
214257		n.d.	*Bos*	M_3	115·6	3·5	− 20·6	5·6			
6138?		n.d.	*Mammuthus*	molar					− 10·3	26·7	

SP, Smerdon's Passage; NSP, North Sally Port; V, vestibule; sample no. 1, Smithsonian's numbers; sample no. 2, Pengelly's numbers.
*, Samples from the same individual.
n.d., ''Not determined''; b.p., ''Bad preservation'', in cases where samples had a clayish aspect after extraction and yielded very little quantities of gases.
$\Delta^{13}C = \delta^{13}C_{apatite} - \delta^{13}C_{collagen}$.

Table 2. Isotopic composition of collagen and enamel carbonate hydroxylapatite of carnivores and omnivores from Kent's Cavern

Sample no. 1	Sample no. 2	Layer	Taxon	Sample	Yield (mg g^{-1})	Collagen C/N	Collagen $\delta^{13}C$ (‰)	Collagen $\delta^{15}N$ (‰)	Apatite $\delta^{13}C$ (‰)	Apatite $\delta^{18}O$ (‰)	Apatite $\Delta\delta^{13}C$ (‰)
	ac38778-4	n.d.	*Crocuta**	maxillary bone	159·0	3·3	− 18·9	8·0			
61375	15/5308	SP	*Crocuta**	mandible	58·3	3·3	− 20·3	9·3			
	9/5315	SP	*Crocuta**	mandible	45·7	3·5	− 20·3	11·2			
61376	12/5315	SP	*Crocuta**	maxillary bone	205·3	3·3	− 19·4	10·8			
61384	9/3478	SP	*Crocuta**	mandible	25·6	3·7	*− 20·0*	*9·0*			
61387	8/3536	SP	*Crocuta**	mandible	145·6	3·4	− 19·0	9·0			
					Average (bones)		− 19·6	9·7			
					S.D.		± 0·7	± 1·3			
	ac38778-4	n.d.	*Crocuta**	P^3	198·3	3·3	− 18·8	8·4	− 12·8	25·8	6·0
214259		n.d.	*Crocuta*	M_1	47·3	3·6	− 19·7	13·0	− 13·4	25·6	6·3
214260	20/3446	SP	*Crocuta*	upper C	62·0	3·4	− 19·6	9·4			
61375	15/5308	SP	*Crocuta**	P_3	170·8	3·4	− 20·4	11·0			
	9/5315	SP	*Crocuta**	P_4	50·2	3·4	− 19·1	11·7	− 12·8	26·0	6·3
	9/5315	SP	*Crocuta**	P_3	95·2	3·4	− 18·9	12·2	− 13·5	25·9	5·4
61376	12/5315	SP	*Crocuta**	P^4	130·9	3·2	− 19·3	11·9	− 13·5	25·2	5·8
61377	6/3389	SP	*Crocuta*	P_3	25·0	3·5	− 19·1	9·5			
61382	2/3470	SP	*Crocuta*	dentin	0						
61384	9/3478	SP	*Crocuta**	M_1	112·4	3·4	− 19·9	9·4	− 13·6	25·2	6·3
61384	9/3478	SP	*Crocuta**	P_4	71·4	3·5	− 19·9	9·5	− 14·1	25·3	5·8
61384	10/3478	SP	*Crocuta*	canine	86·4	3·6	− 19·8	9·3	− 13·5	25·2	6·2
61386	3/3528	SP	*Crocuta*	canine	36·6	3·5	− 19·4	11·7			
61386	4/3528	SP	*Crocuta*	dentin	123·0	3·4	− 19·3	9·5			
61387	8/3536	SP	*Crocuta**	M_1	95·9	3·3	− 19·2	9·7	− 12·5	22·1	6·7
					Average (teeth)		− 19·5	10·4	− 13·3	25·1	6·1
					S.D.		± 0·4	± 1·4	± 0·5	± 1·2	± 0·4
61384	3/3478	SP	*Ursus arctos*	canine	140·1	3·6	− 20·0	12·6	− 13·9	26·3	6·1

Key as for Table 1.

Methods of Analysis

To obtain the insoluble organic matter, chunks of bone were demineralized with 0·5 M EDTA, pH 7·2, at 4°C. The residues were washed 15 times with distilled water and lyophilized. When the organic matter is fairly well preserved, the result is a translucent, pale yellow collagen replica (Tuross *et al*., 1988). Isotopic measurements were performed on gases extracted and purified after a ''Dumas'' combustion as described in Estep & Vigg (1985). One to three milligrams of collagen were combusted with copper oxide and metal copper in a sealed quartz tube at 900°C for 1 h. The combustion tube was cooled at a defined rate, and the products of combustion were isolated by cryogenic distillation. On most of the samples, the determination of the C/N atomic ratio was determined with a Carlo-Erba EA1108 elemental analyzer. The range of C/N values for unaltered samples is presumed to be 2·9–3·6 (DeNiro 1985).

The enamel samples were pretreated according to Bocherens *et al*. (1991*b*). The powdered enamel was treated by NaOCl 2–3% during 20 h at 20°C, rinsed carefully with distilled water and then treated with a 1 M buffered solution of acetic acid (pH 4·75) for 20 h at 20°C to remove any exogenous carbonate without dissolving more than 10% of the enamel sample. The CO_2 was then extracted from the inorganic powders by orthophosphoric acid at 50°C for 5 h, following Koch *et al*. (1989).

The isotope ratios are expressed for carbon as $\delta^{13}C$ versus PDB (a marine carbonate), for nitrogen as $\delta^{15}N$ versus atmospheric N_2 and for oxygen as $\delta^{18}O$ verus SMOW (standard mean oceanic water):

$$\delta^E X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000,$$

where $\delta^e X = \delta^{13}C$ and $^{13}R = {}^{13}C/{}^{12}C$; $\delta^E X = \delta^{15}N$ and $^{15}R = {}^{15}N/{}^{14}N$ and $\delta^E X = \delta^{18}O$ and $^{18}R = {}^{18}O/{}^{16}O$ respectively. Carbon and oxygen isotopic ratios were measured on a Finnigan MAT 252, and nitrogen isotopic ratios were measured on a Nier-Johnson type double focusing mass spectrometer. Analytical precisions were 0·1‰ for $\delta^{13}C$, 0·2‰ for $\delta^{15}N$ and 0·2‰ for $\delta^{18}O$ values. The correction is not known for oxygen in carbonate hydroxylapatite, therefore the correction formula for calcite at 50°C was used (Koch *et al*., 1989).

