# Isotopic Biogeochemistry ($^{13}C$, $^{18}O$) of Mammalian Enamel from African Pleistocene Hominid Sites

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*The carbon and oxygen isotope composition of carbonate in enamel hydroxylapatite can provide information on photosynthetic pathways of plants at the base of food webs, and on hydrological conditions. Retrieval of palaeoenvironmental information from isotopic composition of vertebrate fossils is complicated by potential diagenetic overprinting. In this study, alteration has been assessed by examining the extent to which expected biological carbon and oxygen isotope patterns are disrupted in fossils of species whose diets can be independently predicted by other criteria. The biological patterns used are 1) the differences in carbon isotope composition between grazers and browsers, and 2) the differences in oxygen isotope composition between hippopotamus and terrestrial herbivores.*

*Results obtained on enamel samples from Tighenif (Algeria, ≈700,000 yr), Melka-Kunturé (Ethiopia, 0.7–1.5 myr), and Anabo Koma (Djibouti, ≈1.6 myr) suggest that in vivo carbon and oxygen isotope compositions are preserved in most cases. Moreover, in all three regions, modern patterns of $C_3$ versus $C_4$ grass dominance were present within the Pleistocene.*

## INTRODUCTION

The stable isotope composition of vertebrate fossils is used increasingly to reconstruct environmental and ecological information in modern and ancient ecosystems (van der Merwe, 1982; DeNiro, 1987; Koch et al., 1994). A thorough understanding of isotopic fractionations generated by biochemical processes within organisms is required to interpret isotopic signatures in any organism, modern or fossil. For fossils, retrieval of environmental information from isotopic composition is further complicated



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by potential diagenetic overprinting. Several methods are available to identify alteration of collagen (the dominant protein in bones and teeth), including analysis of C/N ratios and amino acid composition (Ambrose 1990, Tuross et al., 1988; DeNiro & Weiner, 1988). Original carbon and nitrogen isotope compositions have been retrieved from organic residues in fossils as old as 80,000 years, though adequate preservation in such ancient specimens is rare (Tuross et al., 1988; Bocherens et al., 1991b, 1994, 1995).

Because the mineral in bones and teeth, carbonate hydroxylapatite, survives much longer than protein, monitors of its isotopic integrity are vital. Independent monitors of alteration using elemental chemistry or crystallinity are under development, but none yet provide a consistent signal of isotopic alteration in hydroxylapatite (Lee-Thorp and van der Merwe, 1991; Bryant et al., 1994). As a result, alteration has been assessed by examining the extent to which expected biological isotope patterns are disrupted in fossils. This approach has been used extensively to study carbon isotope preservation in fossil vertebrate hydroxylapatite; studies of oxygen isotope preservation are neither as extensive nor as conclusive as those for carbon (see discussion below). Here, we examine carbon and oxygen isotope preservation in tooth enamel of Pleistocene mammals from Africa.

## Carbon and Oxygen Isotopes in Enamel as Paleoecological Indicators

We will consider carbon and oxygen present in mammal teeth as carbonate, which is incorporated into the lattice of hydroxylapatite and makes up 2 to 4 weight percent of the mineral (LeGeros, 1981). Variations in the $\delta^{13}C$ value of carbonate hydroxylapatite in herbivores reflect differences in the isotopic composition of food plants, which are primarily controlled by photosynthetic pathway (DeNiro and Epstein, 1978a, b; Sullivan and Krueger, 1981; Lee-Thorp et al., 1989a). $C_3$ plants, which include all trees, most shrubs and herbs, and cool/moist climate grasses, have low $\delta^{13}C$ values ($-26.5 \pm 2‰$), whereas $C_4$ plants, which include warm/dry climate grasses and some herbs, have higher values ($-12.5 \pm 1‰$) (Bender, 1968; Smith and Epstein, 1971; Deines, 1980; O'Leary, 1988). Plants using Crassulacean Acid Metabolism are capable of fixing carbon with either pathway, and therefore display $\delta^{13}C$ values covering the range for $C_3$ and $C_4$ plants (O'Leary, 1988). The $\delta^{13}C$ value of herbivore hydroxylapatite is similar to that of an animal's diet, offset by a characteristic isotope enrichment that ranges from +9 to +12‰ for wild herbivores (DeNiro and Epstein, 1978b; Sullivan and Krueger, 1981; Lee-Thorp et al., 1989a). The precise enrichment value is debated and probably varies among species due to differences in digestive physiology and within species due to environmental influences on diet and physiology (Bocherens and Mariotti, 1992; Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Using a constant enrichment value, the relative proportions of $C_3$ browse (trees and shrubs) versus $C_4$ grasses has been quantified in living and fossil vertebrates (DeNiro and Epstein, 1978b; Lee-Thorp et al., 1989a, b).

Controls on oxygen isotope variation in mammalian apatite are more complex. It is generally assumed that hydroxylapatite carbonate is derived from blood bicarbonate (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Carbonic anhydrase catalyzes an extremely rapid exchange of oxygen between blood bicarbonate and water (Nagy, 1989); thus oxygen in hydroxylapatite carbonate should equilibrate with body water and ultimately be controlled by 1) the temperature of biomineral formation, and 2) the $\delta^{18}O$ value of body water. Because mammals maintain body temperatures around 37° C, body water composition is the dominant control on the $\delta^{18}O$ value of hydroxylapatite carbonate. The composition of body water is controlled by the mass balance and fractionation of oxygen as it enters and exits the body. Oxygen enters the body as ingested water, inspired $O_2$, and dietary solids. Within the body, metabolism produces $H_2O$ and $CO_2$ as byproducts. Oxygen is lost as liquid water in urine, sweat and feces, and as water vapor and $CO_2$ in respiratory gases. At steady state, a predictable relationship exists between the $\delta^{18}O$ value of ingested water and that of body water (Luz et al., 1984; Tatner, 1988; Bryant and Froelich, 1995).

Ingested water in herbivores has two main sources: drinking water and water in plants. The $\delta^{18}O$ value of drinking water is related to the value of meteoric precipitation, which is correlated to mean annual temperature (Dansgaard, 1964). Plant water is enriched in $^{18}O$ relative to groundwater via evapotranspiration. Enrichment is intense in arid areas (Dongmann et al., 1974) and its effects have been detected in oxygen isotope analyses of mammals (Ayliffe and Chivas, 1990; Luz et al., 1990). As discussed in greater detail below, plant water may vary among species within a habitat due to morphological and physiological differences and may also vary substantially with time of day (Sternberg, 1989; Ziegler, 1989; Bariac et al., 1990, 1994; Flanagan et al., 1991).

## Diagenetic Alteration of the Isotopic Composition of Hydroxylapatite

The preservation of *in vivo* signatures is necessary to infer paleoecological information from the isotopic composition of fossils. While early studies of the isotopic fidelity of fossils were contentious (Sullivan and Krueger, 1981, 1983; Schoeninger and DeNiro, 1982; Nelson et al., 1986), most recent studies have demonstrated that hydroxylapatite carbonate and phosphate in bone and dentin are susceptible to diagenetic overprinting that can be pervasive and difficult to identify using independent monitors (e.g., elemental analysis, x-ray diffraction, infrared spectroscopy), even for relatively young Pleistocene specimens (Lee-Thorp and van der Merwe, 1987, 1991; Ayliffe et al., 1994; Wang and Cerling, 1994; Koch et al., in press, see Barrick and Showers, 1994, for a possible exception). Bone and dentin are composed of extremely small ($100 \times 30 \times 5$ nm), disordered, highly-substituted crystals of hydroxylapatite and are susceptible to post-mortem recrystalliza-

tion, which is the likely mechanism for diagenetic overprinting.

