

Isotopic evidence of early hominin diets

Matt Sponheimer^{a,1}, Zeresenay Alemseged^b, Thure E. Cerling^c, Frederick E. Grine^d, William H. Kimbel^e, Meave G. Leakey^{d,f}, Julia A. Lee-Thorp^g, Fredrick Kyalo Manthi^h, Kaye E. Reed^e, Bernard A. Woodⁱ, and Jonathan G. Wynn^j

^aDepartment of Anthropology, University of Colorado, Boulder, CO 80309; ^bDepartment of Anthropology, California Academy of Sciences, San Francisco, CA 94118; ^cDepartment of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112; ^dDepartment of Anthropology, Stony Brook University, Stony Brook, NY 11794; ^eInstitute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287; ^fTurkana Basin Institute, 00502 Nairobi, Kenya; ^gResearch Laboratory for Archaeology, Oxford University, Oxford OX1 3QY, United Kingdom; ^hDepartment of Earth Sciences, National Museums of Kenya, 00100 Nairobi, Kenya; ⁱCenter for the Advanced Study of Hominid Paleobiology, Department of Anthropology, George Washington University, Washington, DC 20052; and ^jDepartment of Geology, University of South Florida, Tampa, FL 33620

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Carbon isotope studies of early hominins from southern Africa showed that their diets differed markedly from the diets of extant apes. Only recently, however, has a major influx of isotopic data from eastern Africa allowed for broad taxonomic, temporal, and regional comparisons among hominins. Before 4 Ma, hominins had diets that were dominated by C₃ resources and were, in that sense, similar to extant chimpanzees. By about 3.5 Ma, multiple hominin taxa began incorporating ¹³C-enriched [C₄ or crassulacean acid metabolism (CAM)] foods in their diets and had highly variable carbon isotope compositions which are atypical for African mammals. By about 2.5 Ma, *Paranthropus* in eastern Africa diverged toward C₄/CAM specialization and occupied an isotopic niche unknown in catarrhine primates, except in the fossil relations of grass-eating geladas (*Theropithecus gelada*). At the same time, other taxa (e.g., *Australopithecus africanus*) continued to have highly mixed and varied C₃/C₄ diets. Overall, there is a trend toward greater consumption of ¹³C-enriched foods in early hominins over time, although this trend varies by region. Hominin carbon isotope ratios also increase with postcanine tooth area and mandibular cross-sectional area, which could indicate that these foods played a role in the evolution of australopithecine masticatory robusticity. The ¹³C-enriched resources that hominins ate remain unknown and must await additional integration of existing paleodietary proxy data and new research on the distribution, abundance, nutrition, and mechanical properties of C₄ (and CAM) plants.

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Diet has long been implicated as a driving force in human evolution. Changes in the type of food consumed and the manner in which it was procured have been linked with encephalization and the emergence of bipedalism, as well as ecological, social, and cultural evolution within the hominin lineage (1–3). Given this interest, a wide variety of methods (4–8) have been used to investigate early hominin diet over the years.

Stable carbon isotope analysis is a relative newcomer to early hominin dietary studies (9). Initial carbon isotope work suggested that southern African hominins and living African apes had markedly different diets (9, 10). Our ability to interpret those data in broader evolutionary terms was limited, however, because no eastern African hominins had been sampled, and because datasets from other sources, such as dental microwear (11–14), were not available. Now, however, carbon isotope data have become available for most early African hominin species, and for the first time, we can make broad taxonomic, regional, and temporal comparisons of hominin carbon isotope compositions. We can also begin to integrate the carbon isotope data with complementary information on hominin diets from other sources.

This paper has a tripartite structure. The first section begins in the past and takes a brief look at why carbon isotope analysis is useful and what the first studies taught us about hominin diet. The second section moves to the present and assesses a hominin dataset that has expanded over 250% in the past 24 mo. It examines

taxonomic, temporal, and regional trends with an eye to integrating the isotopic data with dietary evidence from dental form, mandibular morphology, and dental microwear. The third section looks to the future and makes some suggestions for addressing arising questions about hominin diet.

