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Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans

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Abstract The diet of extant elephants (*Loxodonta* in Africa, *Elephas* in Asia) is dominated by C₃ browse although some elephants have a significant C₄ grass component in their diet. This is particularly noteworthy because high-crowned elephantid cheek teeth represent adaptation to an abrasive grazing diet and because isotopic analysis demonstrates that C₄ vegetation was the dominant diet for *Elephas* in Asia from 5 to 1 Ma and for both *Loxodonta* and *Elephas* in Africa between 5–1 Ma. Other proboscideans in Africa and southern Asia, except deinotheres, also had a C₄-dominated diet from about 7 Ma (when the C₄ biomass radiated in tropical and subtropical regions) until their subsequent extinction.

Key words Elephants · Diet · Stable isotopes
Browsing

Introduction

The emergence of the Elephantidae from Miocene gomphotheres reflects a major adaptive shift in their method of chewing and it was this new adaptation that accounted for the rapid expansion of the family (Maglio 1973). The adaptive shift coincided with the worldwide spread of C₄ vegetation between 8–5 Ma (Cerling et al.

1997) and the corresponding increase in size and hypsodonty of elephantid cheek teeth appears to be a response to help process the newly available food source. Isotopic analysis of fossil proboscidean enamel indicates that, except in deinotheres, C₄ vegetation formed a significant portion of the diet of many African and Asian proboscideans from the late Miocene onwards (Cerling et al. 1997).

Descriptions of the diet of extant elephants, both *Loxodonta* and *Elephas*, indicate a mixture that includes both browse and grass. The detailed studies of diets of *Loxodonta* in the Bunyoro region in Uganda where grazing is very important (Laws et al. 1974) has been widely quoted and it is often believed that savanna elephants are predominantly grazers (e.g., Tangley 1997). However, other observers have noted an important browsing component in elephants (e.g., Jachman and Bell 1985; Dublin 1995). This perception of differences in dietary preferences even extends to observers in the same region: Norton-Griffiths (1979), in quoting other sources, states that Serengeti elephants are primarily grazers but Dublin (1995) says that they are primarily browsers.

Stable isotope analysis provides an excellent way to distinguish between grazing and browsing in the tropics and sub-tropics. Most trees and shrubs use the C₃ photosynthetic pathway and have $\delta^{13}\text{C}$ values between -22 and -35‰ (averaging about -27‰), whereas most tropical grasses use the C₄ photosynthetic pathway and have $\delta^{13}\text{C}$ values between -10 and -15‰ (Fig. 1). (We note that bamboo uses the C₃ photosynthetic pathway and therefore has the same isotope signal as C₃ browse). The $\delta^{13}\text{C}$ of collagen and tooth enamel preserves a record of the diet of mammals (DeNiro and Epstein 1978; van der Merwe and Vogel 1978; Lee-Thorp and van der Merwe 1987; Quade et al. 1992; Cerling et al. 1997). An advantage of this method is that elephants from a wide variety of habitats and regions can be studied by using materials archived in museums and elsewhere. Tooth enamel is resistant to isotopic exchange (Quade et al. 1992; Wang and

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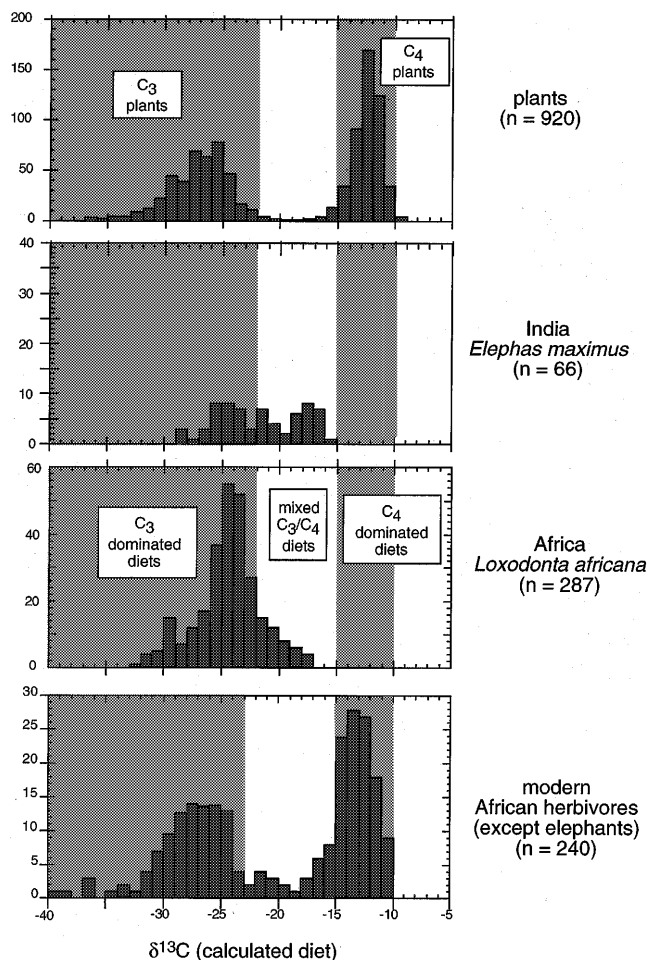


Fig. 1 Histograms showing $\delta^{13}\text{C}$ for modern plants, and estimated diets calculated from tooth enamel or collagen for modern elephants and for modern African herbivores using fractionation as described in the text. Data sources are this study, and from Sukumar et al. (1987), van der Merwe et al. (1988, 1990), Vogel et al. (1990a, b), Sukumar et al. (1987), Sukumar and Ramesh (1992, 1995), Koch et al. (1995), and Bocherens et al. (1996b)

Cerling 1994) and therefore is an ideal material to study for fossil elephants.

In this study we analyzed the $\delta^{13}\text{C}$ of tooth enamel from 43 savanna elephants from Kenya, and 27 forest elephants for Kenya and from the Republic of Congo. This adds to the already large data base of the isotopic composition of modern elephants (van der Merwe et al. 1988, 1990; Tieszen et al. 1989; Vogel et al. 1990a, b; Sukumar and Ramesh 1992; Koch et al. 1995; Bocherens et al. 1996b). We compare these results to other published data from Africa and Asia for modern elephants, and confirm that isotopic studies provide strong evidence that elephants are predominantly browsers.

Little isotopic data have been published on fossil elephants. Here we report data on elephantids, gomphotheres, and deinotheres from Kenya, primarily from the Turkana Basin and environs, and also from Laetoli in Tanzania. In addition, we report data on fossil elephantids from Pakistan. These fossil samples range in

age from middle Miocene through latest Pleistocene and provide strong evidence that unlike their modern counterparts, fossil elephantids were primarily grazers in Africa and Pakistan from 7 million years ago until almost 1 million years ago.

Materials and methods

Enamel from modern and fossil elephants was physically separated from dentine using tungsten-carbide- or diamond-impregnated high-speed rotary tools. The enamel was finely ground and reacted with 1% H_2O_2 or 1% NaOCl followed by reaction with 0.1 M acetic acid (Lee-Thorp and van der Merwe 1987). The cleaned enamel powder was then reacted in vacuum at 25°C for 36 h. CO_2 was cryogenically separated from the reaction products and then reacted at 50°C for 48 h with silver wool to remove SO_2 which we found to be an occasional contaminant in both modern and fossil samples.

