



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Journal of Human Evolution ■■ (2005) ■■■—■■■



# The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australopith origins

Greg Laden <sup>a,\*</sup>, Richard Wrangham <sup>b</sup>

<sup>a</sup> *Department of Anthropology, University of Minnesota, Twin Cities Campus, 301 19th Avenue S, Minneapolis, MN 55455, USA*

<sup>b</sup> *Department of Anthropology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138, USA*

Received 5 July 2002; accepted 30 May 2005

---

## Abstract

We propose that a key change in the evolution of hominids from the last common ancestor shared with chimpanzees was the substitution of plant underground storage organs (USOs) for herbaceous vegetation as fallback foods. Four kinds of evidence support this hypothesis: (1) dental and masticatory adaptations of hominids in comparison with the African apes; (2) changes in australopith dentition in the fossil record; (3) paleoecological evidence for the expansion of USO-rich habitats in the late Miocene; and (4) the co-occurrence of hominid fossils with root-eating rodents. We suggest that some of the patterning in the early hominid fossil record, such as the existence of gracile and robust australopiths, may be understood in reference to this adaptive shift in the use of fallback foods. Our hypothesis implicates fallback foods as a critical limiting factor with far-reaching evolutionary effects. This complements the more common focus on adaptations to preferred foods, such as fruit and meat, in hominid evolution.

© 2005 Elsevier Ltd. All rights reserved.

*Keywords:* *Australopithecus*; Diet; Hominid ecology; Hominid evolution; Last common ancestor; Mole-rats; *Paranthropus*; Roots; Tubers

---

\* Corresponding author. Tel.: +1 612 625 0058; fax: +1 612 625 3095.

*E-mail addresses:* [laden002@tc.umn.edu](mailto:laden002@tc.umn.edu) (G. Laden), [wrangham@fas.harvard.edu](mailto:wrangham@fas.harvard.edu) (R. Wrangham).

## Introduction

In 1980, Hatley and Kappelman pointed out parallels in dental morphology that suggested that bears, pigs, and hominids are all adapted to eating significant amounts of plant underground storage organs (USOs). They summarized their argument as follows: “We believe that postcanine similarities evident among ursids, suids, and hominids are in part an adaptation for processing this tough, fibrous, and gritty plant part. Bears, pigs, and humans are adapted to exploiting plant roots and tubers, although their methods of food gathering are functionally rather than morphologically analogous. Convergence upon the resource of belowground plant storage parts appears to make the responses of nonretractable claws, cartilaginous snout, and digging stick equivalent” (Hatley and Kappelman, 1980: 380).

In this paper, we support and modify Hatley and Kappelman’s hypothesis that hominids are adapted to eating USOs. Specifically, we propose that the way in which USOs were most important for hominids was as fallback foods, much as Wolpoff (1973) argued for South African australopithecids. We further suggest that the development of a USO-eating adaptation was a key contribution to the initial differentiation of hominids from other hominoids, and that various hominid traits are adaptations to the use of USOs as fallback foods. We also note that *Paranthropus* species may have used USOs not only as fallback foods, but also as preferred foods.

Our focus on the importance of fallback foods derives from evidence that changes in the use of such resources (and associated adaptations) tend to be more important than changes in primary (preferred) foods in shaping adaptations related to food-processing (as opposed to food-harvesting) (Robinson and Wilson, 1998). For example, changes in the availability of fallback foods can have rapid and large effects on the size and morphology of bird beaks, which are adapted to processing specialized items eaten during periods of food scarcity (Boag and Grant, 1982; Grant and Grant, 2002). Similarly, among Malagasy lemurs, molar morphology is more highly correlated with differences in fallback foods than with fruit-eating (Yamashita, 1998).

We suggest that an adaptation to the use of new types of fallback foods can, in turn, provide access to novel habitats, and thus bring into play otherwise unlikely selective forces.

We develop several lines of evidence and reasoning to support this hypothesis. First, living African apes require humid habitats partly because they rely on herbaceous vegetation and soft leaves as fallback foods. If early hominids were different from living African apes in that they occupied habitats outside the rainforest, then it is likely that leaves and piths eaten by the forest apes as fallback foods would have been replaced by an alternative fallback food. Accordingly, we discuss the ecology of fallback foods (and USOs in particular) in the context of recent analyses of hominid diets. A shift to USO consumption in the late Miocene (the likely time of the initial split between hominids and other hominoids) depends on the existence of a USO-rich habitat at that time. We document the abundance of USOs in savanna,<sup>1</sup> in contrast to the rainforests principally occupied by contemporary apes. We suggest that the dental features that characterize hominids include adaptations to consuming USOs. We review evidence from the archaeological and

<sup>1</sup> Throughout this paper we use the terms “rainforest” and “savanna” to signify two contrasting tropical ecosystems or biomes. In so doing, we conform to common definitions in use today in African ecological and paleoecological studies. A typical rainforest has a closed canopy and little rain-green vegetation. This includes evergreen and semi-evergreen lowland rainforest and other types of closed canopy forest (Granger, 1996). A typical tropical African savanna has a continuous cover of heliophilous, megatherm, herbaceous rain-green vegetation (such as C4 grasses) (Strahler and Strahler, 1992; Adams, 1996: 181). A savanna may be wooded or open. This definition subsumes into “savanna” finer distinctions such as “parkland,” “wooded savanna,” and “woodland” (if there is a continuous herbaceous cover) on one end of a spectrum, and “grassland” on the other. We include tropical dry deciduous forest, also known as miombo woodland (Granger, 1996) under the term savanna. This conflation is appropriate for the comparison of large-scale ecological zones or biomes. Our purpose here is to specify the contrast between ecosystems with very little vs. significant or even extreme seasonality of rain, and the corresponding distinction of very little vs. significant or even extreme underground plant water or nutrient storage tissues. Fine tuning these definitions beyond this is unnecessary and would perhaps be misleading given that we are speaking of millions of years of time, over which these very ecosystems certainly changed.

fossil records from the Plio-Pleistocene through the Holocene that suggests USO exploitation, as well as the widespread use of USOs by recent or living foraging populations of humans. We begin by considering the use of fallback foods by living African apes, because they offer a model of the species from which hominids evolved.

### Evolution and fallback foods of the forest-living apes

Attempts to understand the evolution of hominid diets sometimes rely on the assumption that Miocene apes related to known fossil taxa gave rise to the australopiths (Teaford and Ungar, 2000). However, there is no direct evidence of phylogenetic continuity between any Miocene ape and known australopith. By contrast, there is substantial support for an alternative proposal, that the australopiths evolved from still undiscovered “forest-ranging, knuckle-walking apes” (Zihlman, 1978: 4; Moore, 1996; Pilbeam, 1996; Wrangham and Pilbeam, 2001).

Molecular data show that gorillas had already split from other hominoids before the evolution of the common ancestor of chimpanzees and hominids (Ruvolo, 1997; Kaessmann et al., 1999). Gorillas and the two species of chimpanzee share many morphological features, including locomotor adaptations for arm-hanging and knuckle-walking, relatively thin-enameled molars adapted to varying degrees to the shearing of leaves and stems, and digestive adaptations for fermentation of hemi-cellulose and cellulose. The similarities appear even greater when body mass is taken into account (Zihlman, 1978; McHenry, 1984; Shea, 1985; Milton, 1999). These points strongly suggest that the morphological and dietary similarities among gorillas and the two species of chimpanzee are homologies. The alternative is that there has been a series of parallel evolutionary adaptations in *Pan* and *Gorilla*. The similarities are sufficiently close and numerous that we judge such convergence as improbable.

The hypothesis that dietary similarities among living African apes are homologies implies that they were present not only in the common ancestor

of gorillas, chimpanzees, and humans, but also in the common ancestor of chimpanzees and humans. This means that the australopiths evolved 5–7 Ma from a forest-living species that shared homologies with gorillas, chimpanzees, and bonobos. The similarities between early hominid fossil crania and those of chimpanzees are consistent with this idea (Falk et al., 1994; Berger and Tobias, 1996; Haile-Selassie, 2001).

There are two key dietary similarities among the living African apes. First, the preferred foods are ripe tree-fruits for chimpanzees (Wrangham et al., 1996; Tutin et al., 1997), bonobos (Hashimoto et al., 1998; White, 1998), and gorillas (Yamagiwa et al., 1996; Doran and McNeilage, 2001). Second, when ripe fruits are in short supply, these species exploit leaves and piths as fallback foods, particularly from terrestrial herbs (Yamagiwa et al., 1996; Doran and McNeilage, 2001). Species variation in reliance on herbaceous leaves and piths is broadly correlated with masticatory adaptations (Taylor, 2002). This suggests that, at 5–6 Ma or earlier, the ancestor of the hominids would have been an ape that, like the living species, used herbaceous leaves and piths as its principal fallback foods and had thin-enameled molars adapted to processing these foods.

Available data on *Ardipithecus ramidus* (White et al., 1994, 2000), and to a lesser extent *Australopithecus anamensis* (Ward et al., 2001), indicate that dental features of some early hominids were in some ways intermediate between later hominids and chimpanzees; for example, enamel thickness in *Ar. ramidus* is near to or within the range of living chimpanzees. Later hominids have large, thickly enameled cheek teeth and low shearing quotients compared to the African apes (Teaford and Ungar, 2000). It would appear, then, that in the early evolution of hominids, a shift occurred from a chimpanzee-like diet towards one that required large, thick-enameled molars and, to varying degrees, molarized premolars. We suggest that this shift was away from herbaceous leaves and piths, and that it became an organizing factor in australopith dental and masticatory morphology. Additional fossils will allow the temporal and biogeographical pattern of this change to be better characterized.

The postulated shift away from teeth suitable for shearing herbaceous leaves and piths makes sense because the more seasonal habitats increasingly occupied by early hominids would have had relatively low densities of these foods compared to the rainforest habitats occupied by hominid ancestors. For example, even in the relatively high-rainfall areas of Gabon, savannas have insufficient herbs to sustain apes, whereas the adjacent rainforests commonly produce large densities of edible leaves and piths (White et al., 1995). Occupation of savannas by early hominids therefore implies that when preferred foods were scarce, a new type of fallback food was required.

### Distribution of USOs across habitats

The subterranean parts of plants form a large proportion of total plant material, commonly more than 50% and sometimes approaching 90% by weight of individual organisms (Andersen, 1987). Most of this consists of roots, which can be fibrous parts that function merely in nutrient uptake or mechanical support without any storage function, and are too highly lignified to be eaten by mammals. But subterranean parts also include underground storage organs (USOs), such as rhizomes, tubers, corms, bulbs, and caudex. Storage of plant resources in specialized organs is hypothesized to be primarily an adaptation to surviving unfavorable conditions during some growth phase or season (Hladik et al., 1984). The nutritional value of USOs therefore varies widely, not only between species, but also within species, as a result of seasonal changes in energy content and presence of toxins, water, and other nutrients (Andersen, 1987).

Because USOs are considered to be adapted to adverse growing conditions, we predict them to be relatively diverse and abundant in areas with long dry seasons and/or little rainfall, but less diverse and common in rainforest habitats because areas with tropical rainforests have only short dry periods, i.e., “unpredictable spells lasting only a few days or weeks” (Whitmore, 1990: 9). We tested this prediction by comparing rainforest and savanna habitats.

Available data suggest that the diversity of all USOs, both edible and inedible by humans, is high in savanna compared to rainforest. In their study of a central African rainforest, Hladik et al. (1984) reported 29 species of plants with tubers, representing 12 families, including both edible (to humans) and inedible species. This is substantially less than the number of USOs recorded by Lee (1979) to be eaten by !Kung San in the semi-desert of the Kalahari (69 species from 12 families). If inedible USOs were included, the number in the Kalahari would presumably be considerably higher.

Speciesity of genera with USOs appears to show the same trend. The only genus in African forests known to include at least three USO-growing species is the yam, *Dioscorea*. By contrast, seven genera that contain at least three species that grow edible USOs have been recorded in savanna regions (*Ceropegia*, *Raphionacme*, *Commiphora*, *Coccinia*, *Cyperus*, *Vigna*, *Dipcadi*). This comparison is preliminary because many plant species have not yet been examined to determine whether or not they have USOs (Hladik et al., 1984), but it clearly suggests that total USO diversity is higher in savannas than in rainforests.

The diversity of edible USOs should similarly be greater in savanna than rainforest. To test this hypothesis, we compiled reports of USOs eaten by African foragers from six savanna sites and six rainforest sites (Table 1). The rainforest sites yielded a total of 24 edible species vs. 80 for the savanna sites. The rainforest USOs were concentrated in the Dioscoreaceae (the principal USO at each site), and were found in a total of 11 families. Savanna USOs, on the other hand, were spread relatively evenly across 20 families of vascular plant and one fungus. Table 1 shows that the most prominent USO-bearing families are Asclepiadaceae, Leguminosae, Liliaceae, Dioscoreaceae, and Cucurbitaceae, which together account for 62% of USO records.

Edible USOs should be more abundant in savanna than in rainforest. Two sites are available as a test. In a northern Tanzanian savanna, Vincent (1985) found that the biomass density of tubers eaten by Hadza foragers averaged 40,000 kg/km<sup>2</sup>. In a rainforest in the Central African Republic, by contrast, biomass density of USOs eaten by Aka

Table 1  
Diversity of USOs eaten by African foragers in relation to habitat

Family	Species per family	Species	Biome	
			Rainforest (mainly lowland)	Savanna (woodland, bush, and grassland)
(Fungus)	1	<i>Tenaris schultzei</i>		X
Agavaceae	1	<i>Sansevieria scabrifolia</i>		X
Alismataceae	1	<i>Echinodorus (Ranalisma) humile</i>	X	
Apocynaceae	1	<i>Strophanthus</i> sp.		X
Asclepiadaceae	17	<i>Baseonoma gregorii</i>		X
		<i>Brachystelma barberiae</i>		X
		<i>Brachystelma</i> sp.		X
		<i>Caralluma lutea</i>		X
		<i>Ceropegia</i> cf. <i>euryacme</i>		X
		<i>Ceropegia</i> cf. <i>stenantha</i>		X
		<i>Ceropegia multiflora</i>		X
		<i>Ceropegia</i> sp.		X
		<i>Ceropegia stenoloba</i>		X
		<i>Fockea?</i> <i>monroi</i>		X
		Unidentified		X
		<i>Raphionacme burkei</i>		X
		<i>Raphionacme hirsuta</i>		X
		<i>Raphionacme</i> sp.		X
		<i>Rhyssolobium?</i> sp.		X
		<i>Sarcostemma</i> sp.		X
		<i>Stapelia kwebensis</i>		X
Burseraceae	4	<i>Commiphora africana</i>		X
		<i>Commiphora angoleusis</i>		X
		<i>Commiphora pyracanthoides</i>		X
		<i>Commiphora</i> sp.		X
Campanulaceae	2	<i>Cyphia glandulifera</i>	X	
		<i>Cyphia stenopetala</i>		X
Capparidaceae	1	<i>Maerua edulis</i>		X
Connaraceae	1	<i>Roureopsis ibliquifoliolata</i> (Gilg) Schellenb.	X	
Convolvulaceae	6	<i>Ipomoea chrisochaeta</i>	X	
		<i>Ipomoea longituba</i>		X
		<i>Ipomoea oenotherae</i>		X
		<i>Ipomoea transvaalensis</i>		X
		<i>Ipomoea verbascoidea</i>		X
		<i>Merremia ampelophylla</i>		X
Cucurbitaceae	10	<i>Coccinia</i> cf. <i>grandiflora</i>	X	
		<i>Coccinia rehmannii</i>		X
		<i>Coccinia sessifolia</i>		X
		<i>Coccinia sessilifolia</i>		X
		<i>Coccinia</i> sp.		X
		<i>Corallocarpus bainessi</i>		X
		<i>Cucumella</i> sp.	X	
		<i>Cucumis</i> cf. <i>kalahariensis</i>		X
		<i>Momordica</i> sp.	X	
		<i>Trochomeria macrocarpa</i>		X
Cyperaceae	4	<i>Cyperus blysmoides</i>		X
		<i>Cyperus fulgens</i>		X
		<i>Cyperus rotundus</i>		X

(continued on next page)

Table 1 (continued)

Family	Species per family	Species	Biome	
			Rainforest (mainly lowland)	Savanna (woodland, bush, and grassland)
		<i>Cyperus usitatus</i>		X
Dichapetalaceae	1	<i>Dichapetalum mombuttense</i>	X	
Dioscoreaceae	10	<i>Dioscorea baya</i>	X	
		<i>Dioscorea bulbifera</i>	X	
		<i>Dioscorea burkilliana</i>	X	
		<i>Dioscorea cf. sagittifolia</i>	X	
		<i>Dioscorea dumetorum</i>	X	
		<i>Dioscorea mangelotiana</i>	X	
		<i>Dioscorea minutiflora</i>	X	
		<i>Dioscorea praehensilis</i>	X	
		<i>Dioscorea semperflorens</i>	X	
		<i>Dioscorea smilacifolia</i>	X	
Euphorbiaceae	1	<i>Cephalocroton mollis</i>		X
Gnetaceae	1	<i>Gnetum africanum</i>	X	
Hydnoraceae	2	<i>Hydnora abyssinica</i>		X
		<i>Hydnora</i> sp.		X
Iridaceae	2	<i>Lapeirousa</i> sp.		X
		<i>Lapeirousia coerulea</i>		X
Leguminosae	14	<i>Bauhinia esculenta</i>		X
		<i>Bauhinia macrantha</i>		X
		<i>Cassia biensis</i>		X
		<i>Hoffmannseggia burchellii</i>		X
		<i>Vatovaea pseudolablab</i>		X
		<i>Vigna?</i> <i>decipiens</i>		X
		<i>Vigna?</i> <i>triloba</i>		X
		<i>Vigna dinteri</i>		X
		<i>Vigna frutescens</i>		X
		<i>Vigna macrorrhynca</i>		X
		<i>Vigna membranacea</i>		X
		<i>Vigna oblongifolia</i>		X
		<i>Vigna praecox</i>		X
		<i>Vigna</i> sp.		X
Liliaceae	13	<i>Asparagus</i> sp.		X
		<i>Dipcadi longifolium</i>		X
		<i>Dipcadi marlothii</i>		X
		<i>Dipcadi rigidifolium</i>		X
		<i>Dipcadi</i> sp.		X
		<i>Dipcadi viride</i>		X
		<i>Eriospermum</i> sp.		X
		<i>Kyllinga alba</i>		X
		<i>Ledebouria</i> sp.		X
		<i>Ornithogalum</i> sp.		X
		<i>Scilla</i> sp.		X
		<i>Walleria muricata</i>		X
		<i>Walleria nutans</i>		X
Menispermaceae	2	<i>Dioscoreophyllum cumminsii</i>	X	
		<i>Jateorhiza</i> sp.	X	
Nymphaeaceae	1	<i>Nymphaea</i>		X

Table 1 (continued)

Family	Species per family	Species	Biome	
			Rainforest (mainly lowland)	Savanna (woodland, bush, and grassland)
Orchidaceae	2	<i>Eulophia hereroensis</i> <i>Eulophia</i> sp.		X X
Pandaceae	1	<i>Microdesmis puberula</i>	X	
Pedaliaceae	1	<i>Harpagophytum procumbens</i>		X
Portulacaceae	1	<i>Talinum crispatulatum</i>		X
Simaroubaceae	1	<i>Kirkia wilmsii</i>		X
Smilacaceae	1	<i>Smilax</i> sp.	X	
Umbelliferae	1	<i>Peucedanum linderi</i>	X	
(29 families)	(104 species)		24	80

X = present. Records were compiled from six rainforest sites and six savanna sites for which edible USOs were reported. Rainforest sites are from Gabon and Central African Republic (Hladik et al., 1984; Bahuchet, 1990a, b; Hladik and Hladik, 1990; Bahuchet et al., 1991); the Ituri Forest, Democratic Republic of the Congo (Tanno, 1981; Terashima et al., 1988; Center for African Area Studies, 2002); south of the Congo River near Wamba (Kano, 1983; Center for African Area Studies, 2002); and western Congo near Kinshasa (Center for African Area Studies, 2002). Savanna sites are from Kenya (Sept, 1984); Suiei lands of Kenya (Ichikawa, 1980); Botswana and Namibia (Lee and DeVore, 1976; Silberbauer, 1981; Center for African Area Studies, 2002); Makapan area in South Africa (Peters and Maguire, 1981); and Lake Eyasi in Tanzania (Vincent, 1985).

pygmies was a mere 100 kg/km<sup>2</sup> (Hladik et al., 1984). The figure of 100 kg/km<sup>2</sup> may be high in comparison to humid forest because the Hladik et al. study included patches of forest from the interior to margins, with USO-stem density increasing approximately 200 times towards the forest edge. Thus, this comparison suggests that compared to rainforest, the biomass density of edible USOs in savanna environments is greater by at least 400 times, or 2–3 orders of magnitude. In the Ituri Forest, Laden (1992) observed plant utilization by Efe Pygmies over several months and found that all wild edible USOs were *Dioscorea*; all were found in a very limited range of habitats, including on large rock outcrops with limited tree cover and in agricultural gardens that had been abandoned within recent decades.

The greater diversity of USOs in savannas can be expected to include more species that are edible without cooking than occur in rainforest. This prediction is currently supported. For example, only one out of 11 species of rainforest USOs eaten by humans was reported to be edible without cooking, i.e., 9.1% (*Dioscoreophyllum cumminsii*, Menispermaceae; Hladik and Hladik, 1990). By contrast, the percentage of USO-bearing species

from savanna areas reported to be eaten raw is 65% (26 of 40 species with relevant information given; data from sources in Table 1). The fact that many savanna USOs were eaten raw suggests that toxin levels were lower in savanna environments, or that carbohydrates were more often stored in relatively easily digestible forms. (Even in savanna areas, however, most USOs were considered to be improved by roasting.)

Thus, despite a paucity of studies, current data suggest a consistent increase in the diversity, biomass density, and edibility of USOs in savanna compared to rainforest. This is striking because rainforest sites are floristically more diverse than savannas. The fact that taxonomic diversity does not account for the USO production in savannas supports the prediction that USOs are adapted to seasonal climatic conditions and can therefore be expected to be routinely abundant in African habitats outside, but not inside, rainforest.

### USOs as fallback foods for modern humans

To evaluate the potential importance of USOs as fallback foods in African Pliocene savannas, we

consider the way that they are used by contemporary foragers.

Human foragers' reliance on USOs is well documented for the savanna and semi-desert habitats of tropical Africa and in similar environments elsewhere through ethnography, ethnoarchaeology, and archaeology. In the Kalahari, roots indeed conform to the concept of fallback foods because, although they are not preferred compared to meat, fruits, honey, or fatty seeds, for example, they become the dominant dietary item during periods of food scarcity. For example, Silberbauer (1981: 202) reported that the G/wi used 13 plant species as staple foods. Sweet fruits were preferred, whereas USOs were mainly fallback foods eaten when preferred foods were not available. The worst time of year was early summer, when people complained of hunger and thirst, body weight was low, illness was more common, and there were even occasional episodes of starvation. At this time, the density of food that a household gathered (and, by inference, that it is likely capable of gathering) was measured as 0.15 kg/km<sup>2</sup> per household per day (i.e., per woman). All foods came from four species of tuber. This annual minimum compares to a maximum of 128 kg/km<sup>2</sup> per day when local fruit crops are abundant, i.e., almost 10,000 times higher.

A similar kind of reliance on USOs was observed for the !Kung at Nyae Nyae:

The roots are of the utmost importance to the !Kung diet in the Nyae Nyae area. Whereas many items of food, especially the fruits, are available only in the season of the rains and for a time after, the underground parts remain preserved in the ground throughout the year. In the territory of Band 1, they are the mainstay during the winter—the dry season (Marshall, 1976: 108).

Roots and bulbs are likewise explicitly claimed by informants to be available all year for Hadza in northern Tanzania and for !Kung San in Botswana (Lee, 1979; Vincent, 1985). However, they become important in the diet only on a seasonal basis. They are eaten by Hadza principally during the main rainy season and the late dry season and by !Kung San during the winter dry season, when the major summer foods are not available (Lee, 1979). In both cases, the ethnographers noted that

the degree of difficulty in harvesting roots is a major factor affecting the degree to which they are preferred. Accordingly, the fact that USOs are eaten more when fruits are not available may have more to do with their being hard to extract from the ground than with their merit as a good-tasting or highly valued food item.

Plant underground storage organs were also important to Australian Aborigines. The magnitude of this importance is seen not only in foraging strategies, but also in some cosmogonies. For example, the origin story of the Kakadu people in Arnhemland refers to the ancestress “Imberombera,” who arrived from across the sea with her “womb filled with children and from her head... suspended woven dilly bags in which she carried yams, bulbs and tubers” (Flood, 1983: 30). There is even an art form in the Northern Territory based on the anthropomorphism of yams (Flood, 1983: 133). Aboriginal Australians in many areas are documented to have made important use of USOs (Gott, 1982). One of the few archaeological examples of a USO from a non-agricultural area is a lily tuber found in Rocky Cape Cave in Tasmania (Flood, 1983: 164).

The use of USOs in the African Later Stone Age (LSA) is inferred from the widespread occurrence of torus-shaped, bored stone artifacts, believed to be digging stick weights (Phillipson, 1982), as well as a number of actual digging sticks. When a sharpened stick is found at an archaeological site, it may be referred to as a digging stick or as a spear, possibly depending on the proclivities of the interpreter. Nonetheless, there are morphological characteristics that can separate the two, and some relatively recent examples of digging sticks claimed for southern Africa are probably legitimate. Gwisho Hot-springs, an LSA site in Zambia with excellent preservation, contained digging sticks dating to nearly 5,000 years ago (Fagan and van Noten, 1971). De Hangen found digging sticks in other locations of the Cape coastal region [reported in Phillipson (1977: 245)].

Thus, USOs are known to be fallback foods for people in at least two African savannas, as well as in the Australian bush. For a primate that cannot readily eat leaves, USOs provide a systematic



supply of food during periods when seeds and fruits are not available, as inevitably occurs.

### Evolution of the USO niche

As pointed out by Hatley and Kappelman (1980), reconstruction of the Omo Basin suggests that USOs would have been common in the Pliocene (Bonnefille, 1976; Carr, 1976). A similar conclusion about the presence of USOs at Laetoli comes from palynological evidence (Harris, 1985; Bonnefille et al., 1987; Andrews, 1989). However, at most sites, the fossil record contains no direct information about past USO abundance. We propose that the presence of fossorial herbivores offers a useful way to assess the distribution and importance of an ancient USO niche in the absence of direct paleobotanical evidence.

Fossorial herbivores are found in 10 orders: insects (7 orders), nematodes (2 orders) and rodents (1 order) (Andersen, 1987). There are no relevant data on the distribution and evolutionary history of the USO-eating insects or nematodes in Africa, but information on rodents comes from two families of mole-rats, the Bathyergidae and Rhizomyidae.

The Rhizomyidae are unknown in rainforest. The only African genus, *Tachyoryctes*, is currently confined to upland areas in eastern Africa, including montane grasslands up to 4000 m in elevation, from Ethiopia to Malawi (Nevo, 1979; Kingdon, 1997; Nevo et al., 2000). The restriction of modern Rhizomyidae to upland habitats means that they have little value for reconstructing the paleoecology of USOs in lowland savannas. Rhizomyids first appear in Africa in the early Pliocene, with *Tachyoryctes* associated with *Ar. ramidus* in a lowland habitat (White et al., 1994).

There are five genera of extant Bathyergidae (*Bathyergus*, *Cryptomys*, *Georhynchus*, *Heliophobius*, and *Heterocephalus*). No member of this family occurs in a rainforest (Honeycutt et al., 1991; Jarvis et al., 1994; Kingdon, 1997). All are found in seasonally dry, non-rainforest habitats, where annual rainfall can be as low as 400 mm or less (Brett, 1991; Jarvis and Bennett, 1991). Their

distribution includes more than 90% of the non-rainforest area in eastern, central, and southern Africa (see map in Jarvis et al., 1994). Their presence is thus a strong predictor of habitat type.

The presence of Bathyergidae species also indicates the availability of USOs, as mole-rat population densities have been shown to be related to USO availability (Huntly and Reichman, 1994). Average USO biomass density for *Heterocephalus glaber* in a Kenyan savanna was 203,000 kg/km<sup>2</sup> (Brett, 1991), i.e., five times the density recorded in Tanzania for USOs edible by humans (Vincent, 1985).

Such high USO densities could indicate the presence of USOs edible by hominids if there is overlap between human and bathyergid diets. To examine this possibility, we reviewed available data on diets of *Bathyergus* (Davies and Jarvis, 1986), *Cryptomys* (Genelly, 1965; Davies and Jarvis, 1986; Lovegrove and Jarvis, 1986; Jarvis and Bennett, 1991), *Georhynchus* (Davies and Jarvis, 1986; Lovegrove and Jarvis, 1986), *Heliophobius* (Jarvis and Sale, 1971; Davies and Jarvis, 1986), and *Heterocephalus* (Hill et al., 1957; Jarvis and Sale, 1971; Brett, 1991; Jarvis and Bennett, 1991). Out of 40 USOs reported to be eaten and identified to species, we found three that were eaten elsewhere by humans (*Ipomoea batatas*, *Vigna membranaceae*, and *Moraea fugax*) (Table 1; see also Peters and O'Brien, 1981). A further 12 species of the 44 USOs eaten by bathyergids and identified at least to genus were in the same genera as species with USOs eaten by humans (*Asparagus*, *Babiana*, *Coccinia*, *Cyperus*, *Dipcadi*, *Mariscus*, *Ornithogalum*, *Oxalis*, *Stylochiton*, *Talinum*, *Trochomeria*, and *Vigna*). Thus, 15 out of 44 bathyergid-eaten USOs (34.0%) were identical or congeneric with human-eaten USOs. To some extent, therefore, bathyergids can index not only the presence of abundant USOs, but also the presence of species edible by hominids.

Thus, the fossil history of the bathyergids is of interest. Their earliest record comes from the early African Miocene, from which a fully fossorial Namibian species has been assigned to the modern Bathyergidae (*Paracryptomys mckenna*), as well as another said to be related to it [*Bathyergoides neotertiarius* (Bathyergoididae)] (Lavocat, 1978).

Bathyerigids are subsequently abundant in the fossil record of the early Miocene in Namibia and eastern Africa, and in the Plio-Pleistocene (Wood, 1985). Their presumed continuous presence implies that USOs have been potentially important food sources from the Miocene to the present. Accordingly, it is likely that there has been an equally persistent niche for USO-eating apes.

If the presence of bathyerigids does indicate the availability of USOs edible by hominids, bathyerigids and hominids should be correlated in the fossil record. To test this prediction, we surveyed faunal data from 68 African fossil-bearing sites or sampling units within the known geographical range of hominids, covering the period from ca. 6.0 Ma to 1.5 Ma. Of these 68 localities, we found 38 with both a microfaunal and macrofaunal record. Of these, 28 southern and eastern African localities had either mole-rats, hominids, or both. These sites are summarized in Table 2.

Inspection of these data shows that there is a consistent co-occurrence of mole-rats and hominids throughout the entire time range. Taphonomic vagaries introduce potential errors because mole-rats are rare relative to other microfauna and hominids are rare relative to other macrofauna. Furthermore, the taphonomic and depositional settings of microfauna and macrofauna are often different, and it may be common for the two sets of faunas to be studied by different individuals and reported at different times. It is very likely, therefore, that some of the seven sites shown in Table 2 that have hominids only will eventually be shown to have mole-rats as well.

Taking into account all 38 micro- and macrofaunal data sets, it is possible to offer a preliminary test of association between hominids and mole-rats. Thus, 17 of the 21 sites at which mole-rats are present also had hominids (44.7%), whereas only seven (18.4%) of the sites without mole-rats had hominids present. With the presently available, though admittedly limited, data, there seems to be a correlation between the presence of hominids and mole-rats in the fossil record (two-tailed Fisher's exact test,  $P = 0.0184$ ). By inference, we suggest that these hominids were associated with USO-rich habitats.

## USOs and hominid evolution

According to McHenry's (1992) "megadontia quotient," australopith species had chewing surfaces substantially larger than the living African apes. Associated with these large teeth were massive masticatory muscles. The australopith dentition, especially that of *Paranthropus*, exhibits little evidence for shearing, which suggests that leaves would not have been their fallback food (Teaford and Ungar, 2000; Wood and Strait, 2004). The thick enamel of australopiths, especially in *Paranthropus* (Grine and Martin, 1988; Macho and Thackeray, 1992; Schwartz et al., 1998), suggests a shift away from leaves as fallback food, as relatively thin enamel, together with a high shearing quotient, is more frequently associated with leaf eating (Kay, 1981; Teaford and Ungar, 2000). This thick enamel may have served as protection against breakage while chewing hard objects *and* to prolong tooth life in an animal with an abrasive diet (Wood and Strait, 2004). We hypothesize that the large jaw muscles, megadonty, and thick enamel, as well as molarization of the premolars (Wood and Strait, 2004), characters developed to varying degrees among australopiths in general, and to a great degree in *Paranthropus* in particular, were adaptations to handle repeated chewing of USOs.

In addition to the increase in enamel surface area, the palates of at least some australopiths are deep (high) relative to those of modern humans and great apes,<sup>2</sup> and thus the oral cavity was large compared with that of chimpanzees. The predominant energy source in USOs consists of carbohydrates that would be initially digested by amylase released by the parotid salivary glands in this large mouth (Conklin-Brittain

<sup>2</sup> This is based on simple observation supported by a check of measurements of the internal palate height and width of readily available materials, as follows. Internal palate height (depth) (mm) from occlusal surface to palate and width (mm), mesial to M1 at alveolar surface, and depth/width: OH 5 cast 31.3/36.5 = 0.858; Chimpanzee UMN UC 1 male 27.7/40.0 = 0.693; Chimpanzee UMN UC 2 female 20.9/36.2 = 0.577; Chimpanzee cast UMN AFR 00 6 male 22.9/42.9 = 0.534; Orangutan (zoo specimen) UMN Orang #2 30.4/51.1 = 0.595; Human UMN HSP 8-1 23.9/36.9 = 0.648; Human UMN HSP 1-1 20.4/36.5 = 0.559.

Table 2  
Co-occurrence of mole-rats and hominids at fossil sites<sup>1</sup>

East Africa	Southern Africa	Age
Olduvai Bed 2	<b>Swartkrans Member 3</b>	
<b>Olduvai Bed 1</b>	<b>Swartkrans Member 2</b>	
	Swartkrans Member 1	
	<i>Humpata level 2</i>	
	<b>Kromdraai<sup>2</sup></b>	~ 2 Ma
<b>Omo G</b>	<b>Taung</b>	
Omo F	<b>Sterkfontein Member 4</b>	
Chemeron Formation	<i>Nosib</i>	
<b>Omo E</b>		
Omo D		
Omo C		
<b>Hadar</b>	<b>Makapan exit quarry red mud</b>	~ 3 Ma
<b>Upper Ndolanya Beds</b>	<b>Makapan Member 4</b>	
<b>Upper Laetoli</b>	Sterkfontein Member 2	~ 4 Ma
Omo Usno		
<i>Lower Laetoli, Kakesio</i>		
<b>Aramis</b>		
Tabarin		~ 5 Ma
<b>Lukeino Formation</b>	<i>Langebaanweg</i>	
<b>Summary</b>		
Sites with mole-rats only	4	
Sites with mole-rats and hominids	17	
Sites with hominids only	7	
Total	28	

<sup>1</sup> Sites with both taxa are in bold, sites with only mole-rats are in italics, and sites with only hominids are in plain-text. Faunal data were surveyed for the presence or absence of hominids and mole-rats (which included the Bathyergidae genera *Cryptomys*, *Gypsochrychus*, *Georychus*, *Bathyergus*, and *Heterocephalus*, along with the Rhizomyinae genus *Tachyoryctes* and indeterminate species in either family). The 28 sites listed are within the temporal and geographical range of hominids and had published records indicating that both macrofauna and microfauna had been collected and studied. An additional 10 sites or localities had macro- and microfaunal records, but neither hominids nor mole-rats were reported. The 38 sites were identified by inspection of 68 reported sites. Data were taken from a number of sources, with the compilation of Turner et al. (1999) serving as a key source. Additional sources include Hay (1976), Partridge (1978, 1979, 1982), Asfaw (1983), Bonnefille (1984), Harris (1985), Hill (1985), Ward and Hill (1987), Andrews (1989), McKee et al. (1995), Reed (1997), Fernández-Jalvo et al. (1998), Leakey et al. (1998), Ward et al. (1999), Avery (2001), Haile-Selassie (2001), Leakey et al. (2001), Senut et al. (2001), Winkler (2001), WoldeGabriel et al. (2001), Asfaw et al. (2002), Behrensmeier et al. (2002), Hill (2002). See text for important caveats regarding taphonomy and sampling difficulties.

<sup>2</sup> Kromdraai A and B were combined because Kromdraai A has physical remains of hominids, but the microfaunal material is still under study, while Kromdraai B has mole-rats, but no hominid bones, but it does contain stone tools.

et al., 2002). Based on the premise that raw USOs require more protracted chewing than the herbaceous leaves and piths eaten by African apes, we hypothesize that the large oral cavity of australopiths functioned to accommodate a large volume of ingesta, allowing long periods of chewing.

We expect that, in the future, tooth-surface microwear analysis will help to clarify australopith diets. At this time, studies in this area have included modern comparative material of a very limited range of diet types, and to our knowledge, there have been no studies that directly test the USO-eating hypothesis. What we do know is that

australopith teeth tend to be more pitted than most ape teeth, with *Australopithecus* teeth being approximately as pitted as those of *Pongo*, and those of *Paranthropus* being more heavily pitted (Grine, 1986; Teaford, 1994). These patterns appear compatible with USO-eating (Ryan and Johanson, 1989; Ungar, 2004). Thus, in discussing work by Grine (1986), Teaford (1994: 25) concluded that “given the molar microwear patterns of *Paranthropus*, something in or on the food was probably hard and abrasive, and the food itself must have required extensive mastication.”

In sum, large, relatively flat, heavily enameled teeth and a large mouth are potentially explicable as adaptations to USO-eating. These occur in gracile australopiths and to an even greater degree in “robust” australopiths.

Pilbeam and Gould (1974) proposed that the ecological separation of the “robust” and “gracile” australopiths species might be analogous to the differences between gorillas and chimpanzees. Their suggestion was based in part on the belief that “robust” australopiths had larger bodies than the “gracile” forms (Pilbeam and Gould, 1974). However, since it is now known that both forms had approximately the same body size (McHenry, 1992, 1994), the gorilla-chimpanzee analogy is imperfect.

However, we suggest that it may have merit as a way to think about dietary differences between the two forms of early hominid, specifically in their use of fallback foods. Gorillas differ from chimpanzees in being able to subsist entirely on their fallback foods (leaves and piths), such as in montane regions or for several weeks of a fruit-poor season. Chimpanzees, in contrast, often use fallback foods similar to those of gorillas, but they require year-round access to fruits (Wrangham et al., 1998). Their fallback foods are eaten not as complete diets for certain fruit-poor seasons, but as filler foods, eaten later in the day during periods when fruits are harder to find.

By analogy, then, gracile australopiths could have been chimpanzee-like in their dietary behavior. According to this scenario, gracile australopiths would have searched year-round for high-quality foods such as fruits, seeds, honey, insects, and meat. Plant USOs would have

provided fallback foods in the same way that leaves and piths provide fallback foods for chimpanzees. The more specialized masticatory apparatus of the robust australopiths, by contrast, could have allowed them to be more gorilla-like in the sense of being able to subsist entirely on their fallback foods. This capability would have enabled them to colonize habitats that had so few high-quality foods (fruit, honey, meat, and seeds) that they were forced to rely for months or years on a diet dominated by USOs.

Stable isotopic studies of australopith remains from Makapan and Swartkrans in South Africa suggest the use of C4 resources by these hominids, which implies the consumption of either C4 plants or the animals that consumed C4 plants (grazers). It has also been suggested that dry season use of the USOs of C4 plants, such as Cyperaceae, is another potential C4 source in this environment (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999). Further research is needed to ascertain the distribution and relative abundance of edible C3 vs. C4 USOs in modern environments, with the aim of eventually reconstructing this aspect of ancient environments.

## Discussion and conclusions

The idea that hominids incorporated USOs into their diets has been with us since Hatley and Kappelman’s (1980) paper, and even before. Archaeologists (e.g., Clark, 1982) have long argued from analogy with modern foragers for the importance of digging sticks and USOs. More recently, the use of USOs has been classified as a critical step in human evolution (Wrangham and Peterson, 1996; Hawkes et al., 1997; Wrangham et al., 1999; Ragir, 2000). The composition and nutritional qualities of USOs has also been the subject of interest (e.g., Schoeninger et al., 2001). Recently, Conklin-Brittain et al. (2002) suggested that USOs increased hominid dietary quality by giving them lower levels of fiber in the overall diet. Thus, the potential importance of USOs for hominids has been widely considered.

We have complemented those approaches by suggesting more specifically how USOs may have contributed to hominid diets. Our hypothesis is that the evolution of hominids from the last common ancestor shared with chimpanzees depended partly on the substitution of USOs for herbaceous vegetation as fallback foods.

Our hypothesis is supported by four points. First, the dental and masticatory adaptations of the African apes and the hominids show clear inter-taxon differences that are well accounted for by a shift to USOs as fallback foods. Second, the commitment to adaptations indicative of USO exploitation increases during hominid evolution. Third, the ecology of USOs indicates that they would have been an abundant resource for hominids throughout their evolution, an assertion further supported by the evidence of the evolution and distribution of USO-eating mole-rats. Fourth, the fossil record indicates a correlation between hominids and mole-rats, suggesting that hominids tended to occur in USO-rich habitats.

There is growing evidence that middle to late Miocene hominoids, mainly in Europe, exploited relatively open habitats, and may have exhibited dietary adaptations (Teaford and Ungar, 2000; Smith et al., 2003; Smith et al., 2004) that we claim here to be related to USO consumption. This lends support to our assertions that a USO niche may have emerged during the Miocene, that this niche may have been important for non-fossorial mammals, and that certain features, such as thick enamel and large teeth, can arise in response to this niche. However, we do not wish to make claims beyond the hominid taxon at this time, other than to note that this may be a fertile area of future research.

We conclude that the hypothesis that USOs were key elements in the fallback diet for Pliocene hominids is worth further investigation. A research program to investigate this idea would involve collecting additional data on modern and ancient distributions of USOs, and the study of isotopic and possibly trace element signatures of this food source to better evaluate ancient chemical ecology inferred from early hominid fossils. Use-wear studies that more directly consider the use of USOs are also necessary. In addition, further

consideration of the effects USO usage may have had on body size, social structure, and biogeography is warranted.

### Acknowledgements

The following people provided valuable insight, assistance, and support in the production of this manuscript: Catherine Smith, the late Eitan Tchernov, Emily Weglian, David Pilbeam, Larry Flynn, Nancy Lou Conklin-Brittain, Patricia Fitzgerald, and Theresa Early. We thank the JHE reviewers and editors for many useful comments.

### References

- Adams, J.M., 1996. Towards a better vegetation scheme for global mapping and monitoring. *Journal of Biogeography/Global Ecology and Biogeography Letters* 5, 3–6.
- Andersen, D.C., 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. *Q. Rev. Biol.* 62, 261–286.
- Andrews, P.J., 1989. Palaeoecology of Laetoli. *J. Hum. Evol.* 18, 173–181.
- Asfaw, B., 1983. New hominid parietal from Bodo, Middle Awash Valley, Ethiopia. *Am. J. Phys. Anthropol.* 61, 367–371.
- Asfaw, B., Gilbert, W.H., Beyene, Y., Hart, W.K., Renne, P.R., WoldeGabriel, G., Vrba, E., White, T.D., 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. *Nature* 416, 317–320.
- Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *J. Hum. Evol.* 41, 113–132.
- Bahuchet, S., 1990a. The Aka pygmies: hunting and gathering in the Lobaye forest. In: Hladik, C.M., Bahuchet, S., Garine, I.D. (Eds.), *Food and Nutrition in the African Rain Forest*. UNESCO, Paris, pp. 14–18.
- Bahuchet, S., 1990b. Food sharing among the pygmies of central Africa. *African Study Monographs* 11, 27–53.
- Bahuchet, S., Garine, I.D., McKey, D., 1991. Wild yams revisited: is independence from agriculture possible for rain forest hunter-gatherers? *Human Ecology* 19, 213–243.
- Behrensmeyer, A.K., Deino, A.L., Hill, A., Kingston, J.D., Saunders, J.J., 2002. Geology and geochronology of the middle Miocene Kipsaramon site complex, Muruyur Beds, Tugen Hills, Kenya. *J. Hum. Evol.* 42, 11–38.
- Berger, L.R., Tobias, P.V., 1996. A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*. *J. Hum. Evol.* 30, 343–348.
- Boag, P.T., Grant, P.R., 1982. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science* 214, 82–85.

- Bonnefille, R., 1976. Palynological evidence for an important change in the vegetation of the Omo Basin between 2.5 and 2 million years. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology, and Evolution*. Chicago University Press, Chicago, pp. 421–431.
- Bonnefille, R., 1984. Palynological research at Olduvai Gorge. Research reports – National Geographic Society 17, 227–243.
- Bonnefille, R., Vincens, A., Buchet, G., 1987. Palynology, stratigraphy and palaeoenvironment of a Pliocene hominid site (2.9–3.3 M.Y.) at Hadar, Ethiopia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 60, 249–281.
- Brett, R.A., 1991. The population structure of naked mole-rat colonies. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), *The Biology of the Naked Mole-Rat*. Princeton University Press, Princeton, pp. 97–136.
- Carr, C.J., 1976. Plant ecological variation and pattern in the Lower Omo Basin. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology, and Evolution*. Chicago University Press, Chicago, pp. 432–467.
- Clark, J.D., 1982. The cultures of the Middle Palaeolithic/Middle Stone Age. In: Clark, J.D. (Ed.), *Cambridge History of Africa*. Cambridge University Press, Cambridge, pp. 248–341.
- Conklin-Brittain, N.L., Wrangham, R.W., Smith, C.C., 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., Teaford, M.F. (Eds.), *Human Diet: Its Origin and Evolution*. Bergin and Garvey, London, pp. 61–76.
- Davies, K.C., Jarvis, J.U.M., 1986. The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the south-western Cape, South Africa. *J. Zool. Ser. A* 209, 125–147.
- Doran, D.M., McNeilage, A., 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Robbins, M.M., Sicotte, P., Stewart, K.J. (Eds.), *Mountain Gorillas: Three Decades of Research at Karisoke*. Cambridge University Press, Cambridge, pp. 123–149.
- Fagan, B.M., van Noten, F., 1971. The Hunter-Gatherers of Gwisho. Musée royal de l'Afrique Centrale, Tervuren.
- Falk, D., Vannier, M., Hildebolt, C., 1994. Relationship of squamosal suture to asterion on external skull surfaces versus endocasts of pongids: implications for Hadar early hominid AL 162-28. *Am. J. Phys. Anthropol.* 93, 435–439.
- Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *J. Hum. Evol.* 34, 137–172.
- Flood, J., 1983. *Archaeology of the Dreamtime*. University of Hawaii Press, Honolulu.
- Genelly, R.E., 1965. Ecology of the common mole-rat (*Cryptomys hottentotus*) Rhodesia. *J. Mammal.* 46, 647–665.
- Gott, B., 1982. Ecology of root use by the Aborigines of southern Australia. *Archaeology in Oceania* 17, 59–67.
- Granger, A., 1996. Forest environments. In: Adams, W.M., Goudie, A.S., Orme, A.R. (Eds.), *The Physical Geography of Africa*. Oxford University Press, Oxford, pp. 173–195.
- Grant, P.R., Grant, B.R., 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707–711.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Grine, F.E., Martin, L.B., 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine, F.E. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 3–42.
- Haile-Selassie, Y., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412, 178–181.
- Harris, J.M., 1985. Age and paleoecology of the upper Laetoli Beds, Laetoli, Tanzania. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York, pp. 76–81.
- Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E.J., Idani, G., Furuichi, T., 1998. Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* 19, 1045–1060.
- Hatley, T., Kappelman, J., 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of below-ground food resources. *Human Ecology* 8, 371–387.
- Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr. Anthropol.* 38, 551–577.
- Hay, R.L., 1976. Environmental setting of hominid activities in Bed I, Olduvai Gorge. In: Isaac, G.L., McCown, E.R. (Eds.), *Human Origins: Perspectives on Human Evolution*, Vol. 3. Benjamin, Menlo Park, WA, pp. 209–225.
- Hill, A., 1985. Early hominid from Baringo, Kenya. *Nature* 315, 222–224.
- Hill, A., 2002. Paleanthropological research in the Tugen Hills, Kenya. *J. Hum. Evol.* 42, 1–10.
- Hill, W.C.O., Porter, A., Bloom, R.T., Seago, J., Southwick, M.D., 1957. Field and laboratory studies on the naked mole-rat (*Heterocephalus glaber*). *Proc. Zool. Soc. Lond.* 128, 455–513.
- Hladik, A., Bahuchet, S., Ducatillion, C., Hladik, C.M., 1984. The tuberous plants of the central African rain-forest. *Revue d'Ecologie (la Terre et la Vie)* 39, 249–290.
- Hladik, C.M., Hladik, A., 1990. Food resources of the rain forest. In: Hladik, C.M., Bahuchet, S., Garine, I.D. (Eds.), *Food and Nutrition in the African Rain Forest*. UNESCO, Paris, pp. 14–18.
- Honeycutt, R.L., Allard, M.W., Edwards, S.V., Schlitter, D.A., 1991. Systematics and evolution of the family Bathyergidae. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), *The Biology of the Naked Mole-Rat*. Princeton University Press, Princeton, pp. 45–65.
- Huntly, N., Reichman, O.J., 1994. Effects of subterranean mammalian herbivores on vegetation. *J. Mammal.* 75, 852–859.
- Ichikawa, M., 1980. The utilization of wild food plants by the Suiet Dorobo in northern Kenya. *The Journal of the Anthropological Society of Nippon* 88, 25–48.
- Jarvis, J.U.M., Bennett, N.C., 1991. Ecology and behavior of the family Bathyergidae. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), *The Biology of the*

- Naked Mole-Rat. Princeton University Press, Princeton, pp. 66–96.
- Jarvis, J.U.M., O'Riain, M.J., Bennett, N.C., Sherman, P.W., 1994. Mammalian eusociality: a family affair. *Trends Ecol. Evol.* 9, 47–51.
- Jarvis, J.U.M., Sale, J.B., 1971. Burrowing and burrow patterns of East African mole-rats *Tachyorydes*, *Heliophobius* and *Heterocephalus*. *J. Zool. Lond.* 163, 451–479.
- Kaessmann, H., Wiebe, V., Pääbo, S., 1999. Extensive sequence diversity among chimpanzees. *Science* 286, 1159–1162.
- Kano, T., 1983. An ecological study of the pygmy chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *Int. J. Primatol.* 4, 1–31.
- Kay, R., 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthropol.* 55, 141–151.
- Kingdon, J., 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, San Diego.
- Laden, G., 1992. Ethnoarchaeology and land use ecology of the Efe (pygmies) of the Ituri rain forest, Zaire: a behavioral ecological study of land use patterns and foraging behavior. Ph.D. Dissertation, Harvard University.
- Lavocat, R., 1978. Rodentia and Lagomorpha. In: Maglio, V.J., Cooke, H.B.S. (Eds.), *Evolution of African Mammals*. Harvard University Press, Cambridge, pp. 69–89.
- Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., Walker, A., 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393, 62–66.
- Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N., McDougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410, 433–440.
- Lee, R.B., 1979. *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge University Press, New York.
- Lee, R.B., DeVore, I., 1976. *Kalahari Hunter–Gatherers: Studies of the !Kung San and Their Neighbors*. Harvard University Press, Cambridge.
- Lee-Thorp, J.A., van der Merwe, N., Brain, C., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *J. Hum. Evol.* 27, 361–372.
- Lovegrove, B.G., Jarvis, J.U.M., 1986. Coevolution between mole-rats (Bathyergidae) and a geophyte, *Micranthus* (Iridaceae). *Cimbebasia* 8, 79–85.
- Macho, G.A., Thackeray, J.F., 1992. Computed tomography and enamel thickness of maxillary molars of Plio-Pleistocene hominids from Sterkfontein, Swartkrans, and Kromdraai (South Africa): an exploratory study. *Am. J. Phys. Anthropol.* 89, 133–143.
- Marshall, L., 1976. *The !Kung of Nyae Nyae*. Harvard University Press, Cambridge.
- McHenry, H.M., 1984. Relative cheek-tooth size in *Australopithecus*. *Am. J. Phys. Anthropol.* 64, 297–306.
- McHenry, H.M., 1992. How big were early hominids? *Evol. Anthropol.* 1, 15–20.
- McHenry, H.M., 1994. Behavioral ecological implications of early hominid body size. *J. Hum. Evol.* 27, 77–87.
- McKee, J.K., Berger, L.R., Thackeray, J.F., 1995. Faunal assemblage seriation of southern African Pliocene and Pleistocene fossil deposits. *Am. J. Phys. Anthropol.* 96, 235–250.
- Milton, K., 1999. Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition* 15, 488–498.
- Moore, J., 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew, W.C., Marchant, L., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 275–292.
- Nevo, E., 1979. Adaptive convergence and divergence of subterranean mammals. *A. Rev. Ecol. Systemat.* 10, 269–308.
- Nevo, E., Ivanitskaya, E., Gracia Filippucci, M., Beiles, A., 2000. Speciation and adaptive radiation of subterranean mole rats, *Spalax ehrenbergi* superspecies, in Jordan. *Biol. J. Linn. Soc.* 69, 263–281.
- Partridge, T.C., 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature* 275, 282–287.
- Partridge, T.C., 1979. Re-appraisal of lithostratigraphy of Makapansgat limeworks hominid site. *Nature* 279, 484–488.
- Partridge, T.C., 1982. Some preliminary observations on the stratigraphy and sedimentology of the Kromdraai B hominid site. *Palaeoecology of Africa and the Surrounding Islands* 15, 3–12.
- Peters, C.R., Maguire, B., 1981. Wild plant foods of the Makapansgat area: a modern ecosystems analogue for *Australopithecus africanus* adaptations. *J. Hum. Evol.* 10, 565–583.
- Peters, C.R., O'Brien, E.M., 1981. The early hominid plant-food niche: insights from an analysis of plant exploitation by *Homo*, *Pan*, and *Papio* in eastern and southern Africa. *Curr. Anthropol.* 22, 127–134.
- Phillipson, D.W., 1977. *The later prehistory of eastern and southern Africa*. Africana Pub. Co., New York.
- Phillipson, D.W., 1982. *The Later Stone Age in sub-Saharan Africa*. In: Clark, J.D. (Ed.), *The Cambridge History of Africa, Vol. I: From the Earliest Times to c. 500 BC*. Cambridge University Press, London, pp. 415–477.
- Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol. Phylogenet. Evol.* 5, 155–168.
- Pilbeam, D., Gould, S.J., 1974. Size and scaling in human evolution. *Science* 186, 892–901.
- Ragir, S., 2000. Diet and food preparation: rethinking early hominid behavior. *Evol. Anthropol.* 9, 153–155.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Robinson, B.W., Wilson, D.S., 1998. Optimal foraging, specialization, and a solution to Liem's paradox. *Am. Nat.* 151, 223–235.
- Ruvolo, M., 1997. Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol. Biol. Evol.* 14, 248–265.
- Ryan, A.S., Johanson, D.C., 1989. Anterior dental microwear in *Australopithecus afarensis*. *J. Hum. Evol.* 18, 235–268.

- Schoeninger, M.J., Bunn, H.T., Murray, S.S., Marlett, J.A., 2001. Composition of tubers used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis* 14, 15–25.
- Schwartz, G.T., Thackeray, F., Reid, C., Reenan, J.F.V., 1998. Enamel thickness and the topography of the enamel-dentine junction in South African Plio-Pleistocene hominids with special reference to the Carabelli trait. *J. Hum. Evol.* 35, 523–542.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *C. R. Acad. Sci. Earth Planet. Sci.* 332, 137–144.
- Sept, J., 1984. Plants and early hominids in East Africa: a study of vegetation in situations comparable to early archaeological site locations. Ph.D. Dissertation, University of California, Berkeley.
- Shea, B.T., 1985. Ontogenetic allometry and scaling: a discussion based on the growth and form of the skull in African apes. In: Jungers, W.L. (Ed.), *Size and Scaling in Primate Biology*. Plenum Press, New York, pp. 175–205.
- Silberbauer, G.B., 1981. Hunter and Habitat in the central Kalahari Desert. Cambridge University Press, Cambridge.
- Smith, T.M., Martin, L., Leakey, M., 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J. Hum. Evol.* 44, 283–306.
- Smith, T.M., Martin, L., Reid, D., de Bonis, L., Koufos, G., 2004. An examination of dental development in *Graecopithecus freybergi* (= *Ouranopithecus macedoniensis*). *J. Hum. Evol.* 46, 551–577.
- Sponheimer, M., Lee-Thorp, J.A., 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283, 368–370.
- Strahler, A.H., Strahler, A.N., 1992. *Modern Physical Geography*. John Wiley & Sons, New York.
- Tanno, T., 1981. Plant utilization of the Mbuti pygmies—with special reference to the material culture and use of wild vegetable foods. *African Study Monographs* 1, 1–53.
- Taylor, A.B., 2002. Masticatory form and function in the African apes. *Am. J. Phys. Anthropol.* 117, 133–156.
- Teaford, M.F., 1994. Dental microwear and dental function. *Evol. Anthropol.* 3, 17–30.
- Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. *Proc. Natl. Acad. Sci.* 97, 13506–13511.
- Terashima, H., Sawada, M., Ichikawa, M., 1988. Wild plant utilization of the Balese and the Efe of the Ituri Forest, the Republic of Zaire. *African Study Monographs* 8 (Supplementary Issue), 1–78.
- Turner, A., Bishop, L.C., Denys, C., McKee, J.K., 1999. Appendix: a locality-based listing of African Plio-Pleistocene mammals. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, New York, pp. 369–399.
- Tutin, C.E.G., Ham, R.M., White, L.J.T., Harrison, M.J.S., 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *Am. J. Primatol.* 42, 1–24.
- Ungar, P.S., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J. Hum. Evol.* 46, 605–622.
- Vincent, A.S., 1985. Plant foods in savanna environments: a preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeol.* 17, 131–148.
- Ward, C., Leakey, M., Walker, A., 1999. The new hominid species *Australopithecus anamensis*. *Evol. Anthropol.* 7, 197–205.
- Ward, C.V., Leakey, M.G., Walker, A., 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* 41, 255–368.
- Ward, S., Hill, A., 1987. Pliocene hominid partial mandible from Tabarin, Baringo, Kenya. *Am. J. Phys. Anthropol.* 72, 21–37.
- White, F.J., 1998. Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *Int. J. Primatol.* 47, 1013–1027.
- White, L.J.T., Rogers, M.E.R., Tutin, C.E.G., Williamson, E.A., Fernandez, M., 1995. Herbaceous vegetation in different forest types in the Lopé Reserve, Gabon: implications for keystone food availability. *African Journal of Ecology* 33, 124–141.
- White, T.D., Suwa, G., Asfaw, B., 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371, 306–312.
- White, T.D., Suwa, G., Simpson, S., Asfaw, B., 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am. J. Phys. Anthropol.* 111, 45–68.
- Whitmore, T.C., 1990. *An Introduction to Tropical Rain Forests*. Clarendon Press, Oxford.
- Winkler, A.J., 2001. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *J. Hum. Evol.* 42, 237–256.
- WoldeGabriel, G., Halle-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S., Asfaw, B., Heiken, G., White, T., 2001. Geology and palaeontology of the late Miocene Middle Awash Valley, Afar Rift, Ethiopia. *Nature* 412, 175–178.
- Wolpoff, M.H., 1973. Posterior tooth size, body size, and diet in South African gracile australopithecines. *Am. J. Phys. