Corrections

ANTHROPOLOGY; EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES

The authors note that on page 10501, left column, line 13 of the abstract, “ca. 35/65 ratio” should instead appear as “ca. 65/35 ratio.” Both the online article and the print article have been corrected.

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COMMENTARY

The author notes that on page 10470, middle column, first paragraph, lines 13 and 16, “$\partial^{13}$C‰” should instead appear as “$\delta^{13}$C‰.”

Also, on page 10471, middle column, first paragraph, line 3 “65%” should instead appear as “35%.”

Both the online article and the print article have been corrected.

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Stable isotope-based diet reconstructions of Turkana Basin hominins

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Hominin fossil evidence in the Turkana Basin in Kenya from ca. 4.1 to 1.4 Ma samples two archaic early hominin genera and records some of the early evolutionary history of Paranthropus and Homo. Stable carbon isotopes in fossil tooth enamel are used to estimate the fraction of diet derived from C3 or C4 resources in these hominin taxa. The earliest hominin species in the Turkana Basin, Australopithecus anamensis, derived nearly all of its diet from C3 resources. Subsequently, by ca. 3.3 Ma, the later Kenyanthropus platyops had a very wide dietary range—from virtually a purely C3 resource-based diet to one dominated by C4 resources. By ca. 2 Ma, hominins in the Turkana Basin had split into two distinct groups: specimens attributable to the genus Homo provide evidence for a diet with a ca. 65/35 ratio of C3 to C4-based resources, whereas P. boisei had a higher fraction of C4-based diet (ca. 25/75 ratio). Homo sp. increased the fraction of C4-based resources in the diet through ca. 1.5 Ma, whereas P. boisei maintained its high dependency on C4-derived resources.

Theropithecus | hominid

Many approaches have been used to reconstruct the diet of early hominins. Some of the methods focus on the functional morphology of the masticatory system, others focus on tooth wear (both macroscopic and microscopic), and yet others focus on the physicochemical signatures that an animal’s diet leaves within its hard tissues (1, 2). Chemical methods include the use of strontium/calcium and barium/calcium ratios (3, 4), but this study focuses on the analysis of stable isotopes of carbon (5–9).

Modern tropical ecosystems differ from those ecosystems that predate the late Miocene. Tropical grasses were rare until the late Miocene, when they greatly expanded in abundance; therefore, by the latest Miocene and Pliocene, many mammals had changed their diets, and some had become dependent on this relatively new dietary resource (10, 11). The study of this dietary evolution is based on the difference in carbon isotope ratios of plants that use either the C3 or C4 photosynthetic pathway (12). Plants using the C3 pathway have δ13C values that range between ca. −24‰ and −32‰ (13); the more positive values are associated with xeric environments, intermediate values are associated with mesic environments, and the most negative values are associated with closed canopy environments (14, 15). Plants using the C4 pathway have δ13C values that range from about −10‰ to −14‰, with more positive values associated with mesic environments and more negative values associated with xeric environments (16). In the tropics, C3 plants are primarily trees, shrubs, and nongrassy herbs and forbs; C4 plants are primarily grasses and sedges, with some rare dicots. A third photosynthetic pathway, Crassulacean acid metabolism, has δ13C values similar to C4 plants in the tropics; Crassulacean acid metabolism plants are mostly succulents in the African tropics and make up a minor but potentially important dietary resource in some circumstances. Carbon stable isotope values of animal tissues (e.g., bioapatite) are enriched in 13C compared with the diet; for large herbivorous mammals, bioapatite is enriched by ca. 12–14‰ relative to dietary materials (5, 17, 18).

Thus, the δ13C of fossil tooth enamel can distinguish between diets that are predominantly based on C3 resources (leaves and fruits from trees and shrubs along with nongrass forbs and herbs and their fruits) and diets that are predominantly based on C4 resources (primarily grasses or sedges). Meat and most other organic tissues are only slightly enriched in 13C compared with the plant-derived diet (19). Stable carbon isotopes in tooth enamel are unable to distinguish between plant- and meat-based (or insect-based) diet, but they can be used to trace the diet back to the ultimate resource: C3 or C4 plants.

