The Diets of Early Hominins

Peter S. Ungar[1]* and Matt Sponheimer[2]*

Diet changes are considered key events in human evolution. Most studies of early hominin diets focused on tooth size, shape, and craniomandibular morphology, as well as stone tools and butchered animal bones. However, in recent years, dental microwear and stable isotope analyses have hinted at unexpected diversity and complexity in early hominin diets. Some traditional ideas have held; others, such as an increasing reliance on hard-object feeding and a dichotomy between *Australopithecus* and *Paranthropus*, have been challenged. The first known evidence of C_4 plant (tropical grasses and sedges) and hard-object (e.g., seeds and nuts) consumption dates to millions of years after the appearance of the earliest probable hominins, and there are no consistent trends in diet change among these species through time.

Diet is fundamental to an organism's ecology and, unsurprisingly, changes in diet have been hailed as key milestones in human evolution. Our understanding of the diets of our distant forebears, the early hominins, has been honed in recent decades as a result of new methods for dietary inference, the discovery of new fossil species and additional specimens, and improved reconstructions of the environments in which they evolved. Here, we focus on recent contributions from dental microwear and stable isotope analyses, two approaches that have challenged traditional thinking about early hominin dietary ecology over the past few years.

There are four principal groups of interest in early hominin evolution: the Mio-Pliocene probable hominins (*Sahelanthropus*, *Orrorin*, *Ardipithecus*); the Plio-Pleistocene "gracile" australopiths (*Australopithecus*); the "robust" australopiths (*Paranthropus*); and the earliest members of our own genus, *Homo*. The first group dates from about 7 million years ago (Ma), although the best-known species, *Ardipithecus ramidus*, lived about 4.4 Ma. The earliest recovered *Australopithecus* dates to approximately 4.2 Ma, whereas *Paranthropus* and *Homo* have their first known appearances shortly before and after 2.5 Ma, respectively, presumably from *Australopithecus* or *Australopithecus*-like ancestors. All of these groups are represented in eastern Africa, the first two are also known from Chad, and the latter three are found in South Africa (*1*).

What We Thought About Early Hominin Diets

The earliest probable hominins are not all well known, but in some cases their molars are smaller and more thinly enameled than those of later australopiths and more like those of extant chimpanzees (*1*), suggesting a diet of fleshy fruits and soft, young leaves. According to conventional wisdom, the craniodental morphology of later *Australopithecus* (e.g., thickly enameled, large, flat cheek teeth; heavily built crania and mandibles relative to living apes) reflects an adaptive shift from diets dominated by soft, sugary forest fruits to hard, brittle nuts or seeds, or to those with adherent abrasives, such as underground storage organs that were readily available in increasingly open Plio-Pleistocene landscapes (*2*, *3*) (Fig. 1). The larger teeth with well-buttressed skulls and massive chewing muscles of *Paranthropus* have led to the notion that "robust" australopiths relied more heavily on hard foods than did *Australopithecus*. The eastern African "hyper-robust" *Paranthropus boisei* has been considered the quintessence of this "nut-cracking" morphology (*4*) (Fig. 1).

The earliest members of our own genus are believed to have had tools to acquire and process a broad range of foods, such as meat and underground storage organs, bespeaking a generalized and versatile diet (*5*). Morphological evidence suggests that early *Homo* had smaller cheek teeth, thinner dental enamel, and greater occlusal relief than did their *Australopithecus* predecessors or their *Paranthropus* contemporaries (*6*–*8*) (Fig. 1). This may indicate changing selective pressures due to extraoral food processing with tools, but also suggests that early *Homo* teeth could more efficiently shear tough foods (such as leaves and meat) than could those of the australopiths. The possession of larger brains in some cases has also been used to argue that *Homo* required high-energy–yielding foods (*9*, *10*).