Past

The use of carbon isotope analysis in paleodietary studies is based on the simple concept that you are what you eat (15, 16). Isotopic traces of past meals are frozen in tooth enamel, and are recoverable after millions of years, because enamel is essentially pre-fossilized and therefore, resistant to postmortem isotopic alteration (17). Carbon isotopes are especially valuable for distinguishing diets based, directly or indirectly, on plants using C₃ and C₄ photosynthesis.

C₃ plants include almost all tree and bush biomass in African savannas but also many herbaceous species. C₄ plants comprise tropical grasses, some sedges, and little else as a percentage of biomass in African savanna environments (18, 19) (*SI Text*). C₄ plants incorporate relatively more ¹³C into their tissues than do C₃ plants, and the carbon isotope compositions of C₃ and C₄ plants do not overlap (20). The carbon isotope compositions of plant foods are reflected in the tissues of consumers with some additional fractionation (*SI Text*), and thus, the carbon isotope ratios in tooth enamel readily distinguish C₄ grass feeders, like zebras (*Equus quagga*) and wildebeests (*Connochaetes taurinus*), from fruit or leaf eaters, like chimpanzees (*Pan troglodytes*) and giraffes (*Giraffa camelopardalis*) (21, 22). However, carbon isotope analysis cannot readily distinguish between diets based on plants (such as C₄ grasses) and animals that eat those plants (such as C₄ grass-consuming zebras or wildebeests).

Succulent plants use a third photosynthetic pathway (crassulacean acid metabolism, or CAM) that essentially alternates C₃ and C₄ photosynthesis and tends to produce C₄ plant-like carbon isotope compositions in tropical Africa (19, 23). Although they are a minor fraction of plant biomass in most woodland and savanna ecosystems and are rarely important foods for primates (24), CAM plants represent a potential wrinkle for interpreting hominin carbon isotope data in terms of a simple dichotomous (C₃ vs. C₄) system.

The first carbon isotope studies of early hominins showed that the southern African australopithecines (*Australopithecus africanus*

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¹To whom correspondence should be addressed. E-mail: matt.sponheimer@gmail.com.

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and *Paranthropus robustus*) consumed mostly C₃-derived carbon but also ate significant quantities of C₄ or CAM foods (¹³C-enriched foods or resources hereafter) (9, 10). Chimpanzees, in contrast, have diets dominated by C₃ vegetation (25) even when they live in relatively open environments with abundant C₄ grasses (26, 27). These studies suggested that australopiths ate ¹³C-enriched plants, such as C₄ grasses or sedges, or consumed animals that had eaten these plants. The latter possibility elicited the most attention; however, the first possibility was equally important, because it suggested that these hominins used their habitats in different ways than do extant apes.

Another way these australopiths differed from chimpanzees was in the variability of their carbon isotope compositions. The observed ^δ¹³C range for chimpanzees within a given environment is quite narrow (26, 27). *A. africanus* (~2.7–2.1 Ma), in contrast, ranges from nearly pure C₃ to predominantly C₄/CAM consumption (28, 29). Some of the greater variation in these australopiths may reflect time-averaging in the hominin sample (30), but much of it is likely caused by ecological differences. There is also evidence for significant variation in the ^δ¹³C values of southern African australopiths at intra- and interannual timescales (31, 32). This marked variation in australopith ^δ¹³C values might indicate a generalist, more baboon-like, dietary adaptation (24).

What the original studies of southern African hominins did not find, however, was significantly different carbon isotopic compositions in *A. africanus*, *P. robustus*, and early *Homo* (33), species with distinctive masticatory anatomy (4), dental microwear (5), and/or archaeology (34) that implied differences in dietary ecology. Thus, the first carbon isotope analyses opened a new window on early hominin ecology but simultaneously raised new questions. What were the ¹³C-enriched foods consumed (e.g., C₄ plants or animals eating them), and what were their relative proportions? What were the temporal trends in diet, if any, within these taxa? Why were there no carbon isotopic differences between morphologically distinct species? What were the carbon isotope compositions of the abundant, and in some cases, geologically much older eastern African hominins, and more specifically, when did hominins first engage with ¹³C-enriched resources?

