

# Diet in Early *Homo*: A Review of the Evidence and a New Model of Adaptive Versatility

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## Key Words

Hominin, feeding adaptations, *Homo habilis*, *Homo rudolfensis*,  
*erectus*

## Abstract

Several recent studies have stressed the role of dietary change in the origin and early evolution of our genus in Africa. Resulting models have been based on nutrition research and analogy to living peoples and nonhuman primates or on archeological and paleoenvironmental evidence. Here we evaluate these models in the context of the hominin fossil record. Inference of diet from fossils is hampered by small samples, unclear form-function relationships, taphonomic factors, and interactions between cultural and natural selection. Nevertheless, craniodental remains of *Homo habilis*, *H. rudolfensis*, and *H. erectus* offer some clues. For example, there appears to be no simple transition from an australopith to a *Homo* grade of dietary adaptation, or from closed forest plant diets to reliance on more open-country plants or animals. Early *Homo* species more likely had adaptations for flexible, versatile subsistence strategies that would have served them well in the variable paleoenvironments of the African Plio-Pleistocene.

## INTRODUCTION

Over the past few years, scholars have paid increased attention to the evolution of diet in the Plio-Pleistocene hominins of Africa, especially the earliest members of our genus, *Homo rudolfensis*, *H. habilis*, and *H. erectus*. Resulting models have been based largely on nutritional studies combined with direct analogy (to living peoples or nonhuman primates) or on contextual evidence, such as archeological and paleoenvironmental indicators. Although many of these models are elegantly constructed and well reasoned, they do not tell us what the hominins actually ate. They form hypotheses that may or may not be testable given the nature of the fossil record.

Here, we review and evaluate some recent models for dietary adaptations of early *Homo* in the context of the hominin fossil record, the archeological record, and evidence for environmental dynamics during the Plio-Pleistocene. The most notable point from this exercise is the limited scope of what can actually be said about the diets of these early hominins. Nevertheless, the jaws and teeth of early *Homo* do offer some clues to the diets of these species. A synthetic view of this evidence, in the context of archeological and paleoenvironmental indicators, suggests that the origin and early evolution of *Homo* are most likely associated with biological and cultural adaptations for a more flexible, versatile subsistence strategy. This strategy would have put the earliest members of our genus at an advantage given climatic fluctuation and a mosaic of different microhabitats in Africa during the late Pliocene.

## THE FOSSIL EVIDENCE FOR PLIO-PLEISTOCENE *HOMO*

The temporal ranges, taxonomy, and hypodigms of early *Homo* species have all been the subject of intense debate over the past couple of decades, and any meaningful discussion of the role of diet in the origin and early evolution of our genus must be grounded in a firm understanding of these issues.

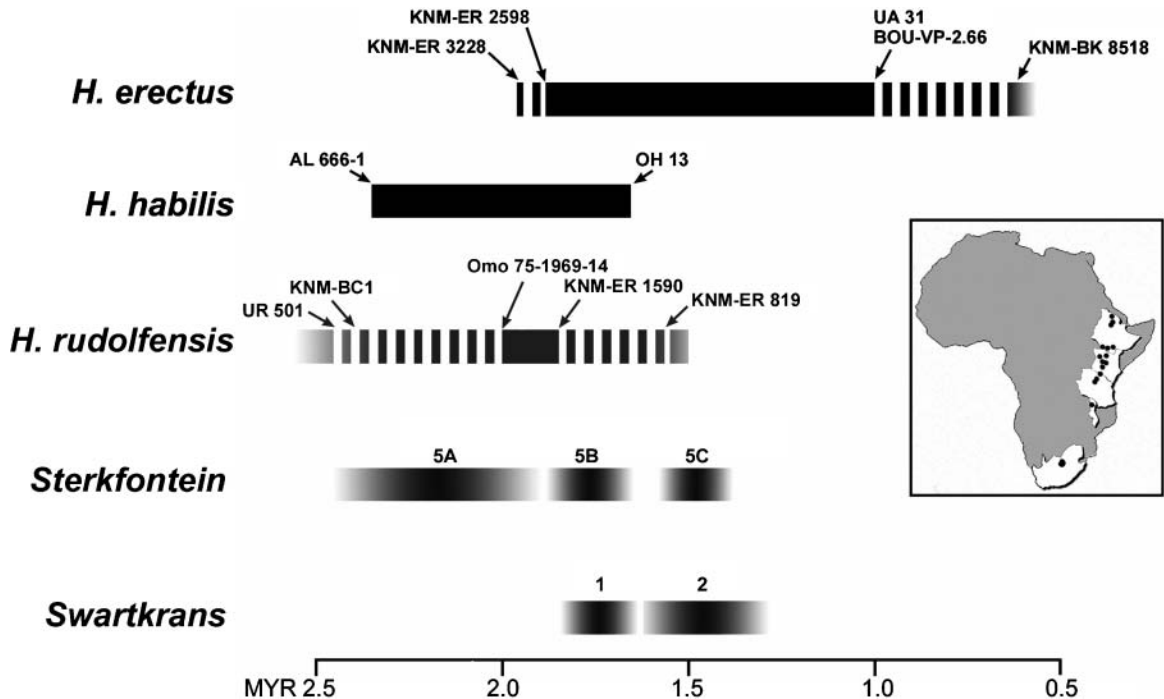
## *Homo habilis* and *Homo rudolfensis*

Many researchers recognize two early species within our genus, *Homo habilis* and *H. rudolfensis* (Stringer 1986, Lieberman et al. 1988, Wood 1991, Rightmire 1993, Strait et al. 1997, Leakey et al. 2001, Dunsworth & Walker 2002, contra Tobias 1991). For the purposes of this review, we accept the hypodigms set forth by Wood (1991) for *H. habilis* and *H. rudolfensis*.