Results

Collagen yields in bone and dentin

The yields of the organic matter, defined as the ratio of dry weight of organic matter after decalcification to the

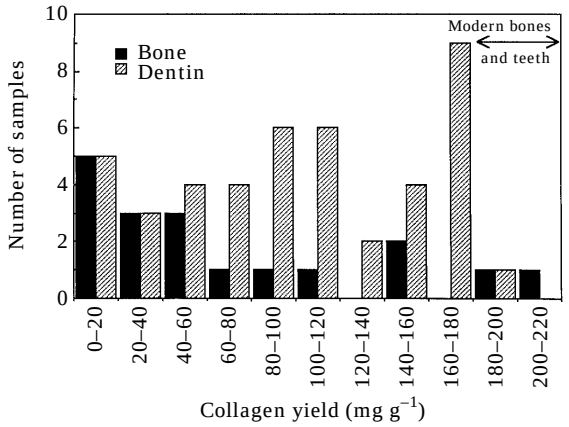

Figure 1. Collagen yields in bone and dentin of Kent's Cavern mammals.

dry weight of fossil bone or tooth, were highly variable within the deposit. A majority of samples yielded a very well preserved collagen, in the form of a yellowish replica of the original sample, with C/N values between 3·2 and 3·6. Only two samples out of 66 yielded no residue after EDTA dissolution. In three samples, the final product consisted of only insoluble minerals, probably clay, that generated only minute quantities of gases after combustion. The C/N values were clearly outside the biological range (no nitrogen for samples nos. 61369-2/4849 and 61372-4871, C/N = 5·7 for sample no. 61389-3643; Table 1). In the well-preserved samples, the amount of collagen was sometimes very close to the amount in fresh bone (around 200 mg g^{-1}); such samples have retained almost all their original collagen. The yields in organic matter extracted from bones and teeth are similar (Tables 1 & 2 and Figure 1), although a majority of bone samples yielded less than 60 mg g^{-1} and the bulk of dentin samples contained more than 80 mg g^{-1} (Figure 1). A comparison of the yields of bone and dentin from the same jawbone specimens, however, indicates that bone did not always contain less collagen than dentin (see Table 4). Thus in terms of total collagen content, bone was preserved as well as dentin.

The range of yield in collagen demonstrates the variability of organics within sites, which has been described in other localities (Bocherens *et al*., 1991*a*,*b*; Tuross & Stathoplos, 1993). Only a few samples with ''biological isotopic values'' (see discussion below) had elevated C/N values (3·7–4·0). Most of the samples with C/N values greater than 3·6 had collagen yields lower than 50 mg g^{-1}, with one exception (horse, no 61370-10/4849: yield of 92·4 mg g^{-1} and C/N = 3·9; Table 1). Samples with collagen yields lower than 10 mg g^{-1} typically had C/N values lower than 3·6. The isotopic compositions measured on the samples with C/N greater than 3·6 are in italics in the tables. Isotopic compositions of these compromised samples were not used for the calculation of average values.

Isotopic compositions in collagen

In herbivores, the $\delta^{13}C$ values of collagen (C/N values 3·2–3·6) range from $-23{\cdot}4$ to $-20{\cdot}1$‰ with a mean of $\delta^{13}C = -21{\cdot}0 \pm 0{\cdot}9$ ($n = 33$) (Table 1 and Figure 2). In carnivores, the $\delta^{13}C$ values of collagen range from $-20{\cdot}4$ to $-18{\cdot}8$‰ with a mean of $-19{\cdot}5 \pm 0{\cdot}5$‰ (n = 20) in carnivores (Table 2 and Figure 2). The $\delta^{13}C$ values between bone and tooth collagen for a given species are not significantly different (Student *t*-test, $P > 0{\cdot}1$). In the deer and hyena jawbones, $\delta^{13}C$ values of bone and tooth collagen within an individual were virtually indistinguishable and the difference was always less than 1‰ (Tables 3 & 4, Figure 3). A paired *t*-test performed on the bone and tooth collagen $\delta^{13}C$ values of the hyena jawbones indicated that these values were not significantly different ($P > 0{\cdot}1$). Thus, the within-species $\delta^{13}C$ values of bone and tooth collagen will be considered together. On average, there is an increase of $\pm 1{\cdot}5$‰ between the $\delta^{13}C$ values of the carnivores relative to the $\delta^{13}C$ values of the herbivores among Kent's Cavern samples. This difference is statistically significant (Student's *t*-test, $P < 0{\cdot}01$). Two of the $\delta^{13}C$ values measured on deer (Table 1; nos. 61371-15/4860 and 61378-5/3400) are depleted relative to the majority of herbivore bone collagen.

Herbivores $\delta^{15}N$ values in bone and tooth collagen (C/N values 3·2–3·6) ranged from 3·3 to 8·4‰ (Figure 2) and averaged $\delta^{15}N = 6{\cdot}3 \pm 1{\cdot}6$‰ ($N = 33$). $\delta^{15}N$ values ranged in carnivores from 8·0 to 13·0‰ (Figure 2), and averaged $\delta^{15}N = 10{\cdot}2 \pm 1{\cdot}4$‰ ($N = 20$). The difference of 3·9‰ between collagen average $\delta^{15}N$ value in herbivores and carnivores is statistically significant (Student's *t*-test, $P < 0{\cdot}01$). In rhinoceros, deer and hyenas, species with a different number of samples of teeth and bones for an intra-individual comparison, the $\delta^{15}N$ values in bone collagen were on average lower than those of tooth collagen (Tables 1 & 2; $5{\cdot}2 \pm 1{\cdot}4$‰ versus $6{\cdot}5 \pm 1{\cdot}8$‰ in the rhinoceros; $5{\cdot}3 \pm 0{\cdot}2$‰ versus $6{\cdot}6 \pm 1{\cdot}1$‰ for deer; $9{\cdot}7 \pm 1{\cdot}3$‰ versus $10{\cdot}4 \pm 1{\cdot}4$‰ for hyenas). Given the large range of $\delta^{15}N$ values, there was no statistically significance in these differences. The single $\delta^{15}N$ value of horse bone collagen was within the range of $\delta^{15}N$ values of horse tooth collagen (Table 1; 8·4‰ versus 3·3–8·5‰). In deer and hyenas, the comparison of $\delta^{15}N$ values in bone and tooth collagen from the same jawbones indicates that tooth collagen is always more positive than bone collagen from the same individual, from 0·4 to 1·7‰ (Table 3 and Figure 3). Moreover, a paired *t*-test performed on the bone and tooth collagen $\delta^{15}N$ values of the hyena jawbones showed that these values were significantly different ($P < 0{\cdot}01$).