Isotopic ratios are reported relative to the isotopic standard PDB using the conventional δ notation where:

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

where R_{sample} and R_{standard} are $(^{13}\text{C}/^{12}\text{C})_{\text{sample}}$ and $(^{13}\text{C}/^{12}\text{C})_{\text{standard}}$, respectively. Enamel or collagen are enriched in ^{13}C compared to diet as expressed using the enrichment factors ϵ :

$$\epsilon_{\text{enamel-diet}} = [(R_{\text{enamel}}/R_{\text{diet}}) - 1] \times 1000$$

and

$$\epsilon_{\text{collagen-diet}} = [(R_{\text{collagen}}/R_{\text{diet}}) - 1] \times 1000$$

where R_{diet} , R_{collagen} , R_{enamel} are the $^{13}\text{C}/^{12}\text{C}$ ratios for diet, collagen, and enamel, respectively. Cerling et al. (1997) and Cerling and Harris (1999) report the enrichment factor of $\epsilon_{\text{enamel-diet}} = 14.1$ for large mammals including elephants, and Vogel et al. (1990a) report an enrichment factor $\epsilon_{\text{collagen-diet}} = 5.5$ for elephants. To compare results from collagen studies and enamel studies, we use these enrichment factors to calculate the original diet which is represented by $\delta^{13}\text{C}_{\text{diet}}$.

A further complication arises in that the isotopic composition of the atmosphere has changed over the last 150 years by 1.5‰, from -6.5‰ to -8.0‰ , due to fossil fuel burning. In this paper we do not normalize all samples to the same year, but note here that any calculations about the fraction of C_3 browse or C_4 grass in the diet is slightly affected by this problem.

Results and discussion

We analyzed a number of modern savanna elephants from Kenya, and compare those results with other published data. These data include the surveys of Asian elephants done by Sukumar et al. (1987) and Sukumar and Ramesh (1992), and those of African elephants by van der Merwe et al. (1988, 1990), Vogel et al. (1990a, 1990b), Koch et al. (1995), and Bocherens et al. (1996b). To compare all these results, which include data for both collagen and for tooth enamel, we discuss these values in terms of the calculated diets using the fractionation factors $\epsilon_{\text{enamel-diet}}$ or $\epsilon_{\text{collagen-diet}}$ to calculate a $\delta^{13}\text{C}_{\text{diet}}$ value. $\delta^{13}\text{C}_{\text{diet}}$ is 14.1‰ or 5.5‰ depleted in ^{13}C compared to the measured enamel or collagen $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{enamel}}$ or $\delta^{13}\text{C}_{\text{collagen}}$), respectively.

Stable isotope analyses of extant elephants from Africa and Asia demonstrate diets dominated by C_3 vegetation although some samples show evidence for a mixed

C₃/C₄ diet (Fig. 1). Diets of non-proboscidean browsers and grazers from East Africa have $\delta^{13}\text{C}_{\text{diet}}$ ranges of -28 to -24‰ and -15 to -10‰ , respectively (Fig. 1). Occasionally diets as negative as -32 to -36‰ are found for ungulates from closed-canopy forests. Elephants have $\delta^{13}\text{C}_{\text{diet}}$ values ranging from -32‰ to -15‰ . Most elephants have diets dominated by C₃ vegetation ($\delta^{13}\text{C}_{\text{diet}} < -23\text{‰}$), but about 25% of *Loxodonta* and almost 50% of *Elephas* have a significant C₄ component in their diet (Fig. 1) with $\delta^{13}\text{C}_{\text{diet}}$ values ranging from -23 to -15‰ . However, no samples showed a predominantly C₄ diet ($\delta^{13}\text{C}_{\text{diet}} < -15\text{‰}$) which is common for other ungulate grazers (Figs. 1, 2). Because the teeth of animals feeding from a mixture of C₃ and C₄ vegetation should produce intermediate $\delta^{13}\text{C}$ values, we used a mixing model to estimate the fraction of C₄ biomass in the diet of elephants. For savanna elephants we estimate the $\delta^{13}\text{C}$ range for available C₃ biomass to be -28 to -23‰ , and the range for available C₄ biomass to be -14

to -11‰ . As noted previously by van der Merwe et al. (1988), the range in $\delta^{13}\text{C}$ values for both C₃ and C₄ plants makes precise dietary C₃/C₄ fractions impossible to calculate, although a range of C₃/C₄ fractions can be made. The maximum C₄ fraction is calculated from the C₃ and C₄ mixing end members of -28‰ and -14‰ , respectively, and the minimum C₃ fraction is calculated from the C₃ and C₄ mixing end members of -22‰ and -11‰ , respectively.

The diets of modern *Loxodonta*: African savanna and forest elephants

Modern *Loxodonta* is restricted to Africa and is the only modern elephant in Africa, although a number of other lineages are well documented in the fossil record. Previously only one species of African elephant was recognized, *Loxodonta africana*, comprising two sub-species. The larger of these, *L. africana africana*, is the savanna, or "bush," elephant and is found in East and South Africa while the smaller, *L. africana cyclotis* inhabits the forests of Central and West Africa. Presently there is debate as to whether these two sub-species should be recognized as individual species. We will discuss the African elephant with the recognition that there are significant physical differences between *L. a. africana* and *L. a. cyclotis*.

It is useful to examine the regional aspects of elephant diet. Figure 2 shows the $\delta^{13}\text{C}_{\text{diet}}$ of *Loxodonta* for different regions and habitats. van der Merwe et al. (1988) showed that forest elephants have diets more depleted in ¹³C than do savanna elephants, which they attributed to the "canopy effect" whereby C₃ plants growing under closed-canopy conditions have significantly lower $\delta^{13}\text{C}$ values than do C₃ plants growing in open conditions (van der Merwe and Medina 1991). The "canopy effect" is also seen in our samples from Mouadje Bai in the Republic of Congo, which is in a primary rain forest. Elephants from the montane forests in Kenya (i.e., the Aberdares, Mt Kenya, Mt Elgon, and Marsabit Mountain) or coastal forest (Shimba Hills, Kiunga) are somewhat depleted in ¹³C compared to elephants from savanna regions, but are not as depleted in ¹³C as elephants from the primary rain forests (Table 1, Fig. 2). van der Merwe et al. (1988) previously found that elephants from primary rain forests had the most negative $\delta^{13}\text{C}$ values, a conclusion with which we concur.

The diets of the savanna elephant, *L. a. africana*, from East, south Central, and South Africa range in $\delta^{13}\text{C}_{\text{diet}}$ from -30‰ to -17‰ , but with most having $\delta^{13}\text{C}_{\text{diet}}$ values between -22 to -28‰ (Figs. 1, 2), indicating a predominantly C₃ diet. Because C₃ plants in arid regions are shifted to slightly more positive values than C₃ plants in mesic environments (Farquhar et al. 1989), the $\delta^{13}\text{C}_{\text{diet}}$ cutoff for C₃ plants is about -22‰ (see discussion in Cerling et al. 1997). Most savanna elephants from Namibia, South Africa, Botswana, Zambia, and Malawi have an essentially pure-C₃ diet

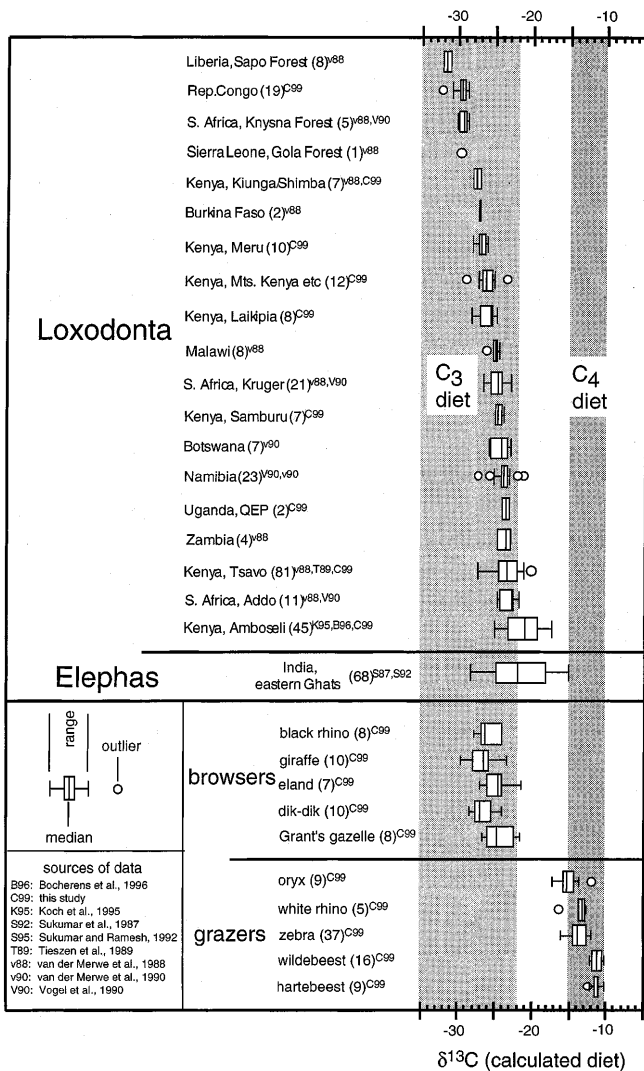


Fig. 2 Ranges in $\delta^{13}\text{C}_{\text{diet}}$ values for *Loxodonta* from different localities, for *Elephas*, and for African browsers and grazers. Data as in Fig. 1

Table 1 New tooth enamel data for modern elephants and latest Pleistocene elephants from Kenya, Uganda, and Congo. All elephants are *Loxodonta africana*

$\delta^{13}\text{C}_{\text{enamel}}$	Sample number ^a	Locality	Tooth ^b (M1–M6)
Forest habitat, Kenya			
–11.7	MGL-7	Aberdares	M4
–15.1	325-Ab	Aberdares	M3
–13.4	223-Ab	Aberdares	M2
–13.1	MGL-11 ^a	Kiunga	M4
–13.7	MGL-11B ^a	Kiunga	M4 or M5
–12.9	MGL-5	Mt Elgon	M4
–12.9	MGL-2	Mt Kenya	M3
–12.6	256-MtK	Mt Kenya	M1
–13.0	257-MtK	Mt Kenya	m2
–14.2	MGL-10	Shimba Hills	M3
Primary rain forest habitat, Congo			
–18.3	MF-F-1	Mouadje Bai	
–17.1	MF-F-2	Mouadje Bai	
–15.0	MF-F-3	Mouadje Bai	
–14.9	MF-F-4	Mouadje Bai	
–15.8	MF-F-5	Mouadje Bai	
–16.3	MF-F-7	Mouadje Bai	
–16.0	MF-F-8	Mouadje Bai	
–15.7	MF-F-9	Mouadje Bai	
–14.9	MF-F-10	Mouadje Bai	
–15.2	MF-M-1	Mouadje Bai	
–16.0	MF-M-2	Mouadje Bai	
–15.7	MF-M-3	Mouadje Bai	
–15.5	MF-M-4	Mouadje Bai	
–15.3	MF-M-5	Mouadje Bai	
–16.0	MF-M-6	Mouadje Bai	
–16.1	MF-M-7	Mouadje Bai	
–15.8	MF-M-8	Mouadje Bai	
–15.8	MF-M-9	Mouadje Bai	
–16.4	MF-M-10	Mouadje Bai	
Savanna/bush habitat			
–9.2	MGL-25 ^a	Amboseli	M4
–6.6	MGL-25:2 ^a	Amboseli	M4
–7.3	MGL-25B:1 ^a	Amboseli	M4
–11.6	MGL-44	Laikipia	M5
–13.2	MGL-45	Laikipia	M2
–14.4	MGL-46	Laikipia	M3
–11.0	MGL-47	Laikipia	M4
–11.8	MGL-6	Laikipia	M4
–11.8	MGL-14	Laikipia-Kikisi Ranch	M4 or M5
–11.6	MGL-15	Laikipia-Kikisi Ranch	M4
–11.7	MGL-16	Laikipia-Kikisi Ranch	M4 or M5
–9.6	MGL-12	Marsabit	M4
–11.9	MGL-13 A ^a	Marsabit	M3
–11.9	MGL-13 B ^a	Marsabit	M3
–12.2	MGL-13 C ^a	Marsabit	M3
–11.3	MGL-3	Marsabit	M5
–9.7	MGL-8	Masai Mara	M4
–13.7	MGL-41	Meru	M2
–12.5	MGL-42	Meru	M3
–13.2	MGL-43	Meru	M4
–12.5	MGL-17	Meru	M4 or M5
–12.9	MGL-18	Meru	M4 or M5
–12.9	MGL-19	Meru	M4 or M5
–11.9	MGL-20	Meru	M4 or M5
–12.9	MGL-21	Meru	M4 or M5
–12.1	MGL-22	Meru	M4 or M5
–12.1	MGL-24	Meru	M4 or M5
–10.1	QEP-211	Queen Elizabeth Park	M4
–9.1	QEP-212	Queen Elizabeth Park	M6
–10.4	MGL-1 ^a	Samburu	M3
–10.8	MGL-1A ^a	Samburu	M3
–10.3	MGL-4	Samburu	M4
–11.0	404E-Sam-M4	Samburu	M4
–11.2	404E-Sam-rM2	Samburu	M2
–11.1	404E-Sam-rM2	Samburu	M2

Table 1 (Contd.)

