12. Environmentally Driven Dietary Adaptations in African Mammals

Thure E. Cerling, John M. Harris, and Meave G. Leakey

12.1 Introduction

From the late Miocene to early Pliocene, global terrestrial ecology underwent a major change, from a world where plants used C_3 photosynthesis almost exclusively to one where C_4 photosynthesis was a major component (Cerling et al. 1997b). This is especially true in the tropics, where C_4 photosynthesis might have comprised 50% of the net primary productivity. Evidence for this change is found in changes in the $^{13}C/^{12}C$ ratios in soil organic matter paleosol carbonates, and in reconstructions of the diets of large mammals (Quade and Cerling 1995; Cerling et al. 1997b; Freeman and Colarusso 2001). This change has so far been well documented in Africa, Asia, North America, and South America. Europe and Antarctica are at latitudes where C_4 photosynthesis does not occur in significant amounts. Comparable events in Australia might have occurred slightly later in time and are currently being studied by Ayliffe and co-workers. The principal method for documenting changes of this nature in the geological past is the determination of carbon isotope ratios, because the $^{13}C/^{12}C$ ratios are significantly different for plants using the C_3 versus the C_4 photosynthetic pathways.

The abrupt change from the C_3-world to the C_4-world makes it possible to study the response of mammals to a major change in food resources. In tropical Africa, dicotyledonous plants (hereafter, dicots) use C_3 photosynthesis almost exclusively, whereas monocotyledonous plants (hereafter, monocots) use the C_4

photosynthetic pathway. This means that most browsers, because they consume dicots, will have a dietary record of C_3 plants, whereas grazers will have a record of a C_4 plant diet preserved in their tissues. This isotopic distinction is very useful for quantifying dietary differences in mammals: grasses and dicots differ in chemical composition (hence, in nutrition content, toxin content, digestibility, etc.) as well as preferred habitat (e.g., openness of canopy, height above ground level, etc.). The paleontological record has many examples of morphological changes in mammals that are attributed to dietary shifts from browsing to grazing. Therefore, stable isotope studies coupled with observations on morphological change in mammals can test some of these hypotheses of dietary change.

In this study we use the well-dated, and very fossiliferous, collections from the Turkana basin in Northern Kenya to document evolutionary change in mammalian lineages, considering in turn equids, proboscideans, suids, and giraffids.

12.2 Methods and Materials

Fossil teeth from various localities in the Lake Turkana basin of Northern Kenya were sampled in the field and from the paleontological collections of the National Museums of Kenya, Nairobi. We use the stratigraphic and geochronological scheme of Brown, Fiebel, and McDougall (Feibel, Brown, and McDougall 1989; McDougall et al. 1992; Brown 1995; McDougall and Feibel 1999) to place fossils in their chronological order. Teeth of extant species from various African localities were sampled in the field and from the osteological collections of the National Museums of Kenya, Nairobi.

The stable isotopic composition of tooth apatite was determined using standard methods and is reported using the standard per mil (‰) isotopic notation:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1)\ 1000 \qquad (12.1)$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios in the sample and standard, respectively. For carbon the standard is PDB. The apparent isotope enrichment factor ε^* between diet and enamel is 14.1‰ where:

$$\square\varepsilon^* = [(1000 + \delta_{enamel})/(1000 + \delta_{diet}) - 1] * 1000 \qquad (12.2)$$

(Cerling and Harris 1999). In this paper we are assuming that the isotope enrichment is the same for all large ungulate mammals.

The $\delta^{13}C$ composition of the tooth enamel of mammalian herbivores reflects the proportion of C_3 versus C_4 vegetation that the animal was ingesting at the time the tooth germ was being formed. For mammals living in warm climates with rain during the growing season (a prerequisite for C_4 vegetation), it is thus possible to infer whether an individual was a browser, grazer, or mixed feeder.

12.3 Mammalian Tooth Enamel as a Paleoenvironmental Recorder

The isotope enrichment from diet to bioapatite is about 14‰ for ruminant bovids and is similar for other large mammals (Cerling and Harris, 1999). Therefore, the average $\delta^{13}C$ of diet can be estimated from the $\delta^{13}C$ of bioapatite. Enamel is the preferred substance to work with for paleodiet studies because it is the least susceptible to recrystallization during diagenesis (Ayliffe, Chivas, and Leakey 1994). In addition, because of the high selectivity in dietary preferences, studies of the isotopic composition of tooth enamel amplify the ecosystem-level isotope signal. The presence of a significant C_4 component in one species indicates that it would have been available for all other extant species.