The Turkana Basin has an excellent, well-dated record (20–23) of hominin fossils from ca. 4 Ma to the present. Thus, the diets of the hominin taxa represented at sites within the Turkana Basin (Fig. 1) can be used to study dietary preferences within the hominin clade across this time interval. All samples come from collections held at the National Museums of Kenya in Nairobi. We analyzed 110 teeth from 94 different individual hominins for their stable carbon isotopes. For practical reasons, we could not always sample specimens with unambiguous taxonomic assignments, and in some cases, we could sample only associated material. Therefore, we discuss the results in the context of generic rather than specific taxonomic attributions. The genera that we discuss include Australopithecus (ca. 4 Ma), Kenyanthropus (ca. 3–3.6 Ma), Paranthropus (ca. 2.5–1.4 Ma), and Homo (ca. 2.3–0.01 Ma). We use the taxonomy favored by Wood (24) and Wood and Leakey (25), although we make no distinction among earlier Homo species (e.g., H. habilis and H. rudolfensis) because of the limitations of the size and quality of the sample. We then compare the results of our analysis of hominins from sites in the Turkana Basin with data from hominins recovered at other locations in eastern and southern Africa.

Results

In this section, we present the results of the stable isotope analyses. We group the Turkana Basin hominin specimens by their geological age (Fig. 2 and Table S1) and discuss the taxa represented in each of the major age groupings.


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See Commentary on page 10470.

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For 10 individuals, stable isotope ratios $\delta^{13}C$ from densely forested environments in eastern Democratic Republic of Congo have $\delta^{13}C_{1750}$ values of $-11.2 \pm 1.1\%$ (8). $\delta^{13}C_{1750}$ refers to isotope values corrected for the anthropogenic addition of $^{13}C$-depleted CO$_2$ to Earth’s atmosphere (Methods), whereas gorillas (Gorilla beringei) from densely forested environments in eastern Democratic Republic of Congo have $\delta^{13}C_{1750}$ values of $-13.5 \pm 1.2\%$ (n = 1) (Table S1). Tooth enamel from modern baboons (Papio) from Kenya and Ethiopia have $\delta^{13}C_{1750}$ values that average $-9.1 \pm 3.1\%$ (n = 19) and range from ca. $-13\%$ to ca. $-2\%$; baboons from forested regions in Democratic Republic of Congo have $\delta^{13}C_{1750}$ values that average $-12.2 \pm 2.3\%$ (n = 5) (Methods and Table S1).

Thus, the $\delta^{13}C$ results for Au. anamensis suggest either a C$_2$-dominated diet or a diet with a small C$_3$ component. Published $\delta^{13}C$ values for Ardihiphicus ramidus are similar: $-10.2 \pm 1.0\%$ (n = 5) (27). Intertaxon comparison using ANOVA shows that the diets of Au. anamensis, Ar. ramidus, and modern G. camelopardalis (Tsavo) are indistinguishable in $\delta^{13}C$ space, but the diets of all three taxa are significantly different ($P < 0.0001$) from G. beringei from forested habitats (Fig. S1 and Table S1). As is seen below, the diet of Au. anamensis differs from the diet of all later hominins from the Turkana Basin.

### 3.4–3.0 Ma. K. platyops is found in the Turkana Basin between ca. 3.0 and 3.4 Ma (28). The only hominin recovered from deposits of similar age in the Awash region of Ethiopia is Au. afarensis (29); 21 teeth from 18 different individuals assigned to K. platyops were analyzed. The observed range in $\delta^{13}C$ of this sample (average = $-6.2 \pm 2.7$, n = 20; maximum = $-2.7$, minimum = $-11.1$) is broader than any other hominin included in this study. The only other hominins with such a large range of values are Au. afarensis (average = $-7.5 \pm 2.6$, n = 20; maximum = $-2.9$, minimum = $-13.0$) (30) and Au. africanus (average = $-6.5 \pm 2.3$, n = 23; maximum = $-1.8$, minimum = $-11.3$) (data in refs. 6, 8, and 31). Compared with modern taxa with a similar sample size, the range and SD for K. platyops is broad and large, respectively (14, 32). The $\delta^{13}C$ values for the 18 K. platyops individuals are normally distributed,
and the Akaike Information Criterion (33, 34) does not support a bimodal distribution for this population.