There is growing evidence that tooth enamel, unlike bone and dentin, retains *in vivo* carbon isotope signatures in hydroxylapatite carbonate. The expected isotopic distinction between $C_3$ browsers and $C_4$ grazers has been recovered from tooth enamel as old as 7 myr (Lee-Thorp and van der Merwe, 1987, 1991; Quade et al., 1992; Morgan et al., 1994; Wang et al., 1994). Comparison of $\delta^{13}C$ values in herbivore enamel with contemporary paleosol and marine carbonates suggests the preservation of original signals in enamel through the whole Cenozoic (Koch et al., 1992) and perhaps as far back as the Permian (Thackeray et al., 1990).

Preservation of oxygen isotope composition in carbonate hydroxylapatite from tooth enamel is largely unexplored, and there is reason to believe that adequate carbon and oxygen isotope preservation may be uncoupled. Wang and Cerling (1994) created a model to examine the effects of isotope exchange between pore fluids and hydroxylapatite carbonate, incorporating the concentrations of carbonate in hydroxylapatite and bicarbonate in pore fluids, equilibrium fractionation of carbon and oxygen isotopes between fluid and mineral, and representative values for the isotopic compositions for apatite, meteoric water, and bicarbonate. In their model, under typical surface conditions, the oxygen isotope composition of hydroxylapatite is significantly altered by mild to moderate exchange, whereas the carbon isotope composition is robust until exchange is pervasive. Oxygen isotope preservation has been demonstrated in relatively pristine, late Pleistocene tooth enamel (Bocherens et al., 1991a, in press; Koch et al., in press), but study of preservation in ancient enamel is lacking. Lack of study of oxygen isotope preservation is due, in part, to the fact that expected biological isotope signals are less clear for oxygen than for carbon.

This article has three goals. First, we will examine the pattern of isotopic segregation among mammals in Amboseli National Park, Kenya, a modern savanna ecosystem, focusing on oxygen isotopes. Second, we will determine the oxygen and carbon isotope compositions of fossil mammals from several African Pleistocene faunas, ranging in age from 0.7 to 1.5 myr. Through comparison to the pattern of isotopic segregation among closely related modern mammals, we will assess the fidelity of isotopic preservation in these fossils. Finally, we will briefly consider the paleoecological significance of our results from these mammalian faunas.

## MATERIALS

Modern samples were collected in Amboseli N.P., Kenya. Tooth enamel from herbivorous mammals in three African Pleistocene localities was studied: Tighenif (Algeria), Anabo Koma (Republic of Djibouti) and Melka-Kunturé (Ethiopia). Site locations are shown on Figure 1.

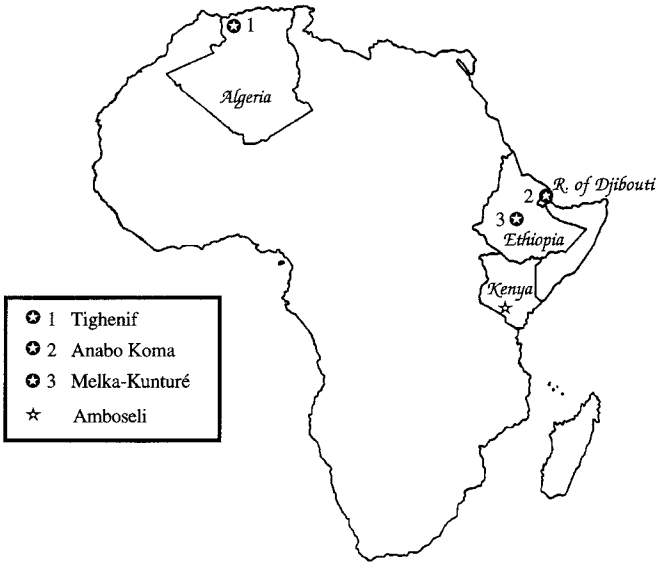


**FIGURE 1**—Map of Africa showing the location of the fossil and modern sites discussed in this study.

### Amboseli

Amboseli N.P., Kenya, lies immediately north of Mt. Kilimanjaro on the Tanzanian border (20°40′ S, 37°15′ E, mean elevation 1140 m). The climate is semi-arid (average temperature 23° C, annual range 15 to 31° C) and rain falls in two seasons (≈350 mm/year) (Western, 1975). Most of the park area occupies an internally-drained Pleistocene lake basin that now contains a seasonal lake and a constant supply of spring water from Kilimanjaro. The flanks of Kilimanjaro to the south of the basin are covered by Afromontane woodlands, whereas bushed grassland of the Somalia-Masai floral province covers the Precambrian bedrock to the north (Western, 1975; White, 1983; Western and Lindsay, 1984). In the 1950's, the basin contained a mixture of habitats, including dense and open woodlands with abundant browse, as well as swamps, lake edge, and plains grasslands dominated by grasses and sedges. Since that time, tree cover has decreased drastically, whereas grasslands have expanded, due to a rise in the water table and to intensified browsing on trees by elephants (Western and Van Praet, 1973; Western, 1975; Western and Lindsay, 1984; Moss, 1988).

Amboseli grasses and sedges have $\delta^{13}C$ values typical for $C_4$ plants ($-13.2 \pm 0.9‰$, n = 12), as do several rare euphorbs and agave, and one abundant shrub, *Sueda monoica* (data in Koch et al., 1991). One succulent herb, *Trianthema ceratosepala,* has a value of $-21.8‰$, suggesting CAM photosynthesis. All other trees, shrubs and herbs have $\delta^{13}C$ values characteristic of $C_3$ plants (herbs, $-27.4 \pm 1.9‰$, n = 13; tree and shrubs, $-27.6 \pm 2.5‰$, n = 9). Submerged aquatic plants, *Ceratophyllum* sp., have intermediate $\delta^{13}C$ values, averaging $-21.4‰$ (n = 2). Thus, as in other African ecosystems with a warm growing season, there is a strong dichotomy in $\delta^{13}C$ value between $C_4$ grass

and $C_3$ browse and herbs (Vogel, 1978a; Tieszen and Imbamba, 1980).

The Amboseli ecosystem supports a large, partly migratory population of mammals, including forty-nine species of large (≥1 kg) wild mammals (Western, 1975). Most samples were collected from carcasses found in 1990 and 1993, though several specimens were collected from recently deceased animals by A.K. Behrensmeyer in 1975. Actualistic experiments on bone weathering in Amboseli indicate that bones survive at the surface for 15 to 20 years (Behrensmeyer, 1978; Behrensmeyer, pers. com.). Consequently, our sample represents park fauna from ≈1970 to 1993.

### Tighenif

The Tighenif (Ternifine) quarry is located 20 km east of Mascara, Algeria. It was first excavated by Arambourg and Hoffstetter in 1954–56, yielding several *Homo erectus* specimens (Arambourg and Hoffstetter, 1963). Excavations by a French-Algerian team in 1982–83 provided additional material and an age of approximately 0.7 myr for the locality (Geraads et al., 1986). The material used in the present study comes from sands deposited over the basal varicolor and gray clays in the bottom of an artesian lake. The large herbivore fauna is diverse (18 species), and may be divided into open, dry country forms (e.g., gazelles, alcelaphines, zebra, white rhinoceros, and warthog-like suids), which predominate, a few mixed feeders (kudu and *Loxodonta atlantica,* a presumed mixed-feeding elephant), and rare, wet country grazers (kob and hippopotamus) (Geraads et al., 1986).

Today, Tighenif is located in the Mediterranean floral province and it receives rainfall primarily in the winter months (Winter et al., 1976, White, 1983). Prior to anthropogenic influences, much of this province was covered by forest, which would have been dominated by $C_3$ trees and grasses (Winter et al., 1976; White, 1983). Despite the fact that the region is currently more open, grasses in this region today largely employ $C_3$ photosynthesis. $C_4$ grasses are more abundant to the south in the foothills of the Atlas Mountains, where the Mediterranean and Saharan floral provinces meet (Winter et al., 1976; White, 1983).

### Anabo Koma

A survey of the sedimentary basins of the Republic of Djibouti, conducted by L. de Bonis, J.-J. Jaeger and coworkers in 1983–86, led to the discovery of several Pleistocene localities, among which Anabo Koma is the richest. It has yielded Oldowan industry artifacts and has been dated biochronologically at 1.6 ± 0.3 myr (Bonis et al., 1988). The large mammal fauna contains a hippopotamus, a presumably grazing elephant (*Elephas recki*), and smaller grazers, such as wildebeest and springbok, which today prefer dry habitats, and kob, which today is closely associated with water (Estes, 1991). Two extinct suids also occur. Their dental morphology is intermediate between that of the browsing bushpig and grazing warthog. Dental morphology suggests that *Kolpochoerus limnetes* was more of a browser, whereas *Metridiochoerus andrewsi* seems more adapted to grazing, but less so than its descendant at Tighenif (Cooke, 1985).

Anabo Koma is located within the Somalia-Masai floral province today. The vegetation in this region is semi-desert shrubland and grassland. Shrubs are dominantly $C_3$, although succulent CAM shrubs (e.g., *Euphorbia*) may be locally abundant. Dominant grasses are in exclusively $C_4$ genera (*Aristida, Brachiaria, Cenchrus, Chloris*) (White, 1983; Smith, 1982).

### Melka-Kunturé

This locality, 50 km south of Addis-Abeba, Ethiopia, was excavated by J. Chavaillon from 1965 to 1980. It includes several archaeological levels, all close to the paleo-Awash river, ranging from Oldowan (Gomboré I, ≈1.5 myr) to Middle Stone Age, through the developed Oldowan of Garba IV (≈1.2 myr) and the Acheulean of Gomboré II (0.7 myr). The fauna analyzed here does not differ much from that of Anabo Koma, with hippopotamus, alcelaphines, zebra, and kob (Geraads, 1979, 1985).

Melka-Kunturé is located near the transition between the Somalia-Masai floral province, occurring in the Great Rift, and the forests of the Afromontane province on nearby highlands. The flora in this region includes bushland and thicket with secondary grassland and wooded grasslands. Grasses are dominantly $C_4$ in the hot/dry rift lowlands (White, 1983).

## METHODS

Enamel from fossils, and enamel, dentin, and bone from modern mammals were collected by drilling. The enamel from fossils was pretreated according to Bocherens et al. (1991a). Powdered enamel was soaked in 2–3% NaOCl for 20 hrs at 20° C to oxidize organic residues, rinsed with distilled water, then treated with 1M acetic acid-Ca acetate buffer (pH = 4.75) for 20 hr at 20° C to remove exogenous carbonate. Pretreatment of modern enamel followed this protocol as well. Pretreatment of modern bone was slightly different. Because of its high organic content, bone was soaked in 2–3% NaOCl for up to 3 days, rather than 20 hr.

Carbon dioxide was produced from the treated powders by dissolution in 100% $H_3PO_4$. For fossils, dissolution was performed at 25° C for 3 days on ≈40 mg of powder. Carbon dioxide was collected and purified by cryogenic distillation in a vacuum line, and carbon and oxygen isotope compositions were measured on a VG Optima gas source mass spectrometer at the Laboratoire de Biogéochimie Isotopique, University of Paris 6. Isotopic analysis of modern samples was conducted in the Stable Isotope Laboratory, Dept. of Earth Sciences, Princeton University, using a VG Optima with an ISOCARB automated carbonate system. Small samples of inorganic powder (≈8 mg) were dropped into a constantly stirred volume of 100% $H_3PO_4$ and reacted at 90° C for ≈10 minutes. All signs of reaction cease by ≈4 minutes. The $CO_2$ and $H_2O$ generated by sam-

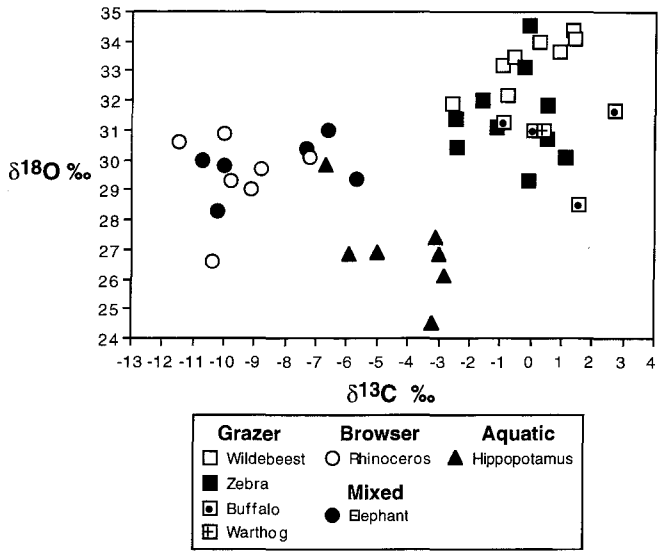


**FIGURE 2**—Enamel hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for modern herbivore bones from Amboseli National Park, Kenya.

ple dissolution are immediately trapped and separated cryogenically, then $CO_2$ is released to the inlet of the mass spectrometer and analyzed. Following sample reaction, the reaction vessel was stirred under vacuum for at least 5 minutes prior to reacting the next sample. Between sample memory for apatite samples reacted under these extraction conditions was similar to that for calcite (e.g., ≈1%).

Isotopic abundances are normalized to international and internal laboratory calcite standards that are analyzed concurrently with the apatite samples. The magnitude of oxygen isotope fractionation during dissolution of carbonate hydroxylapatite in 100% $H_3PO_4$ is not known, therefore we applied a fractionation identical to that for calcite (Koch et al., 1989). The delta value for each isotope is calculated as $\delta^E X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where $\delta^E X = \delta^{13}C$ or $\delta^{18}O$, and $R = {}^{13}C/{}^{12}C$ or ${}^{18}O/{}^{16}O$, respectively. The standards are PDB for carbon and SMOW for oxygen. For fossil samples, analytical precision was better than 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{18}O$ values (Bocherens, 1992). For modern samples, analytical precision for repeated analysis of an enamel apatite standard was 0.2‰ for both carbon and oxygen isotope values, and analytical precision for calcite standards is <0.1‰ for both isotopes.

## RESULTS

In the modern fauna from Amboseli grazers (zebra, wildebeest, warthog, and buffalo) have hydroxylapatite with high $\delta^{13}C$ values typical of $C_4$ feeders (−0.1 ± 1.4‰) and high $\delta^{18}O$ values (32.0 ± 1.6‰) (Fig. 2; Table 1). Unlike the other grazers, the warthog routinely consumes the roots and rhizomes, as well as the leaves of grass, yet it has a $\delta^{13}C$ value similar to other grazers. T-tests performed using STATWORKS demonstrate that carbon isotope values do not differ significantly among grazers ($P > 0.05$ for all comparisons), whereas for oxygen isotopes, buffalo (30.6 ± 1.4‰) and zebra (31.5 ± 1.5‰) have significantly lower $\delta^{18}O$ values than wildebeest (33.4 ± 0.9), but buffalo and zebra do not differ significantly from each other. The $\delta^{13}C$ and $\delta^{18}O$ values of black rhinoceros (−10.0 ± 1.9‰ and 29.5 ± 1.3‰, respectively) are significantly lower than those of the grazers ($P < 0.001$), though their $\delta^{13}C$ values are higher than predicted for a 100% $C_3$ diet. The $\delta^{13}C$ and $\delta^{18}O$ values of mixed feeding elephants (−8.4 ± 2.1‰ and 29.8 ± 0.9‰, respectively) are not significantly different than values from rhinoceros. However, collagen $\delta^{13}C$ values from a larger sample of Amboseli elephants reveal a much greater consumption of $C_4$ grass by some individuals than is indicated in this limited data set from tooth enamel (Koch et al., 1995). The aquatic dwelling hippopotamuses have $\delta^{13}C$ values (−4.2 ± 1.6‰) indicating a strong, although clearly not exclusive, reliance on $C_4$ grasses. Oxygen values from these animals are the lowest observed in Amboseli (26.9 ± 1.6‰). T-tests demonstrate that the differences in oxygen isotope values among grazers, rhinoceros/elephant, and hippopotamus are significant ($P < 0.001$ for all comparisons). Finally, there are no consistent differences in oxygen or carbon isotope value between enamel and bone within each category (Table 1).

At Tighenif, $\delta^{13}C$ values are similar in all taxa, ranging from −12.5 to −8.4‰ (Fig. 3; Table 2). In contrast, hippopotamuses have significantly lower $\delta^{18}O$ values (26.2 ± 0.8‰) the terrestrial herbivores (28.8 ± 0.8‰) ($P < 0.001$), and there is no overlap between these two groups in $\delta^{18}O$ value.

At Melka-Kunturé, fauna from the youngest level, Gomboré II, have $\delta^{13}C$ values ranging from −1.9 to 1.9‰, with no clear taxonomic segregation. The sole hippopotamus has a $\delta^{18}O$ value (25.4‰) lower than the mean for non-aquatic mammals (30.5 ± 1.5‰) (Fig. 4; Table 3). Fauna from Garba IV have slightly more variable $\delta^{13}C$ values (−4.7 to 2.7‰). Again, $\delta^{18}O$ values from hippopotamuses (26.2 ± 2.5‰) are substantially lower than those for open country grazers (mean 31.3‰) (Table 3). At Gomboré I, the oldest level at Melka-Kunturé, $\delta^{13}C$ values range from −1.2 to 3.1‰ and $\delta^{18}O$ values range from 27.0 to 33.1‰ (Table 3). The two wildebeests have different $\delta^{18}O$ values; one has a low value similar to the hippopotamus, whereas the other is much higher.

Fauna from Anabo Koma show the greatest range in $\delta^{13}C$ values (−6.4 to 3.9‰) (Fig. 5; Table 4). The grazers have the most positive $\delta^{13}C$ values (3.2 ± 0.8‰), whereas the two suids have much more negative values (−6.3‰ for *Kolpochoerus* and −2.7‰ for *Metridiochoerus*). The sole hippopotamus has a low $\delta^{18}O$ value (25.7‰), whereas the grazers have the most positive values (28.4 ± 0.5‰) (Table 4). *Kolpochoerus,* which consumed more $C_3$ browse, has the lowest $\delta^{18}O$ value at the site (25.4‰), whereas Metridiochoerus, which consumed more $C_4$ grass, has a $\delta^{18}O$ value similar to other grazers at the site (Table 4).