Temporal ranges for these taxa are presented in **Figure 1**. *Homo habilis* and *H. rudolfensis* were largely synchronous. Most *H. habilis* specimens come from Olduvai and Koobi Fora and date to between 1.87 and c. 1.65 Myr, although A.L. 666-1 from the Hadar extends its range back to 2.33 Myr (Kimbel et al. 1997). Specimens attributed to *H. habilis* at Sterkfontein (Tobias 1991) come mostly from Member 5, which probably also dates to between 2.3 and 1.8 Myr. Most *H. rudolfensis* specimens come from Koobi Fora and date to between 1.90 and 1.85 Myr, although specimens from the Omo Shungura Formation extend this range to 2.02 Myr and perhaps back even to 2.40 (Suwa et al. 1996). If the UR 501 mandible from Malawi and KNM-BC 1 temporal from Chemeron are attributable to *H. rudolfensis* (Bromage et al. 1995, Sherwood et al. 2002), this lends further support to a first appearance date for this taxon of c. 2.4 Myr. Furthermore, if KNM-ER 819 from Koobi Fora is *H. rudolfensis* (Wood 1991), that would extend the range for this taxon forward to between 1.65 and 1.55 Myr (**Figure 1**). Even so, there is little doubt that, as with other paleontological species, the fossil record does not accurately sample the entire geochronological ranges of either *H. habilis* or *H. rudolfensis*.

## *Homo erectus*

Whereas Wood (1991) has argued for taxonomic distinction of *Homo ergaster* from *H. erectus* and other early *Homo* species, other workers have noted continuous morphological variation between specimens attributed



**Figure 1**

Early *Homo* timeline.

to *H. ergaster* and *H. erectus* (Wolpoff 1984, Kramer 1993, Rightmire 1998, Anton 2002, Asfaw et al. 2002, Dunsworth & Walker 2002). We here concur with these workers, who regard the earlier and later African specimens as sampling a single evolving species, *H. erectus*.

*Homo erectus* was a long-lived species, with a temporal range in Africa extending well over a million years (Figure 1). It was synchronous in the earlier part of its range with both *H. habilis* and *H. rudolfensis*. The oldest undisputed *H. erectus* specimen (the KNM-ER 2598 cranial fragment) dates to 1.89 Myr, well within the ranges of both *H. habilis* and *H. rudolfensis* (Feibel et al. 1989). The enigmatic KNM-ER 3228 hipbone might extend the range of this taxon as far back as 1.95 Myr (Susman et al. 1983, Rose 1984). The youngest African *H. erectus* fossils came from Baringo, and probably date to less than 660 Kyr (Wood & Van Noten 1986), and from Tighenif, Alge-

ria, between 800 Kyr and 600 Kyr (Geraads et al. 1986). *Homo erectus* has also been identified in Member 2 at Swartkrans (Robinson 1961, Rightmire 1990, Wood 1991, Tobias 1991), dating to between 1.9 and 1.65 Myr and perhaps younger (Vrba 1985, McKee et al. 1995).

## ENVIRONMENTAL DYNAMICS AND DIETS OF EARLY *HOMO*

Given that diet is a direct link between an animal and its environment, environmental dynamics likely played an important role in dietary changes related to the origin and evolution of early *Homo*. Recent investigators have attempted to explain the origins of individual hominin species by relating first appearances of taxa during the late Pliocene to major episodes of global cooling and drying (see Vrba et al. 1995). Although researchers debate the tempo of faunal turnover at the

time (see Potts 1998), most agree that cooler and more variable climatic conditions had a broad effect on mammalian diversity. Conventional wisdom associates adaptive radiations of *Paranthropus* and *Homo* to these environmental changes.

Cerling (1992) has noted that after 2.5 Myr, C<sub>4</sub> grasslands spread across East Africa, concomitant with periodic fluctuations in climate. If any of the early hominins had critical keystone foods (i.e., foods essential for survival and reproduction) found only in more closed habitats, then extinction would likely have followed. By contrast, if early hominins developed craniodental specializations for consuming savanna resources, such as roots, seeds, and tubers, they would have flourished. An alternative would be to face environmental change with versatility rather than specialization (e.g., Teaford et al. 2002, Wood & Strait 2004). This act would have been advantageous given variable, unpredictable environments, or a mosaic environment comprised of many different microhabitats (Behrensmeyer et al. 1997, Potts 1998, Wood & Strait 2004).

## THE ARCHEOLOGICAL RECORD

The archeological record can provide important evidence for the diets of Plio-Pleistocene hominins. The earliest archeological remains, both lithic and faunal, probably relate directly to feeding activities. Modern orangutans and chimpanzees use hammerstones and wooden probes to open hard-husked fruits, sticks for digging and probing for insects in hard-to-reach places, and other implements fashioned to allow procurement or preparation of foods that would otherwise be inaccessible to them (Fox et al. 1999, Whiten et al. 1999). The earliest hominins likely also used such tools (Panger et al. 2002).

The earliest evidences we have for tool manufacture and use by hominins are stone artifacts from Gona, Ethiopia, dated to at least 2.5 Myr (Semaw et al. 1997) and faunal re-

mains with cut marks from Bouri, Ethiopia, dated to about the same age (De Heinzelin et al. 1999). The actual origin of material culture is almost certainly much older, however, because the earliest tools were likely perishable (Mann 1972, Panger et al. 2002). The archeological record also likely underestimates the functional versatility of the early hominin tool kit. The use of stone tools in butchery is evinced by cut marked bones, but tools were probably also used to process many other types of foods, as is evident from microwear of slightly younger Oldowan artifacts used to prepare vegetation, presumably for consumption, and perhaps to make other tools from plant tissues (Keeley & Toth 1981). Furthermore, we cannot assume that early stone tools served the same functions for all early hominin groups, especially given differences in both material toolkits and diet among living chimpanzee groups (Whiten et al. 1999) and human foragers (Milton 2002). Indeed, we might reasonably view early stone tools as indicative of an expanded toolkit that included perishable and durable implements, thus reflecting increased dietary versatility and flexibility (e.g., Mann 1972, Schick & Toth 1993). Increasing distances by which stones were transported and the recovery of artifacts from a broader range of environments through the late Pliocene (Rogers et al. 1994, Potts 1998) also suggest increasing adaptive versatility for hominins.