$\delta^{13}\text{C}_{\text{enamel}}$	Sample number ^a	Locality	Tooth ^b (M1–M6)
–10.0	404E-Sam-IM3	Samburu	M3
–10.2	MGL-26	Tsavo	M2
–5.7	MGL-27	Tsavo	M3
–11.5	MGL-28	Tsavo	M3
–9.1	MGL-29	Tsavo	M3
–9.3	MGL-30	Tsavo	M3
–7.0	MGL-31	Tsavo	M4
–7.3	MGL-32	Tsavo	M4
–10.9	MGL-33	Tsavo	M2
–13.0	MGL-34	Tsavo	M2
–9.3	MGL-35	Tsavo	M2
–12.1	MGL-36	Tsavo	M1
–9.7	MGL-37	Tsavo	M1
–10.7	MGL-38	Tsavo	M1

^a Multiple sample numbers from the same tooth are from different parts of the same tooth or individual and therefore represent a different time in the individual's life history

^b Molars are numbered from M1 to M6 because elephants erupt their molar and premolar teeth sequentially unlike other mammals. No distinction is made between upper and lower molars

(van der Merwe et al. 1988). Addo Park in South Africa is an interesting exception which, as noted by van der Merwe et al. (1988), is a region where crassulacean acid metabolism plants may make a significant contribution to the diet of elephants. In Kenya most savanna elephants' diet is also C_3 dominated. Elephants from Meru, Masai Mara, Marsabit, and Laikipia have $\delta^{13}\text{C}_{\text{enamel}}$ values ranging from -10 to -14‰ (Table 1), corresponding to $\delta^{13}\text{C}_{\text{diet}}$ values from -24‰ to -28‰ , indicating little, if any, C_4 biomass in their diet.

Only in the Tsavo and Amboseli region of Kenya have we found elephants with a significant ($> \text{ca } 20\%$) fraction of C_4 biomass in their diet (Fig. 2). The diet of modern savanna elephants is often described as including much grass (Kingdon 1979; Tangley 1997), in some cases up to 90% based on stomach contents of elephants from the Bunyoro region in Uganda (Laws et al. 1974). These isotopic results agree with observations that on occasion some elephants have a mixed C_3/C_4 diet, but on the whole they show that most elephants have diets that are dominated by C_3 plants. Significantly, the two African localities where the elephants have the highest fraction of C_4 biomass in their diet are Amboseli and Tsavo in Kenya. These sites have had the most intensive observational data on elephant behavior and where grazing by elephants has been recorded both by observation (Moss 1988) and by stable isotope analyses (Tieszen et al. 1989; Koch et al. 1995). Except for bamboo, which is found at high elevations, grasses in East, Central, and South Africa are C_4 grasses. Therefore, grass makes up a small fraction of the diet of most of the savanna elephants although some individuals from the Tsavo-Amboseli region of Kenya do have a high fraction of C_4 grass in their diet.

This brings up the interesting question of nutritional differences among the various elephant groups because grasses are known to be less nutritious than dicots. van der Merwe et al. (1988) conclude that grass is under-represented in collagen in elephants and suggest that

elephants may not digest C_4 grass as efficiently as they digest C_3 dicots. While this is an attractive hypothesis for the apparent mismatch between observations and isotope studies, it presents problems when considered in the context of fossil elephants. In our following discussion of results from fossil elephants, we show that fossil *Loxodonta* and *Elephas* both relied on C_4 grass as their primary diet source for several million years. It seems unlikely that elephants would use a diet source for which they were poorly suited.

Some interesting results were found in this survey. For example, tooth enamel from a single individual from Masai Mara in Kenya (Table 1) has a $\delta^{13}\text{C}$ value of about -9.7‰ corresponding to a diet of about -24‰ , indicating a C_3 -dominated diet similar in composition to that of dik-dik, Grant's gazelle, or eland (Fig. 2). The Masai Mara region has abundant grasslands, yet the C_4 dietary component of elephants is very low. Dublin (1995) points out that elephants in the Mara browse on seedlings in grasslands, an activity that could easily be mistaken for grazing. According to Lamprey et al. (1967), there were no elephants in the northern Serengeti (north of the Kenya border) until 1937 or in the southern Serengeti until 1955. It is believed Serengeti elephants migrated from the Lambwe Valley in Kenya, from which they had been driven out by the Kenya Game Department's elephant control operations. Following their arrival in the Serengeti, they caused substantial changes in the vegetation including the destruction of the larger trees at the rate of 6% per year. This is circumstantial evidence for the African elephant's preference for browse versus graze and an explanation for the low proportion of grass in the diet of the Masai Mara specimens.

Multiple analyses were made from a single tooth from an individual from Amboseli, chosen to further investigate the possibility of diet variability observed in some elephant populations. Three samples taken vertically along the same plate gave $\delta^{13}\text{C}_{\text{enamel}}$ values of -9.2 ,

–6.6, and –7.3 (Table 1), showing dietary variability during the formation of the tooth. On the other hand, seven samples (not shown in Table 1) taken from different plates along the actively abrading surface gave the same $^{13}\text{C}_{\text{enamel}}$ value within $\pm 0.2\text{‰}$, which is the replication of the analyses. This indicates that enamel records differences in diet during different times in an animal's life.

In summary, data from many modern *Loxodonta* samples from a variety of localities in Africa show that their diet is generally dominated by C_3 biomass. A few individuals show evidence for a significant C_4 component in their diet, but these samples are restricted to a few localities.

Elephas: the Asian elephant

We have not analyzed any modern elephants from Asia, but isotopic results are reported by Sukumar (Sukumar et al. 1987; Sukumar and Ramesh 1992, 1995). These $\delta^{13}\text{C}$ values are of particular interest in the context of $\delta^{13}\text{C}$ values of fossil *Elephas* from both Asia and Africa.

Sukumar and Ramesh (1992, 1995) found that the diet of *Elephas maximus* was dominated by C_3 browse or was a mixture of C_3/C_4 biomass, as is shown in Figs. 1, 2. The average $\delta^{13}\text{C}_{\text{diet}}$ is about -21‰ , which is significantly enriched in ^{13}C compared to that for African *Loxodonta*. The range in $\delta^{13}\text{C}_{\text{diet}}$ is from -15 to -29‰ indicating a variety of diets, but in general the diet of *Elephas* is predominantly C_3 biomass (on average, 55–89% based on the mixing model described above).

Sukumar and Ramesh (1992, 1995) also suggest their results indicate that young Asian elephants have a higher fraction of C_4 biomass in their diets than older elephants. The pattern of dietary change from young to older animals, with younger animals having a higher C_4 component in their diet, is compatible with the data of Koch et al. (1995) and our data from Tsavo and Amboseli. Tieszen et al. (1989) did not find any age structure to the $\delta^{13}\text{C}$ of elephants' diet in the Amboseli region, and Koch et al. (1995) believe that the diet change is due to long-term ecological change in the Amboseli region.

Sukumar and Ramesh (1995) suggest that Asian elephants digest C_4 grasses less easily than C_3 leaves and that the observation of plants ingested may overestimate the importance of C_4 plants in the animals' nutritional needs. A similar conclusion was reached for African elephants (van der Merwe et al. 1988; Vogel et al. 1990a). Yet as with the African elephant, this conclusion needs to be tempered with the observation below that *Elephas* was primarily a grazer for several million years as shown by isotope measurements on fossils (Table 2).

In summary, modern *Elephas* in India have a diet that is mostly C_3 biomass, although some individuals (especially young ones) have a significant C_4 component to their diet. Sukumar and Ramesh (1992, 1995) present convincing evidence that young elephants have a higher

proportion of C_4 biomass in their diets than adults. Thus, one would expect that even if the bulk of a population were browsing, one would often observe grazing behavior of young individuals and their mothers.