**TABLE 1**—Carbonate hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Amboseli mammals.

| Number | Scientific name | Common name | Sample | $\delta^{13}C$ | $\delta^{18}O$ | Diet |
|---|---|---|---|---|---|---|
| 1-50-18 | *Equus burchelli* | plains zebra | enamel | 1.1 | 30.1 | G |
| 21-50-13 | *Equus burchelli* | plains zebra | enamel | 0.5 | 30.7 | G |
| P-1/93-tree2 | *Equus burchelli* | plains zebra | enamel | −0.1 | 29.3 | G |
| S-1/93-out1 | *Equus burchelli* | plains zebra | enamel | −0.6 | 34.5 | G |
| S-3/93-44 | *Equus burchelli* | plains zebra | enamel | −0.3 | 33.1 | G |
| S-8/93-3 | *Equus burchelli* | plains zebra | enamel | 0.5 | 31.8 | G |
| W-1/93-38 | *Equus burchelli* | plains zebra | enamel | −2.4 | 30.4 | G |
| 21-5/90-1 | *Equus burchelli* | plains zebra | bone | −1.6 | 32.0 | G |
| 21-9/90-4 | *Equus burchelli* | plains zebra | bone | −2.5 | 31.4 | G |
| 21-13/90-10 | *Equus burchelli* | plains zebra | bone | −1.1 | 31.1 | G |
| P-1/93-7 | *Connochaetes taurinus* | common wildebeest | enamel | −1.0 | 33.2 | G |
| P-3/93-15 | *Connochaetes taurinus* | common wildebeest | enamel | 0.9 | 33.6 | G |
| S-1/93-27 | *Connochaetes taurinus* | common wildebeest | enamel | 1.4 | 34.1 | G |
| S-8/93-4 | *Connochaetes taurinus* | common wildebeest | enamel | 0.2 | 34.0 | G |
| W-2/93-out2 | *Connochaetes taurinus* | common wildebeest | enamel | 1.3 | 34.4 | G |
| 5-5/90-12 | *Connochaetes taurinus* | common wildebeest | bone | −0.8 | 32.2 | G |
| 6-52-32 | *Connochaetes taurinus* | common wildebeest | bone | −2.6 | 31.9 | G |
| 13-4/90-15 | *Connochaetes taurinus* | common wildebeest | bone | −0.6 | 33.5 | G |
| 21-12/90-29 | *Phacochoerus aethiopicus* | warthog | enamel | 0.4 | 31.0 | G |
| 21-12/90-10 | *Syncerus caffer* | buffalo | enamel | 1.5 | 28.5 | G |
| W-1/93-31 | *Syncerus caffer* | buffalo | enamel | 2.7 | 31.7 | G |
| 8-4/90-33 | *Syncerus caffer* | buffalo | bone | −0.9 | 31.3 | G |
| 21-7/90-21 | *Syncerus caffer* | buffalo | bone | 0.1 | 31.0 | G |
| | | Grazer: average ± 1 σ | | −0.1 ± 1.4 | 32.0 ± 1.6 | |
| 21-5/90-13 | *Diceros bicornis* | black rhinoceros | enamel | −9.8 | 29.3 | B |
| 21-12/90-33 | *Diceros bicornis* | black rhinoceros | enamel | −10.4 | 26.6 | B |
| 21-50-8 | *Diceros bicornis* | black rhinoceros | enamel | −7.2 | 30.1 | B |
| S-3/93-out1 | *Diceros bicornis* | black rhinoceros | enamel | −10.0 | 30.9 | B |
| ALT CAMP | *Diceros bicornis* | black rhinoceros | enamel | −9.1 | 29.0 | B |
| 1-27-76 | *Diceros bicornis* | black rhinoceros | bone | −13.6 | 30.1 | B |
| 6-50-33 | *Diceros bicornis* | black rhinoceros | bone | −11.5 | 30.6 | B |
| 21-5/90-33 | *Diceros bicornis* | black rhinoceros | bone | −8.8 | 29.7 | B |
| | | Rhino: average ± 1 σ | | −10.0 ± 1.9 | 29.5 ± 1.3 | |
| Harriet | *Loxodonta africana* | african elephant | enamel | −7.3 | 30.4 | M |
| M178 | *Loxodonta africana* | african elephant | enamel | −5.7 | 29.3 | M |
| Teresia | *Loxodonta africana* | african elephant | enamel | −10.2 | 28.3 | M |
| Zach | *Loxodonta africana* | african elephant | enamel | −10.7 | 30.0 | M |
| Zoe | *Loxodonta africana* | african elephant | enamel | −6.6 | 31.0 | M |
| 21-12/90-25 | *Loxodonta africana* | african elephant | enamel | −10.0 | 29.8 | M |
| | | Elephant: average ± 1 σ | | −8.4 ± 2.1 | 29.8 ± 0.9 | |
| 5-5/90-19 | *Hippopotamus amphibius* | common hippopotamus | enamel | −2.8 | 26.1 | |
| 6-51-20 | *Hippopotamus amphibius* | common hippopotamus | bone | −3.1 | 27.4 | |
| 21-5/90-7 | *Hippopotamus amphibius* | common hippopotamus | bone | −5.0 | 26.9 | |
| 21-9/90-2 | *Hippopotamus amphibius* | common hippopotamus | bone | −3.0 | 26.8 | |
| 21-50-3 | *Hippopotamus amphibius* | common hippopotamus | enamel | −3.2 | 24.5 | |
| 75-7:76 | *Hippopotamus amphibius* | common hippopotamus | bone | −5.9 | 26.8 | |
| S-4/93-7 | *Hippopotamus amphibius* | common hippopotamus | bone | −6.7 | 29.8 | |
| | | Hippo: average ± 1 σ | | −4.2 ± 1.6 | 26.9 ± 1.6 | |

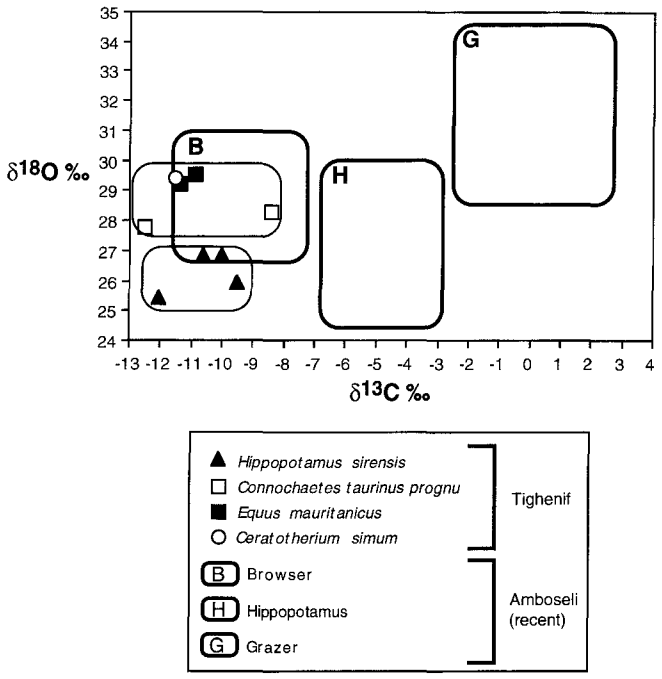


**FIGURE 3**—Enamel hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Tighenif herbivores, compared to those of modern herbivores from Amboseli.

## DISCUSSION

### Controls on Isotope Variation in Amboseli Mammals

Amboseli mammals show the expected pattern of carbon isotope segregation between browsers and grazers. The low $\delta^{13}C$ values for hippopotamuses are somewhat surprising, given that previous observational studies have suggested that hippopotamus were nearly exclusively grazers (Field, 1970; Clemens and Maloiy, 1982; Owen-Smith, 1988). However a previous study of carbon isotopes in dung also uncovered unusually low $\delta^{13}C$ values for Amboseli hippopotamus (Tieszen and Imbamba, 1980). The Amboseli population must be consuming $C_3$ browse and/or submerged aquatic vegetation, which has $\delta^{13}C$ values intermediate between $C_3$ and $C_4$ plants.

Even more unexpected is the strong discrimination among browsers, grazers, and aquatic dwellers in oxygen isotopes. If this segregation is typical, oxygen isotopes may provide a new source of ecological information (terrestrial versus aquatic) and an independent probe of isotopic fidelity in fossils. Before applying oxygen isotopes as a paleoecological or diagenetic monitor, however, the source of oxygen isotope discrimination must be examined.

Considering first the fully terrestrial mammals, there are two explanations for the observation that grazers have higher $\delta^{18}O$ values than the browsing rhinoceros and mixed feeding elephants. First, the grazers are much less massive than the rhinos and elephants; grazers range in size from ≈75 kg for the warthog to ≈700 kg for the buffalo, whereas black rhinoceros reach ≈1350 kg and elephants reach ≈5000 kg (Estes, 1991). Metabolic rate scales negatively with body size, thus rhinoceros and elephant have slower rates of metabolic $H_2O$ and $CO_2$ production (Peters, 1983). Metabolic water contains oxygen derived from atmospheric $O_2$ ($\delta^{18}O$ = +23‰, Dole et al., 1954) and plant cellulose ($\delta^{18}O$ up to +35‰, Sternberg, 1989), which are $^{18}O$-enriched relative to meteoric water. Consequently, smaller mammals with high metabolic rates have higher body water $\delta^{18}O$ values than larger animals with low metabolic rates (Luz et al., 1984; Bryant and Froelich, 1995).

Second, many mammals ingest a significant amount of water from plants. Water in $C_4$ plants may be $^{18}O$-enriched relative to water in $C_3$ plants in the same habitat (Sternberg et al., 1986; Sternberg, 1989; Ziegler, 1989; Flanagan et al., 1991). During photosynthesis, plants open their stomata to admit $CO_2$ for fixation and to allow evapotranspiration to carry water and nutrients to leaves. Because $C_4$ plants use water and fix $CO_2$ more efficiently than $C_3$ plants, they photosynthesize under arid conditions that cause $C_3$ plants to shut their stomata to prevent dehydration. Leaf water in $C_4$ plants undergoes more extensive $^{18}O$-enrichment due to evapotranspiration. Therefore, differences in the $\delta^{18}O$ value of plant water between $C_3$ and

**TABLE 2**—Enamel carbonate hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Tighenif mammals (~700,000 yr).

| Number | Scientific name | Common name | $\delta^{13}C$ ‰ | $\delta^{18}O$ ‰ |
|---|---|---|---|---|
| 63700 | *Hippopotamus sirensis* | hippopotamus | −12.0 | 25.4 |
| 63800 | *Hippopotamus sirensis* | hippopotamus | −10.6 | 26.8 |
| 64000 | *Hippopotamus sirensis* | hippopotamus | −10.0 | 26.8 |
| 84400 | *Hippopotamus sirensis* | hippopotamus | −9.5 | 25.9 |
| 84700 | *Connochaetes taurinus prognu* | wildebeest | −8.4 | 28.3 |
| 84800 | *Connochaetes taurinus prognu* | wildebeest | −12.5 | 27.8 |
| 84600 | *Ceratotherium simum* | white rhinoceros | −11.5 | 29.4 |
| 63900 | *Equus mauritanicus* | zebra | −11.3 | 29.2 |
| 84500 | *Equus mauritanicus* | zebra | −10.9 | 29.5 |

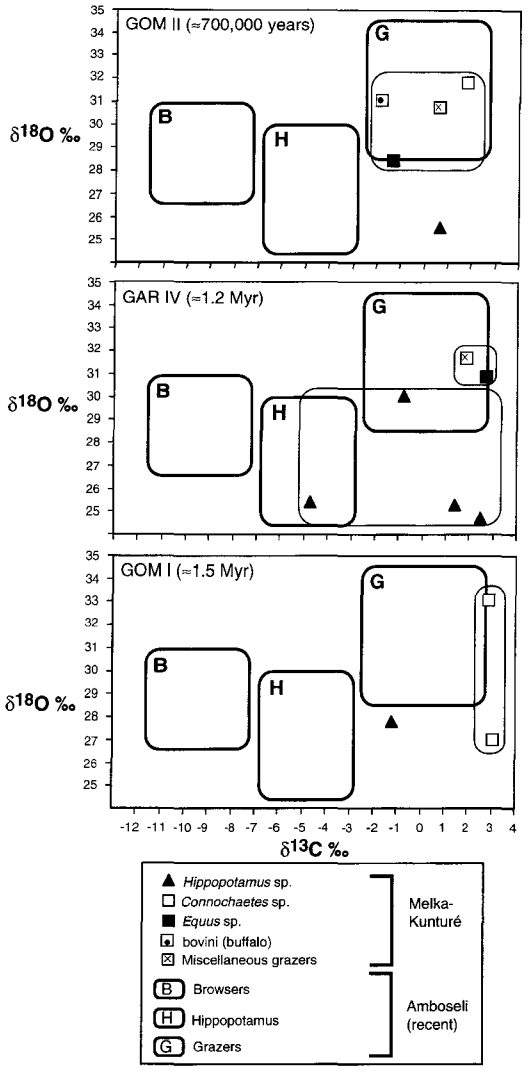


**FIGURE 4**—Enamel hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Melka-Kunturé herbivores, compared to those of modern herbivores from Amboseli. GOM II, Gomboré II; GAR IV, Garba IV; GOM I, Gomboré I.

$C_4$ plants may contribute to oxygen isotope segregation among terrestrial herbivores.

Hippopotamus deviate from the pattern described above. They consume a substantial fraction of $C_4$ plants, yet they have the most negative $\delta^{18}O$ values. The large size of hippopotamus (up to 2000 kg), through its correlation to metabolic rate, would contribute to low $\delta^{18}O$ values. However, hippopotamuses are only half as massive as elephants, yet significantly more $^{18}O$-depleted, indicating that body size cannot be the sole cause of their low values. We will consider three alternative hypotheses low oxygen isotope values in hippopotamus.

A reviewer suggested that hippopotamuses might obtain a greater fraction of their ingested water from drinking water (relative to the oxygen obtained from $O_2$, plant organic matter, and plant included water) than other large mammals. Because the other sources of oxygen are likely to have higher $\delta^{18}O$ values than drinking water, a greater proportion of drinking water could lower the $\delta^{18}O$ value of body water. We could find no data on water consumption rates of hippopotamus, most likely due to the extreme difficult of accurately measuring this variable in a semi-aquatic mammal. We might expect, however, that hippopotamuses would drink less than terrestrial mammals, because they lose less water from their bodies via evaporation than terrestrial mammals.

Hippopotamuses are diurnally aquatic and nocturnally terrestrial (Estes, 1991). Past observational studies have indicated that they graze at night, and that they eat little aquatic forage during the day (Field, 1970; Clemens and Maloiy, 1982; Owen-Smith, 1988). However, a recent study has documented substantial aquatic foraging when the nutritional content of terrestrial forage was low (Mugangu and Hunter, 1992) and our carbon isotope data demonstrate a significant $C_3$ browse and/or aquatic component in Amboseli hippopotamus diets. Because evapotranspiration is reduced when plants are not photosynthetically active, plant water is not as $^{18}O$-enriched at night as it is during the day (Bariac et al., 1990, 1994). Likewise, water in aquatic plants is not as $^{18}O$-enriched as water in land plants (Sternberg et al., 1986). Thus either exclusively nocturnal terrestrial foraging or diurnal feeding on aquatic vegetation may supply hippopotamuses with plant water that is $^{18}O$-depleted when compared to water in the foods of other vertebrates.

The aquatic lifestyle of hippopotamuses may also contribute to low $\delta^{18}O$ values. By remaining submerged during the heat of the day, they substantially reduce the loss of water from their body via transcutaneous evaporation. Unlike water vapor lost via evaporation from the lungs, which is in isotopic equilibrium with body water, water lost by transcutaneous evaporation experiences a strong kinetic isotope fractionation. The isotope value of this water vapor may differ from body water by as much as −24‰ (Schoeller et al., 1986). Consequently, submergence may reduce the transcutaneous evaporative loss of $^{18}O$-depleted water, generating low $\delta^{18}O$ values in hippopotamus body water relative to terrestrial mammals with large evaporative water loss fluxes.

Given the variety of hypotheses offered to explain $\delta^{18}O$ segregation among Amboseli mammals, what can be said about the likelihood of these patterns being characteristic of fossil mammals from different ecological settings? Body size related differences in $\delta^{18}O$ values should be consistent and predictable, although the mass of the fossil taxa must be estimated (Anderson et al., 1985; Gingerich, 1990). Changes among mammals due to differences in the $\delta^{18}O$ value of leaf water may be affected by climate. Under conditions of high humidity, the evapotranspirative enrichment of leaf water is reduced and more comparable among $C_3$, $C_4$, and aquatic plants (Sternberg, 1989; Ziegler, 1989). Thus segregation among mammals based on leaf water differences may vary temporally and spatially with relative humidity. Finally, if hippopotamuses have low $\delta^{18}O$ values because they are diurnally aquatic, then fossil hip-

**TABLE 3**—Enamel carbonate hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Gomboré II (GOM II, ~700,000 yr), Garba IV (GAR IV, ~1.2 myr) and Gomboré I mammals (GOM I, ~1.5 myr).

| Number | Layer | Scientific name | Common name | $\delta^{13}C$ ‰ | $\delta^{18}O$ ‰ |
|---|---|---|---|---|---|
| 89200 | GOM II | *Hippopotamus* sp. | hippopotamus | 0.7 | 25.4 |
| 89200 | GOM II | *Connochaetes taurinus taurinus* | wildebeest | 1.9 | 31.8 |
| 89300 | GOM II | *Kobus* sp. | kob | 0.7 | 30.7 |
| 89400 | GOM II | *Equus* (young) | zebra | −1.4 | 28.4 |
| 89500 | GOM II | bovini | buffalo | −1.9 | 31.1 |
| 89000 | GAR IV | *Hippopotamus* sp. | hippopotamus | −4.7 | 25.3 |
| 98800 | GAR IV | *Hippopotamus* sp. | hippopotamus | 1.4 | 25.2 |
| 98900 | GAR IV | *Hippopotamus* sp. | hippopotamus | 2.5 | 24.6 |
| 88900 | GAR IV | *Hippopotamus* sp. | hippopotamus | −0.8 | 29.9 |
| 88800 | GAR IV | *Damaliscus* sp. | bontebok | 1.9 | 31.7 |
| 89400 | GAR IV | *Equus* sp. | zebra | 2.7 | 30.9 |
| 88700 | GOM I | *Hippopotamus* sp. | hippopotamus | −1.2 | 27.7 |
| 88600 | GOM I | *Connochaetes* sp. | wildebeest | 3.1 | 27.0 |
| 99000 | GOM I | *Connochaetes* sp. | wildebeest | 2.9 | 33.1 |

popotamuses should have low values as long as they too were aquatic. Morphologic and taphonomic analyses of fossil species assigned to the genus *Hippopotamus* indicate that these animals were aquatic organisms (Gèze, 1985). Generally, the potential causes of oxygen isotope segregation among Amboseli mammals, particularly between hippopotamuses and the terrestrial animals, are likely to apply to fossil mammals from different ecologic settings.

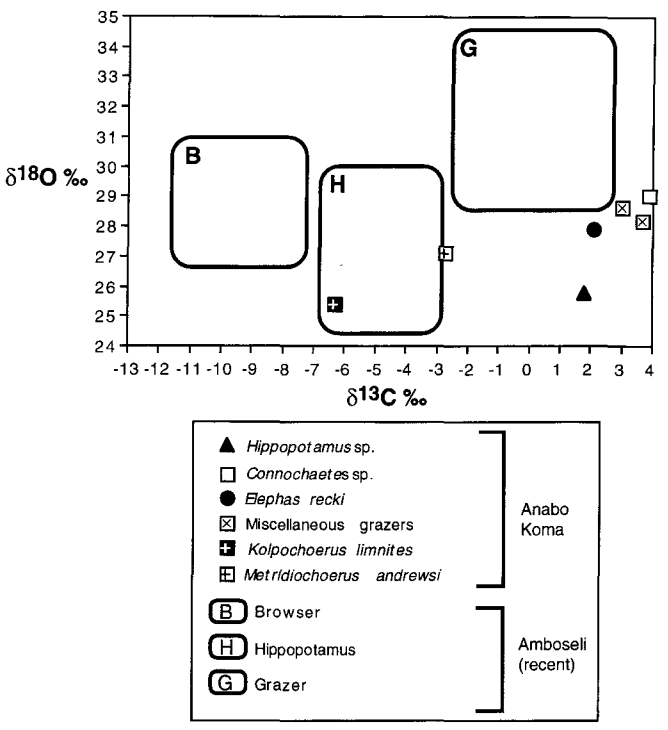


**FIGURE 5**—Enamel hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Anabo Koma herbivores, compared to those of modern herbivores from Amboseli.

## Preservation of Biogenic Oxygen Isotope Values in Hydroxylapatite Carbonate

At Tighenif, Gomboré II, and Garba IV, there is no overlap in $\delta^{18}O$ value between hippopotamuses and fully terrestrial herbivores (Figs. 3–5). Like the modern study group from Amboseli, these fossil hippopotamuses have, on average, $\delta^{18}O$ values from 3 to 5‰ lower than co-occurring terrestrial herbivores (Table 2–4). At Garba IV, one hippopotamus (#88900) has a higher $\delta^{18}O$ value than the others, however, this unusual individual still has a lower $\delta^{18}O$ value than any non-aquatic animal at the site. Thus, there is strong evidence for preservation of $\delta^{18}O$ values in enamel in the 700,000 year old samples from Tighenif and Gomboré II, and in the 1.2 myr old samples from Garba IV. At Anabo Koma (1.6 myr), the one hippopotamus has a $\delta^{18}O$ value 3‰ lower than the average value for non-aquatic mammals. However *Kolpochoerus limnetes,* which has the lowest $\delta^{13}C$ value at the site, also has a lower $\delta^{18}O$ value than this hippopotamus. This may indicate either diagenetic alteration, or perhaps, that this browsing animal consumed $^{18}O$-depleted water. It is impossible to distinguish between these hypotheses with the data at hand. Finally, in the 1.5 myr old samples from Gomboré I, the two alcelaphines are highly variable, while the hippopotamus has a low $\delta^{18}O$ value. Again, with such limited data, it is difficult to deduce whether the disruption of the expected offset between the hippopotamus and the alcelaphines is due to diagenesis or some other taphonomic pro-

**TABLE 4**—Enamel carbonate hydroxylapatite $\delta^{13}C$ and $\delta^{18}O$ values for Anabo Koma mammals (~1.6 myr).

| Number | Scientific name | Common name | $\delta^{13}C$ ‰ | $\delta^{18}O$ ‰ |
|---|---|---|---|---|
| 88200 | *Hippopotamus* sp. | hippopotamus | 1.8 | 25.7 |
| 87700 | *Connochaetes* sp. | wildebeest | 3.9 | 29.0 |
| 88000 | *Elephas recki* | elephant | 2.1 | 27.9 |
| 88300 | *Antidorcas recki* | springbok | 3.0 | 28.6 |
| 88500 | *Kobus* cf. *kob* | kob | 3.7 | 28.2 |
| 87800 | *Metridiochoerus andrewsi* | extinct warthog | −2.7 | 27.1 |
| 87900 | *Kolpochoerus limnetes* | extinct bushpig | −6.3 | 25.4 |

cess that could contribute to isotopic variability in an assemblage, such as transport or time-averaging.

### Paleoecological Implications of Carbon Isotope Abundances

At Tighenif, almost all the terrestrial species have $\delta^{13}C$ values indicating a nearly exclusive diet of $C_3$ plants. Since dental morphology and comparison to closest living relatives strongly indicate that *Connochaetes taurinus, Ceratotherium simum,* and *Equus mauritanicus* were exclusively grazers, $C_4$ grasses must have been missing from the environment of Tighenif. Low $\delta^{13}C$ values for hippopotamuses at Tighenif indicate that their nocturnal grazing areas contained only $C_3$ plants as well. One specimen of *Connochaetes taurinus* (#84700) has a $\delta^{13}C$ value outside the range expected for modern 100% $C_3$-feeders, such as those from western Europe (−12 to −13‰, Bocherens and Mariotti, 1992). This may indicate either diagenetic alteration of this specimen, that this individual consumed a small amount of $C_4$ or CAM plants, or that $C_3$ plants in the ecosystem had somewhat higher values than normal due to water stress (Elheringer, 1989).

The dominance of $C_3$ plants in the diets of fossil grazers suggests that the pattern of winter rainfall occurring in the region today was present 700,000 years ago. In an ecosystem dominated by $C_3$ plants, it is impossible to determine the relative proportion of grassland to woodland using carbon isotopes. However, none of the mammals from Tighenif have extremely negative $\delta^{13}C$ values (<−12‰), as might be expected for forest floor dwellers in a closed canopy woodland, where $CO_2$ recycling produces excessive $^{12}C$-depletion in forest floor plants (Vogel, 1978b; Medina and Minchin, 1980). This fact, coupled with the dominance of grazers in the fauna (Geraads et al., 1986), suggests that 700,000 years ago the area may have contained an open $C_3$ grassland and not the more closed Mediterranean woodland that occurred prior to anthropogenic influences (White, 1983).

At Melka-Kunturé, the Gomboré II level is approximately the same age as Tighenif. However, $\delta^{13}C$ values of all herbivores from this Ethiopian site are ≈0‰, indicating an exclusively $C_4$ diet, as is seen in modern East African grazers from Amboseli. This is consistent with the results of palynology, indicating that grasses were more abundant than today (Bonnefille, 1972), and with the occurrence of the rodent *Tachyoryctes,* also suggesting an open environment (Sabatier, 1979). The megafaunal species also suggest an open environment, at least in Garba IV and Gomboré I (Geraads, 1985). The isotopic results do not support the interpretation of Eisenmann (1985), who deduced that Gomboré II was humid from equid metapodial robustness. The exclusively $C_4$ diet of the single Gomboré II hippopotamus does not match the values from Amboseli, suggesting that it relied less on $C_3$ and/or aquatic plants than modern Amboseli hippopotamuses. Carbon isotope values from two grazers (alcelaphine and zebra) at the 1.2 myr old Garba IV level are slightly higher than at the Gomboré II level, yet clearly within the range expected for grazers from Amboseli. Carbon isotope values for three of the hippopotamus specimens at Garba IV indicate a predominantly $C_4$ diet, whereas specimen 89000 has a lower value more similar to the value for modern Amboseli hippopotamuses.

At Anabo Koma, the oldest site in this study, the hippopotamus has a $\delta^{13}C$ value slightly more negative than grazing herbivores (*Connochaetes, Antidorcas,* and *Kobus*). On the other hand, both suids have much lower $\delta^{13}C$ values (−2.7‰ for *Metridiochoerus* and −6.3‰ for *Kolpochoerus*). These suids must have consumed $C_3$ and/or CAM plants, with *Kolpochoerus* consuming significantly more browse than *Metridiochoerus,* as expected from dental morphology. Lower $\delta^{13}C$ values in fossil suids are correlated with lower $\delta^{18}O$ values. Thus the limited Anabo Koma data suggest a pattern of relative differences in $\delta^{13}C$ and $\delta^{18}O$ values between grazers and more browse dependent animals similar to that between modern browsers and grazers in Amboseli (Fig. 2).

At these East African sites, particularly Anabo Koma, $\delta^{13}C$ values in some grazers are more positive than expected for modern grazers (up to 2‰). A consistent, small positive deflection of $\delta^{13}C$ values in fossils has been detected in several earlier studies of enamel apatite, and has been attibuted to subtle diagenetic alteration or to shifts in the $\delta^{13}C$ value of atmospheric $CO_2$ on Pleistocene/Holocene time scales (Lee-Thorp and van der Merwe, 1987; Quade et al., 1992; Marino and McElroy, 1991; Bocherens et al., 1995). Overall, however, carbon isotope values from these

East African sites at 1.6, 1.2, and 0.7 myr are similar to those seen in closely related taxa from the region today. There is no evidence from grazers that $C_3$ grasses, indicative of cooler temperatures during the wet, growing season, were present at these sites during these three time intervals.

A dominance of $C_4$ grasslands in lowlands of Ethiopia and Djibouti is in agreement with the pattern of late Pleistocene floral transition documented further south in Kenya and Tanzania. Cerling (1992), reporting carbon isotope data from soil carbonates at Laetoli/Olduvai (northern Tanzania), Olorgesailie (south west Kenya), and the Turkana Basin (northern Kenya), has argued that $C_4$ grasslands and savannas became dominant in East Africa only $\approx$1.7 myr ago, and have been continuously present for only $\approx$0.6 myr. In the Baringo Basin (west central Kenya), analysis of soil carbonates and mammalian enamel demonstrates that $C_4$ grasses have never been dominant, although they have increased in abundance over the last 2 myr (Morgan et al., 1994; Kingston et al., 1994). Our East African sites extend this pattern of late $C_4$ dominance northward to the Red Sea. Obviously, we cannot presently determine whether or not $C_4$ grasslands arrived in this region any earlier than 1.6 myr, as we lack older sites.

## CONCLUSIONS

Oxygen isotope analysis of vertebrate fossils is an under-utilized monitor of paleoclimate and paleoecology. This gap results, in part, because most previous workers have focused on analysis of oxygen in hydroxylapatite phosphate, which is technically difficult and time consuming, and in part, because of very real concerns about diagenetic alteration of oxygen isotope signatures in hydroxylapatite carbonate. Finally, relatively little is known about natural variations in the oxygen isotope composition of modern mammals. Through analysis of the well-studied and geographically discrete modern fauna from Amboseli, we demonstrate that clear differences exist in oxygen isotope composition among mammals of different size and life habit. Oxygen isotope analysis of herbivore tooth enamel from three African sites ranging in age from 0.7 to 1.6 myr revealed that the same pattern of isotopic discrimination existed among fossil mammals, suggesting that *in vivo* isotope values can be preserved, at least in some cases. In localities where preservation is high, oxygen isotope values can be used jointly with carbon isotopes to retrieve paleoecological and paleoenvironmental information. For example, the persistance of modern patterns of $C_3$ versus $C_4$ dominance of grass floras during earlier intervals within the Pleistocene has been demonstrated at all three sites. Ultimately, oxygen isotope analysis of mammals may provide a tool for reconstructing paleoclimatic parameters such as mean annual temperature or relative humidity (Longinelli, 1984; Luz and Kolodny, 1985; Koch et al., 1989; Luz et al., 1990; Ayliffe and Chivas, 1990; Ayliffe et al., 1992; Bryant et al., 1994). However, our study of oxygen isotopes in a modern fauna demonstrates that several intriguing patterns of variation must be explored in order to adequately predict the relationship between oxygen isotopes in mammals and meteoric water.

## ACKNOWLEDGMENTS

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