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Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya

Tooth enamel of nine Middle Miocene mammalian herbivores from Fort Ternan, Kenya, was analyzed for $\delta^{13}C$ and $\delta^{18}O$. The $\delta^{18}O$ values of the tooth enamel compared with pedogenic and diagenetic carbonate confirm the use of stable isotope analysis of fossil tooth enamel as a paleoenvironmental indicator. Furthermore, the $\delta^{18}O$ of tooth enamel indicates differences in water sources between some of the mammals. The $\delta^{13}C$ values of tooth enamel ranged from $-8{\cdot}6$–$-13{\cdot}0$‰ which is compatible with a pure C_3 diet, though the possibility of a small C_4 fraction in the diet of a few of the specimens sampled is not precluded. The carbon isotopic data do not support environmental reconstructions of a Serengeti-typed wooded grassland with a significant proportion of C_4 grasses. This study does not preclude the presence of C_3 grasses at Fort Ternan; it is possible that C_3 grasses could have had a wider geographic range if atmospheric CO_2 levels were higher than the present values.

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Introduction

Fort Ternan is one of the more interesting fossil localities in sub-Saharan Africa for a variety of different reasons. It is one of the few sites of Middle Miocene age, dating to between 13·9 and 14·0 Ma (Shipman *et al.*, 1981), it has yielded prolific vertebrate fossil remains whose taxonomic diversity has been interpreted to document the fragmentation of the Miocene equatorial rain forest (Andrews & Nesbit-Evans, 1979), and it has yielded several species of hominoids (Harrison, 1992). This site was once widely considered to contain crucial evidence for the first use of open habitats by the first hominoids (Simons & Pilbeam, 1978). A battered lava cobble and depressed fractures on a bovid skull were once interpreted as direct evidence for hominid tool use and predation (Leakey, 1967, 1968) but hominids are now considered to have appeared much later, in the late Miocene or early Pliocene (Hill & Ward, 1988), nullifying Leakey's behavioral interpretations (Shipman, 1981, 1982; Pickford, 1986). However, the appearance of savanna grasslands during the Middle Miocene is considered a prime stimulus for hominid evolution, and debate continues over the interpretation of the vegetation then present at Fort Ternan.

Despite, or perhaps because of, the wealth of paleoenvironmental evidence afforded by this site, a variety of different habitat interpretations have been published. Shipman (1977, 1982, 1986) concluded that the site represented savanna at or near its ecotonal junction with a more

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distant forested area. Andrews & Nesbit-Evans (1979) interpreted the mammalian fauna to be derived from a woodland or woodland–bushland habitat. Kappelman (1991) studied the functional morphology of bovids and concluded that they were best suited to living in a woodland habitat. Pickford (1985) concluded, on the basis of the fossil gastropods, that Fort Ternan was a moist highland forest. A cenogram analysis of the Fort Ternan faunal assemblage is consistent with a tropical closed habitat (Cerling *et al.*, 1992). Andrews & Nesbit-Evans (1979) suggested that the Fort Ternan woodland habitat had similarities to the woodland–bushland–grassland habitat inferred from Bed I at Olduvai Gorge. Bonnefille (1984) studied pollen from Fort Ternan and noted the abundance of grasses. Retallack *et al.* (1990) and Retallack (1992) subsequently inferred from fossil grass remains that a Serengeti-like habitat had been present at Fort Ternan, and Dugas & Retallack (1993) suggest affinities of these grasses to C_4 grasses.

The modern Serengeti grasslands are comprised of C_4 grasses, which have higher $^{13}C/^{12}C$ ratios than C_3 plants (gymnosperms, most dicotyledons, and many monocotyledons) (Smith & Epstein, 1971). Soils formed under C_4 grasslands have higher $^{13}C/^{12}C$ ratios than those formed under C_3 grassland and forests (Cerling, 1984; Cerling & Quade, 1993; Ambrose & Sikes, 1991). Modern East African grazing herbivores have higher $^{13}C/^{12}C$ ratios than modern East African browsers and forest-feeding herbivores (Ambrose & DeNero, 1986). However, investigation of soil carbonates from the Fort Ternan sequence did not yield results consistent with the presence of C_4 vegetation (Cerling *et al.*, 1991, 1992). The isotope results indicate that C_4 plants must have been relatively rare, if present, at Fort Ternan. If the ecosystem were a grassland, or even a wooded grassland, it must have been very different than modern tropical grassland in which C_4 grasses are abundant. On the other hand if C_4 grasses were rare, isotopic measurements on paleosols may not record their presence unambiguously.

The isotopic composition of the tooth enamel of both fossil and extant mammalian herbivores can be used to determine the percentage (if any) of C_4 vegetation in their diet (Lee-Thorp & van der Merwe, 1987; Lee-Thorp *et al.*, 1989; Cerling *et al.*, 1993; Wang *et al.*, 1994). Shipman (1982) reported dental microwear evidence for grazing (*Oioceros tanyceras*) and mixed feeding (*Kipsigicerus labidotus*), respectively, in the two bovid species that dominate the faunal assemblage at Fort Ternan. Gentry (1970) observed heavy dental attrition in one of these species (*O. tanyceras*) and suggested that it had a harsher diet. If C_4 grasses did occur in the vicinity of Fort Ternan, they should be reflected in the carbon iotopic composition of the grazing herbivores. We here report the results of an investigation of the isotopic composition of mammalian herbivore teeth from that locality.

Materials and Methods

Fossil teeth used for this project were sampled from the archives of the National Museum of Kenya. We selected teeth from nine herbivorous mammal species in the hope of sampling a wide dietary range of vegetation. All teeth were molars or premolars and are from different individuals. The selected species comprised four bovids *Gazella* sp., *O. tanyceras*, *K. labidotus*, and ?*Pseudotragus potwaricus*; two proboscideans *Prodeinotherium hobleyi* and *Choerolophodon ngorora*; the giraffid *Palaeotragus primaevus*; the rhinocerotid *Paradiceros mukirii*; and the suid "*Listriodon*" sp.

Samples of pure enamel from individual teeth were prepared by physically removing all dentine and cementum. Cleaned enamel was crushed and prepared following modifications to the method of Lee-Thorp & van der Merwe (1987); treatment in 10% H_2O_2 (T.E.C. and J.M.H.) or 3·25% NaOCl (S.H.A.) to extract any organic matter and then thoroughly rinsed in water before being treated with 1 M acetic acid to remove any calcite present in micro fractures. The treated samples were again thoroughly rinsed with water and then ethanol before analysis. Samples were reacted in vacuo with 100% H_3PO_4 at 25°C (T.E.C. and J.M.H.) or 60°C (S.H.A.). The resultant CO_2 was cryogenically purified and reacted with Ag wool (T.E.C. and J.M.H.) to remove SO_2 (sometimes produced from modern and fossil teeth as a reaction byproduct).

For three samples we analyzed calcite in matrix adhering to the fossils. The matrix was roasted at 350°C before treatment with phosphoric acid, as described above.

Two specimens of fossil wood that had fallen from the open section at Fort Ternan were collected from the surface of the exposure. Both appeared to be completely replaced by calcite. Sample A is branch or stem fragment with a diameter of about 4 cm. The surface has a vein-like network of fibrous wood, like that found beneath the bark of a thick-stemmed succulent, liana, or vine. The interior is filled with well-developed large calcite crystals up to 3 mm long. Sample B is a tree branch with a knot, with a diameter of about 5 cm. The wood surface preserves the texture of a fine-grained hardwood tree. One large crack was filled with well-developed large calcite crystals up to 3 mm long. Scraping a few millimeters into the calcified surface with a sterile scalpel revealed dark brown streaks of softer material that appeared to be organic matter, so samples were prepared for organic carbon isotopic analysis.

Outer subsurface wood scraped from sample B was roasted under vacuum, resulting in a 22% loss in weight of volatilizable material; the calcite crystals had negligible weight loss. Substantial weight loss suggests the presence of significant amounts of organic matter in specimen B. Two samples drilled from the dark streaky interior of sample B were demineralized in 1 M HCl. The acid-insoluble residues had organic carbon concentrations of 0·3–2·1% by weight, which is three to ten times higher than that of the soils (Cerling *et al.*, 1991), confirming the presence of indigenous organic matter.

$\delta^{13}C$ and $\delta^{18}O$ values were measured on a mass spectrometer using the conventional notation

$$\delta^{13}C \text{ (or } \delta^{18}O) = (R_{sample}/R_{PDB} - 1) \times 1000$$

where R_{sample} and R_{PDB} are the ratios $^{13}C/^{12}C$ (or $^{18}O/^{16}O$) in the sample and the standard, respectively, where the isotope reference standard is PDB. We report our results for $\delta^{18}O$ relative to PDB (Pee Dee Belemnite) assuming the acid–calcite fractionation factor for calcite. Samples were analyzed both at the University of Utah and at the University of Illinois. $\delta^{18}O$ values for water are reported relative to the isotopic standard SMOW (standard mean ocean water).

Using techniques described by Solounias & Moelleken (1993*a*,*b*) *P. primaevus*, *O. tanyceras*, and *Kipsigicerus labidotus* were examined for tooth microwear and *P. primaevus* and *K. labidotus* for snout shape. Tooth replicas were examined with an electron microscope at 500 × . Photomicrographs were digitized and the results were compared with a data base of 35 extant species representing modern browsers, grazers, and mixed feeders.

Results

Evaluation of diagenetic alteration of tooth enamel

Tooth enamel is less suspectible to diagenetic alteration than is bone (Wang & Cerling, 1994) although a number of studies have shown and discussed problems interpreting the $\delta^{13}C$ and

Table 1 **$\delta^{13}C$ and $\delta^{18}O$ values from fossil tooth enamel from Fort Ternan, Kenya**

Sample number	Species	$\delta^{13}C$	$\delta^{18}O$	CO_2 yield* (μmol/mg)
Bovids				
KNM FT 920	*Gazella* sp.	− 13·0	− 0·7	0·81
KNM FT 932	*Gazella* sp.	− 11·0	1·4	0·67
KNM FT 118	*Oioceros tanyceras*	− 8·6	1·9	0·83
KNM FT 123	*O. tanyceras*	− 9·7	1·7	0·74
KNM FT 379	*O. tanyceras*	− 11·2	3·4	0·69
KNM FT 388	*O. tanyceras*	− 10·3	− 0·6	0·70
KNM FT 511	*Kipsigicerus labidotus*	− 11·0	0·5	0·61
KNM FT 520	*K. labidotus*	− 11·4	3·0	0·75
KNM FT 590	*K. labidotus*	− 10·4	2·8	0·81
KNM FT 632	*K. labidotus*	− 10·8	2·5	0·81
KNM FT 1032	?*Pseudotragus potwaricus*	− 9·9	2·0	0·65
Proboscideans				
KNM FT 3355	*Prodeinotherium hobleyi*	− 10·4	0·3	0·74
KNM FT 2785	*Choerolophodon ngorora*	− 10·5	0·8	0·69
KNM FT 2786	*C. ngorora*	− 12·1	2·2	0·59
Giraffids				
KNM FT 2998	*Palaeotragus primaevus*	− 9·8	4·2	0·65
KNM FT 3003	*P. primaevus*	− 11·1	3·4	0·59
Rhinocerotids				
KNM FT 2842	*Paradiceros mukirii*	− 11·5	0·4	0·61
KNM FT 2846	*P. mukirii*	− 11·6	− 0·1	0·56
KNM FT 2858	*P. mukirii*	− 10·2	1·3	0·60
KNM FT 2885	*P. mukirii*	− 11·9	1·0	0·59
Suids				
KNM FT 3321	*Listriodon* sp	− 11·3	− 0·3	0·61

*Average yield for 150 modern mammals from East Africa is 0·65 ± 0·18 (2σ) μmol/mg.