Diets of fossil elephants and other proboscideans

That extant *Loxodonta* and *Elephas* clearly favor a C_3 biomass diet is especially interesting in the context of the estimated diets of their fossil relatives. In this section we show that deinotheres have a C_3 diet from early Miocene through the early Pleistocene, but that other proboscideans have C_4 -dominated diets beginning about 7.5 Ma and continuing into the early Pleistocene.

The low-crowned lophodont teeth of deinotheres, like those of tapirs, have beveled cutting edges that are maintained, though at different angles, throughout the life of the individual for processing the food prior to digestion. Deinotheres teeth remain essentially unchanged in morphology throughout the history of the group but 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 an increase in complexity of the crown pattern and increase in the length of the teeth in different lineages. 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 teeth of elephantids contain a large number of transverse plates instead of the trefoliate bunes characteristic of gomphotheres; owing to the increased length of the teeth, normally only one cheek tooth is erupted and functional in each side of the jaw. The earliest elephantids (*Primelephas* spp.) have low-crowned teeth but the ensuing *Loxodonta*, *Elephas*, and *Mammuthus* lineages are all hypsodont and each demonstrates an increase in crown height and plate number and a decrease in enamel thickness through time. The change in crown height between gomphotheres and elephantids appears to indicate adaptation to 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.

The only Neogene proboscideans with a consistent C_3 diet are the deinotheres (Table 2, Fig. 3) which, in contrast to gomphotheres and elephantids, retained simple bilophodont brachyodont teeth and never developed horizontal tooth replacement. Nineteen samples of *Deinotherium* and *Prodeinotherium* from Kenya and Tanzania, ranging in age from middle Miocene to early Pleistocene, have an average $\delta^{13}\text{C}_{\text{enamel}}$ value of $-11.6 \pm 1.2\text{‰}$, ranging from -9.5‰ to -13.7‰ (Table 2), corresponding to a $\delta^{13}\text{C}_{\text{diet}}$ of about -26‰ .

Table 2 $\delta^{13}\text{C}$ of fossil proboscideans from East Africa. Stratigraphic details are given in Fig. 4

$\delta^{13}\text{C}_{\text{enamel}}$	Sample	Locality	Formation (or informal designation)	Member	Species
<i>Anancus</i>					
-0.1	KP 30442	Kanapoi	Nachukui	Lonyumun	<i>Anancus</i> sp.
-2.1	LT 28567	Lothagam	Nachukui	Apak	<i>Anancus</i> sp.
0.2	LT 361	Lothagam	Nawata		<i>Anancus kenyensis</i>
-9.0	NA-260	Nakali			<i>Anancus</i> sp.
<i>Archaeobelodon</i>					
-9.0	WS 78	Buluk	Warata		<i>Archaeobelodon</i> aff. <i>A. filholi</i>
<i>Choerolophodon</i>					
-10.5	FT 2785	Fort Ternan			<i>Choerolophodon ngorora</i>
-12.1	FT 2786	Fort Ternan			<i>Choerolophodon ngorora</i>
-10.4	MB 403A	Maboko			<i>Choerolophodon kisumuensis</i>
-10.0	WS 12681	Buluk	Warata		<i>Choerolophodon</i> sp.
<i>Deinotheres</i>					
-11.8	ER 2258	Koobi Fora	Koobi Fora	KBS	<i>Deinotherium bozasi</i>
-12.5	ER 4294	Koobi Fora	Koobi Fora	Upper Burgi	<i>Deinotherium bozasi</i>
-12.3	ER 2885	Koobi Fora	Koobi Fora	Lokochot	<i>Deinotherium bozasi</i>
-13.1	ER 3188	Koobi Fora	Koobi Fora	Tulu Bor	<i>Deinotherium bozasi</i>
-13.7	ER 3198	Koobi Fora	Koobi Fora	Tulu Bor	<i>Deinotherium bozasi</i>
-10.9	ER 17896	Koobi Fora	Koobi Fora	Lokochot	<i>Deinotherium bozasi</i>
-12.5	Lit '59 192	Laetoli	Laetolil Beds	Upper	<i>Deinotherium bozasi</i>
-12.6	261-1D	Koobi Fora	Koobi Fora	Lonyumun	<i>Deinotherium bozasi</i>
-12.7	MS 4857	Koobi Fora	Koobi Fora	Lonyumun	<i>Deinotherium bozasi</i>
-12.3	WT 14987	West Turkana	Nachukui	Kataboi	<i>Deinotherium bozasi</i>
-12.4	WT 3617	Kanapoi	Nachukui	Lonyumun	<i>Deinotherium bozasi</i>
-9.5	SH 12306	Samburu Hills	Namurungule		<i>Deinotherium bozasi</i>
-10.4	FT 3355	Fort Ternan			<i>Prodeinotherium hobleiyi</i>
-11.2	MB 12503	Maboko			<i>Prodeinotherium hobleiyi</i>
-11.2	MB 12505	Maboko			<i>Prodeinotherium hobleiyi</i>
-11.1	MB 12495	Maboko			<i>Prodeinotherium hobleiyi</i>
-11.8	NH 5233	Nabwal Hills	Warata?		<i>Prodeinotherium hobleiyi</i>
-11.8	NH 5233	Nabwal Hills	Warata?		<i>Prodeinotherium hobleiyi</i>
-10.9	WS 63	Buluk	Warata		<i>Prodeinotherium hobleiyi</i>
-10.4	Buluk 5204	Buluk	Warata		<i>Prodeinotherium hobleiyi</i>
-9.7	Buluk 5212	Buluk	Warata		<i>Prodeinotherium hobleiyi</i>
<i>Primelephas and Elephas</i>					
-3.4	ER 767	Koobi Fora	Koobi Fora	Okote	<i>Elephas recki recki</i>
-1.5	ER 1693	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki atavus</i>
0.2	ER 1691	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki ileretensis</i>
-2.8	ER 927	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki ileretensis</i>
0.3	ER-1302 ^a	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki ileretensis</i>
0.4	ER-1302 ^a	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki ileretensis</i>
0.4	ER-1302 ^a	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki ileretensis</i>
-0.7	ER 1700 ^a	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki shungurensis</i>
-0.8	ER 1700 ^a	Koobi Fora	Koobi Fora	KBS	<i>Elephas recki shungurensis</i>
-0.1	ER 4102	Koobi Fora	Koobi Fora	Upper Burgi	<i>Elephas recki shungurensis</i>
0.1	ER 4113	Koobi Fora	Koobi Fora	Upper Burgi	<i>Elephas recki shungurensis</i>
0.3	ER 5871	Koobi Fora	Koobi Fora	Upper Burgi	<i>Elephas recki shungurensis</i>
-1.9	ER 2894	Koobi Fora	Koobi Fora	Tulu Bor	<i>Elephas recki brumpti</i>
-2.0	ER 2895	Koobi Fora	Koobi Fora	Tulu Bor	<i>Elephas recki brumpti</i>
-1.3	ER 3191	Koobi Fora	Koobi Fora	Tulu Bor	<i>Elephas recki brumpti</i>
0.2	ER 4106	Koobi Fora	Koobi Fora	Tulu Bor	<i>Elephas recki brumpti</i>
-1.7	KP 30173	Kanapoi	Nachukui	Lonyumun	<i>Elephas ekorensis</i>
-1.5	WT 3570	Kanapoi	Nachukui	Lonyumun	<i>Elephas ekorensis</i>
-2.5	WT 3614	Kanapoi	Nachukui	Lonyumun	<i>Elephas ekorensis</i>
-0.8	LT 26323	Lothagam	Nachukui	Apak	<i>Primelephas</i> sp.
-1.6	LT 23783	Lothagam	Nawata	Upper	<i>Primelephas</i> sp.
<i>Loxodonta</i>					
-11.9	MGL-9	Kakamega	(Late Pleistocene)		<i>Loxodonta</i> sp.
-7.5	KNM-LB-128	Loboi	(Late Pleistocene)		<i>Loxodonta</i> sp.
-1.4	KNM-BK-95	Tugen Hills	Kapthurin		<i>Loxodonta</i> sp.
0.0	ER 1299	Koobi Fora	Koobi Fora	Upper Burgi	<i>Loxodonta adaurora kararae</i>
0.5	ER 4910	Koobi Fora	Koobi Fora	Upper Burgi	<i>Loxodonta adaurora kararae</i>
0.3	ER 338	Koobi Fora	Koobi Fora	Upper Burgi	<i>Loxodonta adaurora kararae</i>
-3.1	ER 4939	Koobi Fora	Koobi Fora	Tulu Bor	<i>Loxodonta exoptata</i>
-11.5	KNM-3189 ^b	Koobi Fora	Koobi Fora	Tulu Bor	<i>Loxodonta exoptata</i>
-11.3	KNM-3189 ^b	Koobi Fora	Koobi Fora	Tulu Bor	<i>Loxodonta exoptata</i>
-3.6	Lit '59 114	Laetoli	Laetolil	Upper	<i>Loxodonta exoptata</i>