Nevertheless, we are limited to the available evidence, and this evidence indicates that by 2.5 Myr, Pliocene hominins were making and using stone tools to process animal remains, almost certainly for consumption. Many researchers have thus argued that the earliest stone tools indicate the beginnings of a substantive increase in meat consumption by hominins (e.g., Dart 1953, Isaac 1971, Harris 1983). Although the early evidence is limited, additional possible cut marked bones have been found in deposits dated to 2.33–2.34 Myr in both West Turkana and the Hadar (Kibunjia 1994, Kimbel et al. 1997).

At first glance, it would seem that the near synchrony of appearances of *Homo* and the first stone tools and cut marked bones are connected, particularly in light of long-standing assumed associations between *H. habilis* and Oldowan artifacts (Leakey et al. 1964). However, there were at least three genera and four species of hominins in East Africa around 2.4–2.5 Myr, and there is no way to know which one(s) was responsible for these artifacts. The earliest known cut marks, for example, are found in the same stratigraphic horizon as hominin fossils referred to “*Australopithecus garhi*” (Asfaw et al. 1999). Also, the earliest evidence for *Paranthropus* (Walker et al. 1986) dates to 2.5 Myr, and some scholars have suggested that at least *P. robustus* used durable, identifiable tools (Susman 1988, Backwell & d’Errico 2001). At this point, then, we cannot argue that durable tool manufacture reflects a new, unique adaptive zone that can help define and distinguish the genus *Homo*. Regardless of whether *Australopithecus* or *Paranthropus* left an archeological record, however, most would agree that one or more species of early *Homo* probably did make and use Oldowan tools.

What about associations between major archeological advances and the appearance of *Homo erectus*? The first major technological innovation, the Acheulean, appears at ~1.4 Myr (Asfaw et al. 1992), and so it post-dates the appearance of *H. erectus*. Furthermore, we cannot associate *Homo erectus* with the control of fire for cooking (another important advance in food-processing technology). Although early evidence for fire at Plio-Pleistocene sites includes reddened patches at Chesowanja and Koobi Fora, and burnt bones at Swartkrans (Gowlett et al. 1981, Brain 1993, Bellomo 1994), most researchers question whether this indicates controlled use of those fires (see Bunn 1999). The oldest unequivocal hearths date only to the middle Pleistocene of Eurasia and are attributed to *Homo heidelbergensis* (James 1989), and even the most recent finds do not push control of fire back beyond 790 Kyr (Goren-Inbar et al. 2004).

On the other hand, the earliest large concentrations of stone tools and modified bones at sites such as DK and FLK 22 at Olduvai and FxJj 1 at Koobi Fora are approximately coincident with the appearance of *Homo erectus* (Blumenschine & Masao 1991). Such sites show that animal tissues had become an important part of early hominin diets by the beginning of the Pleistocene (Potts 1983, Shipman 1983, Blumenschine 1995, Bunn 2001). Still, because *H. habilis*, *H. rudolfensis*, and *Paranthropus boisei* are also found at these sites, it is not possible to associate these concentrations definitively with any specific hominin. Nevertheless, it is reasonable to assume that *H. erectus* did make and use stone tools for animal processing, given similar sites outside of Africa, where no other hominins have been found (e.g., Dennell et al. 1988, Gabunia & Vekua 1995).

## DIET MODELS AND EARLY *HOMO*

The apparent contemporaneity of the earliest *Homo*, Oldowan technology and the spread of C<sub>4</sub> grasslands across East Africa have made for compelling models of the origin and evolution of diet in early *Homo*. The argument suggests that environmental change during the late Pliocene (whether directional or an increase in fluctuation) would have led to changes in resources available to hominins. If early *Homo* used a greater range of habitats, or more variable habitats, an expanded toolkit would have allowed these hominins to process and consume foods that would have been otherwise unavailable. Environmental change provides the motive, and technological innovation offers the opportunity for new dietary adaptations. There remains, however, no consensus on which foods were key and how these foods contributed to the evolution of more human-like subsistence practices. Most models stress increased reliance on either animal products or on savanna-based plant resources.

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**USO:** underground storage organ

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## Meat Eating and Human Evolution

For more than a half century, researchers have stressed the predatory nature of humankind and the key role that hunting must have played in human evolution (e.g., Dart 1953). The basic idea has been that, as savannas began to spread, forest resources became increasingly scarce, and grassland-adapted ungulates became more abundant. Hominins began to incorporate more meat into their diets, with improved hunting abilities following from an expanding toolkit and increasing intelligence. A feedback loop followed, as the new high-protein diet allowed for larger brains, and hunting strategies led to a division of labor, more complex social systems, and selection for yet greater intelligence (Washburn 1963, Isaac 1971; see Lee & DeVore 1968).

Models emphasizing the role of meat eating in human evolution continue to dominate the literature today, but they approach the issue from a variety of perspectives (see Stanford & Bunn 2001). Models relating diet to brain size, for example, have suggested that meat became an increasingly important nutritional resource for early *Homo*, especially *H. erectus* (Milton 1987; Leonard & Robertson 1992, 1994). According to Aiello & Wheeler (1995), we maintain our basal metabolic rates by balancing brain size with gut size. Splanchnic organs and brains are roughly equally expensive tissues to maintain, so decreasing our guts would have allowed brain expansion without the need for a marked increase in energy intake. Animal products would provide readily digestible nutrients for hominins with small guts, so an increase in meat consumption may be tied, indirectly, to the evolution of a large brain. At the same time, animal fat would also provide important nutrients, such as long-chain polyunsaturated fatty acids used to form brain tissue (Hayden 1981, Speth 1989, Eaton et al. 2002).

Eaton and coauthors (2002) argue that as hunting and/or scavenging assumed greater significance, increased complexity of interpersonal and social interactions, together with

animal fat, provided the necessary “psychonutritional nexus” for brain expansion. Indeed, many scholars have emphasized the role of changing subsistence strategies in division of labor and food sharing (Washburn & Lancaster 1968, Isaac 1978, Milton 1987). In this regard, increased meat consumption is seen as having been important to the origins and early evolution of a more human-like adaptive strategy. Recent work on nonnutritional aspects of hunting and meat consumption by chimpanzees and human foragers provides elaborate models for exploring possible roles of food in the evolution of human sociality (Kaplan et al. 2000, Stanford 2001).

## Plant Eating and Human Evolution

Whereas most researchers have stressed increasing animal consumption as the savannas spread across eastern and southern Africa, others have proposed that early *Homo* included more xeric plants in their diets and that gathering was a motive force in human evolution (Linton 1971, Coursey 1973, Wolpoff 1973). As Zihlman & Tanner (1978) noted, plants often account for 60%–70% of the human forager diet. Thus, tools may well have been used first to gather and process plants.

More recent models emphasizing the role of xeric plant foods [especially underground storage organs (USOs) such as tubers, roots, corms, and bulbs] in early hominin evolution have followed, taking their leads from studies of human and nonhuman primate behavioral ecology. O’Connell and coauthors (1999) suggested that after 2 Myr, environmental changes led to reduced access to foods that children could gather themselves. The authors argued that these hominins showed a shift from ape-like to human-like life-history patterns in early *Homo* and that this shift implies an extended postmenopausal life span, allowing grandmothers to help gather food for their grandchildren. They proposed that USOs are the most likely keystone resource



for early *Homo* and that increased reliance on material culture, such as digging sticks and ultimately cooking fires, would have improved access to these foods and the nutrients they contain. Although subsequent work casts doubt on life-history changes in early *Homo* (Dean et al. 2001), other work has also suggested USOs were important parts of early hominin diets.

Wrangham et al. (1999) proposed, as an alternative, that cooking appeared with early *Homo* and that associated delays in food consumption might have selected for a more human-like social system to protect food from theft. Like O'Connell and coauthors, Wrangham and coauthors emphasized the role of plant foods, especially USOs, in early *Homo* diets. Cooking, they argued, can increase digestibility of USOs and break down their mechanical and chemical defenses. It should be noted, however, that Schoeninger and coauthors (2001) have shown that USOs are of limited nutritional value in any case.

O'Connell's and Wrangham's models both suggest a transition from ape-like *Homo habilis* and *H. rudolfensis* subsistence strategies to a more human-like strategy for *H. erectus*. Furthermore, both models suggest larger female body mass and reduction of tooth size in *H. erectus*, compared with earlier *Homo*, as evidence for this transition (although we know of no data for relative female body mass in any of these taxa). Finally, both suggest that because evidence for the consumption of vertebrate tissues (cut marks on faunal remains found at hominin sites) predates *H. erectus*, meat eating is not likely central to the origins of a more human-like substance strategy.

## PALEONTOLOGICAL EVIDENCE FOR DIET IN EARLY HOMO

The above-mentioned foraging models may generate testable hypotheses, but they do not provide any direct evidence of what *Homo rudolfensis*, *H. habilis*, or *H. erectus* actually ate. The archeological evidence is also im-

portant but is of limited utility given its bias toward durable resources and a lack of associations between artifact accumulations and specific hominin taxa. Furthermore, ecological models tell us about available resources but not about which ones were actually exploited. Nutritional models and those derived from human and nonhuman behavioral ecology suggest possible scenarios but do not allow us to choose among them.

The only direct source of data on the diets of early *Homo* is the fossil record of the hominins themselves. Researchers have developed a number of tools for teasing aspects of diet from these fossils. This work has focused on both biological adaptations (tooth size, shape and structure, and jaw biomechanics) and nonadaptive lines of evidence relating to the effects of foods on individuals during their lifetimes (dental microwear and mineralized tissue chemistry) (Ungar 1998, 2002). Although applications of these approaches to early *Homo* have been limited, some investigators have looked to the fossils for evidence of diet.

## Tooth Size

Researchers have argued for more than a half century that tooth size differences among hominins reflect dietary differences (Robinson 1954, Jolly 1970, Kay 1985). Recent work has taken an allometric approach, evaluating data for fossil hominins relative to regressions of tooth size over body weight for extant primates with known diets. Relative incisor breadths suggest that *Homo habilis* and *H. rudolfensis* had large front teeth, with values above the 95% confidence limits of the extant regression line, whereas *H. erectus* fell on the line, along with the australopith species (Teaford et al. 2002). Because extant taxa with larger front teeth tend to eat foods requiring more extensive or intensive incisal preparation, we posited that *H. habilis* and *H. rudolfensis* probably also consumed foods requiring more anterior tooth use than did their australopith predecessors or *H. erectus*. We

speculated that larger incisor sizes of *H. habilis* and *H. rudolfensis* compared with the australopiths relate to changes in diet and that incisor breadth reduction from *H. habilis* and *H. rudolfensis* to *H. erectus* reflects changing selective pressures with increasing tool use to prepare foods prior to ingestion. However, we also cautioned that the small samples for early *Homo* were “embarrassingly small” (see below) and that these inferences should be viewed with caution.

Other work has focused attention on molar allometry, suggesting that bigger cheek teeth provided larger working surfaces to process more low-quality foods. Researchers have noted a trend toward reduction in molar surface area through time in the *Homo* lineage (see Brace et al. 1991, McHenry 1994). Wood & Collard (1999) suggested, for example, that *Homo habilis* and *H. rudolfensis* have relatively large, australopith-sized molar teeth and, like their predecessors, had a “mechanically more demanding” diet than did *H. erectus*. They argued partly on this basis that *H. habilis* and *H. rudolfensis* occupied the same adaptive zone as did australopiths and should be reassigned to the genus *Australopithecus*. McHenry & Coffing (2000) challenged this assertion, however, suggesting that *H. habilis* and *H. rudolfensis* evince reduced cheek tooth area relative to reconstructed body size compared with australopiths and that this relative decrease is actually a key unique feature that *H. habilis* and *H. rudolfensis* share with later species of *Homo*.

### Tooth Shape

The shapes of primate molar teeth reflect the fracture properties of foods that these animals eat. Taxa that often eat tough leaves, for example, have more occlusal relief than do species adapted to consume hard objects (e.g., Kay 1984, Meldrum & Kay 1997). Recent work confirms that dental topography differences between ape species track diet even for worn teeth (M’Kirera & Ungar 2003; Ungar & M’Kirera 2003, Ungar 2006a).

Dental topographic analysis on a mixed sample of early *Homo* specimens suggests occlusal relief and surface slope values intermediate between those of like-worn *Pan troglodytes* and *Gorilla gorilla* (Figure 2) (Ungar 2004). Further, the early *Homo* sample had higher occlusal relief and surface slope values than did *Praeanthropus afarensis*,<sup>1</sup> with differences on the same order as those between chimpanzees and gorillas. These apes differ mostly in fallback foods in places where they are sympatric; gorillas rely more on tougher foods such as leaves and stems when preferred resources are less available. Perhaps then, early *Homo* species “fell back” on tougher foods, such as pliant plant parts or meat, than would have their predecessors (see Lucas & Peters 2000). Still, no hominin has reciprocally concave shearing blades like gorillas and siamangs, whose molars are specialized for fracturing tough foods (Kay 1985). Unfortunately, sample sizes of available undamaged molars of each individual *Homo* species are too small to compare *H. habilis*, *H. rudolfensis*, and *H. erectus*.

### Enamel Thickness

Tooth enamel thickness has been argued to be an adaptation to protect teeth against breakage given a diet including hard, brittle foods requiring high occlusal forces to initiate fracture (Kay 1981, Dumont 1995). Notwithstanding methodological differences between studies, scholars generally agree that the australopiths and early *Homo* had relatively thick enamel on their molar crowns compared with modern humans and most other living primates. Although it is difficult to separate early *Homo* from australopiths given isolated measures of enamel thickness from various sources (Tobias 1991, Ramirez-Rozzi 1998), *H. erectus*

<sup>1</sup>The genus *Australopithecus* as advocated by many to include *A. africanus*, *A. afarensis*, and other species is most probably paraphyletic. Strait et al (1997) adopted the name *Praeanthropus africanus* for this taxon, which was later changed to *Praeanthropus afarensis* (ICZN 1999).



specimens had the absolutely thinnest enamel of those Plio-Pleistocene hominins analyzed by Beynon & Wood (1986). Thinner enamel facilitates quicker dentin exposure, which can increase surface jaggedness. This might therefore suggest another adaptation for efficient fracturing of tough foods (Kay 1981, Ungar & M'Kirera 2003).

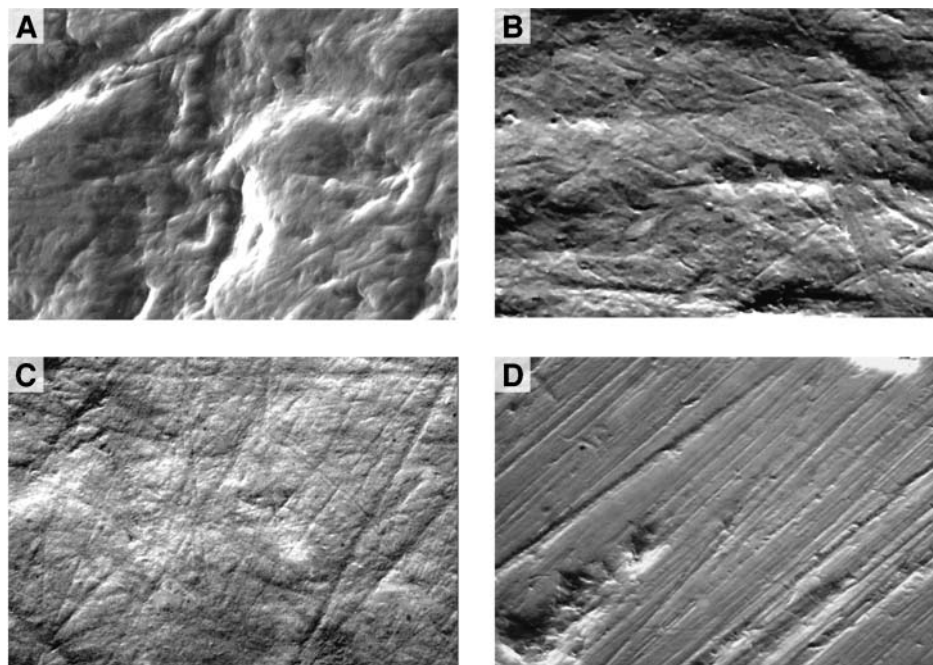
### Jaw Biomechanics

Mandibular corpus shape likely reflects forces acting on the jaw during chewing, potentially providing important clues concerning mechanical properties of foods eaten by early hominins (Hylander 1988, Daegling & Grine 1991). Although *Homo erectus* corpora are somewhat thinner than those of *H. habilis* and *H. rudolfensis*, all early *Homo* mandibular corpora are thicker than those of any extant ape and comparable in robusticity to those of “gracile” australopiths. If thicker corpora resist extreme torsion associated with high bite forces and/or muscle activity during chewing,

early *Homo*, and especially *H. habilis* and *H. rudolfensis*, retained the ability to dissipate unusually high masticatory stresses.

### Dental Microwear

The patterns of microscopic use-wear on primate molar teeth also relate to food preferences. Diets dominated by hard, brittle foods, for example, tend to leave large pits in teeth, whereas those dominated by tougher foods tend to leave more microwear striations and perhaps smaller pits (Teaford 1988, Teaford & Runestad 1992). Our own study of dental microwear in early *Homo* showed that these specimens tend to group with extant primates that do not regularly eat very fracture-resistant foods (Ungar et al. 2006). Nevertheless, we noted variation within the sample, such that *H. erectus* had, on average, more small pits than did *H. habilis* specimens (Figure 3). This finding suggests that *H. erectus* may have, at least on occasion, consumed more brittle or tough items than did *H. habilis*.