$\delta^{18}O$ of fossil bone due to recrystallization (e.g., Kolodny *et al.*, 1996). Recrystallization is clearly evident in dentine or bone but not in enamel (Ayliffe *et al.*, 1994). In addition, precipitation of carbonate in microfractures in enamel should change the CO_2 concentration of diagenetically altered samples, and should change the isotopic composition of such samples. The results from Fort Ternan reported here are strong evidence that diagenesis does not readily alter the stable isotopic composition of tooth enamel, corroborating evidence presented by Quade *et al.* (1992) and Wang & Cerling (1994).

The $\delta^{18}O$ of apatite is more readily altered than the $\delta^{13}C$ of apatite (Wang & Cerling, 1994) as is expected based on water/rock interaction models for isotope exchange. Figure 2 shows that diagenetic carbonate and pedogenic carbonate have $\delta^{18}O$ values that are significantly more depleted in $\delta^{18}O$ than are the tooth enamel samples. Twenty-one samples of fossil tooth enamel (Table 1) have a range in $\delta^{18}O$ from +4·2 to − 0·7‰ relative to PDB, whereas 19 paleosol (Cerling *et al.*, 1991) and diagenetic (Table 2) carbonate samples have a $\delta^{18}O$ range between − 4·6 and − 6·6‰ relative to PDB. The CO_2 content of fossil tooth enamel samples from Fort Ternan (Table 1) is indistinguishable from that of modern mammals with values of 0·68 ± 0·19 and 0·65 ± 0·18 μmol/mg, respectively, where the quoted uncertainties are the 2σ values for sample sizes of 21 and 150, respectively.

Table 2 **Isotopic composition of carbonate associated with fossil wood and with matrix carbonate associated with fossil tooth enamel, Fort Ternan, Kenya**

Sample		$\delta^{13}C$	$\delta^{18}O$	Calcite (%)
KNM FT 118	Matrix carbonate	− 11·6	− 5·6	49·1
KNM FT 590	Matrix carbonate	− 10·9	− 4·6	49·1
KNM FT 632	Matrix carbonate	− 11·7	− 5·7	54·6
Wood A	White crystals	− 11·7	− 4·7	97·8
Wood A	Yellow crystals	− 13·5	− 5·3	97·7
Wood B	Yellow crystals	− 15·8	− 5·0	100
Wood B	Outer wood	− 12·7	− 6·4	84·5

The lack of overlap in $\delta^{18}O$ values between tooth enamel and other carbonate samples at Fort Ternan, and the similarity in CO_2 content of the fossil enamel compared with modern enamel is strong evidence that diagenetic alteration of the $\delta^{13}C$ or $\delta^{18}O$ signal is not significant in the Fort Ternan tooth enamel samples.

Carbon isotopes in fossil tooth enamel

Table 1 shows that all of the herbivores sampled from Fort Ternan have a clear dietary preference for C_3 plants, having tooth enamel ranging in $\delta^{13}C$ from − 8·6 to − 13‰. This is in agreement with the previous stable isotope analysis on paleosols (Cerling *et al.*, 1991) which indicated a virtually pure C_3 ecosystem based on $\delta^{13}C$ averages of − 12 and − 27‰ for pedogenic carbonate and organic matter, respectively.

Because of recent speculations that Serengeti-type grasslands containing a significant fraction of C_4 grasses were present at Fort Ternan (Retallack *et al.*, 1990; Retallack, 1992) we here review the range of $\delta^{13}C$ values in fossil tooth enamel in light of their paleoecological implications. C_3 plants growing without significant moisture stress in relatively open conditions have average values in the range of − 26 to − 27‰. However, under certain conditions, of particular interest to paleoecologists, observed ranges of the $\delta^{13}C$ in C_3 plants can extend from about − 22‰ to about − 35‰. In dense closed canopy conditions, the exchange of CO_2 of forest floor air with open tropospheric air is inhibited by the canopy; thus, the concentration of CO_2 near the forest floor is considerably higher than that of the average troposphere—resulting in a depletion of ^{13}C in the forest floor air. In addition, very low light levels are associated with maximum isotope discrimination in C_3 plants which also results in ^{13}C depletion in C_3 plants. Plants growing and photosynthesizing in such environments, with low light levels and with poor exchange with the troposphere, have negative $\delta^{13}C$ values. Medina and others (Medina & Minchin, 1980; Medina *et al.*, 1986; van der Merwe & Medina, 1989) have shown that depletion in ^{13}C reaches $\delta^{13}C$ values of − 37‰ on the forest floor. At the other extreme is the isotopic enrichment of C_3 plants caused by water stress. Plants close their stomata to decrease water loss; in so doing they inhibit CO_2 transport and there is an enrichment in ^{13}C producing more positive values up to − 22‰ (Ehleringer *et al.*, 1986; Ehleringer & Cooper, 1988; Ehleringer, 1991). In contrast, C_4 plants have a very small $\delta^{13}C$ range. Because they do not grow under closed canopy conditions, and because they do not change $\delta^{13}C$ in response to high water stress, the $\delta^{13}C$ values of C_4 plants range from about − 13 − 10‰, although more extreme values have occasionally been observed. Based on the