The $\delta^{13}C$ and $\delta^{15}N$ values of the degraded collagen with C/N values greater than 3·6 were in most of the cases within the range of the isotopic compositions measured on samples with C/N values between 3·2 and 3·6. A horse tooth (sample no. 61372-4/4871) was the exception; $\delta^{13}C$ and $\delta^{15}N$ were lower than all

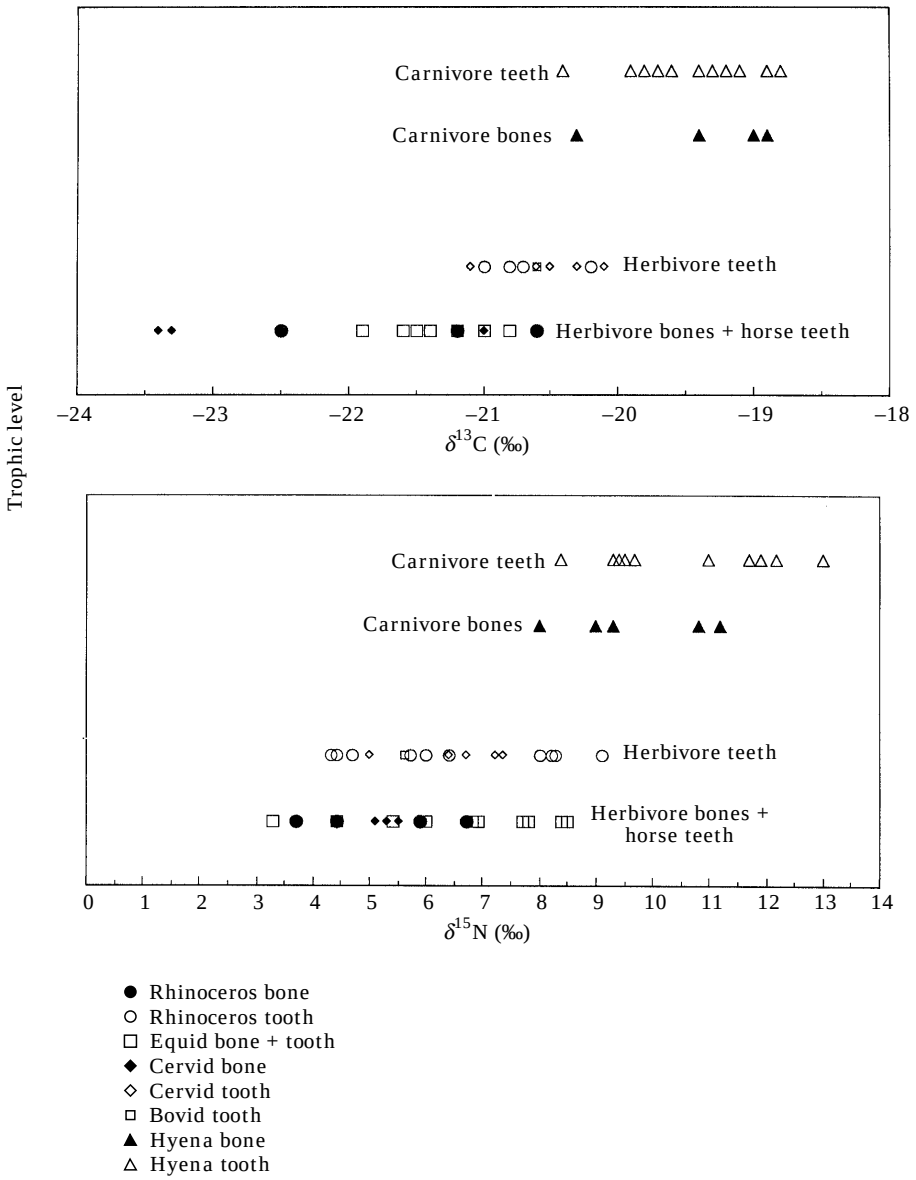

Figure 2. Variations of $\delta^{13}C$ and $\delta^{15}N$ values in Kent's Cavern mammal tooth and bone collagen according to the trophic level as determined from anatomical data. Only samples with C/N values comprised between 3·2 and 3·6 have been plotted.

Table 3. Isotopic composition of collagen from bone and tooth of individual deer from Kent's Cavern

Sample no. 1	Sample no. 2	Layer	Taxon	Sample	Yield (mg g^{-1})	Collagen C/N	Collagen $\delta^{13}C$ (‰)	Collagen $\delta^{15}N$ (‰)	$\Delta\delta^{13}C$ (‰)	$\Delta\delta^{15}N$ (‰)
214257		n.d.	cervid	max. bone	15·1	n.d.	−21·0	5·1		
214257		n.d.	cervid	M^2	103·7	3·4	−20·1	6·7	0·9	1·6
214257		n.d.	cervid	M^3	65·1	3·4	−20·5	6·4	0·5	1·3
61370	13/4849	NSP	cervid	M_2	44·4	3·7	*−21·0*	*8·0*		
61370	13/4848	NSP	cervid	M_3	68·6	3·5	−20·3	7·4		

Key as for Table 1.
$\Delta\delta^{13}C = \delta^{13}C_{tooth} - \delta^{13}C_{bone}$; $\Delta\delta^{15}N = \delta^{15}N_{tooth} - \delta^{15}N_{bone}$.

Table 4. Isotopic composition of collagen from bone and tooth of the same hyena individuals from Kent's Cavern

Sample no. 1	Sample no. 2	Layer	Taxon	Sample	Yield (mg g^{-1})	Collagen C/N	Collagen $\delta^{13}C$ (‰)	Collagen $\delta^{15}N$ (‰)	$\Delta\delta^{13}C$ (‰)	$\Delta\delta^{15}N$ (‰)
	ac38778-4	n.d.	*Crocuta*	max. bone	159·0	3·3	− 18·9	8·0		
	ac38778-4	n.d.	*Crocuta*	P^3	198·3	3·3	− 18·8	8·4	0·1	0·4
61375	15/5308	SP	*Crocuta*	mandible	58·3	3·3	− 20·3	9·3		
61375	15/5308	SP	*Crocuta*	P_3	170·8	3·4	− 20·4	11·0	− 0·1	1·7
	9/5315	SP	*Crocuta*	mandible	71·6	3·5	− 19·6	11·1		
	9/5315	SP	*Crocuta*	P_4	50·2	3·4	− 19·1	11·7	0·5	0·6
	9/5315	SP	*Crocuta*	P_3	95·2	3·4	− 18·9	12·2	0·3	1·1
61376	12/5315	SP	*Crocuta*	max. bone	205·3	3·3	− 19·4	10·8		
61376	12/5315	SP	*Crocuta*	P_4	130·9	3·2	− 19·3	11·9	0·1	1·1
61384	9/3478	SP	*Crocuta*	mandible	25·6	3·7	*− 20·0*	9·0		
61384	9/3478	SP	*Crocuta*	M_1	112·4	3·4	− 19·9	9·4	0·1	0·4
61384	9/3478	SP	*Crocuta*	P_4	71·4	3·5	− 19·9	9·5	0·1	0·5
61387	8/3536	SP	*Crocuta*	mandible	145·6	3·4	− 19·0	9·0		
61387	8/3536	SP	*Crocuta*	M_1	95·9	3·3	− 19·2	9·7	− 0·2	0·7
							Average		0·1	0·8
							s.d.		± 0·2	± 0·4

Key as for Table 1.
$\Delta\delta^{13}C = \delta^{13}C_{tooth} - \delta^{13}C_{bone}$; $\Delta\delta^{15}N = \delta^{15}N_{tooth} - \delta^{15}N_{bone}$.