Much research on early hominin diets has focused on archaeological and morphological data, but like all lines of evidence for subsistence of fossil species, they have limitations. Stone tools and butchered bones tell us little about the plant foods that likely dominated early hominin diets. Moreover, although the earliest known stone tools and cut-marked bones date to at least 2.6 Ma and possibly earlier (*11*, *12*), they still postdate the earliest

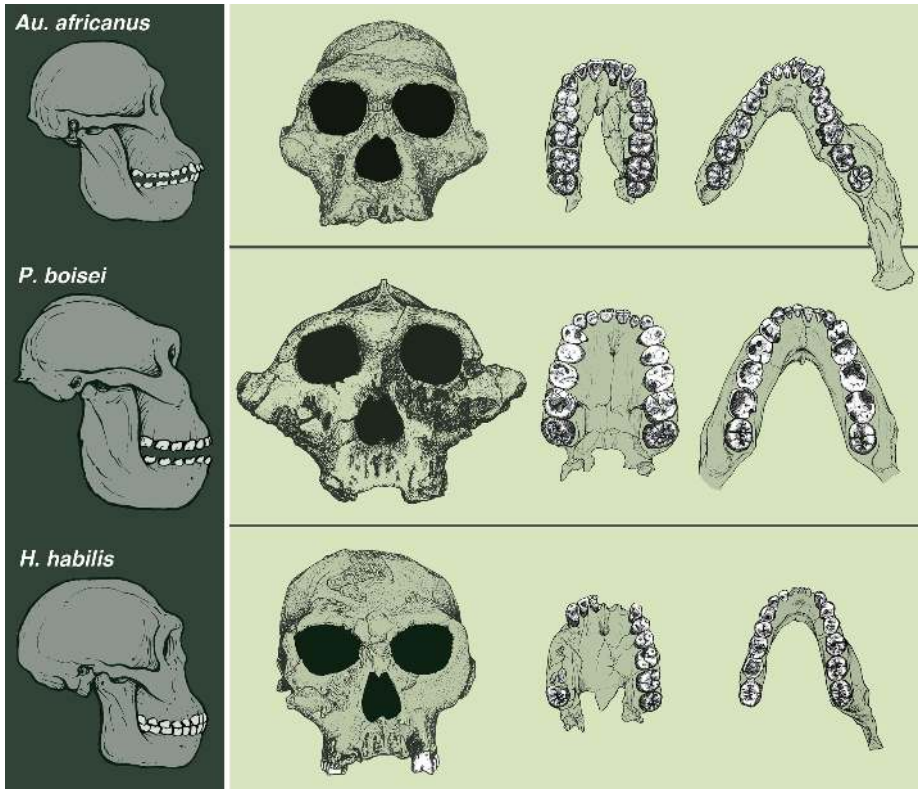
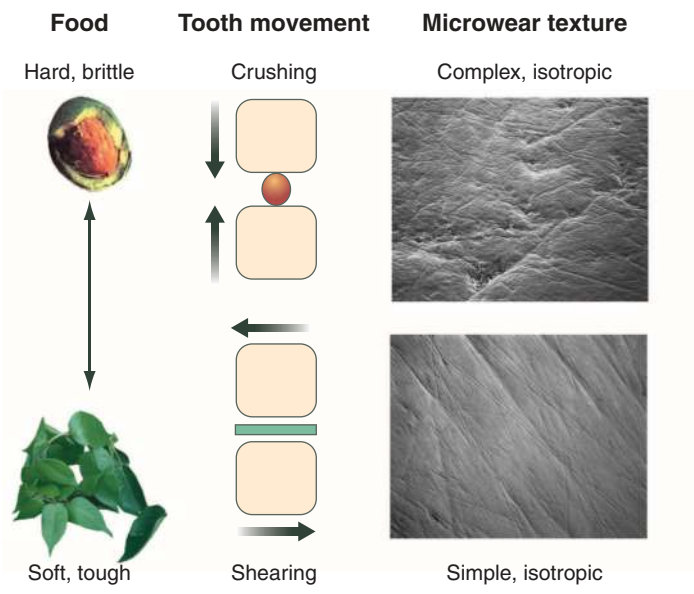


Fig. 1. Composite skulls (**left**) and specimen sketches (**right**) of the crania, maxillae, and mandibles of *Australopithecus africanus* (Sts 5, Sts 52a, and Sts 52b), *Paranthropus boisei* (KNM-ER 406, OH 5, Peninj), and *Homo habilis* (OH 24, KNM-ER 1813, OH 13). Differences in craniodental size and shape underscore the importance of diet for understanding hominin diversity and evolution. [Composites and specimen sketches are modified and reproduced from (*50*) and (*51*) with permission from the publishers and authors (©1988 Academic Press and ©1991 Waveland Press)]

[1]Department of Anthropology, University of Arkansas, Fayetteville, AR 72701, USA. [2]Department of Anthropology, University of Colorado, Boulder, CO 80309, USA.