Although C_3 and C_4 plants have average $\delta^{13}C$ values of about −27% and −13‰, respectively (Bender 1971), there is considerable variation about the mean. C_4 plants tend to have slightly more positive values in mesic environments and more negative values in xeric environments, whereas C_3 plants have the opposite trend. For tropical ecosystems, Cerling, Harris, and Passey (2003) found $\delta^{13}C$ values averaging between −31% to −34‰ for closed canopy forest understory plants; in African tropical savanna and bushland ecosystems, the $\delta^{13}C$ for C_3 plants averaged between −29% and −25‰ while the $\delta^{13}C$ value for C_4 plants averaged between −14% to −12‰. The isotope separation between average C_3 and C_4 plants at the ecosystem scale was as high as 17‰ in some mesic environments and as low as 11‰ in certain xeric environments (see examples in Cerling et al. 2003). The isotope composition of plants is also related to the $\delta^{13}C$ of the atmosphere from which plants derive CO_2. The isotopic composition of the atmosphere has changed by 1.5‰ since 1850 because of fossil fuel burning, and it is likely that the $\delta^{13}C$ of the atmosphere has undergone natural variations of a few ‰ over the past several million years. Therefore, in the following discussion we distinguish only the broad classes of a predominantly C_4-diet, a mixed C_3-C_4 diet, and a predominantly C_3-diet, with $\delta^{13}C$ values of >−2‰, −2 to −8‰, and <−8‰, respectively. Because of the uncertainty in the $\delta^{13}C$ of the local ecosystem mixing endmembers and the uncertainty in the $\delta^{13}C$ of the atmosphere, an enamel $\delta^{13}C$ value of −8‰ is treated as a cutoff for indicating a measurable C_4 component in the diet as recorded by tooth enamel. Thus a value of −8‰ could indicate any dietary component between 0 and about 25% C_4 biomass.

For the past 7 to 8 million years, the C_3 and C_4 distinction in the tropics is between C_3-dicots and C_4-grasses, as it is today. Therefore the isotope distinction that is made is between browsers and grazers, where browsing animals consume dicots and grazers consume grasses. We note that this distinction is lost in regions where the growing season is at cooler temperatures (< 15–20°C) because C_3-grasses dominate in such regions. This includes most of Europe, some Mediterranean climates, and alpine environments including those above about 3000 m in the tropics. Prior to 8 million years ago C_4 plants had very low abundances even in tropical and subtropical regions where they are common today (Cerling et al. 1997b). Therefore, before 8 million years ago it is not possible to use the isotope composition of enamel to indicate the fraction of browse versus grass in the diet, because the isotope distinction is lost. Cerling et al. (1997b) found that equids in southern North America, Pakistan, and Africa all had a predominantly C_3 diet before 8 million years ago; this could have been either C_3 browse or C_3 grass.

12.4 Case Histories of Diet Change in the Turkana Basin

In this section we look at four different mammalian lineages found in the Turkana basin: equids, proboscideans, suids, and giraffids. The Turkana basin is ideally suited for studying mammalian evolution associated with diet change. Neogene sediments of the region are exceptionally fossiliferous, and the frequency of volcanic ash layers throughout the basin has allowed a detailed chronology to be established. The principal fossiliferous localities in the Lake Turkana basin sample the following times: early Miocene (Buluk, Kalodirr), late Miocene (Lothagam), and Pliocene through early Pleistocene (Kanapoi, Koobi Fora, West Turkana, lower Omo Valley). We also include in our discussion data from the nearby Samburu Hills (Namurungule Formation) and Nakali, as well as isolated samples from the Baringo basin, Laetoli, and South Africa.

12.4.1 Equids

The evolution of the horse—from the small, multi-toed, browsing forest-dwellers of the Eocene to the large, single-toed, open country grazers whose undomesticated representatives can still be found in Africa and Asia—has long been construed as a classic example of evolution in action. Equids underwent much of their early evolution in North America and first appear in East Africa at about 10.5 million years ago, when three-toed hypsodont hipparionines became widespread throughout the Old World. There were evidently two episodes of hipparionine migration into Africa from Eurasia, the earlier characterized by species of *Hippotherium* and the later by *Eurygnathohippus* species (Bernor and Harris 2003). We analyzed samples of equids from Nakali and from the Namurungule Formation in the Samburu Hills, in addition to those from the Nawata and Nachukui formations at Lothagam and the Koobi Fora Formation. The Samburu Hills sequence overlaps, in part, with the lowest part of the Lower Nawata Member. The sediments at Nakali predate both the Samburu Hills and the Lothagam sequences.

