

Diet of *Paranthropus boisei* in the early Pleistocene of East Africa

Thure E. Cerling^{a,1}, Emma Mbua^b, Francis M. Kirera^b, Fredrick Kyalo Manthi^b, Frederick E. Grine^c, Meave G. Leakey^{b,c,d}, Matt Sponheimer^e, and Kevin T. Uno^a

^aDepartment of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112-0111; ^bNational Museums of Kenya, P.O. Box 40658, Nairobi, Kenya; ^cDepartment of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364; ^dTurkana Basin Institute, P.O. Box 24926-00502, Nairobi, Kenya; and ^eDepartment of Anthropology, University of Colorado, Boulder, CO 80309-0233

Contributed by Thure E. Cerling, March 26, 2011 (sent for review February 27, 2011)

The East African hominin *Paranthropus boisei* was characterized by a suite of craniodental features that have been widely interpreted as adaptations to a diet that consisted of hard objects that required powerful peak masticatory loads. These morphological adaptations represent the culmination of an evolutionary trend that began in earlier taxa such as *Australopithecus afarensis*, and presumably facilitated utilization of open habitats in the Plio-Pleistocene. Here, we use stable isotopes to show that *P. boisei* had a diet that was dominated by C₄ biomass such as grasses or sedges. Its diet included more C₄ biomass than any other hominin studied to date, including its congener *Paranthropus robustus* from South Africa. These results, coupled with recent evidence from dental microwear, may indicate that the remarkable craniodental morphology of this taxon represents an adaptation for processing large quantities of low-quality vegetation rather than hard objects.

C₄ photosynthesis | C₃ photosynthesis

The East African hominin *Paranthropus boisei* possessed large and low-cusped postcanine dentition, large and thick mandibular corpora, and powerful muscles of mastication, which are generally believed to be adaptations for a diet of nuts, seeds, and hard fruit (1–3). This notion emerged from interpretations of *P. boisei*'s morphology, but gained indirect support from dental microwear studies of its congener, *Paranthropus robustus*; these concluded that wear on the molars of South African *Paranthropus* was consistent with its having ingested and chewed small, hard food items, if not as primary resources, then at least as fallback foods (4–6). Although some have suggested that the craniodental morphology of *P. boisei* is consistent with the consumption of tough rather than hard foods (7, 8), this idea has been largely eschewed by most workers. Thus, when a recent study using dental microwear texture analysis revealed no evidence for the consumption of hard foods by *P. boisei* (9), it challenged decades of received wisdom, and underscored the need for independent lines of paleodietary evidence.

Stable carbon isotope analysis has proven a powerful tool for testing hypotheses about the diets of extinct herbivorous mammals (10, 11). It is based on the idea that carbon isotope compositions vary predictably between plant foods [e.g., plants using the C₃ photosynthetic pathway (most dicotyledonous plants including trees, shrubs, forbs, herbs) and those using the C₄ pathway (predominantly tropical grasses and sedges, which are monocotyledonous plants)], and further that dietary carbon remains locked in tooth enamel even after millions of years (10). Carbon isotope studies of *P. robustus* from South Africa indicated that it consumed some plants using C₄ photosynthesis such as tropical grasses or sedges, but were also consistent with most of its dietary carbon (approximately 70%) having been derived from the C₃ food items favored by extant chimpanzees (*Pan troglodytes*) such as tree fruits (12, 13). In contrast, stable isotopes measurements of two *P. boisei* specimens from Tanzania suggested a high component of C₄ biomass in its diet (14), which would make its diet fundamentally distinct from all known modern or fossil

hominoid taxa. However, it is unclear whether the data for these two individuals is characteristic of the species, or whether its diet varied over time and space, as the variability in previously analyzed hominin taxa is substantial (e.g., ref. 13).

We present stable isotope data for an additional 22 *P. boisei* individuals from central and northern Kenya that range between 1.9 and 1.4 million years in age, and extend the spatial range of the Tanzanian specimens by more than 700 km. These data inform not only our understanding of the diet of *P. boisei*, but given its occasional morphological similarities with other australopithecine taxa (e.g., *Australopithecus afarensis*, *Australopithecus garhi*, *Australopithecus africanus*), potentially our understanding of the role of diet in early hominin evolution.

