

Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma

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A large stable isotope dataset from East and Central Africa from *ca.* 30 regional collection sites that range from forest to grassland shows that most extant East and Central African large herbivore taxa have diets dominated by C₄ grazing or C₃ browsing. Comparison with the fossil record shows that faunal assemblages from *ca.* 4.1–2.35 Ma in the Turkana Basin had a greater diversity of C₃–C₄ mixed feeding taxa than is presently found in modern East and Central African environments. In contrast, the period from 2.35 to 1.0 Ma had more C₄-grazing taxa, especially nonruminant C₄-grazing taxa, than are found in modern environments in East and Central Africa. Many nonbovid C₄ grazers became extinct in Africa, notably the suid *Notochoerus*, the hipparion equid *Eurygnathohippus*, the giraffid *Sivatherium*, and the elephantid *Elephas*. Other important nonruminant C₄-grazing taxa switched to browsing, including suids in the lineage *Kolpochoerus-Hylochoerus* and the elephant *Loxodonta*. Many modern herbivore taxa in Africa have diets that differ significantly from their fossil relatives. Elephants and tragelaphin bovids are two groups often used for paleoecological insight, yet their fossil diets were very different from their modern closest relatives; therefore, their taxonomic presence in a fossil assemblage does not indicate they had a similar ecological function in the past as they do at present. Overall, we find ecological assemblages of C₃-browsing, C₃–C₄-mixed feeding, and C₄-grazing taxa in the Turkana Basin fossil record that are different from any modern ecosystem in East or Central Africa.

carbon isotopes | evolution | diet

The expansion of C₄ biomass beginning in the late Miocene marks a major vegetation change in the history of Earth. Today C₄ plants comprise *ca.* 50% of net primary productivity (NPP) in the tropics (1) yet contributed less than 1% of NPP only 10 million years ago. C₄ plants are primarily grasses and sedges, although C₄ photosynthesis is known to be used in ~20 plant families (2, 3). C₄ photosynthesis is an adaptation to low (*ca.* <500 ppm by volume) concentrations of CO₂ in Earth's atmosphere along with high growing-season temperatures (4). Although genetic evidence indicates an Oligocene origin of C₄ photosynthesis in the grasses (5, 6), macrofossil evidence for C₄ photosynthesis in grasses is extremely sparse (7, 8).

The expansion of C₄ biomass has been documented through stable isotopes in paleosols (9–12), grass phytoliths (13), herbivore tooth enamel (14–16), and biomarkers in deep-sea sediments (17, 18). At 10 Ma in Africa, Asia, and North America, the δ¹³C values for equid tooth enamel indicate a diet dominated by C₃ vegetation; by *ca.* 7 Ma, equids in Africa have a diet dominated (>75%) by C₄ vegetation (14, 15). In East Africa today there is a distinct difference in diets of major herbivores, with most mammals either being predominantly browsing (>*ca.* 75% C₃)

or grazing (>*ca.* 75% C₄), and there are relatively few mixed feeders (Fig. 1).

A recent study of the early transition of C₃ to C₄ dietary change in the Turkana Basin from 10 Ma to *ca.* 4 Ma (15) showed that equids were the earliest mammals to fully exploit the C₄ dietary resource, attaining a predominantly C₄-grazing diet by 7 Ma. Other mammal groups (hippopotamids, elephantids, and bovids) changed to a C₄ diet later than did the equids. In this paper we document dietary changes in the major Artiodactyla-Perissodactyla-Proboscidea (APP) taxa in the Turkana Basin between *ca.* 4 Ma and 1 Ma and compare those to dietary preferences of extant APP taxa in East and Central Africa. The Turkana Basin has an excellent stratigraphy (19–22) with excellent preservation of fossils from 4 to 1 Ma; this study focuses on fossils recovered from the Koobi Fora, Kanapoi, and Nachukui Formations of northern Kenya.

We compare dietary changes within the major APP taxa through the past 4 Ma in the formations listed above using >900 individual fossils that represent the major taxa collected within the principal stratigraphic intervals of these formations. Fossil mammalian diets are compared with those of >1,900 extant mammal individuals sampled from >30 different regions and habitats in eastern and central Africa. We compare the ecosystem structure

Significance

Stable carbon isotopes give diet information for both modern and fossil mammals and can be used to classify diets as C₄ grazers, C₃–C₄ mixed, or C₃ browsers. We show that diets of some major African herbivore lineages have significantly changed over the past 4 million years by comparing fossils from the Turkana Basin in Kenya with modern mammals from East and Central Africa. Some fossil assemblages have no modern analogues in East and Central Africa, suggesting different ecological functions for some mammals in the past as compared with their modern counterparts. The development of modern tropical grassland ecosystems are products of the coevolution of both grasses and herbivores.

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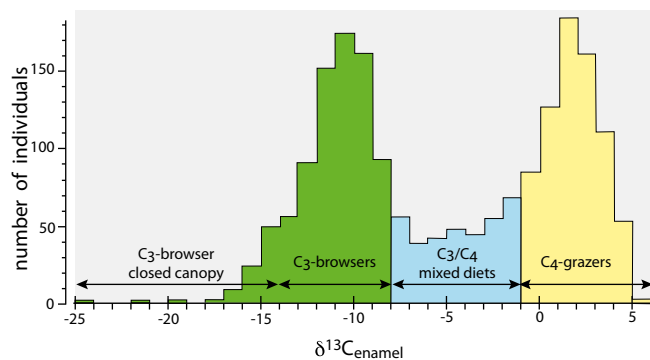


Fig. 1. $\delta^{13}\text{C}_{1750}$ values for tooth enamel (or equivalent) for >1,900 mammals from East and Central Africa (principal localities in *SI Appendix, Table S1*; data from *Dataset S1*).

(C_3 browsers, C_3/C_4 mixed diets, and C_4 grazers) through the Pliocene and Pleistocene and document changes in ungulate diets over time.

Results

The distinction between C_3 dicots and C_4 grasses makes stable isotopes a very useful tracer of diet in tropical ecosystems. Although C_4 dicots are known from Africa, they are uncommon in most biomes (23). Likewise, plants using the Crassulacean acid metabolism pathway (mostly succulents) are also uncommon in most African ecosystems and also often have chemical defenses that deter mammalian herbivory. In the discussion below, modern samples for plants and tooth enamel have their respective $\delta^{13}\text{C}$ values corrected for the anthropogenic CO_2 and are corrected to preindustrial values (see *SI Appendix, Detailed Methods*) and are reported as $\delta^{13}\text{C}_{1750}$. Using data reported in ref. 24, we find the $\delta^{13}\text{C}_{1750}$ values for C_3 plants from forest floor in closed canopy (Ituri Forest), mesic (Aberdares, Nairobi region), and xeric (Turkana, Samburu, Laikipia) biomes to be *ca.* -32.6 , -26.6 , and -25.6‰ , respectively. Mesic (panicoids) and xeric (chloridoids and *Aristida*) grasses have $\delta^{13}\text{C}_{1750}$ values of -10.0 and -11.2‰ , respectively. The isotopic distinction between mesic and xeric vegetation within C_3 and C_4 ecosystems has previously been noted for both C_3 plants (25) and C_4 plants (26, 27).

$\delta^{13}\text{C}$ Assignments for C_3 Browsing, Mixed C_3/C_4 , and C_4 Grazing. Diets of African mammals are frequently discussed in terms of C_3 -dominated browsing, mixed feeding, and C_4 -dominated grazing. In this discussion, a browsing diet is dominated by C_3 biomass (primarily dicots), whereas a grazing diet comprises primarily C_4 biomass (mainly grasses). *SI Appendix, Table S1* gives geographic, climatic, and ecological information for 30 geographic localities with measured $\delta^{13}\text{C}$ on keratin, collagen, or enamel from APP mammals. In each collecting region we analyzed the different APP species to determine the characteristic $\delta^{13}\text{C}$ value for individuals in that particular region; thus, each taxon has a region-specific diet. *Dataset S1* presents $\delta^{13}\text{C}_{1750}$ data for >1,900 individuals from East and Central Africa, distributed across >50 species of large mammals; *SI Appendix, Table S2* summarizes data for individual species. For comparison between tissues, all values are reported as enamel values using isotope enrichments in *SI Appendix, Detailed Methods*. Analysis of these data using the Akaike Information Criterion indicates that there are multiple modes for these individual $\delta^{13}\text{C}_{1750}$ values: A three-component mixture analysis identifies C_3 -browsing and C_4 -grazing components with modal $\delta^{13}\text{C}_{1750}$ values of -10.9 ± 1.6 and $1.7 \pm 1.6\text{‰}$ for C_3 -browsing and C_4 -grazing taxa, respectively, with mixed feeders having intermediate values. Isotope enrichment values $\epsilon^*_{\text{enamel-diet}}$ are between 13.3 and 14.6‰ for ungulate mammals (24, 28), with the higher

values being associated with bovid ruminants; we use 14.1‰ for all taxa in this paper (*SI Appendix, Detailed Methods*). Using these enrichment values and the xeric- and mesic-mixing lines for C_3 dicots and C_4 grasses, we have adopted a value of -8‰ as the boundary between C_3 browsers ($<-8\text{‰}$) and mixed C_3/C_4 diets ($>-8\text{‰}$ to $<-1\text{‰}$), and a value of -1‰ for the boundary between C_4 grazers ($>-1\text{‰}$) and mixed C_3/C_4 diets. Thus, defined isotopically, “mixed C_3/C_4 diets” have C_3/C_4 diet ratios between *ca.* 75/25 and *ca.* 25/75, given the uncertainties in the mixing lines (*SI Appendix, Fig. S2*).

Most samples used for stable isotope analysis of fossils are identified only to tribe for bovids and genus for other taxa; therefore, in the discussion below we evaluate taxonomic groups at the tribal level for bovids and at the generic level for other taxa using this diet classification (Table 1). We consider normalized proportions of C_4 grazers (G), mixed C_3 – C_4 diet generalists (M), and C_3 browsers (B), referred to as G:M:B, using the isotope ranges described above and in *SI Appendix*. For comparison within a taxon in each time interval, we compare the fraction of individuals that are C_4 grazers, mixed C_3 – C_4 diet generalists, or C_3 browsers. In contrast, for comparison of taxa with respect to all other taxa within a single ecosystem or a time slice, we use the average $\delta^{13}\text{C}$ value to define the predominant mode of feeding: C_4 grazer, mixed C_3 – C_4 diet generalist, or C_3 browser.

Table 1. Modern East African large mammal taxon groups (tribe for Bovidae, genus for other taxa) used in this study

Taxon	<i>n</i>	%G	%M	%B
Artiodactyla				
Bovidae				
Aepycerotini	66	15	77	8
Alcelaphini	141	100	0	0
Antilopini	122	11	30	60
Bovini	167	84	13	4
Caprini	1	0	0	100
Cephalophini	63	0	2	98
Hippotragini	38	89	11	0
Neotragini	84	2	11	87
Reduncini	90	93	7	0
Tragelaphini	126	0	15	85
Giraffidae				
<i>Giraffa</i>	61	0	7	93
<i>Okapia</i>	2	0	0	100
Hippopotamidae				
<i>Choeropsis</i>	1	0	0	100
<i>Hippopotamus</i>	186	36	61	4
Suidae				
<i>Hylochoerus</i>	26	0	0	100
<i>Phacochoerus</i>	101	80	18	2
<i>Potamochoerus</i>	46	2	22	76
Tragulidae				
<i>Hyemoschus</i>	1	0	0	100
Perissodactyla				
Equidae				
<i>Equus</i>	157	91	8	1
Rhinocerotidae				
<i>Ceratotherium</i>	13	100	0	0
<i>Diceros</i>	145	0	6	94
Proboscidea				
Elephantidae				
<i>Loxodonta</i>	280	0	19	81

Classified by the percentage of individuals that are C_4 grazers (G), mixed C_3 – C_4 feeders (M), or C_3 browsers (B) based on the isotope values ($\delta^{13}\text{C}_{1750}$ values $>-1\text{‰}$, $>-1\text{‰}$ and $<-8\text{‰}$, and $<-8\text{‰}$, respectively). See *SI Appendix* for complete data.

Dataset S2 presents $\delta^{13}\text{C}$ data for tooth enamel from >900 individual specimens from the Turkana Basin ranging in age from *ca.* 4–1 Ma. The same isotopic ranges are used to distinguish between C_3 browsing, mixed C_3 – C_4 diets, and C_4 grazing for both fossil and modern mammals. We assume the $\delta^{13}\text{C}$ value of the atmosphere is constant for the Pleistocene and Pliocene and has the same value as the preindustrial atmosphere (see discussion in *SI Appendix, Detailed Methods*).

Diets of Mammalian Lineages in the Pliocene and Pleistocene. The mammalian lineages considered here derive from different members of the Kanapoi, Koobi Fora, and Nachukui Formations and are of comparable age to the Shungura Formation in the lower Omo Valley as shown in Fig. 2; K/Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ dates from the sequence are derived from all four formations and many volcanic ashes are correlative between the formations. Time intervals used in this study are based on correlative marker horizons between the Koobi Fora and Nachukui Formations, and are as follows from oldest to youngest: >4 Ma, 4.0–3.6 Ma, 3.6–3.4 Ma, 3.4–3.0, 3.0–2.5 Ma, 2.5–2.35 Ma, 2.35–1.9 Ma, 1.9–1.5 Ma, 1.5–1.3 Ma, and 1.3–1.0 Ma.

The APP taxa for modern specimens is discussed using the normalized proportions of C_4 grazing, C_3 – C_4 mixed, and C_3 browsing (G:M:B) for each taxon (*SI Appendix*). These results largely confirm previous isotope surveys (29, 30) for modern African bovids, hippos (31, 32), suids (33), and elephants (34) but expand the database severalfold. However, comparison of individual lineages of APP taxa show significant changes over time; a number of taxa had diets in the fossil record that are quite different from those of their modern representatives (e.g., Aepycerotini, Antilopini, Tragelaphini, and *Loxodonta*; *SI Appendix, Figs. S4 and S5*).

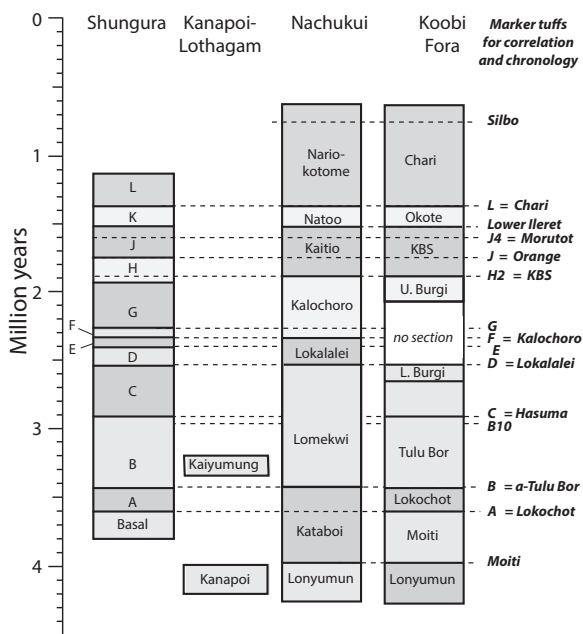


Fig. 2. Stratigraphic relationships in the Turkana Basin for major collecting geographic regions: Shungura, Nachukui, Koobi Fora, and Kanapoi Formations. Dashed lines show some important volcanic ash layers (tuffs) used for correlation between formations; tuff names are in bold. Stratigraphy and correlations based on earlier results (see *SI Appendix, Detailed Methods*).

Discussion

Ecosystem and Dietary Change Through the Past 4 Ma.

Dietary change through time for individual lineages. Many African taxa have diets that remained essentially the same (less than 2‰ change) for much of the past 4 million years (*SI Appendix, Table S4 and Fig. S4*). These include the taxa and lineages that are presently C_4 grazers, Alcelaphini, Bovini, Reduncini, *Ceratotherium* (=Rhino-G), *Metrochoerus-Phacochoerus* and *Equus*, the C_3 – C_4 mixed feeder *Hippopotamus s. l.*, and the C_3 browsers Neotragini, *Giraffa*, *Diceros* (=Rhino B), and *Deinotherium*. Of these, it is notable that modern Alcelaphini have $\delta^{13}\text{C}_{1750}$ values that are consistently more positive relative to fossil Alcelaphini. Such differences could be due to several factors: a slight diagenetic exchange of ^{13}C resulting in the fossils $\delta^{13}\text{C}_{1750}$ values being slightly more negative relative to modern samples, a change in the atmospheric $\delta^{13}\text{C}$ value causing a shift in the $\delta^{13}\text{C}$ of plants and the derived dietary $\delta^{13}\text{C}$ of enamel, an increase in the isotope enrichment (tooth enamel relative to diet) of alcelaphins that occurred in the past million years, or a slight difference in diet whereby many modern alcelaphins are true hypergrazers and the fossil alcelaphins were not. Diagenesis is unlikely to more strongly affect alcelaphins than other taxa, so diagenesis does not explain such differences. Studies of North Atlantic benthic marine carbonates show relatively constant $\delta^{13}\text{C}$ values through the past *ca.* 6 Ma (see discussions in refs. 35 and 36), indicating that the $\delta^{13}\text{C}$ of the atmosphere was similar through the past 4 Ma. At present, we cannot distinguish between the last two possibilities—a change in the isotope enrichment specific to alcelaphins, or a more C_4 -selective diet for alcelaphins than all other taxa—although we favor the latter.

Hippotragin bovids and suids of the *Nyanzachoerus-Notochoerus* lineage changed from a mixed feeding to a grazing diet during the interval represented by this stratigraphic sequence.

Aepycerotini, Antilopini, and Tragelaphini represent three bovid tribes whose diets have recently shifted to more negative $\delta^{13}\text{C}$ values, implying that the fossil representatives of these taxa had a higher C_4 component in their diet than their modern relatives (*SI Appendix, Table S4 and Figs. S4 and S5*). Fossil Aepycerotini in the Turkana Basin are enriched in ^{13}C by several per mil compared with modern *Aepyceros*; only specimens from the Mara and adjoining Serengeti have $\delta^{13}\text{C}$ values comparable to those of most of the fossil Aepycerotini. Fossil Antilopini in all except the lowest stratigraphic intervals have average $\delta^{13}\text{C}$ values between *ca.* –1 and –3‰, indicating a strong C_4 preference, which contrasts with modern antilopins that mostly prefer C_3 browsing. Only the modern antilopin *Eudorcas thomsonii* has values similar to the Turkana Basin fossil Antilopini (*SI Appendix, Table S2*). Thus, the Antilopini have shifted toward browsing since the early to middle Pleistocene. Tragelaphini also have shifted from *ca.* –5‰ in the fossil record to *ca.* –10 to –12‰ in extant tragelaphins. Our survey of 126 modern tragelaphin individuals includes only 7 (i.e., *ca.* 6%) with $\delta^{13}\text{C}$ values >–5‰, whereas 16 of 43 of fossil tragelaphins (i.e., *ca.* 37%) have $\delta^{13}\text{C}$ values >–5‰. Tragelaphins from the Shungura Formation (Members C–G; from *ca.* 3.0–2.0 Ma) also had high $\delta^{13}\text{C}$ values (37) similar to those measured on specimens from the Nachukui and Koobi Fora Formations in the equivalent time interval.

Loxodonta and *Kolpochoerus-Hylochoerus* are lineages that were primarily C_4 grazers from 4 to 1 Ma, but are now C_3 browsers (*SI Appendix, Table S4 and Fig. S4*). Both lineages have gone from average $\delta^{13}\text{C}$ values *ca.* –1‰ between 4 and 1 Ma to the modern average $\delta^{13}\text{C}_{1750}$ value of *ca.* –10 and –14‰, respectively. Such abrupt diet changes imply significant changes in the roles of these genera in the overall ecosystem, and perhaps a change in the ecosystems themselves.

Four C_4 -grazer lineages become extinct in this interval: *Sivatherium*, *Notochoerus*, *Eurygnathohippus*, and *Elephas*

(SI Appendix, Table S4 and Fig. S4). *Sivatherium* was a browser at ca. 4 Ma and switched to grazing between 2 and 1 Ma, becoming extinct after adapting to a C₄-grazing diet. *Notochoerus* was a C₄-grazing suid; it became extinct in the basin by 1.6 Ma. *Eurygnathohippus* was a grazing three-toed equid related to hipparions that became extinct in the early Pleistocene. *Elephas*, a C₄-grazing elephant, was present in the basin from 4 to 1 Ma ago, but it became extinct in Africa in the middle to late Pleistocene.

Cephalophins, neotragins, *Giraffa*, and the browsing rhino lineage represented by *Diceros* have been dedicated browsers throughout their known history. *Deinotherium* was similarly adapted throughout the 4–1 Ma time interval but became extinct in Africa in the middle Pleistocene; it has the most negative $\delta^{13}\text{C}$ values of any taxon for all time intervals in the Turkana Basin for which we have analyses (Dataset S2).

Elephants and tragelaphin bovids are two groups often used for paleoecological interpretations, yet their respective fossil diets were very different from those of their modern closest relatives (SI Appendix, Table S4 and Figs. S4 and S5); therefore, the taxonomic presence of a lineage does not indicate that the earlier fossil representative of the lineage had an ecological function in the past similar to that of the modern representative. For example, *Loxodonta* is often considered to be a keystone species that strongly affects woody cover; although *Loxodonta* is now predominantly a C₃ browser (SI Appendix, Table S2), in the late Pliocene and early Pleistocene *Loxodonta* was primarily a C₄ grazer (SI Appendix, Table S4 and Figs. S4 and S5). Likewise, tragelaphins are commonly assumed to be indicators of forest or woodland (38, 39) because modern tragelaphins are browsers (e.g., see Table 1 and SI Appendix, Table S2); the strongly mixed C₃–C₄ diet of fossil tragelaphins suggests that they should not be considered as indicators of forest or woodland habitat for stratigraphic intervals in the Nachukui and Koobi Fora formations. Thus, the role of tragelaphins in any fossil assemblage should be considered using the $\delta^{13}\text{C}$ of specimens specific to that assemblage.

Ecosystem change through time. This study demonstrates important changes in mammal diets and ecosystem structure through the past 4 million years. Three bovid tribes, the warthog lineage, *Equus*, and grazing rhinos have an essentially unchanged grazing regime through the Omo Group sequence; in contrast, the grazing giraffids, the grazing notochoere suids, grazing three-toed horses, and African representatives of grazing *Elephas* became extinct. The grazing gomphothere, *Anancus*, became extinct early in this record. Two bovid tribes, giraffes, and browsing rhinos remain dedicated browsers; browsing deinotheres became extinct. Three bovid tribes incorporate more C₃ browsing in the diets of extant versus early Pleistocene representatives, whereas the formerly C₄-grazing *Kolpochoerus* lineage culminates in the C₃-browsing *Hylochoerus* and the formerly grazing *Loxodonta* switched to a C₃ browsing-dominated diet. Hippos remain opportunistic feeders throughout.

Modern ecosystems in Africa are characterized by having a large mammal fauna with distinctly different mixtures of G:M:B than faunas in the fossil record. Many of the modern ecosystems sampled are considered to be mosaics, including riparian forest with nearby wooded grassland or grasslands. Forest ecosystems (closed canopy forests, coastal and montane forests, and Afro-alpine in SI Appendix, Table S1) are dominated by C₃ browsers and mixed C₃–C₄ feeders; pure grassland faunas have >80% C₄ grazers, and most of the modern mosaic ecosystems have subequal numbers of C₄ grazers and C₃ browsers, with a minor number of C₃–C₄ mixed feeders (Figs. 3A and 4B).

In this discussion we have assumed that C₃ grasses are insignificant in the isotopic contribution to the C₃ diet resources. If C₃ grasses play a role in this story, strong selectivity would have to be in play because some lineages are essentially C₄ grazers throughout the sequences (e.g., equids, Rhino-G, and alcelaphins). Although C₃

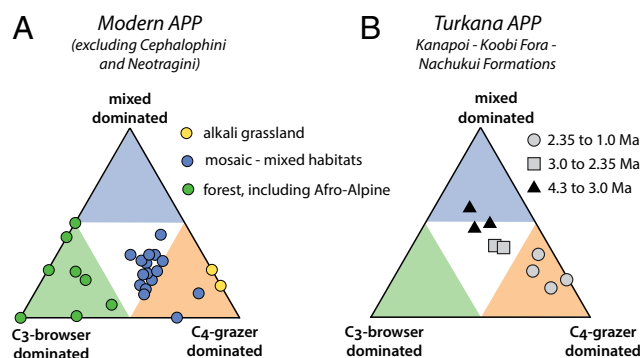


Fig. 3. Ternary diagram showing proportions of C₃ browsers, C₃–C₄ mixed feeders, and C₄ grazers from the orders Artiodactyla, Perissodactyla, and Proboscidea (APP); each taxon in each locality or time interval is represented by the average $\delta^{13}\text{C}$ for that taxon. Each point in the figure represents the respective proportions of APP taxa that are C₃ browsers, C₃–C₄ mixed feeders, or C₄ grazers at one modern locality, or one fossil assemblage from the Turkana Basin of a specific age range. The green, blue, and orange triangles represent regions where >50% of the taxa are C₃ browsers, C₃–C₄ mixed feeders, or C₄ grazers, respectively. (A) Modern ecosystems as described in SI Appendix, Table S1, using data from Dataset S1; Neotragini and Cephalophini are excluded for comparison with fossil assemblages (see SI Appendix, Fig. S3 for comparison with, and without, inclusion of Neotragini and Cephalophini). (B) Fossil assemblages for age ranges discussed in this paper from the Kanapoi, Nachukui, and Koobi Fora Formations; data from Dataset S2.

grasses were possibly present, the selectivity for C₄ grasses by some species and for C₃ grasses by others must be invoked for such dietary differences.

Using this G:M:B ternary classification, the fossil record in the Turkana Basin shows distinctly different patterns for the early (4.3–3.0 Ma), middle (3.0–2.35 Ma), and later (2.35–1.0 Ma) time intervals compared with the modern ecosystems. Before ca. 2.35 Ma, the ecosystems had much higher percentages of C₃–C₄ mixed feeders than are found today in East and Central Africa, with all intervals having >40% C₃–C₄ mixed feeders. For comparison, only a few of the 30 modern ecosystems has such a high percentage of C₃–C₄ mixed feeders; those few are associated with forest or Afro-alpine montane ecosystems with few large mammalian herbivores (e.g., Bale and Mt Kenya). Fig. 3B shows the G:M:B ternary for the individual stratigraphic collection intervals in each of the Kanapoi, Koobi Fora, and Nachukui formations. After ca. 2.2 Ma there was an abrupt change to many more grazing taxa and overall a higher fraction of grazers than are found most of the modern ecosystems studied for comparison (Figs. 3B and 4).

The number of nonruminant grazers after 2.35 Ma is particularly striking, with between five and nine C₄ grazers—in addition to grazing bovids—in these intervals. At the generic taxonomic level with which these comparisons are made, there are only three modern nonruminant C₄ grazers in East and Central Africa: *Phacochoerus*, *Equus*, and *Ceratotherium*, although *Hippopotamus* is locally a grazer in some regions (e.g., Turkana, Nakuru). Many of the nonbovid C₄-grazing fossil taxa are extinct (*Sivatherium*, *Notochoerus*, *Eurygnathohippus*, and *Elephas*) or have switched to browsing (the *Kolpochoerus*–*Hylochoerus* lineage and *Loxodonta*). The time interval from 2 to 1 Ma is noteworthy for the number of nonruminant grazers that are not part of the modern fauna.

Thus, there are several important ecological changes in the Turkana Basin over time: The earlier time interval (ca. 4.1–2.35 Ma) was dominated by C₃–C₄ mixed feeders, whereas the time interval from ca. 2.35–1.0 Ma was dominated by bovid and nonruminant C₄ grazers (Fig. 4A). The timing of this shift in herbivore diet is consistent with previous studies that rely on taxonomic and morphological indicators (38, 39); however, the previously presumed diets are not always consistent with the isotope

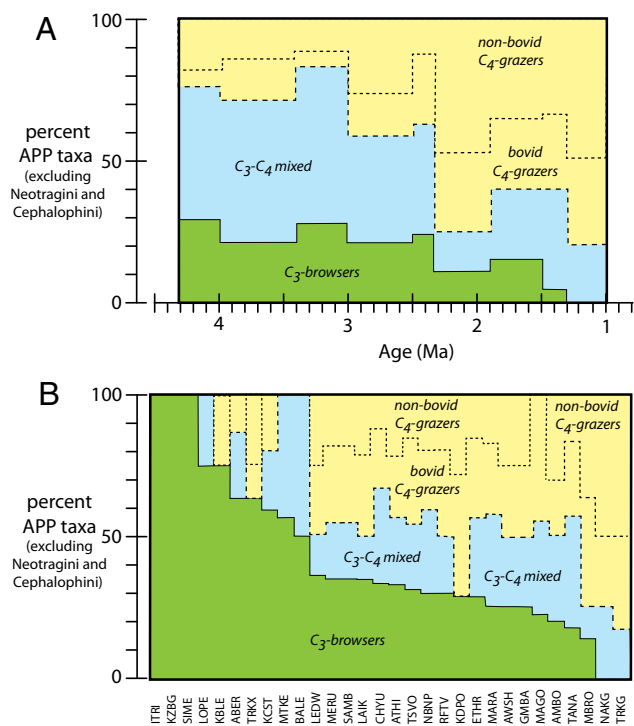


Fig. 4. Trends over time for percentages of C_3 browsers, C_3 – C_4 mixed feeders, bovid C_4 grazers, and nonbovid C_4 grazers in the Kanapoi, Nachukui, and Koobi Fora Formations and modern ecosystems in East and Central Africa for APP taxa (excluding Neotragini and Cephalophini because of their rarity in the fossil assemblages). (A) Fossil assemblages from Kanapoi, Koobi Fora, and Nachukui Formations; time intervals as described in text (data from Dataset S2). (B) Modern ecosystems studied (see SI Appendix, Table S1; data from Dataset S1).

data. Modern analog collections from East and Central Africa do not represent ecosystems dominated by C_3 – C_4 mixed feeders or nonruminant grazers (compare with Fig. 4B). After 1.0 Ma, there was a drastic transformation to the modern Africa dietary distribution, so that most nonruminant C_4 grazers either became extinct or changed their diets to browsing. The timing of the Pleistocene diet changes since 1.0 Ma is uncertain and will come into focus as samples are analyzed from this and other basins (40, 41).

The paleosol record in the Turkana Basin (11, 12, 42) shows a decrease in woody cover with an increase in C_4 biomass from 4 to 1 Ma, but changing from grassy woodland to wooded grasslands; no paleosols indicate open C_4 grasslands. Comparisons between the dietary categories and paleosol ecological reconstructions for the Shungura Formations and the Koobi Fora–Nachukui Formations will be illuminating: From 4 to 1 Ma the Shungura Formation was more wooded than the Koobi Fora and Nachukui formations.

Summary Statement. This study of the history of ecological change in the Kanapoi, Nachukui, and Koobi Fora Formations shows profound changes in ecosystem structure: For the period from 4.3 to 2.5 Ma, large mammal herbivorous taxa were dominated by C_3 – C_4 mixed feeders. No modern dietary analog to this is found in East or Central Africa. From 2.5 to 1.0 Ma, grazing taxa, especially non-bovid grazers, became increasingly abundant; modern environments in East and Central Africa do not have such a high fraction of the nonbovid grazers. Many of the C_4 grazing nonbovid herbivores became extinct between 2 and 0 Ma; in addition, some taxa that previously were C_4 grazers or C_3 – C_4 mixed feeders changed their diet to C_3 browsing. More APP taxa were present in the basin for many of the stratigraphic intervals than exist in any modern equivalent environment (e.g., compare totals for SI Appendix,

Tables S3 and S4); nowhere today in East or Central Africa is such taxonomic diversity found for the APP taxa as was found in the Turkana Basin from 4.3 to 1.0 Ma.

Interaction between the different large mammal herbivore taxa likely plays a role in diet change. In modern African ecosystems megaherbivores (>1,000 kg), particularly elephants and hippopotamus, maintain the structure and function of both wooded and grassy biomes (43, 44) and play a key role in determining the availability of food for mesoherbivores (4–450 kg; ref. 45). Therefore, changes in the diet of large herbivores throughout the 4–1 Ma time interval indicate significant alterations to mammalian dietary ecological structure and competitive interactions and may relate to shifts in vegetation structure. Ecological interactions with carnivores and primates, including hominins, may also be important for understanding the evolution of herbivore diets (46–48).

The interplay of grass expansion in the time period from 10 Ma to the present will be critical in understanding dietary changes that have occurred in the large mammal taxa in Africa. Although NPP of C_4 grasses in the tropics has gone from ca. 1% at 10 Ma to ca. 50% today, there are no known C_4 -grass macrofossils (i.e., fossils exhibiting Kranz anatomy, fossil plants with $\delta^{13}C$ values indicating C_4 photosynthesis, or both) from Africa between 1 and 10 Ma. Which specific C_4 grasses were predominant, or even present, in the Pleistocene or Pliocene of Africa (or elsewhere) is not known; such information will be key toward understanding the development of tropical grasslands and in understanding how fauna used the C_4 -grass dietary resources. Changes in digestibility, toxin level, palatability, nutrient distribution in space and in time, and relative abundances of the different C_4 grasses likely all played an important role in the evolution of the mammalian diet in Africa. These factors may be important in understanding how different APP herbivores competed for dietary resources. It is well known that C_4 photosynthesis is favored by low atmospheric CO_2 concentrations (i.e., less than 500 ppm by volume; refs. 4 and 14); the interval from 4 Ma to the present was continually below this CO_2 threshold (49–51). With each oscillation of CO_2 in the atmosphere, tropical ecosystems are subjected to stresses that could have cumulative effects on ecosystem structure with respect to the comparative success of C_3 and C_4 lineages. The role of climate change, including changes in atmospheric CO_2 , will be better evaluated when details of extinctions and diet change are better known. These records are needed to evaluate the relationships between behavioral, morphological, and environmental change, which may not be synchronous (52).

This study of the dietary history of herbivores in the Turkana Basin shows that modern animals often have diets different from those of their closest fossil relatives. Likewise, for much of the past 4 million years, the large herbivorous fauna used dietary resources in different ways than do their modern analogs.

Methods

Modern samples of APP taxa from East and Central Africa, and fossil samples from the well-dated Turkana Basin in northern Kenya, were analyzed for $\delta^{13}C$ using standard methods (SI Appendix, Detailed Methods).

Ecological comparisons for modern taxa were made based on regional ecological grouping in restricted geographic areas, such as are presented in national parks or reserves (SI Appendix, Table S1). We used the classification of White (53) for discussion of African vegetation (SI Appendix, Classification of African Vegetation).

Fossil samples were grouped by stratigraphic age, using stratigraphic boundaries that are correlated between the Koobi Fora, Nachukui, Kanapoi, and Shungura Formations (Fig. 2).

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