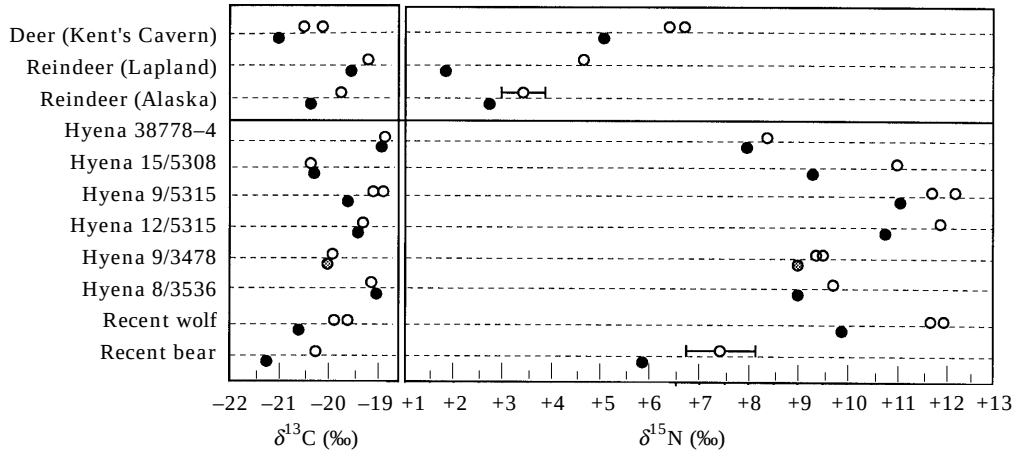

Figure 3. Variations of $\delta^{13}C$ and $\delta^{15}N$ values in Kent's Cavern mammal tooth and bone collagen of deer and hyena jawbones compared to those in modern equivalents (values for modern reindeers and carnivores from Bocherens, 1992). The point for the hyena no. 9/3478 is in grey because of its high C/N value (3·7).

other horse isotopic compositions (Table 1, and see Figure 5).

Isotopic compositions in carbonate hydroxylapatite

The $\delta^{13}C$ values of herbivore enamel from Kent's Cavern ranged from − 12·0 to − 8·9‰ (− 10·9 ± 0·7‰, $N = 20$; Table 1 and Figure 4). In contrast, the one carnivore group, hyenas, had $\delta^{13}C$ values from enamel carbonate hydroxylapatite in range of − 14·1 to − 12·5‰ (− 13·3 ± 0·5‰, $N = 9$; Table 2 and Figure 4). This range did overlap with herbivores. The difference of the average carbonate hydroxylapatite $\delta^{13}C$ values between herbivores and carnivores was statistically significant (Student's t-test, $P < 0·01$). The $\delta^{13}C$ values measured on rock matrix and recrystallized calcite (Table 5 and Figure 4) were more positive than those measured on the enamel samples, ranging from − 8·7 to − 7·5‰.

The difference in the $\delta^{13}C$ values between collagen and carbonate hyroxylapatite ($\Delta^{13}C$) ranged from 9·0 to 10·7‰ in Kent's Cavern herbivores (Table 1). The

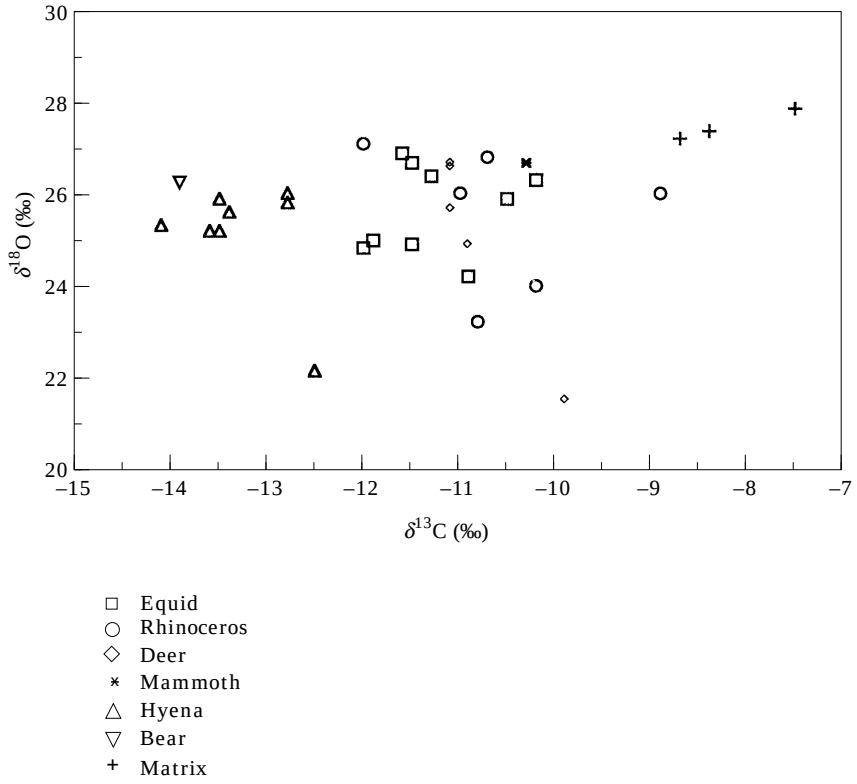

Figure 4. $\delta^{13}C$ and $\delta^{18}O$ values in Kent's Cavern mammal enamel carbonate hydroxylapatite compared to those of rock matrix.

Table 5. Isotopic composition of carbonate from rock matrix surrounding Kent's Cavern samples

Sample no. 1	Sample no. 2	Location	Sample	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)
61384		SP	matrix	− 8·7	27·2
61387	8/3536	SP	matrix around hyena tooth	− 8·4	27·4
	4/3536	SP	calcite in equid tooth	− 7·5	27·9
			Average	− 8·2	27·5
			S.D.	± 0·6	± 0·4

Key as for Table 1.

average $\Delta^{13}C$ values were $10{\cdot}3 \pm 0{\cdot}6$‰ ($N=7$) in horses, $10{\cdot}0 \pm 0{\cdot}7$‰ ($N=7$) in woolly rhinoceros, $9{\cdot}7 \pm 0{\cdot}3$‰ ($N=4$) in deer. There was no significant difference in the $\Delta^{13}C$ values between these different species of herbivores (Student's *t*-test, $P<0{\cdot}01$). In carnivores, $\Delta^{13}C$ values ranged from 5·8 to 6·7‰ (Table 2) and the average value was $6{\cdot}1 \pm 0{\cdot}4$‰ ($N=9$). The difference between the average $\Delta^{13}C$ values of carnivores and each species of herbivores was statistically significant (Student's *t*-test, $P<0{\cdot}01$).