Results

The $\delta^{13}\text{C}$ values of *P. boisei* do not change over the half million years for which samples were available ($r^2 = 0.10$). The average $\delta^{13}\text{C}$ value for these samples was $-1.3 \pm 0.9\text{‰}$ (24 teeth from 22 individuals), with a maximum value of $+0.7\text{‰}$ and a minimum value of -3.4‰ (Table 1). Using estimates of $+2$ and -12‰ for a “pure-C₄ grazing” or “pure-C₃ browsing” diet (14), the $\delta^{13}\text{C}$ values for *P. boisei* correspond to a diet where C₄ biomass comprises $77 \pm 7\%$, with minimum and maximum values of 61 and 91%, respectively.

The carbon isotope composition of *P. boisei* is statistically indistinguishable from that of coeval grass-consumers from the region including Equidae ($x = -0.4\text{‰}$, SD = 0.9‰ , $n = 18$), Suidae ($x = -0.2\text{‰}$, SD = 0.8‰ , $n = 10$), and Hippopotamidae ($x = -1.3\text{‰}$, SD = 1.0‰ , $n = 23$) ($P > 0.05$, ANOVA, Games-Howell), and highly different from C₃ biomass-consuming Giraffidae ($x = -12.5\text{‰}$, SD = 0.8‰ , $n = 4$, $P < 0.0001$). The $\delta^{13}\text{C}$ values of contemporaneous equids, giraffids, hippopotamids, and suids are presented in Table S1. The diet of *P. boisei* differs significantly from that of contemporaneous *P. robustus* ($x = -7.6\text{‰}$, SD = 1.1‰ , $n = 18$) (Fig. 1) in South Africa and early *Homo* throughout Africa ($x = -7.8\text{‰}$, SD = 1.5‰ , $n = 6$) ($P < 0.0001$; data from refs. 13 and 14) (Fig. 2). The $\delta^{13}\text{C}$ values of *P. boisei* are also starkly different from those reported for earlier taxa such as *Ardipithecus ramidus* ($P < 0.0001$) and *Australopithecus africanus* ($P < 0.0001$) (data from refs. 13 and 15). The data for other hominin species are presented in Table S2.

Discussion

C₄ Diet of *P. boisei*. The carbon isotope composition of *P. boisei* is fundamentally different from that of all known living and fossil

Author contributions: T.E.C., E.M., F.M.K., F.K.M., F.E.G., M.G.L., M.S., and K.T.U. designed research; T.E.C., E.M., F.M.K., F.K.M., F.E.G., M.G.L., M.S., and K.T.U. performed research; K.T.U. contributed new reagents/analytic tools; T.E.C., E.M., F.M.K., F.K.M., F.E.G., M.G.L., M.S., and K.T.U. analyzed data; and T.E.C., F.E.G., and M.S. wrote the paper.

The authors declare no conflict of interest.

See Commentary on page 9319.

¹To whom correspondence should be addressed. E-mail: thure.cerling@utah.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1104627108/-DCSupplemental.

Table 1. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of *P. boisei* from the Baringo Basin, Kenya (this study), the Turkana Basin, Kenya (this study) and from Olduvai Gorge and Peninj, Tanzania (14)