One hominin individual (KNM-ER 5431 F) in this time range is assigned to Homininae indet. It is of about the same age as the K. platyops samples discussed above, and its δ13C value (−4.3‰) is within the range of K. platyops.

Modern Papio in East Africa has a similarly wide range of δ13C values. Papio from the Laetoli region of Kenya have values similar to the higher observed values.

2.5–2.3 Ma. Six teeth from five individual hominins in this time range were analyzed in this study. Four individuals attributed to P. aethiopicus had δ13C values ranging between −0.3‰ and −5.1‰. Three of these individuals (KNM-WT 16005, KNM-WT 38351, and KNM-WT 38353) have a very narrow range of δ13C values—from −4.4‰ to −5.1‰. The fourth individual attributed to P. aethiopicus, KNM-WT 17000, is an outlier compared with the other three Panthropus of this age range. Taken together, P. aethiopicus has a diet with a consistently high C4 component (ca. 50% or greater) in this time interval.

One specimen has been assigned to Homo sp. indet. (KNM-WT 42718) (35), and it gave a δ13C value of −7.2‰, which is outside the range of the P. aethiopicus specimens of the same age, although the sample size of P. aethiopicus from this time interval (n = 4 individuals) is small.

1.99–1.67 Ma. The sample from this temporal interval includes two morphologically distinctive hominin taxa, P. boisei and Homo sp. indet.: 13 teeth from 13 different individual P. boisei specimens have an average δ13C value of −1.6 ± 1.0‰ ranging from 0.2‰ to −3.4‰. These values represent a diet dominated by C3 resources (i.e., a C3/C4-based resources ratio of ca. 25/75). The 16 Homo sp. indet. specimens have δ13C values significantly different (P < 0.001, ANOVA, Tukey posthoc) from the P. boisei individuals in the same age range (−7.0 ± 1.5‰, n = 16; i.e., a C3/C4-based resources ratio of ca. 65/35).

Two specimens in this time interval have proven difficult to classify. One of these specimens, KNM-ER 1482 (a taxonomically enigmatic mandible) (24, 36, 37), has a δ13C value of −0.4‰. The other, KNM-ER 2607 (a taxonomically enigmatic lower molar fragment) (24, 36, 38), has a δ13C value of −9.2‰.

1.65–1.45 Ma. Both P. boisei and Homo sp. indet. are represented among the specimens from this time interval. The P. boisei individuals (n = 14) have an average δ13C value (−0.9 ± 1.2‰) that does not differ statistically from the P. boisei individuals in the 1.99–1.67 Ma time range. The −0.9 ± 1.2‰ value corresponds to a C3/C4-based resources ratio of ca. 20/80.

Ten Homo sp. indet. specimens in this age range have an average δ13C value of −4.3 ± 1.1‰ (i.e., a C3/C4-based resources ratio of ca. 45/55). The Homo sp. indet. individuals in this age range differ significantly from the coeval P. boisei sample (ANOVA, Tukey posthoc test, P < 0.001), and they also differ from Homo sp. indet. individuals from the earlier (1.99–1.67 Ma) time range in that there is a ca. 20% increase in the C4 diet component (ANOVA, Tukey posthoc test, P < 0.001).

Two specimens that cannot be easily assigned to either Homo sp. indet. or Paranthropus, KNM-ER 2593 and KNM-ER 42705, were both found in the Area 6/6A region near Ilorot, where many P. boisei specimens have been recovered. They have δ13C values similar to the values of Paranthropus from Area 6/6A and may well be attributable to this genus.

0.01 Ma. Five teeth from four individual hominins from the Galana Boi Formation (Holocene) have an average δ13C value of −4.8 ± 2.3‰ (i.e., a C3/C4-based resources ratio of ca. 50/50). These values are not significantly different from the earlier Homo sp. indet. samples.

**Oxygen isotopes.** The range of variation of the stable oxygen isotopes (δ18O) among the groups discussed above is between 0.7‰ and −1.8‰ (the individual range is from ca. +4‰ to −4‰); SDs within each group are ca. ±1.5‰. These values and ranges of variation are equivalent to water-dependent species such as suids and elephantids (39) as well as carnivores and omnivores. δ18O as a function of time comparing the different hominins is shown in Fig. S2.