The crown height of the teeth of Nakali equids, which are the earliest equids from East Africa, was sufficient to invoke a grazing habit, but analyzed teeth have $\delta^{13}C$ values ranging from -9.2 to $-11.5‰$ and indicate a pure C_3 diet (Fig. 12.1).

Other equids from Ngeringeriwe (ca. 9.5 Ma) in the Tugen Hills have $\delta^{13}C$ values between -9.5 and $-11‰$ indicating little, if any, C_4 contribution to their diet (Kingston, Marino, and Hill 1994). Transition to a C_4 diet took place during

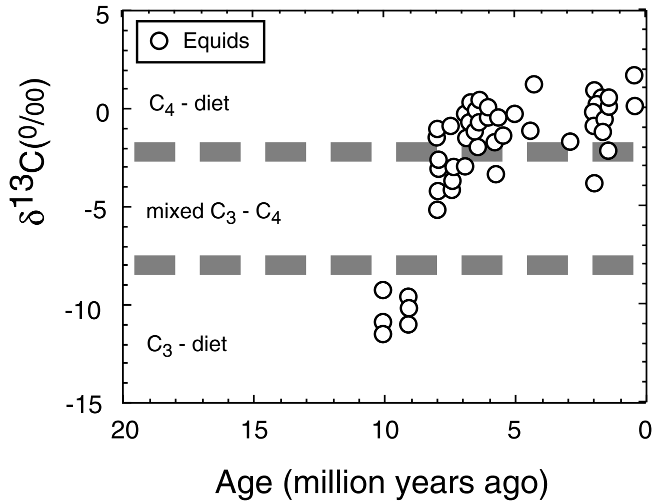

Figure 12.1. $\delta^{13}C$ of tooth enamel versus age for fossil and modern equids from East Africa. The isotope dietary classification is based on an enrichment factor for enamel-diet of 14.1‰.

an interval represented within the Samburu Hills succession and by the lowest part of the Nawata Formation. A mixed C_3/C_4 diet, with $\delta^{13}C$ values between −3 and −5‰ is found in about half (3 of 7) of the samples from the Samburu Hills and in the lower 82 meters of the Nawata Formation (3 of 6 samples). All samples, except one, from later in the Lower Nawata or from younger horizons in the Koobi Fora Formation (n = 14), have $\delta^{13}C$ values more positive than −2‰ (see Fig. 12.1).

Equids appear to have made the transition from a C_3 to a C_4 diet quickly both in Africa and elsewhere, although we have yet to identify a lengthy stratigraphic section where we can document the transition continuously over time. The transition appears to have occurred at about 8 million years ago. Grazing rhinoceroses (*Ceratotherium* species) appear to have begun exploiting C_4 grasses at about the same point in time.

12.4.2 Proboscideans

Three different clades of proboscidean occurred in the African Neogene and are represented by the Deinotheriidae, Gomphotheriidae, and Elephantidae. Deinotheres have low-crowned, lophodont teeth superficially similar to those of tapirs. The lophs have beveled cutting edges that are maintained, though at different angles, throughout the life of the individual for processing the food prior to digestion. Deinothere teeth remain essentially unchanged in morphology throughout the early Miocene to early Pleistocene; however, there is an overall increase in size from the earliest representatives of *Prodeinotherium* to the latest representatives of *Deinotherium.* In contrast, the early gomphotheres have low-crowned bunodont cheek teeth that are adapted for crushing and grinding rather than cutting. There is a general tendency for increase in complexity of the crown pattern and increase in the length of the teeth in different lineages of gomphotheres. This led to a pattern of delayed eruption of the posterior cheek teeth (horizontal tooth replacement), which both allowed the accommodation of larger teeth in the jaw and helped prolong the use of the teeth and, hence, the life of the individual.

The elephantids emerged from gomphothere stock near the end of the Miocene. Morphological differences between gomphotheres and early elephantids suggest a major change in the method of chewing, together with increases in length and hypsodonty of elephantid cheek teeth (Maglio 1973). The teeth of elephantids contain a large number of transverse plates instead of the paired trifoliate bunes characteristic of gomphotheres. Horizontal tooth replacement was further refined so that normally only one cheek tooth was erupted and functional in each side of the jaw. The earliest elephantids (*Primelephas* species) have low-crowned teeth, but the ensuing *Loxodonta*, *Elephas*, and *Mammuthus* lineages have hypsodont teeth; each lineage demonstrates an increase in crown height and plate number and a decrease in enamel thickness through time. The difference in crown height between gomphotheres and elephantids appears to indicate exploitation of different kinds of vegetation; the sequential changes seen in the cheek teeth of elephantid lineages have long been interpreted as progressive modifications for a primarily graminiferous (grazing) diet.

Deinotheres maintain a C_3 diet from their earliest record until their extinction in the early Pleistocene. Early gomphotheres from Maboko (ca. 17 Ma), Buluk (ca. 15 Ma), and Fort Ternan (14 Ma) all have $\delta^{13}C$ values that indicate a pure C_3 diet (Fig. 12.2). Gomphotheres from the Namurungule Formation in the Samburu Hills have $\delta^{13}C$ values between -8 and $-9‰$ indicating a diet dominated by (or solely based on) C_3 plants. Gomphotheres and elephantids, however, evidently changed from a C_3 dominated diet before 8 million years ago, to one that is C_4-dominated by 7 million years ago.

Unfortunately, the gomphotheres sampled from the Samburu Hills assemblages are documented from different sites than the sampled equids, so that in the absence of information about the size and nature of the different localities, it cannot be determined if the transition to C_4 diet in equids preceded that in gomphotheres. The transition from a C_3 to a C_4 diet was rapid in gomphotheres and elephantids (see Fig. 12.2). Elephantid teeth subsequently underwent a series of adaptations to more effectively process an abrasive graminiferous diet, but those of gomphotheres did not; that family became extinct in Africa at about 4 million years ago.

Elephantids have a predominantly grazing diet from about 7 million years ago until less than one million years ago (Cerling et al. 1999). Both fossil *Loxodonta* and *Elephas* were grazers, yet the modern *Loxodonta* in Africa is predominantly a browser as is *Elephas* in Asia (Cerling et al. 1999). Elephants are widely

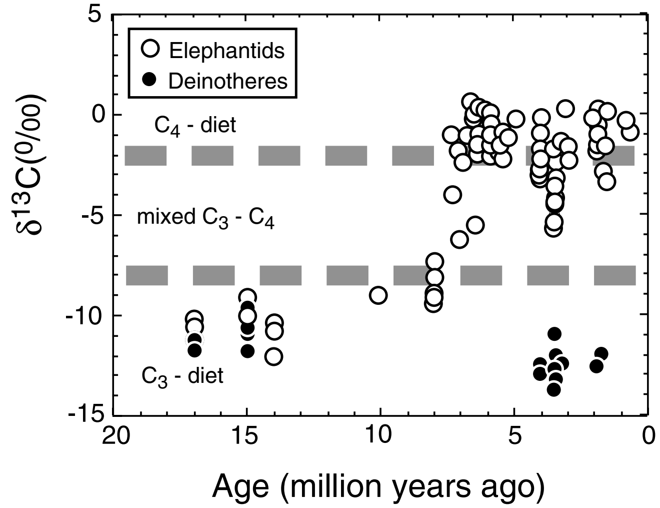

Figure 12.2. $\delta^{13}C$ of tooth enamel versus age for fossil and modern proboscideans from East Africa. The isotope dietary classification is based on an enrichment factor for enamel-diet of 14.1‰.

thought to have an enormous influence on the promotion of grasses in Africa because of their destructive feeding on trees. Their influence on the landscape must have been different in the past than it is today.