*To whom correspondence should be addressed. E-mail: pungar@uark.edu (P.S.U.); msponheimer@gmail.com (M.S.)



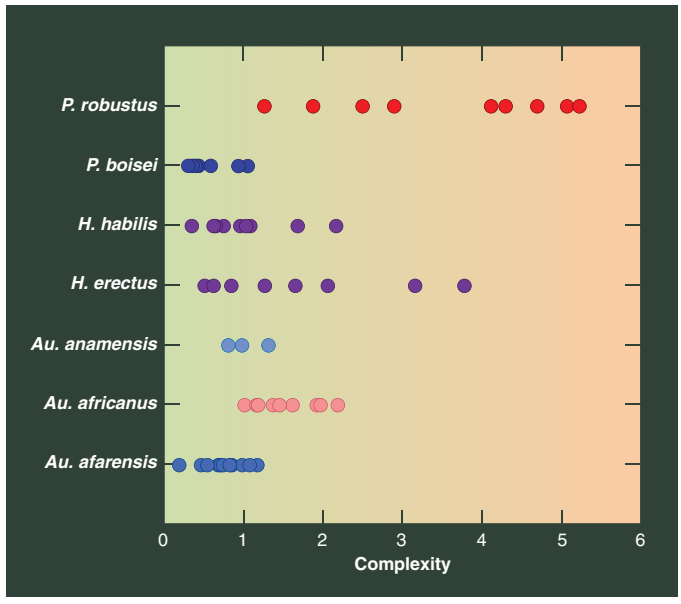


Fig. 2. Microwear textures of early hominins. Left: A model for microwear formation, wherein hard and brittle foods are crushed between opposing teeth, causing pitting with complex, isotropic surface textures; in contrast, soft and tough foods are sheared between opposing teeth that slide past one another, causing parallel scratches and simpler, anisotropic surfaces (*18*). Right: Microwear texture complexity values for individual fossil hominins by species [data from (*21*–*24*)].

hominins by millions of years. And although tooth and jaw size, shape, and structure offer important clues to the fracture properties of foods and associated masticatory stresses and strains to which a species is adapted (*13*–*16*), they indicate what early hominins were capable of eating and suggest the selective pressures faced by their ancestors, rather than what specific individuals ate. For direct evidence of the diets of fossil specimens recovered, we need other sources of information, such as dental microwear and stable light isotope analyses of teeth.

Dental Microwear

Mammals show a strong and consistent association between dental microwear pattern and food fracture properties. Those that crush hard, brittle foods (e.g., nuts, bones) typically have occlusal microwear dominated by pits, whereas those that shear tough items (e.g., leaves, meat) more often show long, parallel striations on their wear surfaces (*17*, *18*). These pits and scratches are traces of actual chewing events; they record activities during a moment in the life of an individual, much like footprints. And like footprints, microwear is fleeting; individual features turn over and are replaced by others as a tooth wears down (*19*). Indeed, microwear textures reflect diet in the days or weeks before death. This "last-supper" phenomenon (*20*) can be an asset, as large samples provide a sense of variation in diet within a species. Taxa with more catholic diets should evince a broader range of microwear textures than those that consume a more limited variety of foods. Several integrated metrics of microwear have proven useful: Surface fractal complexity, or change in apparent roughness with scale of observation, is used as a proxy for food hardness; anisotropy, or directionality of the wear fabric, is used as a proxy for food toughness. High complexity and anisotropy values correspond roughly to surfaces with heavy pitting and highly aligned scratches, respectively.

Dental microwear texture data have not yet been collected for the earliest probable hominins, but results have been published for cheek teeth of 73 specimens of *Australopithecus* (*Au. anamensis*, *Au. afarensis*, *Au. africanus*), *Paranthropus* (*P. boisei*, *P. robustus*), and early *Homo* (*H. habilis*, African *H. erectus*, *Homo* specimens from Sterkfontein Member 5 and Swartkrans Member 1) (*21*–*24*) (Fig. 2, Fig. 3, and table S1). None of the *Australopithecus* specimens have the high complexity values or heavily pitted surfaces of a hard-object feeder, as originally expected given their morphology. And the two eastern African species, *Au. anamensis* and *Au. afarensis*, have similar and homogenous microwear complexity

