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ARTICLE

Stable Isotope Ecology in the Omo-Turkana Basin

THURE E. CERLING, NAOMI E. LEVIN, AND BENJAMIN H. PASSEY

Stable isotopes provide an independent assessment of paleoenvironments in the Omo-Turkana Basin. Stable isotopes track the flow of oxygen and carbon through ecosystems and accordingly are not directly related to changes in mammalian faunal composition or sedimentology. Therefore, isotope studies give insight into the paleoenvironmental conditions in which human evolutionary trends have been recorded. The development of stable isotopes as indicators of continental environmental conditions has proceeded in parallel with questions about the conditions of human environment. What was the vegetation? How hot was it? How dry? What were the diets of animals living among early humans? And most persistently, how important were "savannas" to early hominids? In this review, we take the opportunity to provide extensive background on the use of isotopes in anthropological sites. The application of stable isotope ecology to anthropological sites in the Turkana Basin has a long history, but in many ways the Omo-Turkana Basin has been a proving ground for the development of new proxy methods for understanding tropical terrestrial environments in the Neogene and Quaternary. For that reason, we also describe some of the fundamental aspects of isotope ecology that developed outside the field of paleoanthropology.

Many elements have multiple stable isotopes. Each element is characterized by having a unique number of protons in its nucleus; the number of protons and the balancing number of electrons for an uncharged atom gives it the chemical characteristics that determine its behavior in chemical reactions. Thus, hydrogen, carbon, nitrogen, and oxygen have 1, 6, 7, and 8 protons in their respective nuclei. The nucleus is unstable when only protons are packed together in it. Neutrons provide the nuclear binding energy that keeps the nucleus from flying apart. Each element has a preferred number of neutrons providing stability; for many elements more than one configuration of neutrons is allowed for stability, but usually one is strongly preferred, and hence is the most abundant isotope for that element.

These configurations are stable; that is, they are not radioactive, and thus they are called "stable isotopes." For carbon, the stable isotopes are ^{12}C and ^{13}C, with abundances on Earth of 98.89% and 1.11%, respectively. (In contrast, the radioactive ^{14}C isotope abundances in natural materials are many orders of magnitude lower than this: $^{14}C/^{12}C$ ratios are 10^{-12} or lower for natural materials.) Oxygen has three stable isotopes, ^{16}O, ^{17}O, and ^{18}O, with abundances on Earth of 99.763%, 0.0375%, and 0.1195%, respectively. In the discussion that follows, we will concern ourselves principally with the ratios of $^{13}C/^{12}C$ and $^{18}O/^{16}O$, although other isotope ratios may be important in other applications to the study of environments in the Turkana region.

To discuss stable isotope ratios, we use the conventional terminology and δ-notation:

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

R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratio in the sample and standard, respectively. The analogous expression for oxygen isotope ratios is:

$$\delta^{18}O = (R_{sample}/R_{standard} - 1) * 1000$$

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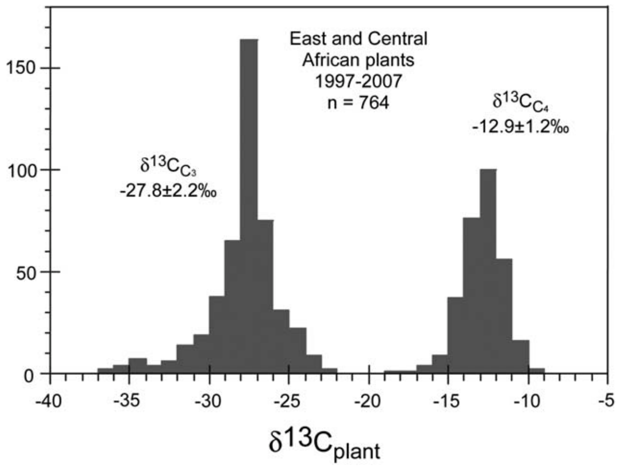

Figure 1. $\delta^{13}C$ of plants collected in East and Central Africa from 1997 to 2007 and analyzed at the University of Utah. No correction has been made for the change in atmospheric $\delta^{13}C$ due to fossil fuel burning. Such a correction would shift all values to more positive levels by about 1.2‰

For both carbon and oxygen, V-PDB is the reference standard. Thus, positive or negative $\delta^{13}C$ and $\delta^{18}O$ values simply mean that the sample has more or less ^{13}C or ^{18}O, than does the standard in units of permil (‰).

Although more and more stable isotope pairs are being shown to have differences in their naturally occurring isotope ratios, the term "light stable isotopes" generally applies to those isotope pairs with masses less than about 40 atomic mass units (that is, the sum of protons and neutrons in the nucleus). They can be analyzed using a multi-collecting gas-source mass spectrometer, which can separate isotopes in the gas phase and simultaneously measure their relative abundances.

Light stable isotopes undergo fractionation; that is, they become separated during chemical reactions or during phase transitions in many natural processes. In many cases, this is an equilibrium reaction that can readily be described in a single reaction. The fractionation factor is the relative difference in the ratios of two phases in equilibrium, such as the reaction involving water vapor in equilibrium with liquid water:

$$H_2^{18}O_{vapor} + H_2^{16}O_{liquid} = H_2^{16}O_{vapor} + H_2^{18}O_{liquid}$$

This can be expressed as an equilibrium constant

$$K_{lv} = [H_2^{16}O_{vapor} * H_2^{18}O_{liquid}]/[H_2^{18}O_{vapor} * H_2^{16}O_{liquid}]$$

$$K_{lv} = [H_2^{16}O_{vapor}/H_2^{18}O_{vapor}] * [H_2^{18}O_{liquid}/H_2^{16}O_{liquid}]$$

$$K_{lv} = [H_2^{18}O_{liquid}/H_2^{16}O_{liquid}]/[H_2^{18}O_{vapor}/H_2^{16}O_{vapor}]$$

$$K_{lv} = R_{liquid}/R_{vapor}$$

Reactions such as these lead to different isotope ratios in waters, minerals, plants, and animals. We will outline some of the ways in which these naturally occurring stable isotope ratios can be used to determine past environmental conditions.

Diagenesis can result in the recrystallization of minerals; this process can reset the isotope signal. Many studies[1–6] have evaluated diagenesis for paleoenvironmental interpretations and have established that fidelity for many isotope fields of study have straightforward relationships (for example, enamel is very robust compared to bone and dentine for deep-time isotope studies).

STABLE ISOTOPE ECOLOGY: CARBON ISOTOPES IN VEGETATION

There is a significant difference between the carbon isotope ratios found in tropical dicots (trees, bushes, herbs) and those found in tropical grasses and sedges, which are monocots. This has to do with the difference in the photosynthetic pathways of the two groups of plants. The C_3 pathway is the older pathway: in it, carbon dioxide is assimilated and reduced in the palisade cells of leaves. The Rubisco enzyme strongly discriminates against the heavy carbon isotope (^{13}C), so the products have very negative $\delta^{13}C$ values, typically -24‰ to -30‰.[7–10] In C_4 photosynthesis (so named because the first photosynthate product has four carbon atoms compared to the three carbon atoms in C_3 photosynthesis), CO_2 is assimilated in the outer mesophyll cells, then transported to bundle sheath cells. The CO_2 is made available to the Rubisco enzyme. However, in this closed environment the Rubisco enzyme consumes virtually all the CO_2. Hence, no isotope discrimination occurs and C_4 plants generally have $\delta^{13}C$ values between -11‰ and -14‰.[7,11] Figure 1 shows the distribution of $\delta^{13}C$ values for East and Central African plants collected between 1997 and 2007. A third photosynthetic pathway, Crassulacean acid metabolism (CAM), is also found in Africa, usually in succulents. However, it is generally found in relatively minor quantities in East African landscapes and will not be further discussed here other than to note that its isotopic values are usually similar to those of C_4 plants in Africa.

Several important factors in the competition between C_3- and C_4-photosynthesis have important implications for ecology and paleoecology. A by-product of photosynthesis is molecular oxygen (O_2). While oxygen is important to animals, high concentrations of oxygen have a negative effect on photosynthesis. The Rubisco enzyme can catalyze two reactions, the carboxylaze reaction (photosynthesis) and the oxygenase reaction (photorespiration); the latter reduces photosynthetic output by consuming fixed carbon without contributing to the energetic needs of the plant.

The early atmosphere on Earth had very high concentrations of carbon dioxide and negligible concentrations of oxygen.[12] That is the reverse of today's atmosphere, in which carbon dioxide is < 250 ppmV inside the leaf (that is, lower than ambient CO_2 of about 380 ppmV) and oxygen is 210,000 ppmV. In such atmospheres with a O_2:CO_2 ratio ≈ 800, C_3 plants have a tendency to make "mistakes," and the oxygen-consuming reaction takes place. This problem is exacerbated by high temperatures. In effect, the oxygen reaction "runs away" at high leaf temperatures. The strategy of C_4 photosynthesis is to increase the internal carbon dioxide concentration to values $> 2{,}000$ ppmV, thus lowering the O_2:CO_2 ratio to ≈ 100. In this way, C_4 plants suppress the photorespiration reaction.[13] Thus, the C_3 versus C_4 competition has elements of both atmospheric chemistry and temperature. Over the long history of geological time, carbon dioxide levels have been low enough to favor C_4 photosynthesis for a relatively short period of time: the last 20 to 30 million years. But today, carbon dioxide is effectively constant in the Earth's atmosphere, and temperature is an important factor for modern ecosystems. Significantly, this temperature effect is seen in the grasses: At cool temperatures, such as those found $> 3{,}000$ meters elevation in Africa, C_3 grasses are found and have the same isotope values as do the other C_3 plants.[14]

In the modern tropics, C_4 photosynthesis is almost exclusively the domain of grasses and sedges, both monocots, whereas C_3 photosynthesis occurs in almost all dicots. These dicots include woody plants such as trees, shrubs, and bushes; they also include nonwoody herbaceous plants. Another important distinction is found in C_3 versus C_4 plants: defense. Most plant toxins are found in C_3 plants, presumably as a defense mechanism, whereas C_4 plants tend to concentrate silica in phytoliths, making them more abrasive. In addition, many of the nutrients in C_4 plants are in the bundle sheath cells, which tend to be protected and are more interior in the leaf structure.[15] C_3 leaves tend to be more nutrient-rich (lower C:N ratio) than are C_4 plants, especially in the nongrowing season. These differences could be important in herbivore diet selectivity between plants using the differing photosynthetic pathways.