Table 2 (Contd.)

$\delta^{13}\text{C}_{\text{enamel}}$	Sample	Locality	Formation (or informal designation)	Member	Species
-2.1	ER 3201	Koobi Fora	Koobi Fora	Lokochot/Moiti	<i>Loxodonta adaurora adaurora</i>
-2.1	ER 3196	Koobi Fora	Koobi Fora	Lokochot/Moiti	<i>Loxodonta adaurora adaurora</i>
-2.7	KP 390	Kanapoi	Nachukui	Lonyumon	<i>Loxodonta adaurora</i>
-1.1	WT 3833	Kanapoi	Nachukui	Lonyumon	<i>Loxodonta adaurora</i>
-3.0	KP 383	Kanapoi	Nachukui	Lonyumon	<i>Loxodonta adaurora</i>
<i>Stegatetrabelodon</i>					
-0.9	LT 26337 ^a	Lothagam	Nachukui	Apak	<i>Stegatetrabelodon orbus</i>
-0.8	LT 26337 ^a	Lothagam	Nachukui	Apak	<i>Stegatetrabelodon orbus</i>
-1.1	WT 2632	Lothagam	Nachukui	Apak	<i>Stegatetrabelodon orbus</i>
-1.1	LOTH-64 ^c	Lothagam	Nawata	Upper	<i>Stegatetrabelodon orbus</i>
-2.0	LOTH-64.a ^c	Lothagam	Nawata	Upper	<i>Stegatetrabelodon orbus</i>
-2.0	LOTH-64.b ^c	Lothagam	Nawata	Upper	<i>Stegatetrabelodon orbus</i>
-1.3	LOTH-64.c ^c	Lothagam	Nawata	Upper	<i>Stegatetrabelodon orbus</i>
0.3	LOTH-66	Lothagam	Nawata	Upper	<i>Stegatetrabelodon orbus</i>
-6.2	LT 26332	Lothagam	Nawata	Lower	<i>Stegatetrabelodon orbus</i>
-1.0	WT 2611 ^a	Lothagam	Nawata	Lower	<i>Stegatetrabelodon orbus</i>
-1.0	WT 2611 ^a	Lothagam	Nawata	Lower	<i>Stegatetrabelodon orbus</i>
-7.3	SH 12381	Samburu Hills	Namurungule		<i>Stegatetrabelodon orbus</i>
<i>Tetralophodon</i>					
-8.1	SH 12308	Samburu Hills	Namurungule		<i>Tetralophodon</i> sp.
Gen. indet.					
-3.8	MS 4891 b	Koobi Fora	Koobi Fora	Lonyumon	Elephantid gen and sp. indet.
-0.4	LOTH-118	Lothagam	Nachukui	Apak	Proboscidea gen. and sp. indet.
-0.2	LOTH-61	Lothagam	Nachukui	Apak	Proboscidea gen. and sp. indet.
-5.5	LOTH-137	Lothagam	Nawata	Lower	Proboscidea gen. and sp. indet.
-0.1	LOTH-154	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-1.5	LOTH-158	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-2.1	LOTH-159	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-0.3	LOTH-162	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-0.2	LOTH-171	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-0.9	LOTH-176	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
0.2	LOTH-60	Lothagam	Nawata	Upper	Proboscidea gen. and sp. indet.
-1.8	LOTH-72	Lothagam	Nawata	Lower	Proboscidea gen. and sp. indet.
-2.3	LOTH-75	Lothagam	Nawata	Lower	Proboscidea gen. and sp. indet.
-3.9	LOTH-84	Lothagam	Nawata	Lower	Proboscidea gen. and sp. indet.
0.7	LOTH-90	Lothagam	Nawata	Lower	Proboscidea gen. and sp. indet.
-1.8	96 JW 17a	Lothagam			Proboscidea gen. and sp. indet.
-9.5	BGJ 506-84	Samburu Hills	Namurungule		Gomphotheriid gen. and sp. indet.
-9.0	BGK 558-84	Samburu Hills	Namurungule		Gomphotheriid gen. and sp. indet.
-9.0	BGS 449-84	Samburu Hills	Namurungule		Gomphotheriid gen. and sp. indet.
-8.0	NA-6	Nakali			Gomphotheriid gen. and sp. indet.
-11.3	MB 12483	Maboko			Gomphotheriid gen. and sp. indet.
-10.0	NH 5234	Nabwal Hills	Warata?		Gomphotheriid gen. and sp. indet.
-9.1	Buluk 5201	Buluk	Warata		Proboscidea gen. and sp. indet.

^a Replicate analyses of the same sample

^b KNM 3189 was sampled twice from the original specimen

^c The four analyses represent different fragments of the same tooth of LOTH 64

Such a diet has essentially no C_4 component to it. The youngest samples are less than 2 Ma and have $\delta^{13}\text{C}_{\text{enamel}}$ values of about -12.4‰ corresponding to a C_3 diet of about -26 to -27‰ .

However, other African and Asian proboscideans sampled from the late Miocene through middle Pleistocene have a significant C_4 component in their diets for most of the interval from 7 to 1 Ma (Fig. 4). Besides deinotheres, we sampled gomphotheres (*Archaeobelodon*, *Anancus*), mammutids (*Cheorolophodon*), and elephantids (*Stegatetrabelodon*, *Elephas*, *Loxodonta*), plus contemporaneous proboscideans that could not be identified to genus. Fifteen non-deinotheres proboscideans from localities older than 8 Ma (Buluk, Fort

Ternan, Maboko, Nabwal Hills, Nakali, and the Samburu Hills) display a $\delta^{13}\text{C}_{\text{enamel}}$ range -7.3 to -12.5‰ indicating a C_3 diet ranging from -22 to -27‰ . The most positive of these samples is from the circa 8 Ma Samburu Hills locality and may represent the first proboscideans to use C_4 as a dietary resource; equids from this locality have a significant C_4 component in their diet (Cerling et al. 1997).

Younger (less than 8 Ma) gomphotheres, including *Anancus*, have a C_4 -dominated diet; the average $\delta^{13}\text{C}_{\text{enamel}}$ value for three late Miocene to early Pliocene specimens of *Anancus* was $-0.7 \pm 1.3\text{‰}$, indicating a C_4 diet with an average $\delta^{13}\text{C}_{\text{diet}}$ value of about -15‰ . Tooth enamel from other samples attributed to *Elephas*,

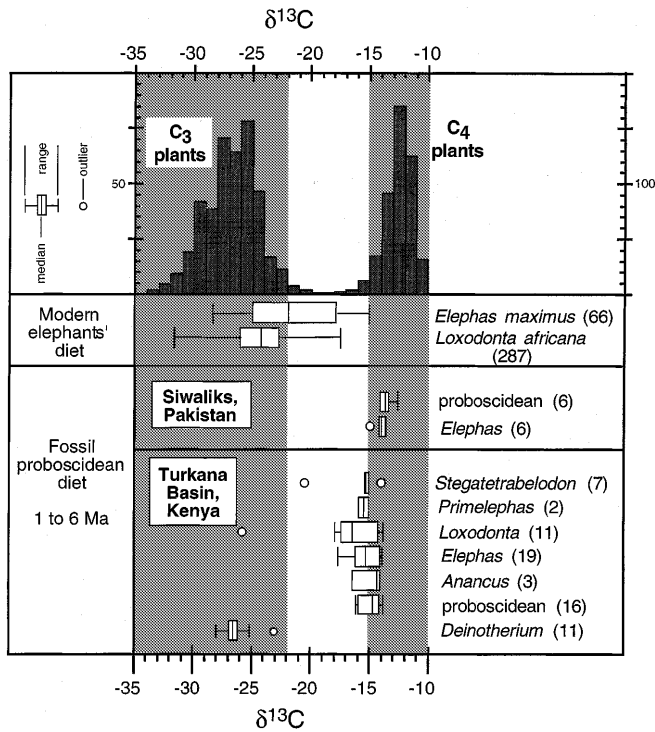


Fig. 3 Estimated diets for modern *Loxodonta* and *Elephas* compared to the estimated diets for fossil proboscideans. Modern data from Figs. 1, 2. Fossil data for Africa from Table 2; fossil data from Pakistan from Stern et al. (1994), Morgan et al. (1994), and from this study

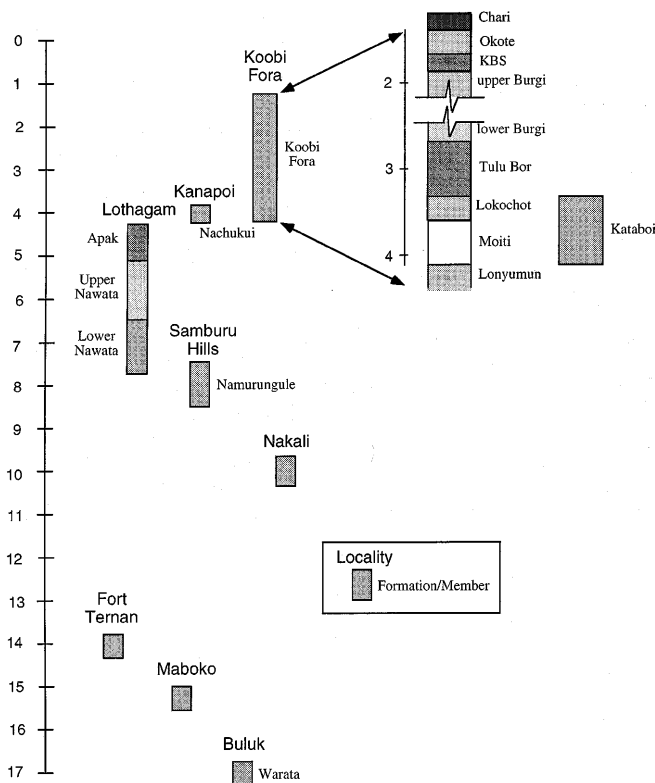


Fig. 4 Generalized diagram showing stratigraphy and ages of important fossil sites used in this study

Loxodonta (excluding one sample, discussed below) *Primelephas*, *Stegatetrabelodon*, and unidentified proboscideans have average $\delta^{13}\text{C}_{\text{enamel}}$ values of $-1.0 \pm 1.2\text{‰}$, $-1.5 \pm 1.4\text{‰}$, $-1.2 \pm 0.4\text{‰}$, $-1.5 \pm 2.1\text{‰}$, and $-0.8 \pm 0.9\text{‰}$, respectively, corresponding to C_4 dietary $\delta^{13}\text{C}_{\text{diet}}$ values ranging from -15 to -17‰ (Fig. 2). Of these samples only one specimen of *L. exoptata* (KNM-ER 3189) indicated a C_3 -dominated diet ($\delta^{13}\text{C}_{\text{enamel}}$ value of -11.5‰ for its tooth enamel, indicating a diet of about -26‰ ; confirmed by a $\delta^{13}\text{C}_{\text{enamel}}$ value of -11.3‰ from a different fragment of the same specimen). Other *L. exoptata* specimens analyzed had predominantly C_4 diets. Indeed, with the exception of that single individual, the fossil record of the African elephantids for the interval from 7 to 1.3 Ma shows all coexisting elephantids and gomphotheres to have had a predominantly C_4 diet. KNM-ER 3189 is a worn posterior fragment of dp4/ (= M3 in some terminologies) that is very modern in appearance with a loxodont abrasion pattern (Beden 1983). It was retrieved as a surface specimen from Area 204 at Koobi Fora and identified as *L. exoptata* but it could, instead, conceivably represent a lag fossil of *L. africana* from the late Pleistocene/Holocene Galana Boi Beds. Similarly, well-mineralized *Equus* and *Phacochoerus* teeth from the Galana Boi Beds occur as surface specimens on outcrops of the Koobi Fora Formation in Area 204 and elsewhere in the Koobi Fora basin.