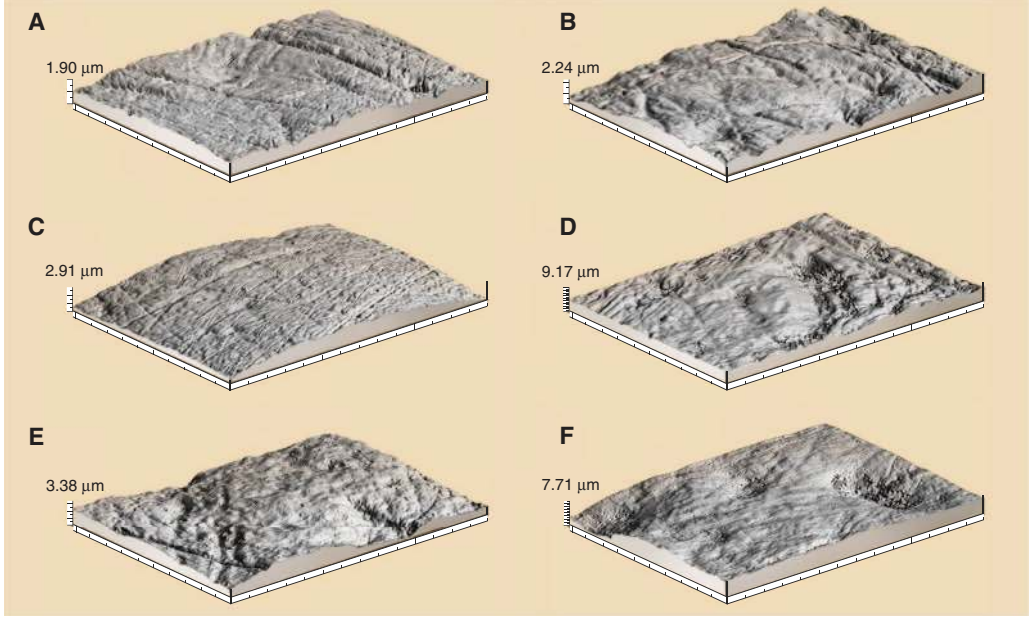


Fig. 3. (**A** to **F**) Photosimulations of microwear surfaces representing (A) *Au. afarensis* (AL 333w-1a), (B) *Au. africanus* (Sts 61), (C) *P. boisei* (KNM-CH1B), (D) *P. robustus* (SK 16), (E) *H. habilis* (OH 16), and (F) *H. erectus* (KNM-ER 807). Each represents an area of 102 μm by 139 μm on facet 9; vertical scales are as indicated.

(within and between taxa) despite a sample distribution spanning more than 1 million years and 1500 km and habitats as different as closed woodland and grassland (*25*). The South African *Au. africanus* has higher average complexity, but this is still lower than that expected of a hard-object feeder. *Australopithecus* spp. also have low to moderate anisotropy, with few values extending into the upper ranges of living folivorous primates. This indicates that they did not shear tough leaves as do modern folivores, perhaps because such foods were not an important part of their diet. However, it is also possible that they ground tough foods in the manner of a mortar and pestle, as their flat teeth might have posed fewer masticatory constraints than those of modern folivores (*23*).

The eastern African "robust" australopith, *P. boisei*, has low microwear texture complexity and low to moderate anisotropy values, suggesting a diet dominated by foods with fracture properties similar to those eaten by *Au. anamensis* and *Au. afarensis* (*22*, *23*). The South African *P. robustus*, on the other hand, has the highest average complexity and lowest anisotropy of any early hominin (*21*). Complexity in South African "robust" australopiths also shows high variance, with a distribution most comparable to hard-object fallback feeders such as gray-cheeked mangabeys (*Lophocebus albigena*) and brown capuchins (*Cebus apella*), which tend to "fall back" on harder items when softer, more preferred foods are unavailable (*21*). This could indicate that their anatomy evolved to cope with infrequently eaten but fracture-resistant foods [see (*15*)].

Microwear textures of early *Homo* suggest that all species had fairly generalized diets lacking specialization for either extremely hard or tough foods (*24*). Of note, *H. erectus* has substantially more variation in microwear complexity values than *H. habilis*, or indeed than that of any other hominin examined to date except *P. robustus*. This suggests that *H. erectus* had a comparatively broad-based diet, spanning a range of fracture properties including some hard and perhaps tough foods, which may also produce small pits through adhesive wear (*26*).