**Figure 3**

Dental microwear of (A) *Lophocebus albigena* (NMNH 220086), (B) *Homo erectus* (KNM-ER 820), (C) *Homo habilis* (OH 15), (D) *Gorilla gorilla* (NMNH 545027). Scale bar = 30  $\mu\text{m}$ .

## Mineralized Tissue Chemistry

Because stable isotope ratios and trace elements in animal tissues relate to foods eaten, studies of tooth and bone chemistry in early hominins may also give us insight into diet and habitat (Sillen & Kavanagh 1991, Schoeninger et al. 1997). Elevated Sr/Ca in *Homo erectus* suggested to Sillen and coauthors (1995), for example, that these hominins ate underground storage organs, which are high in strontium. However, the ability of stable isotope studies to distinguish hominin taxa has been limited. Indeed, specimens of *Australopithecus africanus*, *Paranthropus robustus*, and early *Homo* all show  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values similar to one another and to other primates, with values between those of extant grazers and browsers, perhaps suggesting a comparable mix of  $\text{C}_3$ - and  $\text{C}_4$ -based foods (Lee-Thorp et al. 2000, van der Merwe et al. 2003).

## LIMITS TO INTERPRETATION

Although studies such as these help us glean insights about the diets of early *Homo*, we must acknowledge the limitations of what we can infer from the fossil evidence (Ungar 2006b). Small samples reduce the power of statistical analyses. Relationships between form and function are often unclear when applied to the fossil record. Taphonomic processes alter remains, making interpretations difficult. And, in the case of hominins, there are few appropriate living analogs, particularly for comparative studies on how technological innovation affects selective pressures on biology.

### Sample Size

The single greatest obstacle to reconstructing diet in early *Homo* is sample size. For example, only five I<sup>1</sup>s have been reported for early *Homo* (one for *H. rudolfensis*, two for *H. habilis*, and two for *H. erectus*). This limitation, along with typical variation of about  $\pm 20\%$  for hominoids (see Plavcan 1990),

makes it difficult to consider how incisor size relates to diet in these hominins. Small sample sizes further hamper dental allometry studies because of their dependence on postcranial elements to reconstruct body weights. *H. rudolfensis* has no definitively associated craniodental and postcranial remains. Even if samples were sufficient, Smith (1996) has argued convincingly that confidence intervals for reconstructed weight estimates are so great that most allometric studies of fossil hominins would have to be viewed very cautiously. McHenry (1994), for example, lists a species average body weight for *H. habilis* of  $51.6 \text{ kg} \pm 22.6 \text{ kg}$  for males and  $31.5 \text{ kg} \pm 22.5 \text{ kg}$  for females.

### Unclear Relationships between Function and Morphology

Diet cannot be inferred from fossils where form-function relationships are unclear in living primates (Kay 1984). Molar size presents one case in point. Recent studies have used this attribute to help define adaptive zones for early hominins (Wood & Collard 1999, Leakey et al. 2001), with the basic idea that larger cheek teeth indicate lower-quality diets. Although this may explain why folivorous platyrrhines have relatively larger molars than do frugivorous New World monkeys, it is not clear why frugivorous catarrhines have larger molars than do closely related folivores (Kay 1977, Lucas 1980). Mandibular corpus robusticity provides another example. If thick mandibular corpora are expected to resist stresses and strains associated with a diet involving heavy chewing, why do colobines and gorillas have such thin corpora compared with early hominins? It is no surprise, then, that Brown (1997) found “not a single useful formula whereby a given mandible can be associated with a specific diet” (p. 269).

### Taphonomic Effects

Bones and teeth are exposed to taphonomic agents that can alter them, making the

inference of diet difficult or impossible. Dental microwear, for example, is often obliterated by surface etching or erosion (**Figure 4**)—molars of only 18 of 83 early *Homo* specimens examined from East and South Africa retain antemortem dental microwear (Ungar et al. 2006). This is a problem because large samples are important to infer dietary breadth, given that individual wear features can be worn away and replaced by others in only days (Teaford & Oyen 1989).

The problem is even worse with studies of mineralized tissue chemistry, where it is often difficult to identify and control for the diagenetic effects of fossilization (Schoeninger et al. 2003). Furthermore, there are limitations to the antiquity of fossil specimens suitable for such analyses given current technology, particularly for those elements (e.g., nitrogen) found in the organic phases of bones and teeth. Also, because a specific food type can yield varying results depending on the environment from which it comes, accumulation from different times and places can be especially problematic—particularly for hominins who likely moved among microhabitats during life. One related problem with tissue chemistry studies is that different foods can yield similar results. For example, a folivore can have Sr/Ca levels indistinguishable from those of a carnivore (Sealy & Sillen 1988). Different foods can likewise confer the same  $\delta^{13}\text{C}$  values (see Burton & Wright 1995).

### Technological Innovation and Natural Selection

Conventional wisdom suggests that one key adaptive shift in early *Homo* was an increased reliance on tools for food acquisition and processing (Oakley 1962). As tools began to take on an increasingly important role in obtaining and preparing foods, selective pressures on hominin jaws and teeth probably changed (Brace et al. 1991). Cutting implements, for example, change the mechanical properties of foods before they enter the mouth and, hence, change the demands placed on the cranioden-

tal toolkit for food processing. Tools, therefore, become a confounding variable in assessing form-function relationships between teeth and jaws, on the one hand, and food properties, on the other.

We are further limited by our lack of understanding of the roles that tools played in food acquisition and processing by early *Homo*. Even if we could reasonably reconstruct stone (and bone) tool function, we have no perishable elements of the early Oldowan toolkit, and we have no way of knowing how common and important these tools were to early *Homo*. We cannot, therefore, adequately assess the probable effects of tools on the jaws and teeth of early *Homo*. This problem is further exacerbated by a lack of extant analogs with which to compare effects of habitual tool use on craniodental morphology; there is a substantive gap between chimpanzees and modern humans in degree of tool use in food acquisition and processing.