| Specimen | $\delta^{13}\text{C}$ | $\delta^{18}\text{O}$ | Tooth | Age range | Median age | Nominal % C_4 |
|---------------------|-----------------------|-----------------------|----------------------------------|-----------|------------|------------------------|
| Baringo Basin | | | | | | |
| KNM-CH-302 | -1.3 | -1.5 | m-frag | >1.42 | 1.42 | 76 |
| Turkana Basin | | | | | | |
| KNM-ER-810 | -3.4 | -3.3 | P ₃ | 1.77 | 1.77 | 61 |
| KNM-ER-818 | 0.7 | 1.9 | Lt M ₃ | 1.55-1.65 | 1.60 | 91 |
| KNM-ER-1804 | -1.2 | -0.7 | Lt M ₃ ³ | 1.77 | 1.77 | 77 |
| KNM-ER-3887 | -1.6 | -2.9 | Rt M ₃ ³ | 1.50-1.65 | 1.57 | 74 |
| KNM-ER-6080 | -2.2 | -0.6 | Rt M ₂ | 1.55-1.65 | 1.60 | 70 |
| KNM-ER-13750 | 0.2 | 0.5 | M-frag | 1.87 | 1.87 | 87 |
| KNM-ER-15940 | -1.1 | -0.6 | Lt M ₃ | 1.77 | 1.77 | 78 |
| KNM-WT-17396 | -1.9 | -3.1 | Lt M ₃ | 1.65-1.79 | 1.72 | 72 |
| KNM-WT-37100 | -1.8 | -1.5 | M ₂ or M ₃ | 1.65-1.79 | 1.72 | 73 |
| KNM-WT-37748 | -2.1 | - | Rt M ₃ ³ | 1.65-1.79 | 1.72 | 71 |
| KNM-ER-1171(C) | -0.6 | -1.9 | Lt M ₁ | 1.56-1.60 | 1.58 | 81 |
| KNM-ER-1469(A) | -2.3 | -0.1 | Lt M ₃ | 1.87-1.90 | 1.89 | 69 |
| KNM-ER-1479(A) | -2.3 | 0.2 | M ₃ | 1.87 | 1.87 | 69 |
| KNM-ER-1806(C) | -1.3 | -2 | Rt M ₃ | 1.85 | 1.85 | 76 |
| KNM-ER-3737(B) | -1.6 | -2.5 | Rt M ₁ | 1.56-1.60 | 1.58 | 74 |
| KNM-ER-3952(F) | -1.3 | 0.0 | Lt M ₃ ³ | 1.87 | 1.87 | 76 |
| KNM-ER-729(A) | 0.0 | -0.7 | Lt P ₄ | 1.49-1.55 | 1.52 | 86 |
| KNM-ER-732(A) | -0.1 | -1.8 | P ⁴ | 1.56-1.60 | 1.58 | 85 |
| KNM-ER-733(A) | -1.5 | -2.6 | Rt M ₃ | 1.49-1.55 | 1.52 | 75 |
| KNM-ER-733(D) | -0.5 | -2.2 | Lt P ⁴ | 1.49-1.55 | 1.52 | 82 |
| KNM-ER-802(D) | -0.1 | -1.6 | Lt M ₁ | 1.56-1.60 | 1.58 | 85 |
| KNM-ER-802(G) | -1.9 | - | M ₃ | 1.56-1.60 | 1.58 | 72 |
| KNM-ER-816(B) | -1.9 | -1.3 | Rt P ⁴ | 1.77 | 1.77 | 72 |
| Olduvai | | | | | | |
| OH5 | -1.2* | - | Lt M ₂ | - | 1.82 | 77 |
| Peninj | | | | | | |
| NMT-W64-160 | 0.7* | - | Lt M ₂ | - | 1.62 | 81 |
| Average | -1.3 | - | - | - | - | 77 |
| SD | 0.9 | - | - | - | - | 7 |
| Number [†] | 24 | - | - | - | - | 24 |

*Data from ref. 14.

[†]Number of different individuals. KNM-ER-733 and KNM-ER-802 are represented by two teeth each from two different individuals. The average value for each individual was used to compute the overall average and standard deviation.

The attribution of specimens to *Paranthropus boisei* is as follows: KNM-CH 302 (ref. 48); the "East Rudolf" fossils from the Koobi Fora Formation (refs. 49 and 50 and references therein); and the "West Turkana" teeth from the Nachukui Formation (50, 51).

hominoids, which vary from nearly pure C_3 consumers like gorillas (16) and chimpanzees (17, 18) to variable C_3 consumers like *A. africanus* and *P. robustus* (12, 13). Indeed, the only known hap-

lorrhine primate with a similar carbon isotope composition is the extinct grass-eating baboon *Theropithecus oswaldi* ($x = -2.3\%$, $\text{SD} = 1.5\%$, $n = 12$) (see Table S2 and references therein) from the same general time period. Despite a once broad distribution, the genus *Theropithecus* is now limited to a single species living in the highlands of Ethiopia. These observations suggest that the organisms with which *P. boisei* most likely competed for resources were not contemporaneous *Homo*, *Papio* (savanna baboons), or

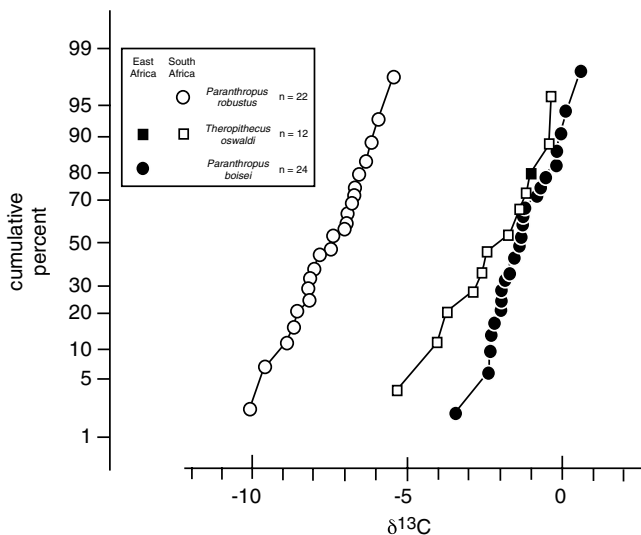


Fig. 1. Cumulative frequencies of *P. boisei* from eastern Africa with contemporaneous *P. robustus* from southern Africa, and for *T. oswaldi* from both eastern and southern Africa. Multiple analyses from single individuals have been averaged.

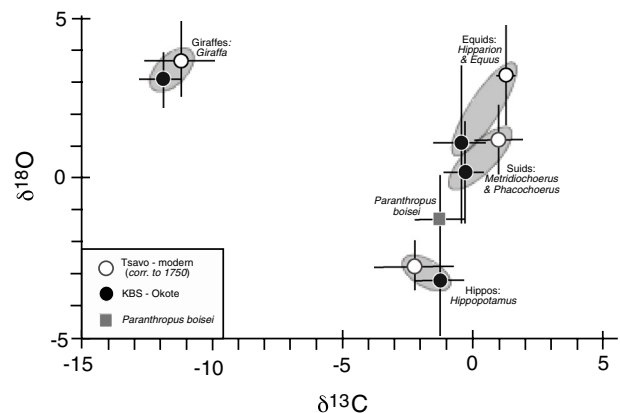


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of *P. boisei* from the Turkana Basin compared with giraffes, suids, hippos, and equids from the KBS and Okote Members of the Koobi Fora Formation, and to their modern counterparts from the Tsavo region in Kenya.

other frugivorous taxa, but probably C₄ biomass consumers including equids, suids, hippos, *Theropithecus*, and some bovids.

The vast majority of C₄ biomass is grass, although there can be large quantities of C₄ sedges, especially in wetland environments such as the Okavango Delta today (19). A much smaller percentage of C₄ dicots and crassulacean acid metabolism plants with similar carbon isotope compositions exists, although the typically low abundance of the former and low abundance and frequent toxicity of the latter make them unlikely to be regular targets for early hominins (20). Thus, it is almost certain that *P. boisei* had a diet focused on grasses, sedges, or both.

It has recently been suggested that sedges were an important hominin resource because they are often found in the riverine woodlands favored by many savanna primates and because their tubers are a potentially high energy resource for which tool-wielding hominins would have had little competition (14, 21). Nevertheless, sedges often utilize C₃ photosynthesis, are not widely distributed in many habitats, and might have been of dubious nutritional value without cooking (22, 23). Moreover, there is no record of any large mammal feeding on sedges to such an extent. Regardless, if *P. boisei* was a wetland sedge specialist, it would suggest an extremely limited distribution in ancient landscapes with important implications for our understanding of early hominin biology and biogeography.

Grasses, in contrast, are widely abundant and use the C₄ photosynthetic pathway in most African savanna environments; they are utilized extensively by taxonomically diverse mammals including the primate *Theropithecus*. A reason for thinking that grass blades were not consumed by *P. boisei* is that the low occlusal relief of its cheek teeth is the opposite of what might be expected for a consumer of leaves. Folivores tend to have great occlusal relief, whereas flat teeth are usually found in hard-object consumers among frugivorous primates (1). Nevertheless, the dental microwear complexity profiles of *P. boisei* and *Theropithecus* are similar, suggesting a diet with comparable mechanical properties (24). Although the high anisotropy (directionality) of *Theropithecus* molar microwear is very different from that of *P. boisei*, it has been suggested that this results from different constraints posed by their dentognathic morphology rather than diet (24). In other words, it is possible that they were utilizing similar foods but chewing them in different ways.

P. boisei cheek teeth display notable gradients of gross wear, resulting in large, deeply excavated dentine exposures, and in this regard, they are similar to other australopith species (e.g., *A. afarensis* and *A. africanus*) that also possess low tooth cusps with thick enamel. Thus, like other australopiths, *P. boisei* undoubtedly had a diet that consisted of foods with abrasive qualities—the gross wear is as likely due to repetitive loading of phytolith-rich tough foods as exogenous grit. Thus, either grass or sedge consumption and/or exogenous grit might well have contributed to *P. boisei*'s notable wear gradient.

Of perhaps greater moment than its potential specific similarities, the microwear of *P. boisei* molars, which shows remarkable uniformity over time from about 2.3 Ma to about <1.4 Ma (9, 24), stands in stark contrast to the wear fabrics exhibited by primate hard-object consumers. Indeed, there is no evidence beyond the anecdotal [e.g., the broken left first permanent molar crown in the KNM-ER 729 *P. boisei* mandible (8) and the observation that a couple of *P. boisei* molars show antemortem enamel chipping (25)] that these food items were hard.

Paleoenvironment of *P. boisei*. Previous interpretations of the environmental conditions of *P. boisei* are varied and include closed wet habitats (26), scrub woodland to arid shrubland (27), and semiarid savanna associated with woodlands and gallery forest (28). The oxygen isotope composition of *P. boisei* and contemporaneous mammal tooth enamel provides further information about its water utilization and environment (29). Fig. 2

shows the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for the water-dependent hippopotamus, the water-independent browser *Giraffa*, and two grazers (equids and suids) from the Kay Behrensmeier Site (KBS) and Okote members (Table S1); it also shows the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for their modern counterparts in the Tsavo region in Kenya (Table S3). These data suggest that *P. boisei* was very water dependent based on its $\delta^{18}\text{O}$ values, which are more negative than those of coeval suids, equids, and giraffids. The similarity in $\Delta(\delta^{18}\text{O}_{\text{giraffe}} - \delta^{18}\text{O}_{\text{hippo}})$ suggests that the environment in the Turkana Basin in KBS-Okote time had a water deficit (30) similar to that in the Tsavo region today (mean annual temperature = 25 °C; mean annual precipitation = 550 mm per year). $\Delta 47$ values from paleosols in the Turkana region indicate soil temperatures between 30 and 37 °C, indicating high mean temperatures and an open habitat in the Koobi Fora and Nachukui regions where these fossils were found (31).

Overall, the stable isotope evidence from paleosols and tooth enamel is compatible with semiarid savanna with riparian woodlands or with woodlands associated with lakes (32). Grasses or sedges would have been highly available in such an environment.

South Africa vs. East Africa: *P. robustus* vs. *P. boisei*. Why the difference in carbon isotope composition between *Paranthropus* in eastern and southern Africa? If these congeners had similar biology then it could be argued that the difference represents a generalist genus eating different things in disparate regional environments. However, most herbivorous taxa do not show evidence of diet change between the regions (compare ref. 33 with ref. 34), including *Theropithecus* (Table S2). Moreover, there is little reason to believe that the potential environments of *P. boisei* in East Africa were homogenous over time and space, or that its habitat was so different from that of *P. robustus* that the carbon isotope compositions of their diets did not overlap. In fact, a variety of paleoenvironments have been reconstructed for *P. boisei* that clearly overlap with those of *P. robustus* (27, 28). Most studies, however, have emphasized open and well-watered habitats for *P. boisei* [e.g., deltaic environments and/or edaphic grasslands (26, 27, 35)]. *P. boisei* and *P. robustus* carbon isotope values could also differ if both were principally sedge consumers and there was a differential distribution of C₃ and C₄ sedges. Indeed, there is some evidence that C₄ sedges are more common in East African habitats today (23).

Given current evidence, however, the simplest explanation is adaptive divergence between the eastern and southern African *Paranthropus* populations, with the former focusing on grasses or sedges and the southern population consuming a more traditional hominoid diet that included tree fleshy fruits, as well as variable C₄ resources. In short, *P. robustus* had an expanded dietary repertoire relative to extant apes that included C₄ resources, whereas *P. boisei* had completely abandoned the presumed ancestral diet (C₃-based foods) to focus on a resource abundant in savanna and wetland environments.

Implications for Craniodental Adaptations. These results might also have broader significance for our understanding of australopith craniodental adaptations. Earlier taxa such as *A. anamensis* and *A. afarensis* exhibit, albeit in an incipient state, craniodental features that have been surmised to indicate a diet that consisted of hard objects (36–39). Traditional thinking has been that such masticatory adaptations permitted hominins to colonize increasingly seasonal and open environments (37). However, recent dental microwear studies suggest that the mechanical properties of *A. afarensis* (and *A. anamensis*) diets were nearly identical to those of *P. boisei* (9, 24, 40–42). If this is so, could it be that the australopith masticatory package represents an adaptation to C₄ resources such as grasses or sedges? The similarity in dental microwear fabrics among the eastern African australopiths, all of which lack any evidence for hard-object food consumption (9, 24,

40–42), is consistent with the notion that their craniodental morphology could reflect “repetitive loading” rather than hard-object consumption (7, 8, 43). If this is borne out, it would suggest our understanding of early hominin ecology and biomechanics needs rethinking, but must ultimately wait on stable isotope data from earlier hominins.

Conclusions

Carbon isotope data show that *P. boisei* had a diet primarily of C_4 resources, most likely grasses or sedges, over a wide range of time (>0.5 Ma) and space (Turkana, Baringo, Natron, and Olduvai regions). These data are irreconcilable with the idea of *P. boisei* having eaten foods even broadly similar to those of African apes. They are also inconsistent with the notion that *P. boisei* ate nuts or hard fruits preponderantly, and also suggest that *Paranthropus* in eastern Africa (*P. boisei*) and southern Africa (*P. robustus*) had very different diets, a notion also supported by dental microwear (6, 9). In sum, this study suggests that the prevailing ideas based on morphological and biomechanical considerations are at least partly in error, and that our understanding of the dietary basis of masticatory differentiation within the hominin lineage may require revision.

Methods

Samples were obtained from the National Museums of Kenya. Approximately 2 mg of powder was obtained using a high-speed rotary drill; *P. boisei* enamel from broken tooth surfaces were sampled so that information concerning morphology was not compromised. Powdered samples were treated with 0.1 M buffered acetic acid for 30 min to remove secondary carbonates

(see Table S4). Samples were reacted with 105% phosphoric acid at 90 °C in silver capsules and analyzed on an isotope ratio mass spectrometer following cryogenic separation of CO_2 ; results are reported using the standard per mil (‰) notation with Vienna Pee Dee Belemnite as the standard for both oxygen and 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 (44). For comparative purposes, modern mammals have had their $\delta^{13}C$ values adjusted to compensate for recent changes in atmospheric $\delta^{13}C$ values (45–47).

Treated and untreated fossil enamel from four samples were analyzed to test for the presence of exogenous carbonate. Fossil enamel samples were treated with 0.1 M buffered acetic acid for 30 min, rinsed four times with ultrapure (Milli-Q) distilled water, and dried overnight at 60 °C. Treated and untreated samples were analyzed back to back for $\delta^{13}C$ and $\delta^{18}O$ on an isotope ratio mass spectrometer. Carrara carbonate standards were used to convert voltages measured on the major mass Faraday cup (44) into CO_2 yields ($\mu mol/mg$). Two of four untreated samples, ER-810-UNT and ER-1806C-UNT, had CO_2 yields of 1.34 and 1.81 $\mu mol/mg$, respectively, indicating the presence of exogenous carbonate (Table S4). Their treated counterparts had yields of 0.75 and 0.59 $\mu mol/mg$, respectively, which fall within the range for modern enamel samples. Carbon isotope values between treated and untreated samples differed by up to 2.7‰ (Table S4). Based on the results from the four pilot samples, all remaining samples were treated as described above.

ACKNOWLEDGMENTS. We thank Frank Brown for discussions and Nick van der Merwe and Bernard Wood for reviews of the manuscript. Research was funded by the National Science Foundation (Grant BCS 0621542) and the University of Colorado Dean’s Fund for Excellence. We thank the National Museums of Kenya for permission for this study.

- Kay RF (1981) The nut-crackers—A new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55:141–151.
- Lucas PW, Corlett RT, Luke DA (1986) Postcanine tooth size and diet in anthropoid primates. *Z Morphol Anthropol* 76:253–276.
- Wood B, Constantino P (2007) *Paranthropus boisei*: Fifty years of evidence and analysis. *Am J Phys Anthropol* 134(Suppl 45):106–132.
- Grine FE (1986) Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: A quantitative analysis of permanent molar microwear. *J Hum Evol* 15:783–822.
- Grine FE, Kay RF (1988) Early hominid diets from quantitative image analysis of dental microwear. *Nature* 333:765–768.
- Scott RS, et al. (2005) Dental microwear texture analysis reflects diets of living primates and fossil hominins. *Nature* 436:693–695.
- Jolly CJ (1970) The seed eaters: A new model of hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Walker AC (1981) Diet and teeth. Dietary hypotheses and human evolution. *Philos Trans R Soc Lond B Biol Sci* 292:57–64.
- Ungar PS, Grine FE, Teaford MF (2008) Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS One* 3:e2044, 10.1371/journal.pone.0002044.
- Lee-Thorp JA, van der Merwe NJ (1987) Carbon isotope analysis of fossil bone apatite. *S Afr J Sci* 83:712–715.
- Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in modern and fossil proboscideans. *Oecologia* 120:364–374.
- Lee-Thorp JA, van der Merwe NJ, Brain CK (1994) Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *J Hum Evol* 27:361–372.
- Sponheimer M, Lee-Thorp JA (2007) Hominin palaeodiets: The contribution of stable isotopes. *Handbook of Paleoanthropology*, eds W Henke and I Tattersall (Springer-Verlag, Berlin), pp 555–586.
- van der Merwe NJ, Masao FT, Bamford MK (2008) Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *S Afr J Sci* 104:153–155.
- White TD, et al. (2009) Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science* 326:87–93.
- Levin NE, et al. (2008) Herbivore enamel carbon isotopic composition and the environmental context of *Ardipithecus* at Gona, Ethiopia. *Geol Soc Am Special Paper*, eds J Quade and JG Wynn 446:215–234.
- Schoeninger MJ, Iwaniec UT, Nash LT (1998) Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Oecologia* 113:222–230.
- Smith CC, Morgan ME, Pilbeam D (2010) Isotopic ecology and dietary profiles of Liberian chimpanzees. *J Hum Evol* 58:43–55.
- Ellery WN, Ellery K, Rogers KH, McCarthy TS (1995) The role of *Cyperus papyrus* L. in channel blockage and abandonment in the northeastern Okavango Delta, Botswana. *Afr J Ecol* 33:25–49.
- Peters CR, Vogel JC (2005) Africa’s wild C_4 plant foods and possible early hominid diets. *J Hum Evol* 48:219–236.
- Conklin-Brittain NL, Wrangham RW, Smith CC, Ungar PS, Teaford MF (2002) A two-stage model of increased dietary quality in early hominid evolution: The role of fiber. *Human Diet: Its Origin and Evolution* (Bergin & Garvey, Westport), pp 61–76.
- Schoeninger MJ, Murray S, Bunn HT, Marlett JA (2001) Composition of tubers used by Hadza foragers of Tanzania. *J Food Compos Anal* 14:15–25.
- Stock WD, Chuba CK, Verboom GA (2004) Distribution of South African C_3 and C_4 species of Cyperaceae in relation to climate and phylogeny. *Austral Ecol* 29:313–319.
- Ungar PS, Krueger KL, Blumenshine RJ, Njau J, Scott RS (2011) Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleoanthropology Project, 1995–2007. *J Hum Evol* in Press.
- Constantino PJ, et al. (2010) Tooth chipping can reveal the diet and bite forces of fossil hominins. *Biol Lett* 6:826–829.
- Shipman P, Harris JM (1988) Habitat preference and paleoecology of *Australopithecus boisei* in eastern Africa. *Evolutionary History of the “Robust” Australopithecines*, ed FE Grine (Aldine de Gruyter, New York), pp 343–381.
- Reed KE (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. *J Hum Evol* 32:289–322.
- Feibel CS, Harris JM, Brown FH (1991) Palaeoenvironmental context for the Late Neogene of the Turkana Basin. *Koobi Fora Research Project*, ed JM Harris (Clarendon Press, Oxford), 3, pp 321–346.
- Kohn MJ, Schoeninger MJ, Valley JW (1996) Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. *Geochim Cosmochim Acta* 60:3889–3896.
- Levin NE, Cerling TE, Passey BH, Harris JM, Ehleringer JR (2006) Stable isotopes as a proxy for paleoaridity. *Proc Natl Acad Sci USA* 103:11201–11205.
- Passey BH, Levin NE, Cerling TE, Brown FH, Eiler J (2010) High temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. *Proc Natl Acad Sci USA* 107:11245–11249.
- Cerling TE, et al. (2010) Comment on the paleoenvironment of *Ardipithecus ramidus*. *Science* 328:1105–d, 10.1126/science.1185274.
- Cerling TE, Harris JM, Passey BH (2003) Diets of East African Bovidae based on stable isotope analysis. *J Mammal* 84:456–471.
- Sponheimer M, et al. (2003) Diets of Southern African Bovidae: Stable isotope evidence. *J Mammal* 84:471–479.
- Behrensmeyer AK (1978) The habitat of Plio-Pleistocene hominids in East Africa: Taphonomic and microstratigraphic evidence. *Early Hominids of Africa*, ed C Jolly (St. Martin’s Press, New York), pp 165–189.
- White TD, Suwa G, Simpson S, Asfaw B (2000) Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am J Phys Anthropol* 111:45–68.
- White TD, et al. (2006) Asa Issie, Aramis and the origin of *Australopithecus*. *Nature* 440:883–889.
- Macho GA, Shimizu D, Jiang Y, Spears IR (2005) *Australopithecus anamensis*: A finite-element approach to studying the functional adaptations of extinct hominins. *Anat Rec* 283A:310–318.
- Kimbel WH, Deleuzene LK (2009) “Lucy” redux: A review of research on *Australopithecus afarensis*. *Am J Phys Anthropol* 140(Suppl 49):2–48.
- Grine FE, Ungar PS, Teaford MF (2006) Was the Early Pliocene hominin ‘*Australopithecus anamensis*’ a hard object feeder? *S Afr J Sci* 102:301–310.
- Grine FE, Ungar PS, Teaford MF, El Zaatari S (2006) Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. *J Hum Evol* 51:297–319.

42. Ungar PS, Scott RS, Grine FE, Teaford MF (2010) Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philos Trans R Soc Lond B Biol Sci* 365:3345–3354.
43. Hylander WL (1975) Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science* 189:1095–1098.
44. Passey BH, Cerling TE, Levin NE (2007) Temperature dependence of acid fractionation for modern and fossil tooth enamels. *Rapid Commun Mass Spectrom* 21:2853–2859.
45. Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347–363.
46. Francey RJ, et al. (1999) A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus* 51:170–193.
47. Keeling RF, Piper SC, Bollenbacher AF, Walker SJ (2010) Monthly atmospheric $^{13}\text{C}/^{12}\text{C}$ isotopic ratios for 11 SIO stations. *Trends: A Compendium of Data on Global Change* (Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN).
48. Gowlett JAJ, Harris JWK, Walton D, Wood BA (1981) Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. *Nature* 294:125–129.
49. Wood BA (1991) *Koobi Fora Research Project, Vol 4: Hominid Cranial Remains*, (Clarendon Press, Oxford), 4.
50. Brown B, Brown FH, Walker A (2001) New hominids from the Lake Turkana Basin, Kenya. *J Hum Evol* 41:29–44.
51. Prat S, Brugal JP, Roche H, Texier PJ (2003) Nouvelles découvertes de dents d'hominidés dans le membre Kaitio de la formation de Nachukui (1,65-1,9 Ma), Ouest du lac Turkana (Kenya). *Comptes Rendus Palevol* 2:685–693 [New discoveries of hominid teeth from the Kaitio Member, Nachukui Formation, West Turkana (French)].