The fraction of C_3 versus C_4 biomass is very important in interpreting past ecosystems. Absorption of sunlight by the ground surface and the thermal mass of soils can result in high surface soil temperatures in direct sunlight. C_4 plants have an ecological advantage in conditions with high photosynthetic temperatures (that is, leaf surface temperatures)[13]; maximum daily ground surface soil temperatures in open regions can be 20° to 30°C hotter than in nearby well-shaded areas. Thus, C_4 photosynthesis is more prevalent in open conditions, where it is much hotter and light intensity is higher. Therefore, the proportion of C_3 versus C_4 plants gives an indication of the openness of the environment. Savannas, which are wooded grasslands to grasslands, in the UNESCO terminology[16] (Table 1), have significantly more open canopy (less than 40% woody canopy cover) than do woodlands to forests. Much debate over the past 40 years has concerned the role of savannas in the evolution of humans, their ancestors, and their close relatives.

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Thus, the vegetation structure of ecosystems could be expressed in the proportion of C_3 versus C_4 biomass. At the landscape scale, this could be preserved in soils or as terrestrial vegetation deposited in lakes (for example, as leaf waxes). At an individual scale, this could be preserved in mammalian diets in which animals choose to eat either C_3 plants (browsers) or C_4 plants (grazers). Absolute temperatures can be derived from the coupling of the rare isotopes of carbon (^{13}C) and oxygen (^{18}O) in the molecule $Ca^{13}C^{18}O^{16}O^{16}O$ based on different ordering relationships related to temperature.

ECOSYSTEM STRUCTURE: STABLE ISOTOPE EFFECTS

Although we have described the general isotope relationships in the C_3 and C_4 photosynthetic pathways, it is worth noting some important subtle isotope variations within each of these pathways. One notable effect is that in closed canopy forests, the $\delta^{13}C$ of C_3 plants can be very negative: -30‰ to -36‰ due to enhanced isotope fractionation at low light levels (low quantum yield) and recycling of CO_2.[17,18] This can be passed on to herbivore consumers, so that a diet comprised of closed-canopy C_3 vegetation would be very depleted in ^{13}C as compared to a normal browsing diet (for example, the Ituri Forest[19]). However, C_3 plants are

TABLE 1. Summary of UNESCO Classification of African Vegetation[a]

Classification	Definition
Forest	A continuous stand of trees at least 10 m tall, their crowns interlocking
Woodland /Bushland / Shrubland	
Woodland	An open stand of trees at least 8 m tall with a canopy cover of 40% or more
Bushland	An open stand of bushes usually between 3 and 8 m tall with a canopy cover of 40% or more
Thicket	A closed stand of bushes and climbers usually between 3 and 8 m tall
Shrubland	An open or closed stand of shrubs up to 2 m tall
Wooded grassland	Land covered with grasses and other herbs, with woody plants covering between 10 and 40% of the ground
Grassland	Land covered with grasses and other herbs, either without woody plants or the latter not covering more than 10% of the ground
Desert	Arid landscape with a sparse plant cover. The sandy, stony, or rocky substrate contributes more to the appearance of the landscape than does the vegetation.

[a] From White.[16] This classification is based on the fraction of woody canopy cover for defining different vegetations types, with forests and woodlands having more than 40% of the surface with woody canopy cover; wooded grassland having between 40% and 10% of the land surface covered with woody canopy; and grassland having less than 10% woody canopy cover. The UNESCO classification does not include a definition of savanna because of its widespread and ambiguous use; however, its definition of trees with an understory of grass would include grasslands, wooded grasslands, and grassy woodlands.

in the δ^{13}C range from about -24‰ to -30‰, with the more positive values associated with more xeric conditions and the more negative values associated with more mesic conditions.[20] This is related to stomatal regulation where, in xeric conditions, partial stomatal closure to prevent water loss results in less isotope discrimination by the Rubisco enzyme.[9]

The δ^{13}C values for C_4 plants also vary according to aridity. NADP-plants tend to have higher δ^{13}C values than do NAD-/PCK-plants; the former are more likely to be found in mesic environments and the latter in more xeric environments.[11] Within each of these pathways, more negative δ^{13}C values are found in xeric environments due to "leakage" in the bundle sheath cells, so that photosynthesis occurs in a less than completely closed system.[21]

Taken together, the mixing lines between C_3 and C_4 plants are different in mesic versus xeric environments.[20] In the former, the difference between the C_3- and C_4-plant δ^{13}C values are larger than in more xeric environments. That is, in mesic environments the end-member values for C_3- and C_4-plants may be ca. -28 and -11‰, respectively, compared to more xeric environments where they may be ca. −25‰ and −14‰, respectively. This means that the particular end-member values of δ^{13}C must be considered in evaluating past environments, resulting in inherent uncertainty in the fraction of C_3- or C_4-component estimated in any calculations.

SOIL ORGANIC MATTER AND THE CARBONATE SYSTEM

An ecosystem comprised of C_3 and C_4 plants leaves a distinctive isotope signature on the ecosystem. An ecosystem consists of both above-ground and below-ground biomass. Plants respire carbon as carbon dioxide in soils. This soil-respired CO_2 (a flux) has a very similar δ^{13}C value to the above-ground carbon. Slight differences have to do with the small differences in δ^{13}C in different chemical compounds produced by the plants, such as lignin, cellulose, and carbohydrate. Soil organic matter has residence times of 10s to 100s of years. Different compounds have different half-lives for decay but, on the whole, organic matter has a similar δ^{13}C value to the above-ground biomass. The isotope composition of soil organic matter collected from underneath the crown cover is very similar to that between canopy crowns.[22,23] This similarity is likely due to two things. First, the residence of carbon in soils is 10s to 100s of years and represents a time-integrated signal; second, the C_3 versus C_4 mix of subcanopy plants is related to the light levels and temperatures near the ground surface. Thus, C_4 plants do not become significant until the woody canopy cover falls below ca. 60%. Likewise, nonwoody C_3 plants, such as herbs and forbs, contribute to the overall soil biomass. Thus, the fraction of woody cover is not a simple mixing line between the C_3- and C_4-end members because of the presence of nonwoody herbaceous C_3 plants.

Soil CO_2 (concentration) is derived from root respiration (flux), which has a δ^{13}C value similar to that of associated plant matter, and microbial respiration, which has a δ^{13}C value similar to that of soil organic matter. Soil CO_2 increases with depth below the ground surface. The mass transport of CO_2 can be described using a diffusion-production model based on soil physics.[24] Thus, the soil CO_2 (concentration) has a different isotope value than does soil-respired CO_2 (flux) in the same soil. Soil carbonate is formed in isotope equilibrium with soil CO_2[25,26] with an enrichment in ^{13}C resulting from diffusion (ca. 4.4‰), isotope fractionation (ca. 9‰ to 12‰ depending on temperature), and mixing with the atmosphere (which results in further enrichment). The atmospheric mixing is important primarily in the upper 15 cm of soils where a steep gradient is observed; mixing at depth is important only in soils with a low res-

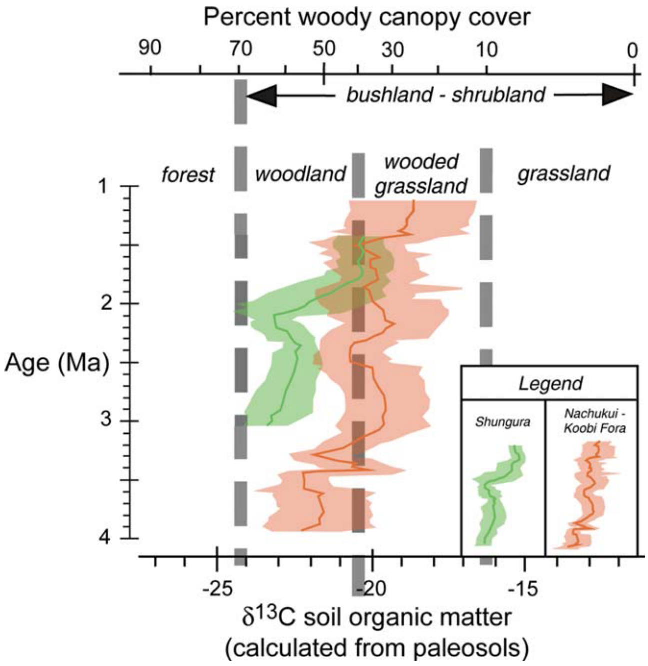

Figure 2. Long-term trends of paleosols in the Shungura compared to the Koobi Fora-Nachukui sections. $\delta^{13}C$ values from paleosol carbonate are assumed to be 14‰ enriched in ^{13}C relative to soil organic matter. Woody cover was estimated using the relationship found for modern tropical soils.[33] Solid line is a 10-point running average of $\delta^{13}C$ values; shaded area is $\pm 1\sigma$ for the 10-point running average.

piration rate. Because soil carbonate is rarely produced in the upper 25 cm of soils, the net isotope enrichment of carbonate compared to soil-respired CO_2 is generally about 14‰ to 16‰.[25]

Here we review stable isotope results from paleosols in the Omo-Turkana region. Levin and coworkers[27] studied approximately 200 soil carbonate nodules, principally from vertisol type paleosols in the Shungura Formation in the lower Omo Valley and in the Koobi Fora and Nachukui Formations, which, respectively, are on the eastern and western shores of Lake Turkana. This work builds on the earlier work of Cerling,[28,29] Wynn,[30,31] and Quinn,[32] which was restricted to the Omo Group sediments within Kenya, and showed an increase in the $\delta^{13}C$ and $\delta^{18}O$ values after about 1.9 Ma. These results suggested an increase in the fraction of C_4 biomass in the local ecosystems and a change in the water cycle toward more enriched ^{18}O in soil water.

The study by Levin and coworkers[27] includes the Shungura Formation, which outcrops near the basin axis and provides valuable comparison to a different part of the basin, whereas much of the Koobi Fora and Nachukui Formations are more representative of basin margin sedimentation. In Figure 2, we show the long-term trends of paleosols in the Shungura compared to the Koobi Fora-Nachukui sections. This figure also includes the estimated woody cover of the environment based on measured soil organic matter and woody canopy cover. Before ca. 1.9 Ma, the Shungura environment was woodier than the Koobi Fora-Nachukui environments. The older Shungura is represented by an ecosystem that was ca. 65%-30% woody cover; using the UNESCO classification, this would be termed a "woodland or forest," likely a riparian forest. After 1.9 Ma, the Shungura region was less woody, on the order of 40% canopy cover, which would be more akin to wooded grasslands to grassy woodlands, and what is commonly called "savanna" in Africa today. The Koobi Fora-Nachukui Formations show a slight decrease in the fraction of woody cover over time; from 4 to 3 Ma, the fraction of woody cover was ca. 50%, and decreased to values between 30% and 40% from 3 to 1.5 Ma. There was another increase in woody cover to ca. 25% after 1.5 Ma. Thus, wooded grasslands have been the dominant ecosystem in the region represented by the Koobi Fora and Nachukui Formations.

STABLE ISOTOPE ECOLOGY: MAMMALIAN DIETS

Stable isotopes provide important information concerning diets of mammals in several ways, including the testing of assumptions concerning diets of certain lineages; monitoring changes in the diets of individual lineages over time; and providing an ecological "snapshot" of mammalian diets in the overall ecosystem with respect to browsing and grazing.

Background: The Relationship Between Diet and Animal Tissues

In the 1980s, it was shown that animal tissues recorded dietary preferences for C_3 and C_4 plants in herbivores.[34] This was certainly true for modern animals, but there was a period of controversy concerning the preservation of the diet signal for fossils.[35,36] Lee-Thorp and van der Merwe[37] showed that fossil tooth enamel was a faithful recorder of diet in fossils. Enamel is originally composed of large crystals, whereas bone and dentine are originally composed of micro-crystallites.[3] Dentine and bone crystallize in diagenesis to large crystals,[3] and in so doing have the opportunity to exchange carbon and oxygen isotopes.[4] Thus, enamel can be used for isotope studies of paleodiet using bioapatites, whereas bone, dentine, and cementum are considered to be highly susceptible to diagenetic alteration.

The isotope enrichment between diet and enamel is about 14‰ for ruminant mammals.[38] Passey and colleagues[39] showed that there was slight variation in this fractionation for herbivores, with nonruminants having a fractionation factor nearer to 12‰. Further, this study resolved the apparent conflict between different diet studies[38,40-42] and overall fractionation factors by showing that blood CO_2-bioapatite has a constant fractionation factor and that differences in animal physiology, which likely are related to methane production, were responsible for the differing overall isotope enrichments between diet and enamel.

Comparison of Fossil Diets with Modern Equivalents

Diets of modern mammals are often used as analogues for the diets of fossil mammals. Diets of most modern mammals are similar to those of their ancestors in the fossil record of 1-2 Ma; for example, alcelaphines, reduncines, hippotragines, and equids are grazers, as were their presumed ancestors; tragelaphines and giraffids are browsers, as were their presumed ancestors. The $\delta^{13}C$ of most bovids is similar to that expected from the literature.[20] However, stable isotopes have provided some surprises. Modern elephants (*Loxodonta*) are predominantly browsers, whereas their ancestors were predominantly grazers[43]; modern forest hogs (*Hylochoerus*) are browsers, but between 1 and 2 Ma their presumed ancestor, *Kolpochoerus,* was a grazer (compare Harris and Cerling[44] with Cerling and Viehl[45]). The difference in elephant behavior is striking. Modern ecologists consider that elephants are crucial in maintaining the savanna environment because of their destructive feeding behavior on trees. For millions of years, most of the elephantids (*Loxodonta*, *Elephas*, *Anancus*) were grazers: What, then, was the role of elephants in savanna dynamics?

Changes in Diets of Individual Lineages Over Time

The detailed chronology provided in the Omo-Turkana Basin, along with the abundant fossil remains, provides an excellent opportunity to compare mammal diets over time. Through the past 4 Ma, three lineages stand out as having undergone important changes: elephants, sivatheres, and suids (Fig. 3).

The modern elephant is primarily a browser. On an annual basis, about 80% of elephant diet comprises C_3 plants; for short times during the rainy season, they switch to a C_4-grass-rich diet.[46–48] However, fossil elephants in the Omo-Turkana Basin were predominantly grazers, with C_4 grass making up ca. 80% of their diets. What we don't yet know is whether this was a constant diet throughout the year or if, in a reversal of today's situation, they had brief periods of intense browsing. The fossil record does show that until ca. 0.2 Ma, the grazing elephant was present in the Omo-Turkana Basin; no browsing elephantids were found. Genetic evidence suggests that elephants went through an important "bottleneck" between ca. 50 and 150 ka.[49] Clues to understanding changes in elephant diets are likely related to this event.

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Suids have long been used in the Turkana Basin as markers of time because of their rapid evolution.[50–52] Through time, the length of the third molar increased and the tooth became more highly crowned; this was thought to be an adaptation for grazing, and provided an excellent case study for stable isotope paleoecology. Indeed, the *Nyanzachoerus-Notochoerus* lineage changed from a predominantly C_3 diet at 7 Ma in the Lothagam sequence to a grazing diet by Tulu Bor Member times (lower part of the Koobi Fora Formation) as the molar length increased from 40 to 90 mm.[44]

Sivatheres provide a third striking example of diet change over time. These large giraffids had shorter necks and limbs than does the modern giraffe *Giraffa camelopardalis*. Over time, as the sivathere's limbs became shorter, it gradually changed its diet from being a browser, at 4 Ma, to being a grazer by 1.7 Ma.[53]

Figure 3 also shows the long-term dietary patterns for hippos and deinotheres. Deinotheres always had a diet dominated by C_3 plants. The constancy of its $^{13}C/^{12}C$ ratio over time is strong evidence that diagenesis does not reset the carbon isotope values of tooth enamel. The $\delta^{13}C$ values for hippos shows that their diet is predominantly C_4 in the Turkana Basin. Modern hippos have a significant range in $\delta^{13}C$ values. The increasingly high fraction of C_4 plants in the hippo diet after 2 Ma suggests that grasses were more abundant after 2 Ma than before 2 Ma.

Other examples, certainly in deeper time, will reveal changes in diets. The C_4 ecosystems expanded in Africa in the late Miocene, so that that before 10 Ma all mammals were C_3-feeders. Recent work[54] documents the different strategies of various mammalian lineages to this change in ecosystem structure and food resources. Equids were the first lineage to fully use the C_4-resource in diet. Use of C_4 plants as a principal dietary resource followed more slowly for other lineages. Thus, proboscideans changed to the C_4 resource more slowly, but were dedicated grazers by 6.5 Ma. Deinotheres prove an exception among the proboscideans and, as noted, have been browsers throughout their dietary history. Hippos and some bovids also gradually adapted to diets comprised principally of C_4 plants. These results have been published relatively recently; our understanding of the drivers of dietary change in this period is incomplete.

Diet of *Paranthropus boisei*

In 2010, the National Museums of Kenya (NMK) initiated a stable iso-

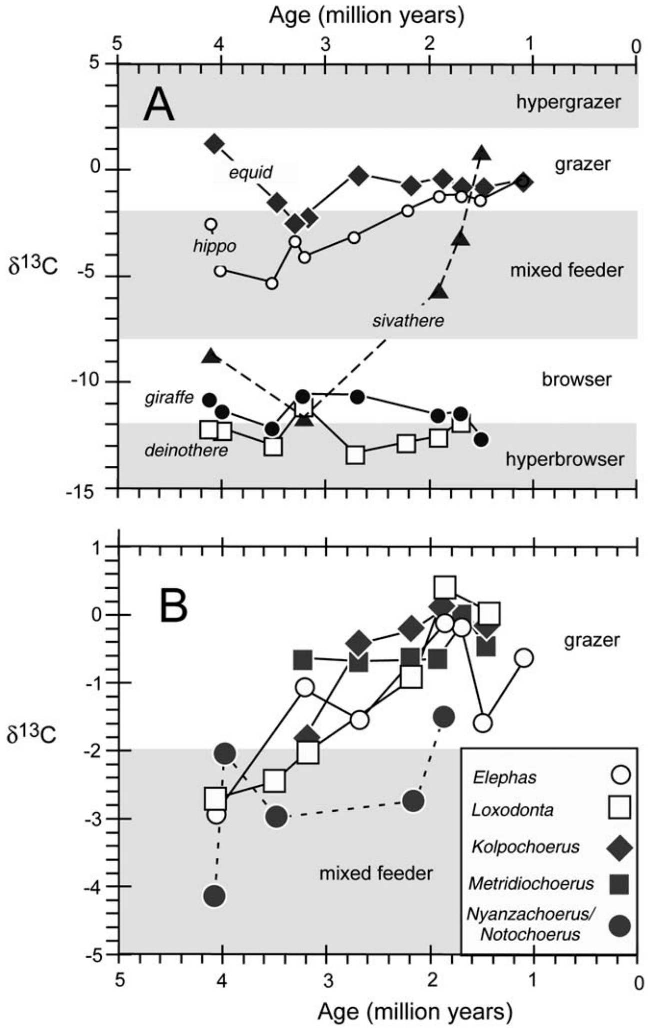

Figure 3. Trends in $\delta^{13}C$ of selected mammals from the Turkana Basin with time, with ranges of $\delta^{13}C$ following Cerling and colleagues:[20] hypergrazers (> 2‰), grazers (+2 to -2‰), mixed feeders (-2‰ to -8‰), browsers (-8 to -12‰), and hyperbrowsers (> -12‰) There is no evidence for feeding in a closed canopy (> -15‰). A. Equids, hippos, sivatheres, giraffes, and deinotheres. B. Elephantids (*Elephas* and *Loxodonta*) and suids.

tope study of hominins from the Turkana region. The first group studied was *Paranthropus boisei*, the iconic "Nutcracker Man," whose large sagittal crest and large molars indicated a powerful masticatory apparatus. This study followed on an early, more limited study in the Olduvai region,[55] which suggested a diet dominated by C_4 plants, most likely grasses or sedges. The NMK study[56] showed definitively that *P. boisei* had a C_4-dominated diet over a wide time interval and a large geographic region, from Olduvai to the northern Omo-Turkana Basin (ca. 1000 km), with a likely much larger range. Twenty-two different individuals had a diet that averaged 77 ± 7% C_4 biomass. This is the highest fraction of C_4 biomass observed in any haplorrhine primate (fossil or modern). Such a high fraction of C_4 biomass in the diet means that it is unlikely to have been competing with coeval hominins for diet resources over the interval from 2 to 1.5 Ma.

THE WATER CYCLE

Oxygen isotopes provide important insight into the role of water in ecology. The meteoric water cycle in stable isotope space has several important effects that result in changes to the isotope composition of water. While water is not preserved in the geological record, it is imprinted in the $\delta^{18}O$ of both soil carbonates and biogenic apatites (for example, tooth enamel). A particularly important process is that of evaporation, in which the light isotope (^{16}O) is preferentially lost to the atmosphere, while residual water, such as is found in lakes, leaves or soils, can become highly enriched in ^{18}O.

The $\delta^{18}O$ of soil carbonates is related to the isotopic composition of soil water, but also to the temperature of carbonate formation. Changes in the $\delta^{18}O$ of soil carbonates are observed in the geologic record,[27–32] but the precise interpretation is difficult because changes could be independently ascribed to temperature, evaporation, changes in storm tracks, or combinations of these.

WHAT OF THE FUTURE? STABLE ISOTOPES AS NEW AND INDEPENDENT MEASURES OF ECOLOGY

Work on rodents by Kyalo Manthi of the National Museums of Kenya is under way. Preliminary results show that the isotopes of micromammals will be yet another useful indicator of ecology. Rodents have smaller home ranges than do larger mammals (although these are complicated by transport of predators), and so may indicate more about local conditions than do larger mammals. Previously, the study of rodent tooth has been hampered because of their small size and the need to separate enamel from dentine. Passey and Cerling[57] improved laser applications to small samples and showed that the *in situ* analysis of individual rodent teeth is possible.

The dietary evolution of bovids is being studied by Francis Kirera. The bovids will provide an interesting case study through time because they partition dietary resources of grass and browse. The evolution of diet change in bovids is likely to be particularly instructive as it is studied in parallel with their radiation in the Neogene. Preliminary results indicate that the fairly robust distinction between grazing and browsing bovids is recent; there were many more mixed-feeder bovids between 4 and 1 Ma than there are today in eastern Africa.

Studies of hominin diets began in South Africa,[58–61] Tanzania,[55] and Ethiopia.[62] These studies have shown that all hominins have a component of C_4 biomass in their diet, indicating a use of savanna resources by at least 4 Ma. Among sampled hominins, *Ardipithicus* has the lowest fraction of C_4 biomass in the diet, with estimates of a minor amount of C_4/CAM biomass in the diet at > 4 Ma.[62] We have described initial work on hominins from the Omo-Turkana Basin.[56] Future work through NMK will compare individual lineages in time and compare co-eval lineages. These studies will enhance understanding of the evolution of diets in humans and their ancestors.

The water balance of past ecosystems has always been an intriguing question. How wet or dry was it in the past? Quantification of aridity has always been elusive to terrestrial sedimentologists. Isotopes provide a route to quantifying this parameter. Levin and colleagues[63] have developed an approach to this by showing that certain mammals have a high dependence on meteoric water, whereas other mammals show increasing independence as they derive water from other sources, such as leaves. Thus, comparison of oxygen isotopes in hippos and giraffes is a promising line of inquiry to quantify paleo-aridity because the $^{18}O/^{16}O$ ratio of leaf water is sensitive to aridity, whereas that of meteoric water is relatively insensitive.

Absolute soil temperatures can be measured by studying the coupling of the rare ^{13}C isotope with the rare ^{18}O isotope. The "Holy Grail" of isotope geochemistry has been to determine paleotemperatures. The basis for paleothermometers is the observation that chemical reactions, including isotope exchange reactions, are temperature sensitive. In traditional studies, the derived equation has three parameters: temperature, the isotope composition of water, and the isotope composition of calcite. In the fossil record, only the latter can be measured, and any such measurement has a field of possible temperatures, each coupled to a particular isotope composition of water. However for the reaction:

$$Ca^{13}C^{16}O_3 + Ca^{12}C^{18}O^{16}O_2$$
$$= Ca^{13}C^{18}O^{16}O_2 + Ca^{12}C^{16}O_3$$

only calcium carbonate is present, so that the isotopologue distributions of $CaCO_3$ molecules can be solved uniquely for temperature and $\delta^{18}O$ of the water in which the mineral formed. (An isotopologue is a unique combination of isotopes within a molecule; the preceding equation shows four different isotopologues of $CaCO_3$). This method is colloquially called the Δ_{47} method because it represents the difference between the measured mass 47 ($={}^{13}C^{18}O^{16}O$) and a randomly $^{13}C^{18}O^{16}O$ mixed molecule[64] derived from the $CaCO_3$ molecule through reaction with phosphoric acid. This determination requires simultaneous high-precision measurements of all isotopologues. Passey and colleagues[65] used this method to show that soil temperatures for the past ~4 Ma in the Turkana Basin have been between 30°C and 40 °C. Such high temperatures have been corroborated in modern soils in the region in areas of dwarf shrubland. This suggests that for much of the past 3 Ma, the Turkana region has been a relatively open, hot environment. Today, it has one of the hottest mean annual temperatures (ca. 30°C) on the planet. The preliminary results of this method have been reported,[65] but concurrent studies of modern soil formation processes, along with monitoring of soil temperatures in different environments, are ongoing. When those are further along, we will be better able to evaluate the compatibility of such high temperatures with estimated woody cover. We anticipate that results to be obtained in the next five years, coupled with our understanding of the relationship of woody cover to soil temperatures and soil carbon isotopes, will greatly enhance our understanding of the environments of early hominins. This will give indications of the "patchiness" of the landscape in terms of temperature, shade, shelter, and food resources.[33]

Studies of hominin diets began in South Africa,[58–61] Tanzania,[55] and Ethiopia.[62] These studies have shown that all hominins have a component of C_4 biomass in their diet, indicating a use of savanna resources by at least 4 Ma. Among sampled hominins, *Ardipithecus* has the lowest fraction of C_4 biomass in the diet...

Seasonality is also a difficult parameter to quantify in terrestrial ecosystems in the fossil record. The problem is having a "clock" that can resolve and record seasonality. Fossil teeth in some mammals take more than a year to develop. However, the maturation of enamel scrambles the signal so that considerable overprinting occurs. Signal processing, a method commonly used in seismology to study periodic signals, offers an opportunity to "unscramble" isotopes recorded in tooth enamel.[66] Thus, seasonality in diet and drinking water, as recorded by stable isotopes in teeth, can be studied as maturation parameters are characterized for different mammals. Kevin Uno is studying enamel maturation in elephants to understand seasonal diet changes in elephants.

A promising area of research is the analysis of the stable isotopes of complex individual organic molecules. Because of their complexity, such molecules do not undergo significant fractionation during degradation. Therefore, each surviving molecule has the potential for ecological characterization. Leaf waxes, lipids produced by soil bacteria, and algal molecules, have the potential to further characterize humidity, soil temperatures, and water temperatures, respectively. Compounds produced uniquely by certain classes of plants, such as sedges, are being explored because they offer the tantalizing possibility of further characterizing the kinds of plants in, and their distribution across, the African landscape at various scales. These methods are currently in development and are being applied to the Omo-Turkana group sediments by Kendra Chritz, Katherine Freeman, and Clayton Magill.

SUMMARY

Stable isotopes provide unique insight into the paleoecology of the Turkana Basin. Their principal use has been to better understand the distribution of C_3-plants, which are primarily trees, shrubs, and nongrassy herbaceous plants, and C_4-plants, which are primarily grasses and sedges. Stable isotope studies of modern and ancient soils show that the dominant environment in the region was equivalent to wooded grassland, with 10% to 40% woody canopy cover. Some open grasslands (< 10% woody canopy cover) and woodlands (> 40% woody canopy cover) were present, but on the whole this ecosystem had significant areas of open habitat. The Shungura region was more densely wooded than were the Koobi Fora and the Nachukui regions. Absolute estimates of paleotemperatures from paleosol carbonates show that climate was similar to that of the region today. Most mammals had diets similar to their modern counterparts, but there were some significant differences. The elephants were primarily grazers, whereas the modern elephant in is primarily a browser. Morphological changes in some mammals, such as the dentition of suids, changed systematically along with change from browsing to grazing.

Continued use of isotopes in exploring the environments of human evolution will open new areas of isotope research in the coming decade. This will greatly enrich our knowledge base for interpreting human evolution and behavior in the Turkana Basin and elsewhere.

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