Present

Taxonomic Comparisons. ^δ¹³C values are presently available for 175 specimens representing 11 early hominin species (9, 10, 28, 29, 31–33, 36–42) (Fig. S1 and Table S1). The specimens, which range in age from about 4.4 to 1.3 Ma, come from sites in southern, eastern, and central Africa. The spate of data from beyond southern Africa pushes back evidence for the earliest consumption of C₄ foods to ~3.5 Ma and provides strong evidence of carbon isotopic niche differentiation (ref. 43 has information on isotopic niche) among the eastern African hominins.

The earliest known candidate hominin taxa (*Ardipithecus ramidus*, ca. 4.4 Ma; *Australopithecus anamensis*, ca. 4.0 Ma) for which we have data have relatively low ^δ¹³C values that indicate diets dominated by C₃ foods, much like contemporary savanna chimpanzees (26, 27). Antithetically, by 1.9 Ma, *P. boisei* had a diet dominated (~80%) by ¹³C-enriched foods, and unexpectedly, *P. boisei*'s ^δ¹³C values do not overlap with those of its southern African congener, *P. robustus* ($P < 0.001$; Wilcoxon). Temporally intermediate *A. afarensis* and *Kenyanthropus platyops*, in contrast, fall between these two extremes. Their ^δ¹³C values are significantly different from the previously mentioned C₃- (*Ar. ramidus* and *A. anamensis*) and C₄/CAM-consuming (*P. boisei*) hominins ($P < 0.05$; Wilcoxon), but they are highly variable and overlap with both. Whatever the taxonomic relationship of *A. afarensis* and *K. platyops* (44–46), these near contemporaries were consuming foods from across a much wider carbon isotope space than their antecedents.

The stark differences in ^δ¹³C values between *P. boisei* and early representatives of the genus *Homo* and *P. robustus* ($P < 0.001$; Wilcoxon) provide the best evidence for isotopic niche differentiation between contemporaneous fossil hominin species. However, three individuals of *A. bahrelghazali* from Chad, a contemporary of *A. afarensis* and *K. platyops* (~3.5 Ma), derived their carbon principally from ¹³C-enriched resources (36), and two individuals of *A. sediba* (~2.0 Ma), a near contemporary of late *A. africanus* and early *P. robustus*, had strongly C₃ diets (41). Both of these hint at additional isotopic niche differentiation.

Temporal Patterns. There is a relatively weak but significant [$r^2 = 0.25$; $t(173) = -7.49$, $P < 0.001$] increase in hominin ^δ¹³C values (more C₄/CAM) over time (Fig. S2A). No similar increase occurs through time in grazing Equidae (principally C₄ consumers), browsing *Giraffa* (C₃ consumers), or mixed-feeding (C₃/C₄) monkeys (*Parapapio* and *Papio*) associated with the hominin fossils (Fig. S3A).

The hominin temporal trend is weakened by differences between regions. For instance, there is no evidence of change through time among southern African hominins, although this lack may partially reflect the more limited time depth of those samples (about 2.7–1.1 Ma) (47) (Fig. S3B). When restricting the dataset to samples from eastern Africa, the temporal relationship is considerably more robust [$r^2 = 0.50$; $t(117) = -10.90$, $P < 0.001$], and when *Homo* is further excluded [because it is believed to be ecologically distinct from its australopith predecessors (3)], a strong relationship between australopith ^δ¹³C and time is apparent [$r^2 = 0.76$; $t(85) = -16.52$, $P < 0.001$] (Fig. S2B).