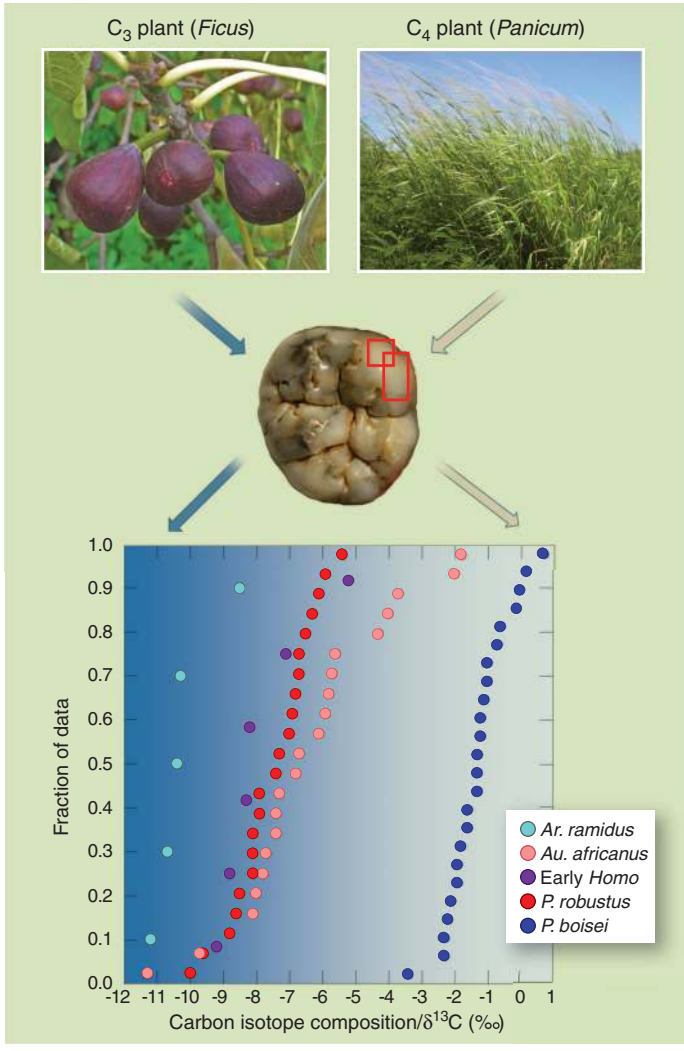


Fig. 4. Carbon isotope compositions ($^{13}C/^{12}C$) of early hominins. Top: Carbon flows from C_3 and C_4 plants (blue and pink arrows, respectively) into the tooth enamel of the consumer (in this case *P. robustus*, SK 1), and its resulting carbon isotope composition reveals the proportions of these plant types consumed. Bottom: Quantile plot with carbon isotope ratio data for all early hominins analyzed to date [data from (*34*–*38*, *49*)]. Darker shading indicates a greater degree of C_3 plant consumption. Each data point reflects a hominin's diet for a period ranging from months to years depending on the sampling procedure used (red rectangles represent hypothetical sampling areas). Carbon isotope ratios ($^{13}C/^{12}C$) are expressed as δ values in parts per thousand relative to the PeeDee Belemnite standard.

Stable Isotopes

Stable isotope analysis of ancient tissues is based on the principle "you are what you eat" (*27*). Stable isotopes in foodstuffs become incorporated into the growing teeth and bones of consumers. These tissues then acquire an isotopic composition related to that of the source food that can reveal much about paleodiets (*28*–*30*). Although dietary studies can be undertaken with bone mineral in some cases, dental enamel is preferred as it is more highly mineralized and thus less susceptible to postdepositional chemical alteration than bone (*31*); it is also an incremental tissue that may allow investigation of intra-individual diet change through time.