The oxygen isotopic values ranged from 21·5 to 27·1‰ (Tables 1 & 2 and Figure 4). The average values of $\delta^{18}O$ were not significantly different between horses ($\delta^{18}O = 25{\cdot}7 \pm 1{\cdot}0$‰), woolly rhinoceros ($\delta^{18}O = 25{\cdot}5 \pm 1{\cdot}6$‰), deer ($\delta^{18}O = 25{\cdot}1 \pm 2{\cdot}1$‰) and hyenas ($\delta^{18}O = 25{\cdot}1 \pm 1{\cdot}2$‰). The $\delta^{18}O$ values measured on samples of rock matrix surrounding the fossils and on some diagenetic calcite formed within a horse tooth were slightly higher than those found in the fossil specimens (27·2–27·9‰; Table 5 and Figure 4).

Discussion

Preservation of the carbon and nitrogen isotopic compositions in organic matter

In addition to the C/N ratio of the extracted organic matter (DeNiro, 1985), one test for the preservation of the isotopic composition of ancient organic matter is to compare those measured to equivalent modern material. As stated previously, two kinds of isotopic differences in the bone and tooth collagen have been

identified in mammals: (1) the difference between herbivores and carnivores; and (2) the difference between bone and dentin collagen of the same individuals in the species where teeth stop their growth around weaning time. A clear enrichment in ^{15}N has been shown to exist between herbivore and carnivore collagen. This enrichment is reported to range in terrestrial ecosystems from 2·8‰ (Schwarcz, 1991) to 5·7‰ (Ambrose & DeNiro, 1986) with an average value between 3 and 4‰ (Schoeninger & DeNiro, 1984; Schoeninger, 1985; Sealy *et al*., 1987). A less obvious enrichment in organic ^{13}C, up to 2‰, has also been reported (van der Merwe, 1989; Lee-Thorp *et al*., 1989), but has not been observed in all terrestrial ecosystems studied to date. The difference in organic $\delta^{13}C$ values between herbivores and carnivores seems to be observed in ecosystems where all the plants have a C_3 photosynthetic pathway, and thus present a small range of carbon isotopic input (van der Merwe, 1989). The other isotopic difference in modern and fossil mammals is the enrichment in ^{15}N in dentin collagen relative to bone collagen in species where teeth stop growing around weaning time (e.g. reindeer, bear, wolf). The $\delta^{15}N$ of bone and tooth overlaps in species with continuously-growing teeth, such as horse (Bocherens *et al*., 1992, 1994).

In Kent's Cavern samples, the isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) are within the range of values measured in modern mammals from temperate and cold areas (Tauber, 1986; Bada *et al*., 1990; Bocherens *et al*., 1994). For instance, the average $\delta^{13}C$ value of modern European herbivores published in Tauber (1986) range from $-21{\cdot}8$ to $-20{\cdot}4$‰ for equivalent species than in Kent's Cavern, and the average $\delta^{13}C$ value of modern European herbivores published in Bocherens *et al*. (1994) is $-21{\cdot}1 \pm 0{\cdot}9$‰ ($N = 7$) (range from $-22{\cdot}1$ to $-19{\cdot}9$‰). Furthermore, isotopic compositions of Kent's Cavern material are similar to those measured on the same species or on species of the same trophic level in other European Upper Pleistocene localities (Bocherens *et al*., 1991*a*,*b*, 1994; Fizet *et al*., 1994). Two of the $\delta^{13}C$ values measured on deer from Kent's Cavern, however, are lower than the $\delta^{13}C$ values measured on the majority of herbivore bone collagen ($-23{\cdot}3$‰ and $-23{\cdot}4$‰ for deer bone nos. 61371-15/4860 and 61378-5/3400, respectively; Table 1). The collagen yield on these two samples is comparable to others, the C/N values are in the upper acceptable range of ratios (3·5 and 3·6) and the $\delta^{15}N$ values are typical of other herbivores. Such negative $\delta^{13}C$ values have been measured only on deer samples coming from two different places in the cave, and not on other species. Therefore, we have no basis for rejecting these values, although analogous results in other deer samples and a careful examination of the biochemical composition of these collagen samples is necessary to confirm the more negative $\delta^{13}C$ values.

In comparing the $\delta^{15}N$ values, those measured in bones and in dentin of species with teeth formed only during infancy are considered first (Bocherens *et al*., 1992, 1994). For this purpose, we compared the values from the tooth and bone collagen of one deer mandible (Table 3) and six hyena fragmentary jawbones (Table 4). For these two taxa, higher values in tooth relative to bone collagen were observed, as in the closely related living groups (reindeer and carnivores such as wolf and black bear, respectively) with a similar dietary pattern. The $\delta^{15}N$ values were lower in bone collagen than in dentin collagen in deer, as observed in modern and fossil reindeer (Figure 2, Bocherens *et al*., 1994) and in hyenas, as observed in modern carnivores such as wolf and black bear (Figure 2; Bocherens *et al*., 1994), and in fossil cave bear (Bocherens *et al*., 1994). The differences between the average $\delta^{15}N$ values of bone and tooth collagen for deer and hyenas are very similar to those measured on individual jaws (1·6‰ for deer and 0·8‰ for hyenas). When two teeth from the same jawbone were analysed (Tables 3 & 4; deer nos. 214257 and 13/4849, hyena nos. 9/5315 and 9/3478), the difference of $\delta^{15}N$ values are rather small (0·1–1·0 per thousand) and of the same magnitude than for modern reindeers and carnivores (Figure 2; Bocherens, 1992). Thus, for these two species, a diet of milk produces higher $\delta^{15}N$ values in tooth than in bone collagen. The $\delta^{15}N$ values of these tissues are, therefore, considered separately in the discussion of the trophic level of these species.

Measurements performed on modern and fossil individuals demonstrated that the $\delta^{15}N$ values of horse dentin collagen reflect the adult diet in a fashion analogous to bone collagen (Bocherens *et al*., 1992, 1994; Fizet *et al*., 1994). For the purpose of a trophic level discussion, the $\delta^{15}N$ values of Kent's Cavern horse tooth collagen were thus reported with the $\delta^{15}N$ values of bone collagen of the other herbivore species. In the case of the woolly rhinoceros, the $\delta^{15}N$ values measured on these two tissues were separated because of the type of tooth growth and the slightly higher average $\delta^{15}N$ value of the dentin collagen relative to the average $\delta^{15}N$ value of the bone collagen ($6{\cdot}5 \pm 1{\cdot}8$‰ versus $5{\cdot}2 \pm 1{\cdot}4$‰, respectively). Future work will resolve the variability of the tissues with more certainty.