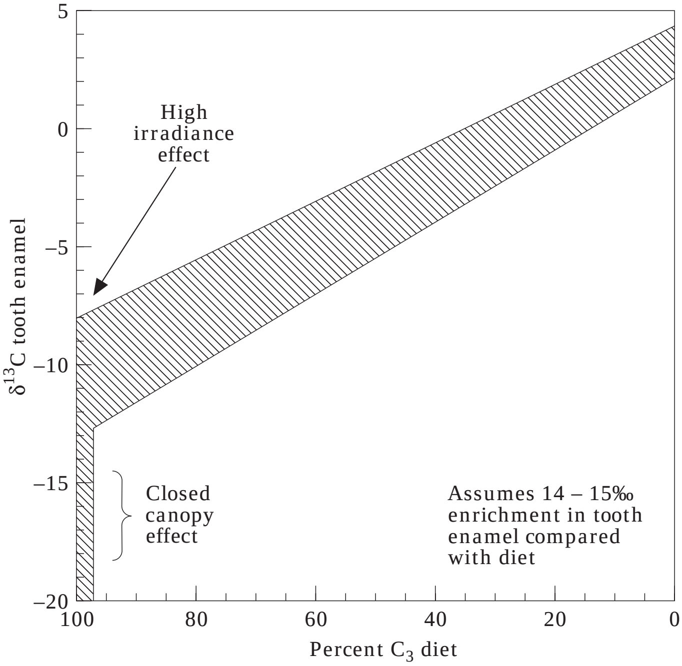

Figure 1. Relationship between diet and δ^{13}C of tooth enamel. The effect of a closed canopy shifts the δ^{13}C of vegetation because of increased biogenic CO_2 on the forest floor; C_4 plants do not have a closed canopy effect because they do not grow under closed canopy conditions. C_3 plants are enriched in arid conditions compared with more humid conditions. Changes in the global δ^{13}C of atmospheric CO_2 would result in a translation of the entire diet field.

estimated δ^{13}C of diets of fossil animals (Lee-Thorp & van der Merwe, 1987) and on the known diets of captive animals (Wang *et al.*, 1994), the isotopic enrichment in ^{13}C between diet and fossil tooth enamel is documented at 14–15‰ compared with the diet. The interpretation of fossil mammals and fossil materials is slightly complicated by the −1·5‰ shift in the isotopic composition of the atmosphere in the last 150 years due to fossil fuel burning (Friedli *et al.*, 1986; Marino *et al.*, 1992). It is mentioned here as a precautionary note and discussed in further detail below.

In light of the above considerations, we estimate that the δ^{13}C of biogenic apatite for diets of a pure C_3 biomass can have a considerable range, from −8 to about −20‰, with the extremes being related to special but important ecological conditions. The range of δ^{13}C values for tooth enamel from mammals utilizing a pure C_4 diet is much smaller, on the order of +1 to +4‰ because the isotopic composition of C_4 plants is more uniform. Figure 1 shows the estimated δ^{13}C values of biogenic apatite and its relation to diet.

The δ^{13}C results from each of the nine species analyzed at Fort Ternan indicate a C_3-dominated diet (Figure 2). In light of the preceding discussion, the most positive δ^{13}C values could represent a pure C_3 diet where the C_3 plants were shifted to slightly more positive values under conditions of high water stress. Alternatively, such results could indicate that a few animals had a diet that included a small proportion (ca. 0–20% for most samples, and from 0–30% for one sample; from Figure 1) of C_4 plants. None of the results is consistent with a diet derived from closed canopy conditions in which the isotopic

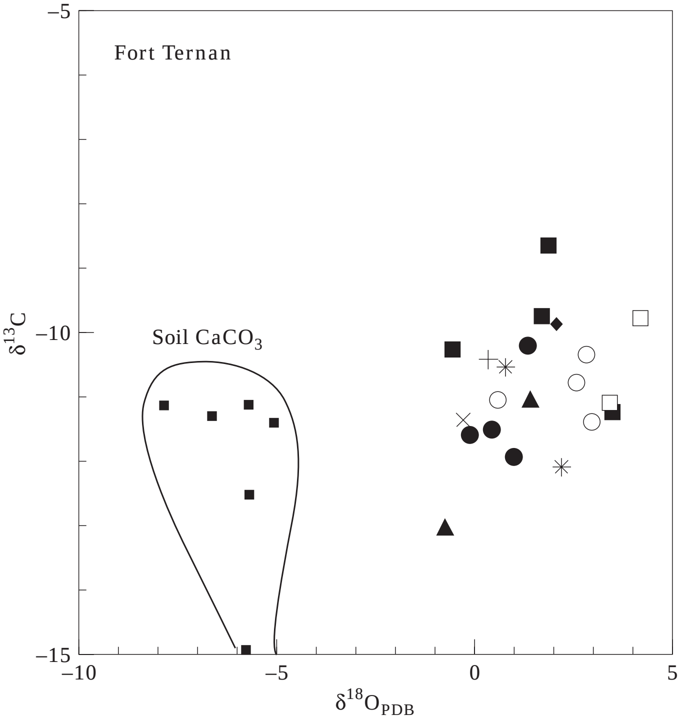

Figure 2. $\delta^{13}C$ and $\delta^{18}O$ values of different Fort Ternan fossil mammals and paleosol nodules horizons from two Chogo-type paleosols. Bovids: (▲) *Gazella*; (■) *Oioceros*; (○) *Kipsigicevus*; (◆) *Pseudotragus*. Giraffid: (□) *Paleotragus*. Proboscideans: (+) *Prodeinotherium*; (*) *Choerolophodon*. Rhino cerotid: (●) *Paradiceros*. Suids: (×) *Listriodon*.

composition of the plants was shifted to more extreme negative values. This is a significant point in the discussion of the Fort Ternan samples, because previously Cerling *et al.* (1991, 1992) had speculated that closed canopy conditions were possible based on the isotopic composition of paleosol organic matter and carbonate; the implications of this will be discussed later in this report.

The negative $\delta^{13}C$ end member for browsers from the Fort Ternan assemblage can be placed in context by comparing the $\delta^{13}C$ values for rhinos, proboscideans, suids, and giraffids. The average $\delta^{13}C$ value for four different specimens of *P. mukirii*, a rhinoceros distantly related to *Diceros bicornis*, is − 11·3‰, ranging from − 10·2–11·9‰. This is comparable to a modern *D. bicornis* from the Turkana Basin with a value of − 10·2 (T.E.C. and J.M.H., unpublished data). *Palaeotragus*, a giraffid, averages − 10·4‰. The proboscideans, *Prodeinotherium* and *Choerolophodon* average − 11·0 which is comparable to figures obtained for modern *Loxodonta africana* from Marsabit Mountain in northern Kenya (− 12‰ for four of five individuals; Figure 3). A single suid, provisionally identified as *Listriodon* sp., had a $\delta^{13}C$ value of − 11·3‰. The range of $\delta^{13}C$ values for all samples is − 9·8 to − 12·1‰, indicating that the isotopic composition of the diet of these mammals was between − 24 and − 27‰. This is compatible with a "normal C_3" ecosystem, such as a woodland or forest, and does not indicate a closed canopy where isotopic depletion of ^{13}C in C_3 plants would be expected.

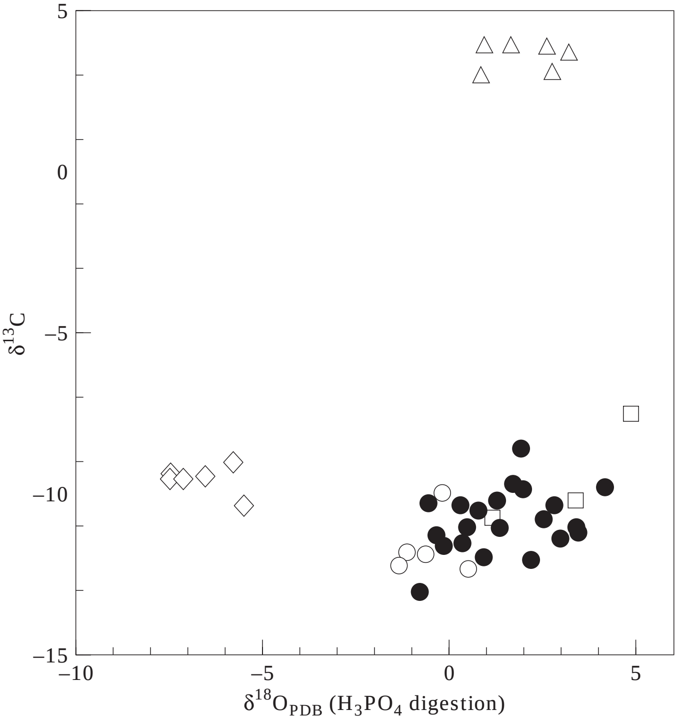

Figure 3. $\delta^{13}C$ and $\delta^{18}O$ values for Fort Ternan fossil mammals compared with that of modern African mammals and to the Ricardo Formation equids. Modern elephants from Marsabit Mountain, Kenya. The modern alcelaphines are hartebeest and wildebeest, and the tragelephine is eland, all from the Athi plains region in Kenya. (●) Fort Ternan; (◇) Ricardo Formation equids; Modern African herbavores. (△) Alcelaphines; (□) Tragelaphines; (○) Marsabit elephants.

Fort Ternan has well-preserved grasses present (Retallack *et al.*, 1990; Retallack, 1991, 1992) which have recently been described as new species (Dugas & Retallack, 1993). Three of the five newly named species are most closely related to modern C_4 grasses although Kranz anatomy was not identified in the fossil specimens. If these grasses were indeed C_4 grasses, then their isotopic signal should be detectable in the dental enamel of mammals that used them as a food source. Bovids are the faunal elements most likely to take advantage of any grasses present. Four different bovids were sampled: *Gazella, Oioceros, Kipsigicerus,* ?*Pseudotragus*. Shipman *et al.* (1981) concluded from dental wear studies that *Oioceros* was a grazer [not substantiated by results obtained by one of us (N.S.)], whereas *Kipsigicerus* was a mixed grazer-browser. Gentry (1970) concluded that both *Oioceros* and ?*Pseudotragus* were ancestral to the Alcelaphini, from which a grazing component might be inferred for the diet of ?*Pseudotragus*. Gentry (1970) noted that *Oioceros* had more occlusal wear than *Protogocerus* (*Kisigicerus*) and may have had a harsher diet. Extant gazelles live in arid habitats and are also grazer-browsers. Thus, all four bovid species sampled from Fort Ternan could conceivably have incorporated at least some graze into their diet. However, all of the bovids sampled indicate a C_3-dominated diet, with $\delta^{13}C$ values ranging from −13 to −8·6‰ (mean=10·7 ± 1·1‰). Only one sample (one of four *Oioceros* specimens analyzed) yielded a value that could possibly be interpreted as representing a diet derived from mixed C_3 and C_4

biomass, and even this is not conclusive. The $\delta^{13}C$ of the Miocene atmosphere is not known; however, the pre-1850 atmosphere had a $\delta^{13}C$ value of about −6·5‰ compared to the late-20th century value of −8·0‰ (Friedli *et al.*, 1986; Marino *et al.*, 1992), with plants undergoing a similar shift to more negative values. Thus, the dietary value of −8·6‰ and the implied dietary average value of −23 to −24‰ is within the range of modern C_3 plants and is within the plausible range of $\delta^{13}C$ values for Miocene C_3 plants.