12.4.3 Suids

Suid assemblages from sub-Saharan Africa underwent a major transformation at the end of the Miocene. Genera representing the subfamilies Kubanochoerinae, Listriodontinae, and Paleochoerinae were replaced by *Nyanzachoerus* species (*Ny. syrticus*, *Ny. devauxi*) that comprised immigrant representatives of the Eurasian Tetraconodontinae. The derived tetraconodontine *Notochoerus jaegeri* appeared in the early Pliocene, and its daughter species *Not. euilus* characterizes the later Pliocene together with *Nyanzachoerus pattersoni*, *Ny. kanamensis*, and *Ny. australis*. The middle Pliocene saw a second wave of immigration from Eurasia that founded the *Potamochoerus*, *Kolpochoerus,* and *Metridiochoerus* lineages. Today these three lineages are represented, respectively, by the bush pig (*Potamochoerus porcus)*, the forest hog (*Hylochoerus meinertzhageni*), and the warthog (*Phacochoerus aethiopicus*).

Four of these suid genera—(*Nyanzachoerus*, *Notochoerus*, *Kolpochoerus*, and *Metridiochoerus*)—were characterized by increases in size, hypsodonty, and in the complexity of the third molar. As in elephantids, these trends were previously interpreted to represent adaptations from a browsing to a grazing diet. This interpretation was confirmed for *Nyanzachoerus* and *Notochoerus* species. The earliest nyanzachoeres had shorter third molars and lower $\delta^{13}C$ values than did the later nyanzachoeres and notochoeres (Fig. 12.3), thereby supporting previous hypotheses that the lengthening of the third molar represented an adaptation to a more abrasive diet. However, of the four species of *Metridiochoerus* recognized in the Plio-Pleistocene portion of the Koobi Fora succession—*M. an-*

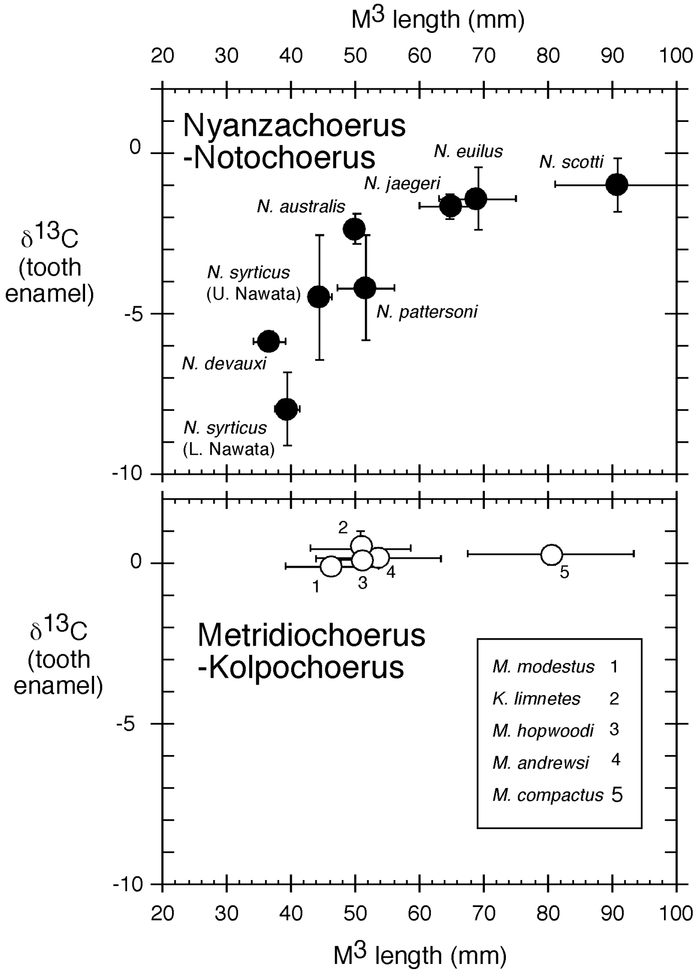

Figure 12.3. $\delta^{13}C$ of tooth enamel versus length of M^3 for fossil suids in the Turkana Basin. The *Nyanzachoerus-Notochoerus* lineage shows increasing length of the M^3 as more C_4 grass is incorporated into their diet. *Metridochoerus* and *Kolpochoerus* do not show any change in the fraction of C_4 biomass in their diet.