We consider only the values measured on rhinoceros bone collagen for the discussion of trophic level. It appears that the difference between the average $\delta^{15}N$ value in herbivore bone (including horse tooth) and carnivore bone ($6{\cdot}0 \pm 1{\cdot}6$ and $9{\cdot}7 \pm 1{\cdot}3$, respectively) is 3·7‰, almost the same as the difference between the average $\delta^{15}N$ value in herbivore and carnivore teeth ($6{\cdot}5 \pm 1{\cdot}5$ and $10{\cdot}4 \pm 1{\cdot}4$, respectively). This difference of 3·7‰ is very similar to others measured between mammal herbivores and carnivores in most modern terrestrial ecosystems, usually between 3 and 4‰ (Schoeninger & DeNiro, 1984; Schoeninger, 1985;

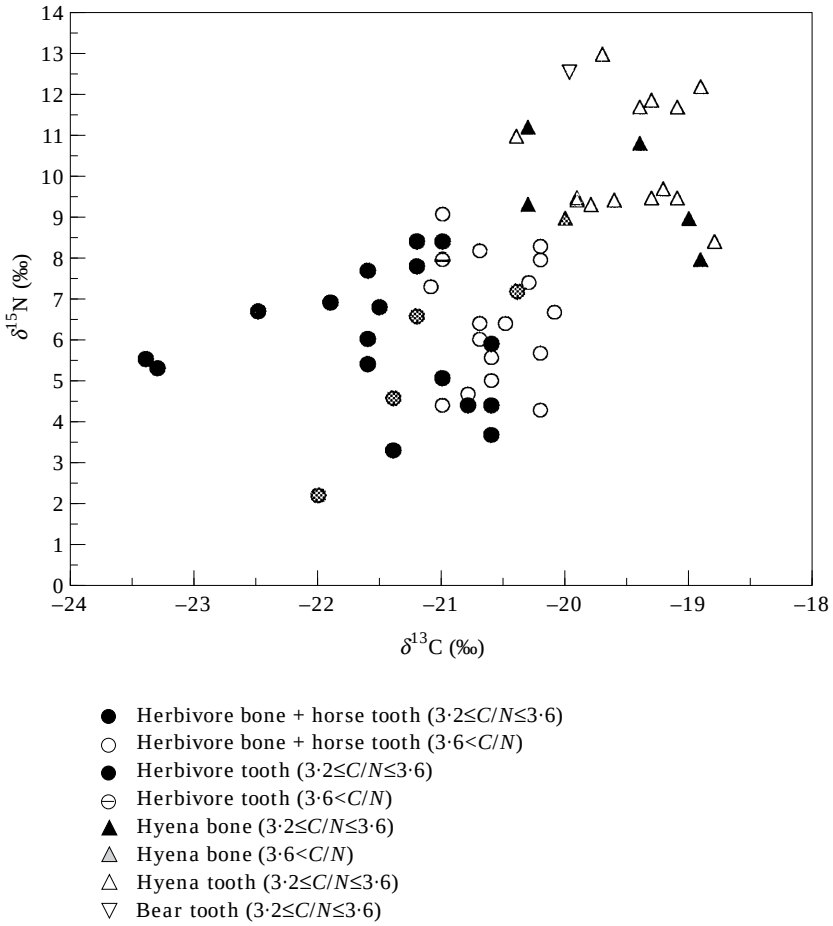

Figure 5. δ^{13}C and δ^{15}N values in Kent's Cavern mammal tooth and bone collagen.

Sealy *et al.*, 1987; Tuross *et al.*, 1994). The δ^{15}N values in herbivores and carnivores in the total population overlap slightly (Figure 1), but when both carbon and nitrogen isotope ratios are considered, herbivores and carnivores form two distinct groups (Figure 5). A comparison of the mean ± 1 S.D. values in Kent's Cavern and three French Upper Pleistocene localities (Figure 6) shows a similar pattern of variations, with lower δ^{13}C values in herbivores and carnivores, and higher δ^{15}N values in carnivores than in herbivores. We conclude that the similarity of the isotopic compositions between fossil and modern equivalents and other fossil material reflects the preservation of some of the biogenic signal.

Preservation of isotopic compositions in carbonate hydroxylapatite

The δ^{13}C values of carbonate generated from hydroxylapatite of herbivores from Kent's Cavern ($-12{\cdot}0$ to $-8{\cdot}9$‰; Table 1 and Figure 4) overlap the range reported by Bocherens & Mariotti (1992) for European and Alaskan modern large herbivores ($-13{\cdot}7$ to $-10{\cdot}3$‰) and for European and Alaskan Pleistocene large herbivores ($-12{\cdot}4$ to $-10{\cdot}1$‰). Only one value for a rhinoceros sample ($-8{\cdot}9$‰ for sample no. 61389) is slightly more positive. The values measured on rock matrix and recrystallized calcite (Table 5 and Figure 4) are less negative than those measured on the enamel samples, with no overlap ($-8{\cdot}7$ to $-7{\cdot}5$‰). In hyenas from Kent's Cavern, the δ^{13}C values of enamel carbonate hydroxylapatite ($-13{\cdot}3 \pm 0{\cdot}5$‰, range from $-14{\cdot}1$ to $-12{\cdot}5$‰) are comparable to those measured in Pleistocene carnivores from other localities (Bocherens *et al.*, 1994). In the fossil samples from French localities, the δ^{13}C values of enamel carbonate hydroxylapatite ranged from $-12{\cdot}6$ to $-12{\cdot}1$‰ for carnivores (Bocherens, 1992; Bocherens *et al.*, 1994). However, they are slightly less negative than for modern carnivores from South Africa with similar collagen δ^{13}C values (-16 to -13‰; Lee-Thorp *et al.*, 1989) and for the very few specimens of carnivores from temperate areas analysed to date ($-15{\cdot}3$‰; Bocherens & Mariotti, 1992). Nevertheless, the difference between the δ^{13}C values of enamel carbonate hydroxylapatite between herbivores and carnivores (2·6‰) is very similar to those measured in modern mammals from defined localities (Bocherens

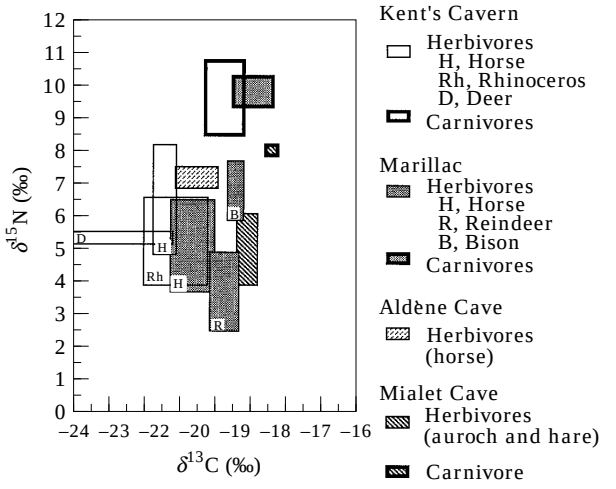

Figure 6. $\delta^{13}C$ and $\delta^{15}N$ average ($\pm$ S.D.) values in Kent's Cavern mammal bone collagen compared with those of three French Upper Pleistocene localities (values for French localities are from Bocherens, 1992, and Fizet, 1992).

& Mariotti, 1992). The $\delta^{13}C$ values of enamel carbonate hydroxylapatite of carnivores, herbivores and rock matrix reveal separated clusters of points for these three categories of samples (Figure 4). When compared to the enamel carbonate hydroxylapatite isotopic compositions of samples from French caves (Figure 6), the $\delta^{13}C$ values appear very similar for the different trophic groups.