Proboscideans from Pakistan demonstrate changes similar to those observed in Africa; those older than about 8 Ma have C_3 -dominated diets, whereas all samples younger than 6 Ma have C_4 -dominated diets (Table 3). For the younger samples, six *Elephas* samples and six unidentified proboscideans have $\delta^{13}\text{C}_{\text{enamel}}$ values of $0.2 \pm 0.5\text{‰}$ and $0.6 \pm 0.6\text{‰}$, respectively, indicating diets with average $\delta^{13}\text{C}_{\text{diet}}$ values of about -14‰ (Fig. 3).

Although this study discusses the diets of modern elephants and their ancestors, we briefly mention the last of the European and New World proboscideans. C_4 grasses are restricted to tropical and sub-tropical regions with rain during the (warm) growth season. Growing conditions preclude C_4 vegetation in Mediterranean and cool climates; thus proboscideans from western Europe and northern Eurasia necessarily had strictly C_3 diets (Bocherens et al. 1994, 1996a). C_4 vegetation is present in the central and eastern portions of southern North America. Isotopic analyses of *Mammuthus* teeth from Florida, Texas and Arizona (Rancholabrean, late Pleistocene) indicate a higher proportion of C_4 vegetation than do the *Mammuthus* teeth from the same regions with $\delta^{13}\text{C}_{\text{enamel}}$ values of about -3 to -0.6‰ for *Mammuthus* and -10.5‰ for *Mammuthus* (Table 4), corresponding to estimated diets of -15‰ and -25‰ , respectively. Fossil equids and bison from these localities also had C_4 -dominated diets (Table 4). However, in Idaho where C_3 grasses are prevalent, *Mammuthus* has a C_3 -dominated diet (Table 3). Based on the data from Africa and Asia and the change in diet of *Elephas* and *Loxodonta* to browse in the late Pleistocene, it is possible

Table 3 $\delta^{13}\text{C}$ values for proboscidean tooth enamel from Pakistan. Data from Quade et al. (1992), Stern et al. (1994), Morgan et al. (1994), and this study

$\delta^{13}\text{C}_{\text{enamel}}$	Sample/source	Formation	Age (Ma)	Species
0.1	ROT-12	Upper Siwaliks	2.0	Proboscidea gen. and sp. indet.
-0.7	Stern et al. (1994)	Upper Siwaliks	2.5	<i>Elephas</i> sp.
0.3	Stern et al. (1994)	Upper Siwaliks	2.5	<i>Elephas</i> sp.
0.6	Stern et al. (1994)	Upper Siwaliks	2.5	<i>Elephas</i> sp.
0.1	Stern et al. (1994)	Upper Siwaliks	2.7	<i>Elephas</i> sp.
0.9	Quade et al. (1992)	Upper Siwaliks	3.5	Proboscidea gen. and sp. indet.
0.2	Quade et al. (1992)	Upper Siwaliks	3.5	Proboscidea gen. and sp. indet.
0.7	Stern et al. (1994)	Upper Siwaliks	4.0	<i>Elephas</i> sp.
1.7	ROT-191	Upper Siwaliks	4.0	<i>Elephas</i> sp.
0.2	Morgan et al. (1994)	Upper Siwaliks	4.2	Proboscidea gen. and sp. indet.
0.8	Morgan et al. (1994)	Upper Siwaliks	4.4	Proboscidea gen. and sp. indet.
0.0	Morgan et al. (1994)	Upper Siwaliks	4.6	Proboscidea gen. and sp. indet.
-8.2	Morgan et al. (1994)	Dhok Pathan	6.6	Proboscidea gen. and sp. indet.
-7.6	GSP 15296	Dhok Pathan	7.0	<i>Choerolophodon corrugatus</i>
-4.8	ROT-196	Dhok Pathan	7.1	Gomphotheriid gen. and sp. indet.
-11.3	Stern et al. (1994)	Dhok Pathan	7.4	<i>Stegodon</i> sp.
-6.6	Morgan et al. (1994)	Dhok Pathan	8.0	Proboscidea gen. and sp. indet.
-11.0	GSP 15638	Dhok Pathan	8.0	<i>Stegolophodon</i> cf. <i>stegodontoides</i>
-12.0	Morgan et al. (1994)	Nagri	9.6	Proboscidea gen. and sp. indet.
-10.4	Quade et al. (1992)	Chinji	11.8	Proboscidea gen. and sp. indet.
-9.8	Quade et al. (1992)	Chinji	13.5	Proboscidea gen. and sp. indet.

Table 4 $\delta^{13}\text{C}$ values for mammoths with coexisting mastodonts, equids, or bison from selected Rancholabrean localities in North America

$\delta^{13}\text{C}_{\text{enamel}}$	Sample	Species
Florida, Ichetucknee		
-0.6	UF V4086	<i>Mammuthus</i> sp.
-10.4	M-92	<i>Mammut</i> sp.
-3.9	B-94	<i>Bison</i> sp.
-2.2	E-90	<i>Equus</i> sp.
Texas, Ingleside		
-0.9	TMM 30967-808	<i>Mammuthus</i> sp.
-10.6	TMM 30967-395	<i>Mammut</i> sp.
-0.8	TMM 30967-2224	<i>Equus fraternus</i>
Arizona, Gila Pueblo		
-3.2	LACM 5111m	<i>Mammuthus</i> sp.
0.7	LACM 5111e	<i>Equus</i> sp.
0.0	LACM 5118	<i>Bison</i> sp.
Idaho, American Falls		
-10.2	IMNH 776/40368	<i>Mammuthus columbi</i>
-9.9	IMNH 72006/16103	<i>Mammut</i> sp.
-9.3	IMNH 65003/23325	<i>Equus</i> sp.
-8.1	IMNH 71004/23690	<i>Bison latifrons</i>

that the last grazing elephantids were the mammoths, which became extinct in North America in the latest Pleistocene (Stafford 1990).

Concluding remarks

Thus we are faced with a very intriguing problem. Both the *Elephas* and *Loxodonta* lineages go back about 5 million years to the late Miocene of Africa. Their initial appearance coincides with the worldwide expansion of the C_4 biomass from which they and contemporary gomphotheres fed almost exclusively. However, after the middle Pleistocene, both *Elephas*

and *Loxodonta* abandoned the diet that had served them well for their previous history and for which their teeth had become increasingly specialized. What mandated the change from C_4 grasses back to C_3 browse? Did the reduction of C_4 grasslands at the end of the Pleistocene due to changing atmospheric CO_2 levels (Cerling et al. 1998) force proboscideans back into the forests due to competition from contemporary hypergrazers such as the antelopes? Were forest habitats sought to avoid predation by humans? Are the supposed lineages of *Elephas* and *Loxodonta* incorrect, and do their presumed ancestors from East Africa and Asia represent open-habitat lineages that did not lead to the extant species? Whatever the reason, it is clear that from their initial appearance in the Pliocene or Miocene up to almost 1 million years ago, *Elephas* and *Loxodonta* were predominantly grazers, yet modern *Elephas* and *Loxodonta* are predominantly browsers in almost all environments. Perhaps the indication of a mixed C_3/C_4 diet in some regions, and the reports of C_4 -dominated diets in a few other localities (Laws et al. 1974), indicates that both *Elephas* and *Loxodonta* are in the last stage of a transition back to being browsers from being grazers.

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