Carbon isotopes are particularly useful for hominin paleodietary studies because they tell us about the relative proportions of plants using the C_3 (trees, bushes, forbs) and C_4 (tropical grasses and some sedges) photosynthetic pathways that were consumed by herbivores, or, in the case of faunivores, the proportions of these foods consumed by their prey (*28*) (Fig. 4). This allows a variety of questions to be addressed. For instance, did the early members of our lineage have diets similar to those of our closest living kin, the chimpanzee (*Pan troglodytes*)? We know that chimpanzees have diets dominated by C_3 tree foods (especially fleshy fruits), whether in their preferred forest habitats or in fairly open savannas with abundant grasses (*32*, *33*). Carbon isotope ratios ($^{13}C/^{12}C$) have been analyzed for more than 75 hominin specimens from sites in Ethiopia, Kenya, Tanzania, and South Africa, ranging in age from about 4.4 to possibly 0.8 Ma (Fig. 4 and table S1). The broad view of these data is that early hominins did not have diets like those of extant African apes, but this conclusion belies the complexity of the varied results. For instance, the earliest taxon analyzed to date, *Ar. ramidus*, had in aggregate a C_3 diet much like that of savanna chimpanzees (*34*). Other taxa, such as *Au. africanus*, *P. robustus*, and early *Homo*, were more middling, as they ate more than 50% C_3 foods but also consumed substantial quantities of C_4 foods (*33*, *35*–*38*) that became increasingly available in the Plio-Pleistocene (*39*, *40*). In marked contrast, *P. boisei* had a diet of about 75 to 80% C_4 plants, unlike that of any other fossil hominin but similar to that of grass-eating warthogs, hippos, and zebras (*18*, *37*, *41*). Carbon isotopic variability between these taxa is also marked, with *Au. africanus* ranging from pure C_3 to nearly pure C_4 diets, whereas other taxa such as *P. boisei* have much reduced ranges.

Thus, carbon isotopes suggest marked dietary diversity within the hominins. This is not surprising, given their temporal and ecogeographic ranges and the variation in masticatory morphology they manifest; however, the isotope data also suggest enormous and unanticipated differences between contemporaneous taxa with strong morphological similarities, notably the "robust" australopiths *P. robustus* and *P. boisei*. Despite their attribution to the same genus, there is no overlap in their carbon isotope compositions (*41*), which is a rarity for congeners among extant mammals. All told, the early hominins analyzed to date fall roughly into three groups: (i) those with carbon isotope compositions indicating strong C_3 diets similar to those of savanna chimpanzees, (ii) those with variably mixed C_3/C_4 diets, and (iii) those with carbon isotope compositions indicating diets of chiefly C_4 vegetation, as is typically seen for grass-eating ungulates in tropical climes.

Integrating and Moving Forward

Microwear and stable carbon isotope studies have challenged long-held assumptions about early hominin diets. The simple textbook model—in which hominin craniodental functional morphology evolved for increasing consumption of hard, brittle foods as savannas spread—is incorrect, or at least too simplistic. None of the *Australopithecus* or even *Paranthropus* specimens examined from eastern Africa show microwear patterns of a hard-object feeder (*18*). And whereas the *Ardipithecus* carbon isotope composition is consistent with a diet similar to those of savanna chimpanzees (as might be expected), that of *P. boisei* indicates that C_4 plant foods such as grasses or sedges provided the vast majority of dietary energy for this taxon. This was almost completely unanticipated [but see (*42*)] and raises the intriguing possibility that earlier eastern African australopiths may have had a similar penchant for C_4 foods, especially given the similarities of their dental microwear to that of *P. boisei*.

Both the microwear and carbon isotope data offer other surprises. First, there seems to be a geographic influence on australopith diets; the microwear texture complexity of eastern African *Australopithecus* and *Paranthropus* is lower than that of their South African congeners. Likewise, *P. boisei* and *P. robustus* have different carbon isotope compositions, with the South African "robust" australopiths consuming a much higher fraction of C_3 foods, like most other early hominins (although not to the extent seen in *Ardipithecus*). This might indicate that a specialized morphological complex can serve more than one function and reflect more than one type of diet; perhaps "robust" morphology functioned in high-stress hard-object feeding for *P. robustus* but in repetitive loading during grinding of tough foods for *P. boisei*.

The apparent continuity of microwear pattern through the putative lineage *Au. anamensis–Au. afarensis–P. boisei* could even suggest that morphological changes reflect increasing efficiency for grinding large quantities of tough food. Although living primates that eat tough items typically have sharp shearing crests, eastern African australopiths and especially *P. boisei* may have evolved a different solution for processing such foods, given the flattened, thickly enameled teeth of their close ancestors (*23*). Natural selection must work with the raw materials available to it. Thus, the present-day ecomorphological diversity within the primates may not be sufficient for making some paleoecological inferences, which is not surprising given that the vast majority of all primates, especially apes, that have ever lived are now extinct.