Taken together, no discernible resource partitioning at Fort Ternan can be demonstrated from the carbon isotope data obtained during this study. The possible grazer *Oioceros* (−10·0 ± 1·1) is more positive than the presumed browser *Paradiceros* (−11·3 ± 0·8) but no obvious difference in preferred vegetation may be inferred. In contrast, resource partitioning is readily observable in data from the modern East African ecosystem (Figure 3).

This brings us to the question of the importance of C_4 plants in the overall ecosystem. So far, the stable isotopic carbon composition of paleosols (Cerling *et al.*, 1993) and fossil tooth enamel provide no indication of C_4 plants at Fort Ternan. If C_4 plants were present, they could only have contributed a very small part of the biota. The first locality where C_4 grasses have been documented by the presence of Kranz anatomy and $\delta^{13}C$ values is the Middle Miocene (Clarendonian) Ricardo Formation in California (Nambudiri *et al.*, 1978; Tidwell & Nambudiri, 1989), with an estimated age of about 12·5 million years (Whistler & Burbank, 1992). The Ricardo Formation has an extensive flora, primarily of fossil woods including oak, pine, and acacia (Webber, 1933). Fossil equids from the Ricardo Formation have $\delta^{13}C$ values of about −9·5‰ (Figure 3), indicating that C_4 plants only made up a small fraction of equid diets at that locality. Indeed, although C_4 plants with Kranz anatomy were clearly present in the Ricardo Formation, they evidently made up only a small proportion of the flora. The same could be true for Fort Ternan.

It seems clear from the fossil record that grasses were present at Fort Ternan, and, as is documented below, that bovids from the Fort Ternan assemblage were utilizing grasses in their diet. It is also probable that these grasses used the C_3 photosynthetic pathway. C_4 grasses must have been rare because a variety of herbivores was sampled and none shows unequivocal evidence of a measurable fraction (>20%) of C_4 biomass in its diet. If, as proposed by Retallack *et al.* (1990), grasses made up a large fraction of the Fort Ternan flora, then the altitude distribution and physiological requirements of grasses must have been very different in the mid-Miocene of Africa compared with today, where C_4 grasses dominate the grass flora below about 2500 m elevation (Tieszen *et al.*, 1979).

Isotopic analysis of fossil wood and sedimentary matrix on teeth

The $\delta^{13}C$ values of calcite crystals and calcified wood from samples A and B range from −11·7 to −15·8‰. They are similar to the results previously obtained for soil carbonates (Cerling *et al.*, 1991) and from matrix adhering to the teeth of two *Kipsigicerus* and one *Oioceros* from Fort Ternan (Table 2). The organic matter $\delta^{13}C$ values for wood sample B range from −23·4 to −24·2‰ (Table 3), which are well within the range for C_3 plants.

A significant amount of original organic carbon was preserved in fossil wood specimen B. The wood organic values are a few permil less negative than the mean for modern plants, but when ∼1‰ is added to account for the fossil fuel effect for modern atmosphere, these values are close to those expected for trees in the Kenya Rift Valley and other countries in Africa (Ambrose & Dechamps, unpublished data). For example, uncarbonized wood of *Tarchonanthus camphoratus* growing between 1600 and 1950 m elevation has $\delta^{13}C$ values of −23·2 and −23·5‰. *Acacia drepanolobium* is −27·5–−26·7‰ and *Juniperus procera* is −22·0‰. *Kigelia*

Table 3 **$\delta^{13}C$ values, insoluble residue concentration, and carbon concentration of fossil wood (after decalcification with 1 M HCl and sealed tube combustion at 860°C)**

Sample	$\delta^{13}C$	Insoluble weight %	C weight %
Wood B outer	− 23·9	7·49	0·31
Wood B inner	− 23·4	7·67	2·11
Wood B inner	− 24·2	4·29	0·57

africana collected in Zaire ranges from − 25·7– − 23·7‰ and in South Africa, Zambia and Ethiopia, it ranges from − 23·6– − 22·9‰.

The $\delta^{13}C$ values of Fort Ternan Wood B are thus within the normal range for tropical African trees. If diagenesis did not alter the original isotopic composition of these samples, they indicate that the $\delta^{13}C$ values of organic matter of some Fort Ternan C_3 plants were only slightly enriched in ^{13}C compared with the preindustrial average for modern plants and that $\delta^{13}C$ values of − 8 to − 9‰ in fossil tooth enamel are compatible with a pure or nearly pure C_3 diet.

The isotopic analysis of tooth enamel of herbivores from Fort Ternan was undertaken with the intent to document the presence of C_4 plants in their diets, and thus to confirm the identification of the C_4 photosynthetic pathway of the grasses identified by Dugas & Retallack (1993). The presence of organic matter in wood from Fort Ternan suggests an additional line of inquiry. If organic matter is preserved in the abundant grass macrofossils at Fort Ternan, its carbon isotope ratios should be in the range of − 14– − 9‰. This would ultimately settle the issue of the presence of C_4 grasses at Fort Ternan.

Oxygen isotopes in fossil tooth enamels

The oxygen isotopes in fossil tooth enamel can also be used to give information about the physiological behavior of mammals. Cerling & Sharp (1996) have shown that the oxygen isotope values derived from H_3PO_4 digestion of tooth enamel (which measures the CO_3 component in apatite), from BrF_5 reaction with purified phosphate (which measures the PO_4 component), and from laser ablation (which measures a weighted average of the CO_3 and PO_4 components) are equally robust measures of the oxygen isotopic composition of enamel. There is a range of about 5‰ in the $\delta^{18}O$ of the CO_3 component of biogenic apatite in the Fort Ternan samples. We estimate that local meteoric waters were about − 6‰ (see discussion below).