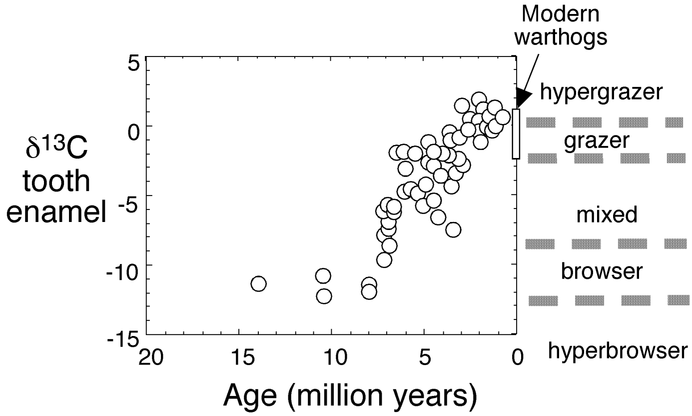

Figure 12.4. $\delta^{13}C$ of tooth enamel versus age for fossil and modern suids from East Africa. The isotope dietary classification is based on an enrichment factor for enamel-diet of 14.1‰.

drewsi, M. modestus, M. hopwoodi, and *M. compactus* (Harris and White 1979; Harris 1983)—all were found to be dedicated C_4 grazers throughout their known history, as were representatives of the *Kolpochoerus* lineage. Third molars of the *M. andrewsi* and *K. limnetes* lineages display a progressive increase through time in the length, height, and number of pillars of the third molars, so it was somewhat surprising to find that even the earliest and least progressive representatives from the Nachukui Formation were dedicated C_4 grazers (and that there is no relationship between M^3 length and $\delta^{13}C$). In this case, it appears that even the earliest kolpochoeres and metridiochoeres had adapted to grazing and that the progressive lengthening of the molars does not reflect an overall change in diet but, as with the elephantids, an adaptation for increased efficiency in processing a graminiferous diet. Overall, suids show a gradual increase in the fraction of C_4 grass in their diets over several million years, becoming 100% grazers by about 3 million years ago (Fig. 12.4).

12.4.4 Giraffids

The Giraffidae is today represented by only two living species, although approximately 30 fossil species have been recognized from the fossil record (Solounias et al. 2000). The family is characterized by the presence of a bifurcate lower canine and the presence of skin-covered ossicones; most representatives are of large size and have elongate legs and necks. Although seldom comprising significant elements of the African biota, giraffe relatives are represented by *Prolibytherium* and *Zaraffa* in the early Miocene of North Africa, by *Climacocerus*, *Paleotragus,* and *Samotherium* species in the middle to late Miocene of East Africa, and by *Sivatherium* and *Giraffa* species during the past five million years.

Despite the diversity of extinct forms, most have small and low-crowned teeth, and until recently the consensus had been that giraffids were committed browsers. However, Solounias and Dawson-Saunders (1988) used tooth microwear analysis to demonstrate that representatives of the Eurasian genus *Samotherium* were mixed feeders and hypothesized that *Samotherium* species seasonally alternated between browsing and grazing. A grazing component of the diet was further substantiated by the proportionately wide nature of the premaxilla (Solounias and Dawson-Saunders 1988; Solounias and Moelleken 1993). More recently, Solounias et al. (2000) have expanded their database of extant ruminant tooth wear and in so doing were able to recognize in the Giraffidae five dietary categories: grazers, facultative grazers, seasonal mixed feeders, nonseasonal mixed feeders, and browsers.

In sub-Saharan Africa, the middle Miocene giraffoids, *Climacoceras* and *Paleotragus primaevus,* both seem to have had a pure or nearly pure C_3 diet (Fig. 12.5). However, the $\delta^{18}O$ value for *Paleotragus* teeth indicated a more evaporated water source suggesting that, like extant giraffes, *Paleotragus* may have obtained much of the water it required from its food (Cerling et al. 1997a). Specimens of *Paleotragus* from the Samburu Hills are slightly more positive than those from Fort Ternan, although specimens from both localities plot as browsers. The difference may reflect a slight increase in the C_4 dietary component but could suggest that the later and more northerly locality was drier and more water-stressed.