The microwear and isotope evidence also gives insight into food choices and foraging strategies. The *P. robustus* microwear complexity distribution suggests that individuals ate hard objects only on occasion, perhaps in a manner akin to the lowland gorilla's (*Gorilla gorilla*) falling back on lower-quality, tough foods during times when preferred soft, sugar-rich items are unavailable (*43*). Laser ablation analysis, which allows isotopic sampling along the rough growth trajectory of teeth, also reveals considerable variation in within-tooth carbon isotope compositions of *P. robustus* at inter- and intra-annual time scales (*44*). In contrast, the teeth of *Au. afarensis* show little variance in microwear texture complexity despite a range of samples across time and space. In this case, a model involving increased foraging ranges for foods with given fracture or nutritional properties, such as observed for some chimpanzees (*45*), might be more appropriate.

The above evidence challenges certain aspects of our understanding of hominin biology, biogeography, and evolution. For instance, if *P. boisei* was a C_4 sedge consumer (*37*), its distribution was likely limited to the periphery of permanent sources of water. Its eventual extinction might then be linked to the difficulty of dispersing away from water sources despite the vaunted energetic efficiency of bipedalism (*46*). On the other hand, if *P. boisei* was a C_4 grass consumer, it might have thrived in the emerging savannas of the Pleistocene, demanding an explanation other than habitat change for its extinction.

Our understanding of the paleoecology of these organisms is in flux, and a great deal of directed, integrative research remains to be done [e.g., (*47*)]. Microwear and stable carbon isotope analyses are needed for all relevant species, and these results must be integrated with data on masticatory biomechanics, plant distributions and nutritional/mechanical properties, and primate ecology and digestive physiology. An important role for microwear and isotope analyses within contemporary paleodietary research is to focus on underlying processes rather than outcomes, as well as to recognize evolutionary novelties, such as grazing giraffes (*48*) and grass- or sedge-eating apes (*37*). When these behavioral proxies are linked to morphological and paleoenvironmental data sets through time, yoking habitat and dietary change to morphological response, our understanding of the patterns and processes of hominin evolution will be greatly augmented.