Hence, in eastern Africa, we initially observe C₃-focused consumers (*Ar. ramidus* and *A. anamensis*), but by about 3.5 Ma, there is a marked transition to mixed C₃/C₄ consumers that fall broadly across carbon isotope space (*A. afarensis* and *K. platyops*). By about 2.5 Ma, there is an isotopic split: *Paranthropus* becomes a C₄ or CAM specialist, whereas early *Homo* maintains a mixed C₃/C₄ isotopic niche. Nevertheless, the carbon isotope space occupied by the potential ancestral (*A. afarensis* and *K. platyops*) and descendant (*P. boisei* and early *Homo*) taxa is nearly the same (ranges of 10.3‰ and 10.8‰, respectively), although the latter taxa are slightly shifted to higher ^δ¹³C values. This similarity across carbon isotope space could indicate that the broad hominin niche did not fundamentally change over this period, although hominin ^δ¹³C values become more taxonomically structured (i.e., taxa develop distinct carbon isotope compositions) over time.

Environmental Signals. Multiple lines of evidence suggest that hominin environments became grassier between about 4 and 1 Ma (48, 49), and although these changes were neither unidirectional nor consistent across Africa, they do roughly parallel the trend in hominin ^δ¹³C values described above (greater ¹³C-enriched resource consumption over time). However, the temporal increase in hominin ^δ¹³C values is driven by two events: the origin of significant C₄ (or CAM) consumption at about 3.5 Ma and the origin of the genus *Paranthropus* by about 2.5 Ma. The first event may have been tied to environmental change, although if so, it is unlikely to have been a simple increase in available C₄ grasses because there is little reason to believe that the broader environments of *Ar. ramidus* and *A. anamensis* were less grassy than the habitats of *A. afarensis* (42, 49). A stronger case can be made that the origin of *Paranthropus* (and its C₄-dominated diet) coincided with increases in C₄ biomass. There is, however, no evidence that non-*Paranthropus* hominin ^δ¹³C values changed from about 3.5 to 1.5 Ma or across environmental shifts/gradients.

So did environmental change have no impact on the diets of non-*Paranthropus* hominin species? No, not necessarily. Environmental change encompasses far more than shifts in the proportion

of C₄ grass on a landscape. Differences in tree composition (e.g., fine- vs. broad-leaved; high vs. low diversity) or palatability of the grass layer (e.g., *Panicum maximum* vs. *Cymbopogon caesius*; high vs. low crude protein) can have a major impact on mammalian diets (50), but such changes are difficult to detect in the fossil record. It is also conceivable that environmentally driven diet changes occurred in narrower temporal intervals (precessional or shorter) than can be perceived at many hominin sites (30, 42). Hence, the extreme variability in $\delta^{13}\text{C}$ values of some hominin species (e.g., *A. africanus*) could be evidence of generalist taxa with individuals or subpopulations that use broadly similar habitats in diverse ways (see ref. 51), or could indicate habitat change at timescales that cannot be resolved at present in the hominin fossil record.

Nevertheless, it would not be surprising if some hominins (e.g., *Ar. ramidus*, *A. anamensis*) were able to maintain their diets in the face of changing environments by selectively using preferred microhabitats (e.g., gallery forests) regardless of the broader regional environments, much like modern chimpanzees do (52). Such habitat selectivity might have buffered hominins against habitat loss so that only extreme climatic/environmental events elicited isotopically observable dietary responses. As a result, the difficulty of placing hominins within particular microhabitats on a landscape is a major constraint on our ability to interpret hominin $\delta^{13}\text{C}$ data and hominin ecology generally.

Isotopic Data Relative to Other Lines of Evidence. With the exception of *Homo*, the masticatory apparatus of early hominins became increasingly robust (i.e., thicker mandibular bodies and larger postcanine tooth areas) over time, and although there is debate as to what specific foods drove this morphological evolution, an adaptive shift in diet influenced by habitat change is usually implicated (5, 53, 54). The $\delta^{13}\text{C}$ values across time are broadly consistent with a directional change in australopith diet. Significant relationships between early hominin $\delta^{13}\text{C}$ values and postcanine tooth area [$r^2 = 0.86$, $t(5) = 5.50$, $P < 0.01$] (Fig. S4A and Table S2) and mandibular cross-sectional area at M₁ (first lower molar) [$r^2 = 0.83$, $t(5) = 4.91$, $P < 0.01$] (Fig. S4B and Table S2) are also consistent with a concomitant change in diet and morphology (morphological data are from refs. 55–58, the authors, and metrics provided by the Middle Awash Research Project) (Table S2).

In contrast, there is no apparent relationship between hominin dental microwear variables (complexity and anisotropy) and carbon isotopic compositions, postcanine area, or mandibular cross-sectional area at M₁ (data from ref. 59) (Table S2). For example, hominins with the highest and lowest $\delta^{13}\text{C}$ values (and the largest and smallest postcanine tooth area) have similar occlusal microwear. However, both microwear and isotopic datasets strongly differentiate *P. robustus* from southern Africa and *P. boisei* from eastern Africa, which is a surprising result given their craniodental similarities and presently hypothesized phylogenetic relationship (46, 55, 60).

Consilience. Today, research on the evolution of hominin diets pushes along on a number of parallel fronts, all of which ask different questions about diet and operate at different spatio-temporal scales. For example, carbon isotope analysis reveals the photosynthetic pathway from which dietary carbon was derived over a period of months or years, depending on how the tooth was sampled. Dentognathic morphology, in contrast, speaks to the foods to which the masticatory apparatus is adapted and thus, most directly reflects the diet of previous generations. These research fronts are complementary, and in combination, they should provide a more complete picture of ancient diet. Nevertheless, they do not always converge on a simple dietary interpretation, although such difficulties may arise from our limited ability to interpret the various lines of evidence.

The australopith masticatory apparatus has long been interpreted as evidence of hard, tough, or abrasive diets (5, 7, 8, 53, 54, 61–65). The dental microwear of *P. robustus* has complexity values that are similar to the complexity values of savanna generalists (*Papio cynocephalus*) and hard-object feeders (e.g., *Cercocebus atys*) (66, 67) (Fig. S5). Combined with its hypertrophied masticatory apparatus and flat postcanine occlusal surfaces, a diet of small hard objects from savanna-type habitats made considerable sense (5, 61–64). The carbon isotope data fit this scenario with the added suggestion that novel C₄ foods, such as grass seeds or sedge underground storage organs, were added to an otherwise C₃ diet (9, 29). There was little reason to believe that the data for eastern African *Paranthropus* taxa would paint a different picture.

The results of recent dental microwear studies were unexpected, however, in that all of the eastern African australopiths, including *P. boisei* (“Nutcracker Man”), have microwear with low complexity and few pits, quite unlike modern hard-object consumers (11–14, 59) (Figs. S5 and S6). In fact, the only modern primate taxa with such low mean complexity values are *Semnopithecus entellus*, *Trachypithecus cristatus*, *Colobus guereza*, *Alouatta palliata*, and *Theropithecus gelada* (67). These taxa are from different continents and different habitats, and they exhibit different degrees of arboreality/terrestriality. The one thing that they have in common is a predominantly leaf-based diet (grass leaves in the case of *T. gelada*) that includes relatively few hard objects (68). If australopiths were also significantly folivorous, they would be expected to evince skeletal and dental adaptations for generating and resisting highly repetitive, low-magnitude loads during chewing. Australopith skull architecture is consistent with a diet requiring considerable repetitive loading (65, 69, see ref. 70), but the flat occlusal surfaces of their tooth crowns appear to be poorly suited for the comminution of leaves (53, 63).

Carbon isotopes do not directly speak to the possibility of australopith folivory. It is true that the extremely high $\delta^{13}\text{C}$ values of *P. boisei*, *A. bahrelghazali*, and some individuals of other hominin taxa are typical of grass blade (leaf)-consuming herbivores and that, among the catarrhine primates, such high values are only found regularly among fossil relatives of the grass-eating baboon *T. gelada* (71–73). Folivores, however, can have predominantly C₃, C₄, or C₃/C₄ mixed diets (21, 22).

Given this ambiguity, several interpretations of the above evidence have been advanced. Perhaps eastern African australopiths were adapted for durophagy, but hard objects were eaten only during brief periods when preferred foods were unavailable? Such a fallback adaptation might explain their low-complexity microwear surfaces (7, 11, 13, see ref. 74). Perhaps the C₄ foods eaten by *P. boisei* and other taxa were the underground storage organs (USOs) of C₄ sedges? Sedge USOs are reasonably high-quality resources for which hominins would have had little competition (37). Perhaps the C₄ foods consumed by hominins included grass blades, meristems, seeds, and rhizomes depending on seasonal availability? Such a diet squares readily with the carbon isotope data for *P. boisei* and *A. bahrelghazali* (36, 39) and is consistent with dental microwear evidence given that *T. gelada* eats all of these items seasonally (75), but like *P. boisei*, has little microwear pitting (67, 76). There are arguments for and against all of the preceding (and other) alternatives, and we can safely say that all are underdetermined given the available evidence.

Despite these uncertainties, we have increasing confidence in the pattern of hominin dietary evolution from a carbon isotopic perspective. Before 4 Ma, most hominins avoided the abundant C₄ (or CAM) resources that we know were available to them. By about 3.5 Ma, C₄ (or CAM) plants had become a frequent component of an expanded hominin dietary repertoire. After this time, the overall range of African hominin isotope space changed little, although some taxa (e.g., *P. boisei*) followed

isotopically narrow paths, whereas others (e.g., *Homo* and *P. robustus*) remained in mixed C₃/C₄ space. We know that hominin mean $\delta^{13}\text{C}$ values, mandibular robusticity, and postcanine area are significantly correlated, especially among the eastern African australopiths, intimating that C₄ resource consumption was one of potentially several drivers behind the increasing robusticity of the australopith masticatory package. Existing dental microwear data suggest, however, that the mechanical properties of foods consumed were stable in the face of marked isotopic and morphological change.

Future

What steps need to be taken to clear up this rather muddled, if intriguing, picture? There exist clear priorities for morphological and microwear research. Additional work distinguishing the morphological (and microstructural) correlates of diets requiring repetitive vs. high-magnitude loading (7, 8, 69, 70) is required, and effort should be focused on the types of foods that were potentially processed by flat australopith molars. For instance, is there anything about the rotatory movement of the *Paranthropus* mandible during chewing (77) that, when coupled with its occlusal morphology, enamel microstructure, and dental macrowear, allowed more effective processing of tough food items than previously thought possible? Or could it be that, because of phylogenetic constraints, these hominins took a path of maximizing tooth longevity (by having larger, more thickly enameled teeth) rather than maximizing processing efficiency (69)? Particularly relevant might be investigation of nonprimate herbivore dentition, which is sometimes flat despite tough, low-quality diets (see 78). Regardless, additional work on the australopith durophagy hypothesis is warranted.

From a microwear perspective, a key question is what could produce the low-complexity microwear of the eastern African australopiths? Additionally, to intersect with the isotopic data, what ^{13}C -enriched foods are capable of producing such microwear textures (see 79)? More data on the microwear of sympatric fossil primates and other mammals are also required. The southern African record shows that many fossil papionins have less pitting (and presumably, less complexity) than modern *Papio* (80), but we lack similar data from eastern Africa to explore the conspicuously low complexity values of australopiths there. If eastern African papionins have universally low complexity values, for example, questions might be raised about the effect of habitat or taphonomy (e.g., seasonality of death) on microwear textures.

On the carbon isotope front, all early African hominin species for which significant samples exist have been analyzed. Thus, the broad patterns described here are not likely to change substantially. We can look forward, however, to learning more about how the $\delta^{13}\text{C}$ values of hominin species [or individuals (31, 32)] change over time and space and at the extent of isotopic niche partitioning among sympatric hominin taxa and their broader mammalian communities (Fig. S7) (see below on plants).

Yet, the most pressing task is to integrate the evidence from various paleodietary data sources, and to do so, we need to move in new directions. Because we are now confident that ^{13}C -enriched foods were very important resources for many hominins, we need to look at such foods as parts of the hominin fundamental (potential foods) and realized niches more seriously (as in 79). Additional work on the distribution, abundance, nutrition, and mechanical properties of C₄ or CAM plants should be fertile ground for consilience. The nutritional and mechanical properties of plants speak directly to issues of morphology (how well a hominin's morphology is suited for plant foods with particular mechanical/nutritional properties and shapes), dental microwear (could a certain plant resource produce a given microwear texture?), and carbon isotope analysis (is a resource of high quality and/or abundance relative to others of similar isotopic composition?).

We need to continue to look for novel sources of information. For instance, phytoliths may be preserved in the calculus of early hominin teeth (41) and can potentially provide a more specific taxonomic window on hominin diet. There also remains potential in hominin trace element analysis (81, 82). Furthermore, obtaining unadulterated organic material from early hominins for isotopic analysis (83), perhaps offering insight into the importance of animal food consumption in human evolution (see 3), remains a potential, if elusive, possibility.

With regard to individual hominin taxa, a focus on *P. boisei* might bear considerable fruit, because despite a lack of extant comparators (84), its diet might be the easiest to work out. Its combination of high $\delta^{13}\text{C}$ values and low microwear complexity considerably narrows the range of its potential diets. Additionally, understanding what it ate will likely shed light on the australopith masticatory complex generally, because it arguably represents the summit of a broad adaptive trend within the australopiths. Even if we find that its dietary habits were singular, and it is therefore a poor exemplar for other hominins, we will still have learned something important about hominin dietary diversity.

Conclusion

There can be little doubt that our understanding of early hominin diet has changed since the first carbon isotope study of early hominins was published in 1994 (9). Isotopic and other lines of evidence are now forcing us to consider adding foods to early hominin menus that few people would have contemplated 15 y ago. These advances are also helping us ask new questions about hominin interactions with the biotic and physical environment. For instance, the hypothesis that *P. boisei* principally consumed C₄ sedges around watercourses suggests that it had a highly constrained distribution across the landscape, little competition for preferred dietary resources, heightened interaction with aquatic predators, and increased susceptibility to climatically or tectonically driven changes in water availability. In contrast, a hominin that ate grass, or other animals that ate grass, would have used the environment, interacted with the broader mammalian community, and weathered changing habitats in very different ways. Thus, emerging ideas about hominin diet have deep, and possibly underappreciated, implications for our understanding of hominin evolution. Fortunately, the influx of new data over the past few years has given us an opportunity to integrate data sources in ways that were never before realistic. Hence, there is every reason to expect greater collaboration, and deeper understanding, is just around the corner.

Materials and Methods

Samples discussed herein were obtained from the Ditsong National Museum of Natural History, National Museums of Tanzania, National Museums of Kenya, Centre National d'Appui à la Recherche in Chad, and National Museum of Ethiopia. Sampling protocols varied because hominins were sampled during the course of multiple independent studies. Today, about 3 mg of enamel powder are obtained using a high-speed rotary drill (10). Before 1997 larger samples were required (9). Powdered enamel is treated with dilute acetic acid to remove secondary carbonates (9, 17). A small number of specimens were analyzed using laser ablation isotope ratio MS (31, 32, 41), and where appropriate, these $\delta^{13}\text{C}$ values were adjusted by 0.5‰ for comparability with values obtained by conventional acid hydrolysis (41).

Stable isotope ratios are expressed in δ -notation: $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$. R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratio in the sample and standard, respectively. The standard for carbon, Pee Dee Belemnite, had relatively more ^{13}C than most of the terrestrial biosphere, and therefore, plants and animals tend to have negative $\delta^{13}\text{C}$ values. The Pee Dee Belemnite standard has now been exhausted and replaced by the Vienna Pee Dee Belemnite standard.

Postcanine tooth area was taken directly from ref. 56 and supplemented with data for *Ardipithecus* from ref. 58. Mandibular cross-sectional area was calculated from refs. 55 and 57, author datasets, and previously unpublished Middle Awash Research Project data for *Ardipithecus* (Table S2).

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