It is significant that the most positive values (about + 4‰) are from the giraffid *Palaeotragus*, an animal likely to have derived a large fraction of its body fluid from vegetation enriched in ^{18}O. The values more negative than this, observed in all the other mammals, would indicate greater reliance on drinking water. For modern mammal assemblages in East Africa, giraffes have a higher $\delta^{18}O$ value than other mammals in the local ecosystem (T.E.C. and J.M.H., unpublished data). Metabolic water is thought to be a minor component of total body water of large (>100 kg) mammals (Bryant & Froelich, 1995). Relative humidity and temperature affect leaf water and organic matter oxygen isotope ratios (Dongman *et al.*, 1974; Epstein *et al.*, 1977; Sternberg *et al.*, 1989) so that leaf water is significantly enriched in ^{18}O compared with local source water. Forest canopy and dry, open habitats thus have higher $\delta^{18}O$ values than those in a cool, humid forest understory. The relatively high $\delta^{18}O$ in giraffids and other mammals may thus indicate canopy feeding or feeding in relatively open habitats. Given the relatively small size of the Fort Ternan giraffid, the ^{18}O results suggest open habitat.

Implications of paleosol results

Stable carbon and oxygen isotope values for pedogenic carbonate in the Fort Ternan region were documented by Cerling *et al.* (1991, 1992). Retallack *et al.* (1990) and Retallack (1990, 1991) reported carbonate nodule-bearing paleosols with organic matter from Fort Ternan and used them to interpret the soils as mollisols. We analyzed pedogenic carbonate from two Chogo paleosols, as well as carbonate from somewhat later cements associated with Chogo and Onuria paleosols. All values were very similar, with $\delta^{13}C$ and $\delta^{18}O$ values averaging -12 and -6‰ (Figure 2), respectively, for the composite suite of samples. The cements may have been deposited while the system was actively accumulating. $\delta^{13}C$ values for organic matter in the paleosols average -27‰. The carbon isotopic composition of the paleosol nodules and the paleosol organic matter implies that a $\delta^{13}C$ value of about -27‰ for organic matter in the Chogo type paleosols. Because both soil carbonate and enamel apatite CO_3 are enriched in ^{13}C by about 14–15‰ compared with organic matter producing the soil (Cerling, 1984; Cerling *et al.*, 1989; Cerling & Quade, 1993) and in the diet, respectively, it is relatively straightforward to compare the diet with the organic matter derived from the soil. The grasses described by Retallack *et al.* (1990) and Dugas & Retallack (1993) are in the Onuria Formation; organic matter from the Onuria paleosol has $\delta^{13}C$ values average $-26{\cdot}4$‰, virtually the same as for the Chogo soil. Figure 2 shows that the isotopic composition of the paleosol carbonate and that of the fossil tooth enamel is similar, both being close to the C_3 end member, but it implies that some of the diet was a few ‰ enriched in ^{13}C compared with organic matter preserved in the paleosols which represents the average $\delta^{13}C$ of biomass in the soil.

In a preliminary survey of Amboseli National Park in Kenya, Koch *et al.* (1991) found that the $\delta^{13}C$ values of individual C_3 plants within the park ranged from -24–-30‰ with mean values for herbaceous plants of $-27{\cdot}1 \pm 1{\cdot}9$‰ and for woody plants of $-27 \pm 2{\cdot}4$‰. It is reasonable to assume that the Fort Ternan floral assemblage may have had a similar range of $\delta^{13}C$ values. On the other hand, van der Merwe & Medina (1989) reported a range in $\delta^{13}C$ values for a closed canopy tropical rain forest from -30‰ at the canopy top to -37‰ for plants growing on the forest floor. Based on these comparisons and the observation that the diets of all the mammals were dominated by C_3 vegetation, it is likely that the Fort Ternan site was dominated by C_3 plants with few, if any, C_4 plants. It is also likely that, although the soils and diet indicate an average $\delta^{13}C$ for vegetation between -27 and -25‰, the local ecosystem had a range of $\delta^{13}C$ values for different plants. It is unlikely that closed canopy conditions, where CO_2 exchange with the open troposphere was inhibited and light conditions were very low, were present.

The $\delta^{18}O$ of paleosol carbonate was about -6‰ relative to PDB. By comparison to modern soils (Cerling & Quade, 1993) this value implies a $\delta^{18}O$ of local meteoric water to be between about -6 and -10‰ relative to SMOW. Such a value would be compatible with a relatively high elevation (between 1000 and 2000 meters). For example, modern meteoric water in the Nairobi region is about -6‰ (T.E.C., unpublished data). Fort Ternan is at 1660 meters and is not thought to have been lower during deposition of the Fort Ternan sediments, which accumulated on the lower flanks of a volcano (Shipman, 1982).

Isotopic ecology and resource partitioning

Figure 3 shows the isotopic composition of Fort Ternan mammals in comparison with some modern mammals of East Africa. Alcelaphine bovids from the Athi Plains, Kenya have $\delta^{13}C$ values between +3 and +4‰ due to their exclusively C_4 diet. Tragelaphine bovids (eland) have $\delta^{13}C$ values that are similar to the more ^{13}C enriched samples from Fort Ternan; these could indicate either a diet dominated by ^{13}C-enriched C_3 plants that grow in areas of high irradiance, or a small proportion of C_4 plants in the diet. Modern elephants from a woodland habitat (Marsabit Mountain, Kenya) have $\delta^{13}C$ values of about − 12‰, which is similar to the most ^{13}C depleted samples from Fort Ternan. It is likely, however, that these elephants have themselves been shifted to slightly more ^{13}C depleted values because of the 1·5‰ depletion in ^{13}C of the atmosphere in the past 100 years due to fossil fuel burning. In that case, they fall squarely in the middle of the Fort Ternan values of $\delta^{13}C$. The alcelaphines and tragelaphines in Figure 3 were killed in 1968 and were less affected by this shift than the elephants, although they may have been shifted by 0·5 to 1‰ to more negative values compared with pre-industrial values.

The giraffid *P. primaevus* obtained more of its body water from leaves than did the other species, whereas *P. mukirii* and the proboscideans obtained more of their body water through drinking. This pattern persists today in that rhinos and elephants are more dependent on water than giraffes (Kingdon, 1978). High giraffid and low rhinocerotid $\delta^{18}O$ values may also indicate vertical feeding and microhabitat partitioning. Grazing animals are often obligate drinkers, in part because grasses wither during the dry season, while many browsers are comparatively water-independent because leafy plants retain moisture and nutrients in all seasons (summarized in Ambrose, 1991). *Kipsigicerus* has higher $\delta^{18}O$ values than *Oioceros* and may have relied on more leaf water. This would be consistent with the aforementioned evidence for grazing in *Oioceros*.

Morphological analysis

The snout of *P. primaevus* has been restored from a complete arcade of lower incisors and canines from Fort Ternan (Solounias & Moelleken, 1993*a*). The snout is similar to that of the okapi and the giraffe and is thus interpreted to be a browser. In contrast, the snout of *K. labidotus* is rather squared and is interpreted to be most similar to that of mixed feeders (Solounias and Moelleken, 1993*b*).

Microscopic examination of the teeth of 14 individuals of *Palaeotragus* showed them to have a pattern of pits and scratches similar to that of modern giraffes, and this taxon is thus interpreted to have been a browser. Samples of *O. tanyceras* also indicate a browsing diet using microwear analysis, yielding results close to those of two extant browsers—the bay duiker (*Cephalophus dorsalis*) and the black duiker (*Cephalophus niger*). However one extant grazer, the common waterbuck (*Kobus ellipsiprymnus*), falls outside the cluster of typical grazers and closer to typical browsers. It is possible that *O. tanyceras*, like the waterbuck, was adapted for grazing near water-logged habitats.

As demonstrated by Solounias & Moelleken (1993*b*, 1994), mixed feeders furnish bimodal tooth microwear features that represent both a browsing and a grazing domain. Samples of *K. labidotus* ($n = 35$) microwear clearly cluster into two domains that are indistinguishable from the browsing and grazing domains of the extant mixed feeders *Gazella granti*, *Tragelaphus scriptus*, *Taurotragus oryx*, and *Capricornis sumatraensis*. From the bimodal distribution of scratches it can be inferred that *K. labidotus* was a mixed feeder.

The microwear and morphometric analysis of three Fort Ternan species show that *P. primaevus* was a browser by both tooth microwear and snout shape analysis. *K. labidotus* was a mixed feeder by both methods and *O. tanyceras* was a browser or perhaps a grazer similar to the African common waterbuck but with a larger browsing component. That both *Kipsigicerus* and *Oioceros* may have been at least partly adapted for grazing is significant in terms of the isotopic composition of their teeth. Part of their diet probably included grasses, but evidently not C_4 grasses.

Summary and implications

The Fort Ternan site provides strong evidence that the $\delta^{13}C$ and $\delta^{18}O$ of fossil tooth enamel is a robust indicator of paleoenvironmental parameters, and is not readily altered in diagenesis. The CO_2 yields are similar for fossil enamel samples and modern mammals, and the $\delta^{18}O$ of pedogenic and diagenetic carbonate from Fort Ternan is very different than that of fossil tooth enamel from the site.

Stable isotope analysis of paleosol carbonate, paleosol organic matter, and dietary inference based on a suite of nine mammal genera from Fort Ternan show no conclusive evidence for the presence of measurable C_4 biomass. If C_4 grasses were present, they made up only a minor amount of the biomass. This is in keeping with the observed global pattern in which abundant C_4 biomass has not been observed prior to the late Miocene. Between 7·5 and 6 Ma ago, C_4 biomass becomes abundant enough to be the dominant food source of some mammals in Pakistan (Quade *et al.*, 1992; Cerling *et al.*, 1993), Africa (Morgan *et al.*, 1994; Harris & Cerling, 1995, 1996), North America (Cerling *et al.*, 1993; Wang *et al.*, 1994), and South America (MacFadden *et al.*, 1996).

If, at Fort Ternan, the grasses used the C_3 photosynthetic pathway and were an important part of the Fort Ternan ecosystem, then it is important to establish the conditions under which they flourished. At intermediate elevations in the tropics C_4 grasses dominate, except under exceptional circumstances, such as excessive wetness. However, it is known that under the present atmospheric CO_2 conditions where the CO_2/O_2 ratio is very low (350:200,000 ppm) photorespiration inhibits the growth of C_3 grasses in hot conditions (Ehleringer *et al.*, 1991). It is possible that in the Middle Miocene $P(CO_2)$ concentrations were high enough that photorespiration was suppressed, and thus C_3 plants enjoyed their inherent efficiency advantage over C_4 plants. If so, C_3 grasses may have been present in environments such as tropical or subtropical open canopy woodlands and grasslands where, under modern atmospheric CO_2 levels, they no longer successfully compete against C_4 grasses.

The combination of the isotopic data with the non-isotopic allow some interesting inferences. The isotopic signal alone cannot distinguish between C_3 from browse or graze. When we consider the microwear and morphometric data, we find that *K. labidotus*, and to a lesser extent *O. tanyceras*, may have been mixed feeders and thus part grazers. These species evidently utilized C_3 grasses which today grow best in forest glades and in riparian systems by the water edge. It is possible that the origin of grazing in Bovidae may have begun in such biotopes and with the utilization of C_3 grasses initially, or it is possible that C_3 grasses may have been found in more open environments in tropical regions when CO_2 levels were significantly higher than modern values. Although the story of the development of grazing has yet to be thoroughly understood, this work shows that grazing of C_4 biomass was insignificant at Fort Ternan.

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