References and Notes

1. B. Wood, N. Lonergan, *J. Anat.* **212**, 354 (2008).
2. M. F. Teaford, P. S. Ungar, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 13506 (2000).
3. G. Suwa *et al.*, *Science* **326**, 94 (2009).
4. B. Wood, P. Constantino, *Am. J. Phys. Anthropol.* **50** (suppl. 45), 106 (2007).
5. P. S. Ungar, F. E. Grine, M. F. Teaford, *Annu. Rev. Anthropol.* **35**, 209 (2006).
6. A. D. Beynon, B. A. Wood, *Am. J. Phys. Anthropol.* **70**, 177 (1986).
7. P. S. Ungar, *J. Hum. Evol.* **46**, 605 (2004).
8. H. M. McHenry, K. Coffing, *Annu. Rev. Anthropol.* **29**, 125 (2000).
9. L. C. Aiello, P. Wheeler, *Curr. Anthropol.* **36**, 199 (1995).
10. K. Milton, *Evol. Anthropol.* **8**, 11 (1999).
11. S. Semaw, *J. Archaeol. Sci.* **27**, 1197 (2000).
12. S. P. McPherron *et al.*, *Nature* **466**, 857 (2010).
13. D. J. Daegling, F. E. Grine, *Am. J. Phys. Anthropol.* **86**, 321 (1991).
14. W. L. Hylander, in *Evolutionary History of the "Robust" Australopithecines*, F. E. Grine, Ed. (Aldine de Gruyter, New York, 1988), pp. 55–83.
15. D. S. Strait *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 2124 (2009).
16. P. W. Lucas, *Dental Functional Morphology: How Teeth Work* (Cambridge Univ. Press, New York, 2004).
17. P. S. Ungar, *Mammal Teeth: Origin, Evolution, and Diversity* (Johns Hopkins Univ. Press, Baltimore, MD, 2010).
18. See supporting material on *Science* Online.
19. M. F. Teaford, O. J. Oyen, *Am. J. Phys. Anthropol.* **75**, 279 (1988).
20. F. E. Grine, *J. Hum. Evol.* **15**, 783 (1986).
21. R. S. Scott *et al.*, *Nature* **436**, 693 (2005).
22. P. S. Ungar, F. E. Grine, M. F. Teaford, *PLoS ONE* **3**, e2044 (2008).
23. P. S. Ungar, R. S. Scott, F. E. Grine, M. F. Teaford, *Philos. Trans. R. Soc. London Ser. B* **365**, 3345 (2010).
24. P. S. Ungar, K. L. Krueger, R. J. Blumenschine, J. Njau, R. S. Scott, *J. Hum. Evol.* 10.1016/j.jhevol.2011.04.006 (2011).
25. F. E. Grine, P. S. Ungar, M. F. Teaford, *S. Afr. J. Sci.* **102**, 301 (2006).
26. M. F. Teaford, J. A. Runestad, *Am. J. Phys. Anthropol.* **88**, 347 (1992).
27. M. J. Deniro, S. Epstein, *Geochim. Cosmochim. Acta* **42**, 495 (1978).
28. J. A. Lee-Thorp, J. C. Sealy, N. J. van der Merwe, *J. Archaeol. Sci.* **16**, 585 (1989).
29. P. L. Koch, K. A. Hoppe, S. D. Webb, *Chem. Geol.* **152**, 119 (1998).
30. T. E. Cerling, J. M. Harris, M. G. Leakey, *Oecologia* **120**, 364 (1999).
31. J. A. Lee-Thorp, N. J. van der Merwe, *J. Archaeol. Sci.* **18**, 343 (1991).
32. M. J. Schoeninger, J. Moore, J. M. Sept, *Am. J. Primatol.* **49**, 297 (1999).
33. M. Sponheimer *et al.*, *J. Hum. Evol.* **51**, 128 (2006).
34. T. D. White *et al.*, *Science* **326**, 67 (2009).
35. J. Lee-Thorp, J. F. Thackeray, N. van der Merwe, *J. Hum. Evol.* **39**, 565 (2000).
36. N. J. van der Merwe, J. F. Thackeray, J. A. Lee-Thorp, J. Luyt, *J. Hum. Evol.* **44**, 581 (2003).
37. N. J. van der Merwe, F. T. Masao, M. K. Bamford, *S. Afr. J. Sci.* **104**, 153 (2008).
38. J. A. Lee-Thorp, N. J. van der Merwe, C. K. Brain, *J. Hum. Evol.* **27**, 361 (1994).
39. P. B. deMenocal, *Earth Planet. Sci. Lett.* **220**, 3 (2004).
40. R. Bobe, *J. Arid Environ.* **66**, 564 (2006).
41. T. E. Cerling *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 9337 (2011).
42. C. J. Jolly, *Man* **5**, 5 (1970).
43. P. S. Ungar, in *Comparative Dental Functional Morphology*, T. Koppe, G. Meyer, K. W. Alt, Eds. (Karger, Basel, 2009), pp. 38–43.
44. M. Sponheimer *et al.*, *Science* **314**, 980 (2006).
45. W. C. McGrew, P. J. Baldwin, C. E. G. Tutin, *J. Hum. Evol.* **10**, 227 (1981).
46. P. S. Rodman, H. M. McHenry, *Am. J. Phys. Anthropol.* **52**, 103 (1980).
47. N. Dominy, E. R. Vogel, J. D. Yeakel, P. Constantino, P. W. Lucas, *Evol. Biol.* **35**, 159 (2008).
48. N. Solounias, M. Teaford, A. Walker, *Paleobiology* **14**, 287 (1988).
49. M. Sponheimer *et al.*, *J. Hum. Evol.* **48**, 301 (2005).
50. J. G. Fleagle, *Primate Adaptation and Evolution* (Academic Press, New York, 1988).
51. C. S. Larsen, R. M. Matter, D. L. Gebo, *Human Origins: The Fossil Record* (Waveland, Prospect Hills, IL, 1991).

Acknowledgments: Supported by NSF, the Leakey Foundation, and the Wenner-Gren Foundation. We thank C. Campbell, J. Leichliter, O. Paine, Y. Rahman, C. Ross, and P. Sandberg for comments; T. Cerling, D. Codron, D. de Ruiter, F. Grine, J. Lee-Thorp, R. Scott, M. Teaford, and N. van der Merwe for discussions over the years; and D. de Ruiter for the image of SK 1. All raw data referred to in this paper are published in (*21–24*, *34–38*, *49*).

Supporting Online Material

www.sciencemag.org/cgi/content/full/334/6053/190/DC1
SOM Text
Table S1
References

10.1126/science.1207701