The difference between the $\delta^{13}C$ values of enamel carbonate hydroxylapatite between herbivores and carnivores has been attributed to the isotopic difference between lipids and carbohydrates of the food (Krueger & Sullivan, 1984), although more recent investigations (Ambrose & Norr, 1993; Tieszen & Fagre, 1993) support an interpretation of homogenization of dietary carbon through the citric acid cycle. The increased content of isotopically depleted lipids in the carnivore diet would tend to shift the carbonate hydroxylapatite values in the observed direction. It is of interest that Lee-Thorp *et al.* (1989) observed no difference between the absolute $\delta^{13}C$ values of enamel carbonate hydroxylapatite in modern herbivores and carnivores.

Another way to assess the preservation of enamel carbonate hydroxylapatite is to compare the difference of the $\delta^{13}C$ values in collagen and in carbonate hydroxylapatite ($\Delta^{13}C$), which has been related to trophic level and climatic conditions (Figure 7; Krueger & Sullivan, 1984; Lee-Thorp *et al.*, 1989; Bocherens & Mariotti, 1992). These $\Delta^{13}C$ values were $8{\cdot}4 \pm 1{\cdot}4$‰ (range: 6·8–9·6‰) for modern European and Alaskan herbivores and $8{\cdot}6 \pm 0{\cdot}5$‰ (range: 7·8–9·1‰) for Pleistocene French herbivores. In Kent's Cavern herbivores for which both collagen and carbonate hydroxylapatite $\delta^{13}C$ values have been measured present a range of their $\Delta^{13}C$ values from 9·0 to 10·7‰. In Kent's Cavern carnivores, the difference is $6{\cdot}1 \pm 0{\cdot}4$‰, rather larger than for modern carnivores ($4{\cdot}3 \pm 1{\cdot}0$‰, calculated from Lee-Thorp *et al.*, 1989). These $\Delta^{13}C$ values are thus slightly higher in Kent's Cavern herbivores and carnivores relative to their modern and Pleistocene trophic equivalents. This effect is mostly due to more positive carbonate hydroxylapatite $\delta^{13}C$ values in Kent's Cavern specimens, rather than collagen $\delta^{13}C$ values. It remains to be determined what amount of exchange has occurred between the carbonate hydroxylapatite and the exogenous carbon with heavier $\delta^{13}C$ values (Table 5). If this exchange occurred, the spacing between the $\Delta^{13}C$ values of Kent's Cavern herbivores and carnivores is nevertheless similar to that measured in modern mammals from a single ecological environment (Bocherens & Mariotti, 1992). By comparison with $\delta^{13}C$ values of modern mammals of the same geographic and climatic area, the $\delta^{13}C$ values of Kent's Cavern mammals retain the discrimination between carnivores and herbivores. The impact of this potential exchange upon the interpretation of omnivory warrants further studies and the ongoing analysis of radiocarbon dates from paired collagen/apatite CO_2 will help to resolve the issue of isotopic exchange in the inorganic phase.

The state of preservation of the oxygen isotopic values is more difficult to assess. The $\delta^{18}O$ values range from 21·5 to 27·1‰ (Table 1 and Figure 4). Excursions of several ml are known in marine carbonates deposited during the time period from 50,000–30,000 years BP (Bond *et al.*, 1993). The average values of $\delta^{18}O$ are not significantly different between horses ($\delta^{18}O = 25{\cdot}7 \pm 1{\cdot}0$‰), woolly rhinoceros ($\delta^{18}O = 25{\cdot}5 \pm 1{\cdot}6$‰), deer ($\delta^{18}O = 25{\cdot}1 \pm 2{\cdot}1$‰) and hyenas ($\delta^{18}O = 25{\cdot}1 \pm 1{\cdot}2$‰). The $\delta^{18}O$ values measured on samples of rock matrix surrounding the fossils and on some diagenetic calcite formed within a horse tooth are slightly higher than those measured on the fossil specimens, with no overlap (27·2–27·9‰; Table 5 and Figure 4). The $\delta^{18}O$ values measured on the fossil specimens are lower than those measured on roughly contemporaneous specimens from Caves located in Southern France, where they range from 26·3 to 31·0‰ (Figure 8; Bocherens, 1992), and may be due to the latitudinal effect on $\delta^{18}O$ values in rain water (Yurtsever & Gat, 1981).

Paleobiological implications

The $\delta^{13}C$ values of bone collagen are slightly more negative in Kent's Cavern herbivores than in equivalent samples from France (around 1‰; Figure 4). The $\delta^{13}C$ values are significantly different between horses from Kent's Cavern from Marillac (Student's *t*-test, $P < 0{\cdot}01$). This difference may be due to variations in the $\delta^{13}C$ values of the plants at the base of the food webs: the consequence of prevailing environmental conditions (Tiezsen, 1991). Interestingly, van Klinken *et al.* (in press) report more negative $\delta^{13}C$ values in

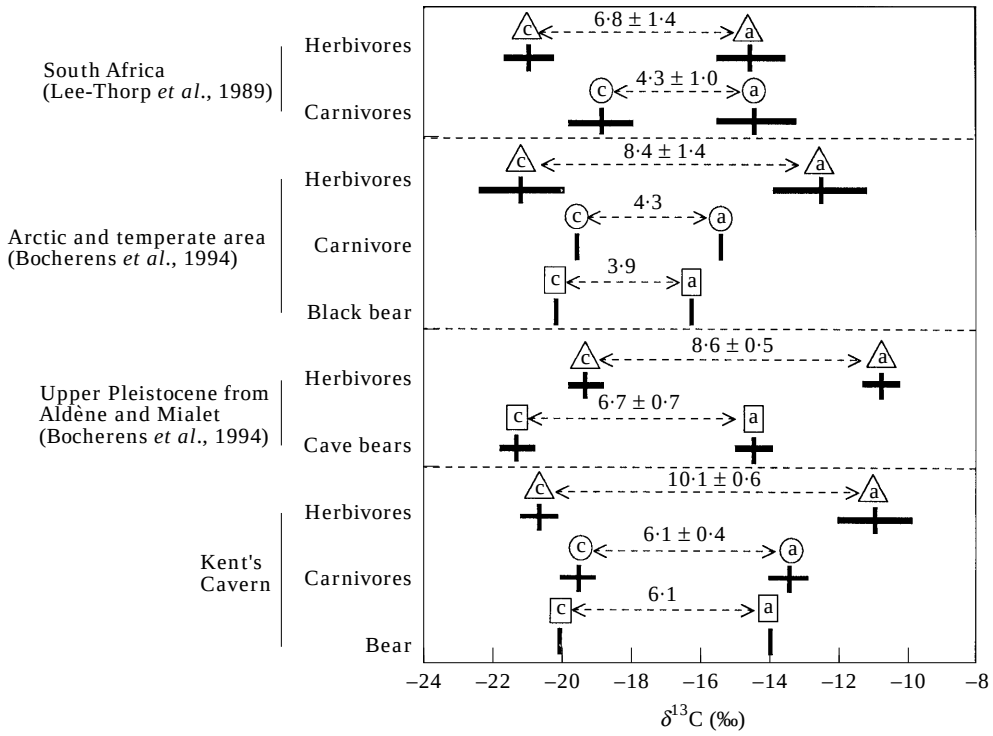

Figure 7. Average collagen (''c'') and carbonate hydroxylapatite (''a'') $\delta^{13}C$ values in modern, Kent's Cavern and Upper Pleistocene French localities herbivores, carnivores and bears (bars represent isotopic values' standard deviation).