Several species of *Giraffa* have been recognized in the East African Plio-

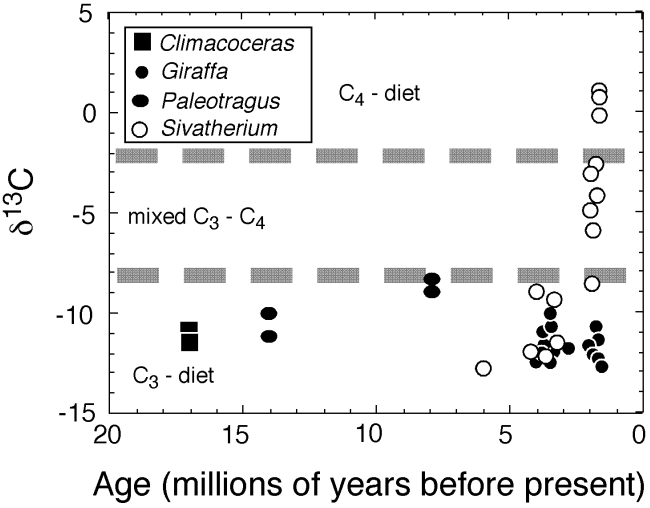

Figure 12.5. $\delta^{13}C$ of tooth enamel versus age for fossil and modern giraffids from East Africa. The isotope dietary classification is based on an enrichment factor for enamel-diet of 14.1‰.

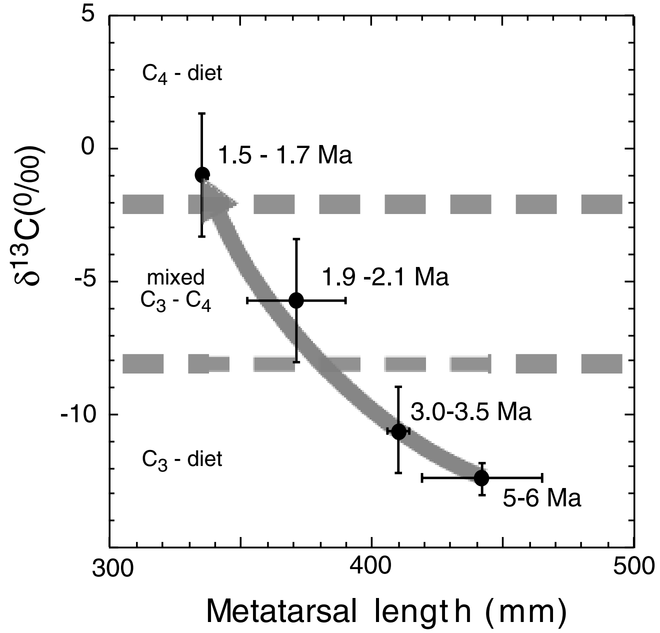

Figure 12.6. $\delta^{13}C$ in tooth enamel compared to metatarsal length in Sivatheres. The metatarsal becomes shorter as more C_4 grass is incorporated into the diet.

Pleistocene. All seem to plot out isotopically as dedicated browsers. Although the samples are small, specimens of *Giraffa jumae* and *G. stillei* from Laetoli appear to be less negative in $\delta^{13}C$ and less positive in $\delta^{18}O$ than specimens from the Lake Turkana basin; this may suggest that the Serengeti specimens drank more water but ate more grass. The findings could also indicate, however, that browse vegetation in the Laetoli region was stressed from lack of water at the time the giraffes were feeding on it.

Two species of *Sivatherium* have been recognized from sub-Saharan Africa: *Sivatherium hendeyi* from Langebaanweg and the more widely distributed *Sivatherium maurusium*. Isotopically, *Sivatherium hendeyi* plots out as a browser, as do the samples of *S. maurusium* from Kanapoi and from the lower portions of the Koobi Fora Formation (Fig. 12.6). However, a change in diet is indicated by specimens from the Upper Burgi Member; one of the specimens plots as a browser, but the other one plots as a mixed feeder. Specimens from the upper part of the Koobi Fora Formation plot as grazers.

It is intriguing that African sivatheres adopted a grazing diet several millions of years after proboscideans, perissodactyls, suids, and bovids exploited C_4 grasses in sub-Saharan Africa. Corroboration of the dietary change is seen in the lengths of the metatarsals: The metatarsal length in the Miocene is considerably longer than those from the younger Pleistocene.

12.5 Discussion

Carbon isotopic analysis is a very powerful tool for determining dietary adaptations of mammals from the tropics of Africa, Asia, and the Americas and can be used for fossil as well as extant specimens. The technique supplements and, in some instances, surpasses the accuracy of dietary information derived from direct observation of extant individuals. The technique may be applied to most, if not all, tissues from living specimens; dentine and bone provide believable results from late Pleistocene fossils, but tooth enamel is the most reliable source of isotopic information for fossil specimens because of possible complications from diagenetic alteration. In particular, stable isotopes can be used to test hypotheses about anatomical characteristics and their relationship to diet if the question can be cast in terms of a C_3-diet versus and C_4-diet.