### DISCUSSION

Although a number of problems limit our ability to reconstruct the diets of early *Homo*, the evidence we have is still valuable for evaluating competing models and generating new hypotheses. It is difficult to assess changes between the australopiths and their early *Homo* successors. Claims of larger incisors and smaller molars in *H. habilis* and *H. rudolfensis* are difficult to evaluate without larger samples and more precise body-weight estimates. Preliminary observations of cheek tooth crown shape hint that early *Homo* had more occlusal relief than did some australopiths (e.g., *Praeanthropous afarensis*). If so, early *Homo* would have been able to process tougher foods better than could *Pr. afarensis*. Technological innovations may have further allowed the consumption of a broader spectrum of foods.

Small samples prohibit assessment of morphological differences between *H. erectus* and *H. habilis* or *H. rudolfensis*. Still, *H. erectus*

may have had thinner dental enamel, narrower mandibular corpora, and more small microwear pits in their cheek teeth. These observations suggest that *H. erectus* may have been less capable of crushing hard objects but better able to shear through tougher foods with their molar teeth than *H. rudolfensis*, *H. habilis*, and earlier hominins. This possible reduction in ability to process a broad spectrum of foods would, at first glance, seem to be a reversal of the trend toward selection for “gracile” australopiths (Teaford & Ungar 2000). Alternatively, this evidence may simply reflect changing selective pressures resulting from food preparation using tools prior to ingestion and mastication, thus indicating the increasing role of technology as an adaptive strategy (Teaford et al. 2002).

### Dietary Versatility as an Adaptive Strategy

The fossil, archeological, and paleoenvironmental evidence taken together suggest a model of increasing dietary versatility with the appearance and early evolution of *Homo*. The concurrence of stone tools, cut marked bones, and early *Homo* by ~2.4 Myr suggests that regardless of what other hominins were doing, *H. rudolfensis* and *H. habilis* probably used durable and perishable tools to increase the range of foods to which they would have had access. Technological innovation likely played a relatively minor role in the dietary adaptations of these taxa, though, because *H. rudolfensis* and *H. habilis* show little evidence of the changing selective pressures expected if tools replaced jaws and teeth in initial food processing. These hominins retain fairly thick molar enamel and broad mandibular corpora perhaps for processing hard foods or those foods requiring repetitive loading, yet they show more molar cusp relief than at least *Praeanthropus afarensis*, suggesting an improved ability to fracture tough foods such as pliable plant parts and meat. Tools would have allowed for more dietary flexibility, but in-

creased dietary versatility still may have been driven more by biological (i.e., dental) than by cultural evolution.

On the other hand, the earliest major concentrations of tools and tool-modified bones coincide roughly with the appearance of *H. erectus*. Although other hominins may have been involved, *H. erectus* almost certainly contributed to these sites, especially given similar accumulations outside Africa. *H. erectus* may also show adaptive changes, such as thinning enamel, to further improve efficiency in shearing and slicing tough foods such as pliable plant parts or meat. Although increasing efficiency for fracturing tougher foods may have resulted in decreased ability to crush hard and brittle foods, tools such as the hammerstones observed for Tai Forest chimpanzees (Boesch & Boesch 1990) could have easily compensated. Thus, a combination of tools and morphological change would have allowed increased dietary versatility for *H. erectus*.

Dietary versatility would have been especially useful given environmental changes, such as the spread of C<sub>4</sub> grasslands across East Africa following 2.5 Myr, when *H. habilis* and *H. rudolfensis* first appear. It would also have served *H. erectus* well because this taxon emerged at the midpoint of a significant faunal turnover spanning 2.1–1.7 Myr. Potts (1998) argued that locomotor versatility was a crucial adaptation to Pliocene climatic fluctuation and mosaic habitats. We suggest that dietary flexibility may have been equally important as an adaptive strategy under these environmental conditions. Craniodental adaptations and material culture would have allowed early *Homo*, and especially *H. erectus*, to eat a broader spectrum of foods than could earlier hominins.

This does not mean that early *Homo* individuals had particularly varied diets, but rather that they may have been capable of eating a broader range of foods. Chimpanzees and gorillas show significant differences in their diets, depending on the individual population and the seasonal availability of resources

within home ranges (e.g., Goodall & Groves 1977, Vedder 1984, Wrangham et al. 1991, Yamagiwa et al. 1992, Tutin et al. 1997, Yamakoshi 1998). Ethnographic studies over the past century have shown human foragers to have an even greater range of diets, from nearly all animal products (e.g., Ho et al. 1972) to mostly wild plant parts (e.g., Gould 1980). This finding led Milton (2002) to argue vehemently against a single hypothetical “Paleolithic diet.”

Perhaps then, early *Homo*, and especially *H. erectus*, had an adaptive strategy of dietary versatility. This versatility would have been advantageous in an unpredictable, changing environment or an environment dominated by many different microhabitats. Perhaps *H. erectus* was the first hominin to leave Africa because it was the first with sufficient dietary versatility to allow it to do so. It may be no coincidence that this species spread into habitats as far north as the Republic of Georgia, and perhaps as far east as Indonesia, so quickly following its origin and first appearance in Africa (Swisher et al. 1994, Gabunia et al. 2000).

### Evaluation of Common Models

A versatility model for early *Homo* diets differs from most published models, which focus on specific keystone resources. Most reconstructions involve a shift from closed-forest C<sub>3</sub> vegetation to meat or more xeric plant underground storage organs. But how important was meat to early *Homo*? Because investigators have found few cut marked bones at archeological sites predating 1.9 Myr, meat-eating by hominins may not have been widespread when early *Homo* first evolved. *Homo rudolfensis* and *H. habilis* retain thick tooth enamel and wide mandibular corpora, indicative of an ability to process hard, brittle foods, but appear to show greater occlusal relief, suggesting increased efficiency for ingesting and shearing tough foods, including meat. Thus, although meat-eating could have remained opportunistic under some condi-

tions, animal tissues may have started to become a more important resource under other conditions.

Evidence of an important role for meat eating is more compelling for *H. erectus*. Large concentrations of stone tools and modified bones after 1.9 Myr combined with thinner enamel may suggest improved abilities to slice and shear tough foods, including meat. A higher incidence of small pits in the enamel may indicate the consumption of soft, tough foods such as meat (Teaford & Runestad 1992). However, did meat dominate their diets? Not necessarily. The little lithic microwear evidence we have suggests that early Pleistocene tools were used to process animal and plant tissues (Keeley & Toth 1981).

What about underground storage organs? Thick tooth enamel, flat occlusal surfaces, and broad mandibular corpora of *Homo rudolfensis* and *H. habilis* are consistent with crushing hard and brittle foods, such as USOs (assuming that these are, in fact, hard and brittle). However, the fact that early *Homo* had more occlusal relief than did their hominin predecessors suggests they were not adapted to hard and brittle roots and tubers. Furthermore, cheek tooth microwear data suggest lower pit percentages than expected of a hard object specialist (Ungar et al. 2006). Although tools might certainly have been used to dig out edible bulbs and roots and to crush them prior to ingestion, the archeological record does not offer evidence for this (see Backwell & d’Errico 2001). In sum, there is little evidence that *H. rudolfensis* and *H. habilis* would have specialized on these foods. Nutritional considerations also make a USO specialization unlikely (Schoeninger et al. 2001).

One could make a similar argument for *H. erectus*. Although tools could have allowed these hominins to procure and process USOs, some morphological evidence may suggest that these hominins would have been less able to process hard, abrasive roots and tubers within the mouth. These hominins



simply do not show clear morphological adaptations suggesting specialization on such resources.

## SUMMARY AND CONCLUSIONS

Many models exist for the origins and early evolution of the genus *Homo*. Most models note an environmental shift to drier, more open conditions in the late Pliocene. Authors argue that the roughly concurrent appearances of early *Homo* and an archeological record suggest that these hominins evolved subsistence strategies to process xeric resources, be they animal or plant tissues, with the help of tools. Resulting hunting or gathering strategies are said to have set in motion psychosocial changes that led from a

more ape-like to a more human-like adaptive strategy.

The fossil and archeological evidence offer little support for adaptive strategies that focus on such specific foods. We propose that the fossil evidence, combined with archeological remains and paleoenvironmental indicators, suggests a more flexible, versatile subsistence strategy. This is not to say that *H. rudolfensis*, *H. habilis*, or *H. erectus* individuals necessarily had very broad diets at any given time. These species were more likely adapted to subsist in a range of different environments with different resources in each. This strategy would have put them at an advantage given climatic fluctuation and a mosaic of different microhabitats in Africa during the late Pliocene.

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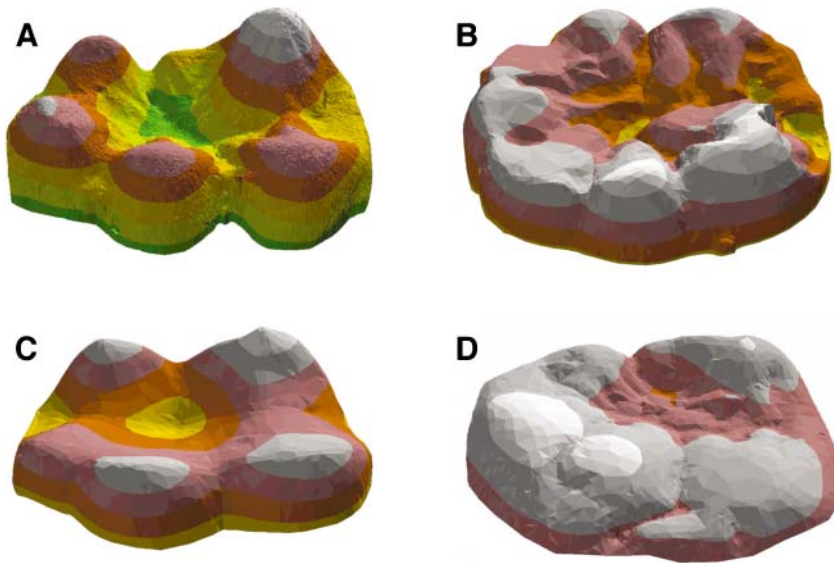
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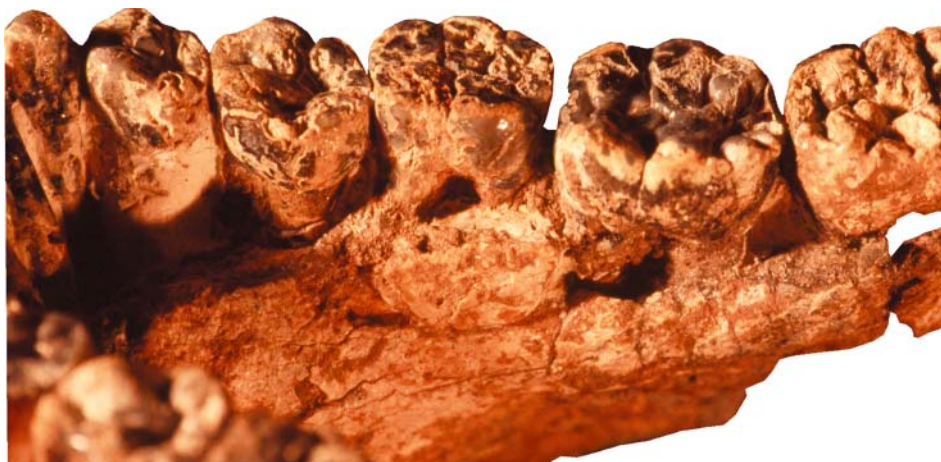
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**Figure 2**

Triangulated irregular network models of surface data for similarly worn  $M_2$ s of (A) *Gorilla gorilla*, (B) *Pan troglodytes*, (C) *Homo erectus* (KNM-WT 15,000), and (D) *Praeanthropus afarensis* (AL 266-1).



**Figure 4**

KNM-ER 3220. Note the taphonomic damage to the teeth. Image copyright by the National Museums of Kenya.



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