**Discussion**

**Diets of Early Hominins: C3- and C4-Based Resources.** We use the terms C3- and C4-based resources throughout our discussion, because our isotopic method cannot distinguish between a plant-based diet, a meat-based diet, and an omnivorous diet. Thus, based on isotopes alone, we consider that the diets of the early hominins that we have investigated could be primarily herbaceous (C3 and C4 plants), or they could be a secondary C3- or C4-based diet, an apparent C3- or C4-dominated diet, or an omnivorous diet. A secondary C3- or C4-based diet could be a meat- or insect-based diet (in which the δ13C values are derived from the basal herbaceous diet of the prey). An apparent C3-based diet is one based on aquatic resources in which algae have elevated δ13C values because of bicarbonate uptake during photosynthesis (40); for this example, algae or fish then have δ13C values with an apparent C4 component (41, 42). Lastly, an omnivorous diet is a combination of the above resources: primary herbaceous diet along with secondary C3- or C4-derived components (i.e., meat or insects) or apparent components (i.e., aquatic).

The stable carbon isotope signature of a meat-based diet depends on the nature of the prey: small bovid herbivores less than ca. 10 kg (e.g., dik-dik and other neotragines) tend to be browsers and have C3-based diets (14, 32), whereas large herbivores can have diets that are C3-based (browsers such as most tragephelines, black rhinos, and giraffes), C3-based (grazers such as warthogs, zebras, aelaphines, reducines, and bovines), or mixed (i.e., impala, and some gazelles). Thus, the size of prey may be important in considering possible secondary diet C3 or C4 resources. Other small mammals (e.g., hyrax, lagomorphs, or rodents) could have been an important dietary resource and would contribute to isotope mixing lines between C3- and C4-based end member values.

**Evolution of Hominin Diets Between 4 and 1.4 Ma in Eastern Africa.**

The earliest hominin taxon sampled in this study, the ca. 4 Ma *Au. anamensis*, has a diet comprised primarily of C4-based resources (an average ca. 90/10 ratio of C3/C4 diet resources with a range from 100/0 to 80/20 for C3/C4 resources). This finding is not entirely unexpected, because the diets of the obvious outgroups for hominins, *Pan* and *Gorilla*, are both predominantly C3-based (43–45). It is impossible to refute the hypothesis that some C4 resources contributed to the diet of these *Au. anamensis* individuals, and we do not attempt to do so. The observed δ13C range of *Au. anamensis* is narrow, and it is similar to the slightly older *Ar. ramidus* found in the Awash region of Ethiopia (27). A diet with this carbon stable isotope signature is likely dominated by plant foods. The only alternative is a diet based on meat/insect resources based on animals that themselves consume almost entirely C3 resources. However, note that initial surveys of fossil mammals from the Turkana region show that, by 7 Ma and on, most herbivores in the Turkana Basin had C2-based diets (10, 11, 46, 47). Thus, *Au. anamensis* would have to have been a very specialized hunter if meat were a significant portion of the diet, because the prey would have to have been exclusively C3 consumers.

By 3.5 Ma, the diet of the hominins that we sampled had expanded to include significant C4 resources. The diet of *K. platyops* shows a broad range, with some individuals having strongly C3-based diets and others having C4-dominated diets. The range of values for 18 *K. platyops* individuals corresponds to δ13C diet average values of ca. −25‰ to −17‰; the average *K. platyops* diet corresponds to a C4/C3-based resources ratio of ca. 60/40, but the range of the C3/C4-based resources ratio, 95/5 to 35/65, is wide. This wide range of dietary C3 vs. C4 resources suggests that *K. platyops* expanded into a dietary niche hitherto unexploited by

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hominins in the Turkana Basin. δ13C values of Au. afarensis (30), another hominin taxon in East Africa of similar age, and Au. africanus in southern Africa of less certain age (6, 8, 31) similarly have a wide range of δ13C values. The work by Sponheimer et al. (48) discusses these similarities and differences in more detail.

One individual in the small sample of P. aethiopicus, the KNM-WT 10000 cranium (49), deserves special comment. Its left M2 has a δ13C value of −0.35‰, indicating a C3-dominated diet (ca. 15/85 for the C3/C4 diet ratio), which is a diet similar to the P. boisei sample in the later time range. The dietary breadth within Paranthropus by ca. 2.3 Ma needs to be investigated with additional samples and analyses.