One drawback of the methodology is that enamel germs are formed only at specific times during the development of young individuals, and thus the dietary information from a specific tooth reflects the diet of the individual (or that of its mother) only when that tooth was being formed. In contrast, hair and horn grow continuously throughout life, but these tissues are seldom fossilized. Microscopic pits and scratches on the wear surfaces of teeth record abrasion by dietary items ingested by the sampled specimen during the course of the previous few months. Thus microscopic wear analysis provides a useful method for refining dietary information provided by isotopic analysis.

This study shows the dietary response of four different mammalian lineages to ecological change. Equids, elephantids, suids, and giraffids/sivatheres responded in different ways to the expansion of C_4 biomass in the East Africa ecosystem. Between 8 million and 7 million years ago, C_4 grasses became abundant in East Africa. Equids responded very quickly to this new diet and became exclusive, or almost so, C_4-grazers by about 7 million years ago. From 7 million years ago to the present, C_4 grasses have been the dominant food source for equids in Africa. The proboscidean response was similar; very shortly after C_4 grasses became abundant, the diet of elephantids was dominated by C_4-grass. However, they have experienced a recent change so that modern elephants are browsers, unlike their fossil relatives.

Suids provide an interesting test case for dietary adaptation as they underwent significant morphological change during this time period. Stable isotopes show this change is accompanied by diet change for only one lineage, while two other lineages underwent similar change (elongation of molars) yet maintained a predominantly C_4 diet throughout. Late Miocene and early Pliocene sivatheres have isotopically similar tooth enamel to giraffines but became grazers in the late Pliocene; this change to grazing was accompanied by a shortening of their limb bones. Among the large herbivores from the African fossil record, giraffines and deinotheres have consistently negative $\delta^{13}C$ tooth enamel values, indicative of a pure C_3 browsing diet throughout their history.

12.6 Summary

The Turkana basin provides an excellent study area to examine dietary adaptations to ecological change. C_4 biomass increased significantly in East Africa between 7 million and 8 million years ago, and the Turkana basin is well dated. It contains abundant fossils, which have been placed in their stratigraphic and chronological context. Because most grasses in sub-Saharan Africa use the C_4 method of photosynthesis, grazing mammals may be readily distinguished from browsing mammals by the isotopic composition of their body tissues. The isotopic composition of tooth enamel distinguishes fossil mammals that fed on C_4 plants from those that exploited C_3 vegetation, thereby documenting dietary changes associated with the late Miocene radiation of C_4 grasses.

Hipparionine horses with hypsodont teeth entered Africa at about 10 Ma but did not start exploiting C_4 grasses until about 8 million years ago. By 7 million years ago they had a predominantly C_4 diet, which continues today in the equids of Africa. Both gomphotheriid and elephantid proboscideans started to exploit C_4 grasses between 8 million and 7 million years ago. Elephantids subsequently developed longer and taller teeth that had more plates with thinner enamel; these represent progressive adaptations to an increasingly graminiferous diet. However, modern African elephants (*Loxodonta*) are predominantly browsers, unlike the fossils from the Turkana basin and elsewhere in Africa. Gomphotheriid teeth did not display comparable changes, and this group became extinct at about 4 million years ago. Deinotheriid proboscideans remained C_3 browsers throughout their known history. Tetraconodontine suids arrived in Africa at about 8 million years ago. The third molars of *Nyanzachoerus* and *Notochoerus* species display changes in length, height, and complexity through time, and such changes were associated with a change in diet from browse to graze as recorded by the carbon isotopes.

The suines *Metridiochoerus* and *Kolpochoerus* migrated into Africa after 4 million years ago; changes in the morphology of their third molars (M^3), like comparable changes seen in elephantid teeth, represent adaptation to a graminiferous diet. The third molar increased in length over several million years although their diet was predominantly C_4 throughout. Giraffids were present in sub-Saharan Africa from the middle Miocene. Whereas giraffines had small and low-crowned teeth and remained browsers throughout their known history, sivatheres started exploiting C_4 grasses during the late Pliocene (i.e., several million years after other African mammals had exploited C_4 vegetation) and became grazers by about 2 million years ago. The adaptation in sivatheres was a shortening of both the fore and hind legs as C_4 grass was increasingly used as a diet resource.

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