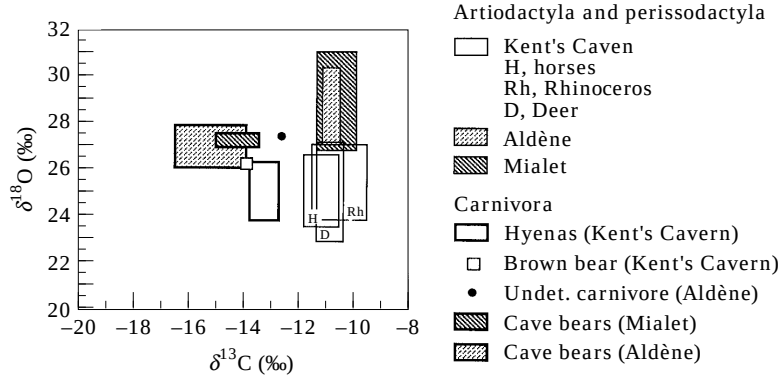

Figure 8. $\delta^{13}C$ and $\delta^{18}O$ average ($\pm$ S.D.) values in Kent's Cavern mammal enamel carbonate hydroxylapatite compared with those of two French Upper Pleistocene localities (values for French localities are from Bocherens, 1992).

Holocene herbivore collagen in England than in France.

The collagen $\delta^{13}C$ values from two deer bones are more negative than the values from the rest of the herbivores from Kent's Cavern and from French upper Pleistocene localities ($-23{\cdot}3$ and $-23{\cdot}4$‰). If these values truly reflect a biological signal, they carry paleobiological meaning, but it is unknown whether a unique food source or ecological variables are causal factors. One ecological factor that causes such negative values in modern herbivore collagen is the canopy effect, due to the recycling of respiratory CO_2 and physiological conditions for the plants under canopy (Tieszen, 1991; van der Merwe & Medina, 1991). However, such an explanation for the more negative bone collagen $\delta^{13}C$ values of deer is unlikely since the paleobotanical data do not support the occurrence of a close-canopied forest in the surroundings of Kent's Cavern at the time of deposition of the ''cave-earth'' layer (Campbell, 1977).

The $\delta^{15}N$ value of the one sample of brown bear from Kent's Cavern collagen was among the most positive of all carnivores and herbivores combined (Table 2). Based on this isotopic composition which are very similar to those of hyenas, the brown bear from Kent's Cavern had most probably a carnivorous diet. In contrast, the isotopic measurements of fossil cave bears indicated a mostly herbivorous diet for this species (Bocherens *et al*., 1994). However, more carnivorous diets are known for some populations of modern brown bears (Herrero, 1978).

The large number of hyenas analysed in this study provides, for the first time, a reference set of data for upper Pleistocene carnivores in Western Europe that we can compare to the results obtained on cave bears of the same age. The cave bear belongs to the order Carnivora but its diet has been shown to be mostly of plants, according to the low $\delta^{15}N$ values of their bone collagen (Bocherens *et al*., 1994). However, the difference of the $\delta^{13}C$ values in collagen and in carbonate hydroxylapatite of cave bears ($6{\cdot}7 \pm 0{\cdot}7$‰) published by Bocherens *et al*. (1994) are similar to those of Kent's Cavern hyenas ($6{\cdot}1 \pm 0{\cdot}4$‰). Nonetheless, these bears clearly presented more negative $\delta^{13}C$ values in both collagen and carbonate hydroxylapatite when compared to the hyenas. The cave bear $\Delta^{13}C$ values appear also close to those reported for herbivores by Lee-Thorp (1989), but those herbivores were from a different climatic zone. True carnivores (such as hyenas) have collagen $\delta^{13}C$ values 1–2‰ more positive than those of their herbivorous prey, and the $\Delta^{13}C$ between collagen and carbonate hydroxylapatite is about 3‰ less than the $\Delta^{13}C$ for grazing herbivores. In these two species of the order Carnivora, the similar $\Delta^{13}C$ values, regardless of trophic position, points out the futility for attempts to distinguish between plant and animal sources in omnivores (e.g. other bears) with these $\Delta^{13}C$ values only. The biochemical composition of the diet and the digestive physiology of the animal are obviously additional important factors that may influence $\Delta^{13}C$ values.

Conclusions

Chemical discrimination of herbivores and carnivores is observed in the organic nitrogen and carbon isotopic values, as well as in the carbonate hydroxylapatite–collagen differences. Between the absolute isotopic values of paleodietary indicator, there is an obvious lack of unambiguous omnivore ''space'', particularly for the $\delta^{13}C$ and the $\delta^{15}N$, but also in the $\delta^{13}C$ of enamel. Combined isotopic paleoindicators such as spacings in organic/inorganic carbon isotopes as a function of absolute organic nitrogen or carbon isotopic values (e.g. Figure 9) may help to resolve some of the difficulties in interpreting omnivorous diets. Full resolution and utilization of these paleodietary indictors will require not only resolution of any diagenetic overprinting, but also an understanding of the metabolic pathways that contribute to the fractionation of isotopes from the diet to the animal's tissue.

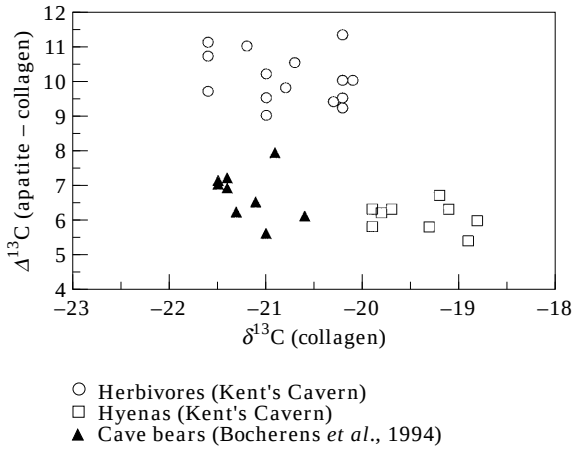

Figure 9. Collagen $\delta^{13}C$ values versus $\Delta^{13}C$ values (difference of $\delta^{13}C$ values in collagen and carbonate hydroxylapatite) in Kent's Cavern herbivores, hyenas, and French cave bears (values for cave bears are from Bocherens *et al*., 1994).

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