Between 2.0 and 1.4 Ma, numerous P. boisei and Homo sp. indet. specimens show that the diets of the two genera were distinct, with Paranthropus having a diet comprised of a 20/80 C3/C4 diet ratio, whereas Homo sp. indet. shows C3/C4-derived ratio values that range from 25/75 to 45/55. Previous comparisons with southern African fossils suggest that P. boisei from East Africa had a diet that was much narrower in terms of C3/C4 resources than P. robustus from southern Africa (9), with a wide range of δ13C values that indicates a much broader dietary niche.

The taxonomically enigmatic mandible KNM-ER 1482 (50) has a δ13C value of −0.4‰, which is intriguing. It has shifted even farther in the direction of being dependent on C4 resources than most P. boisei. Its mandibular and dental morphology offers little or no evidence to assign it to P. boisei. Indeed, some have suggested that it may belong to the same taxon as the KNM-ER 1470 cranium (50) and the KNM-ER 62000 maxilla (51). If this proves to be the case, then within the same region, there may be at least two hominin taxa, almost certainly in different lineages, that have shifted to a diet dominated by C4 resources.

**Paleoecology of the Koobi Fora and Nachukui Formations.** Precessional climatic cycles of ca. 20,000 y duration are widely recognized in marine and lacustrine sequences in tropical latitudes. Between insolation maxima and minima (separated by ca. 10,000 y), there are significant changes in rainfall and ecology. Fluvial strata present challenges for quantitative paleoenvironmental interpretation at timescales less than 20,000 y because of their abrupt and discontinuous mode of deposition. A discrete sedimentary package associated with a particular insolation cycle still does not reveal whether a fossil was deposited at maximum, minimum, or intermediate insolation. Furthermore, matching a fossil with the paleoenvironment in which it lived requires knowing the part of a cycle that a paleoenvironmental indicator (e.g., paleosol carbonate, mineralogy, indicator fossil, or biomarker) records. A vertebrate fossil from the base of a 20,000-y fining upward sequence may have lived during a climatic milieu different from the climate under which carbonate formed in a paleosol at the top of the same sequence. In most situations, it is not feasible to relate a fossil from fluvial sediments to a particular part of a precessional cycle, and it is certainly not possible using legacy collections or surface finds. Nonetheless, long-term ecological changes can be discerned through the 3-Ma record considered here.

Stable isotopes also provide important constraints on the paleoecology of the Turkana Basin. The earliest hominins reported here, from ca. 3 to 4 Ma, lived in an environment that was predominantly ca. 40–60% woody cover, which was determined from paleosol δ13C values (52, 53). For this period, the soil carbon contribution from C3 woody plants, C4 forbs and herbs, and C4 grasses would be ca. 60–40%, 15–20%, and 25–40%, respectively (Fig. 2B and Fig. S3). Such a habitat would be a grassy woodland, grassy shrubland, or grassy bushland (54). Sedimentological evidence (55) shows that the proto-Omo river was present throughout this period; this river likely had a riparian forest (>80 woody cover) that may have been hundreds of meters wide; Δ18O measurements on paleosols indicate that the region had soil temperatures between 30 °C and 40 °C (56), indicating a regional temperature regime similar to the temperature regime of today. Thus, this region had a riparian corridor with cooler temperature and little to no C4 resource availability, but close by, the woodland/shrubland/bushland was a more open habitat with significant C4 resources and much higher daily temperatures than in the riparian corridor. These paleoecological conditions suggest that, based on dietary considerations, Au. anamensis may have been restricted to a narrow riparian corridor, whereas K. platyops must have ventured into open habitats to obtain C4 dietary resources. Thus far, fossils of K. platyops are associated with alluvial fans of a large lateral stream on the western basin margin interfingerling with deposits of the ancestral Omo River.

**Fig. 3.** Images of KNM-ER 45502 before and after sampling. (A) Top view of tooth before sampling. (B) View of the tooth with sample powder (1.8 mg) after sampling. (C) Sample before sampling; the box shows the area chosen for sampling (E). (D) Sample after sampling (same view as C); the boxed area is the close-up view shown in F. (E) Close-up view of the area sampled for stable isotope analysis before sampling. The red arrow shows the broken enamel surface to be sampled. (F) The same area as E but after sampling. The red arrow points to the surface sampled.
Woody cover diminished in the region over time; between ca. 2.0 and 1.4 Ma, woody cover was 20–40% based on δ13C in paleosols (52). Such an ecosystem is equivalent to wooded grassland with soil contributions of C4 woody plants, C3 forbs and herbs, and C4 grasses of ca. 40–20%, 20–30%, and 40–50%, respectively (Fig. 2B); areas of true grassland (<10% woody cover in the United Nations Educational, Scientific, and Cultural Organization terminology (54)) were uncommon, at least on the timescale of paleosol formation (>1,000 y). This change represents a great increase in the availability of C4 plants for Homo and Paranthropus compared with the earlier Australopithecus and Kenyanthropus and a significant opening of the landscape. The 2.0–1.4 Ma interval had intermittent lakes fed by the proto-Omo River; however, it may have been diverted to the Nile drainage for some periods during this interval (55). Geochemical and mineralogic evidence shows that some of these lakes were alkaline (56); δ18O evidence from paleosols indicates high mean annual temperatures, similar to the temperatures of today (57).

Thus, from 4.1 to 1.4 Ma, the region had abundant C4 resources available in the 30-km broad grassy woodland/shrubland to wooded grasslands that bordered narrow (hundreds of meters wide) riparian forests or woodlands associated with the proto-Omo River.

Comparison of Hominin Diets to Theropithecus. Theropithecus was another large-bodied primate in the Turkana Basin at this time. Stable isotope measurements of tooth enamel show that Theropithecus was a heavy C4 consumer by 4 Ma, with ca. 65% C4 resources contributing to the diet (58). Throughout the period from 4 to 1 Ma, Theropithecus had a diet that was as much or more C4-based than any hominin. Paranthropus, from 1.4 to 2.0 Ma, had a diet that was ca. 75% C4-based, whereas the conoeval Theropithecus had a diet that was ca. 75–85% C4-based (58).

Modern Primates as Analogs for Hominin Diets. Modern gorilla and chimpanzees have diets that are entirely or almost entirely C3-based (data in Table S2 and refs. 43–45). Only the earliest hominin in this study could be interpreted as having had a C4-based diet with minimal (if any) C4 components; the δ13C of Au. anamensis had a diet that was as much or more C4-based than any hominin. Paranthropus, from 1.4 to 2.0 Ma, had a diet that was ca. 75% C4-based, whereas the conoeval Theropithecus had a diet that was ca. 75–85% C4-based (58).

Methods

Hominin teeth from the National Museums of Kenya were sampled using a high-speed rotary drill to obtain powder (ca. 2–5 mg) from each sample. Only hominin teeth with broken surfaces were sampled; sampling was from the exposed broken enamel (Fig. 3). Enamel powder from modern gorilla (G. beringei) was obtained from archived samples in Kahuzi-Biega National Park. Modern samples from Democratic Republic of Congo were analyzed in the Archaeology Department at the University of Cape Town using a Kiel device coupled to an isotope ratio mass spectrometer. Results are reported using the standard per million (‰) notation, where 

$\delta^{13}C = \left( \frac{R_{sample}}{R_{standard}} - 1 \right) \times 1,000$

and $R_{sample}$ and $R_{standard}$ are the 13C/12C ratios in the sample and standard, respectively (Vienna–Pee Dee Belemnite is the standard for carbon isotope measurements). Corrections for temperature-dependent isotope fractionation in oxygen were made using modern and fossil internal reference materials that had been reacted at 25 °C (61). For comparative purposes, modern mammals have had their δ13C values adjusted to compensate for recent changes in atmospheric δ13C values (62, 63); these values are referred to in the text as δ13C1950. We use the year of death to calculate the δ13C1950 value; this date will result in a maximum correction, because tooth enamel likely formed ca. 10 y before death for these individuals.

Age estimates for each hominin use the correlations and chronology of the >350-kyr volcanic ash in the basins (20–25, 64); taxonomic assignments are in refs. 24 and 25.

SI Methods has additional information on isotope enrichment factors in mammals, stratigraphic information and age estimates for individual hominins (Table S3), statistical treatment, taxonomic assignments, and biome classifications used in this work.

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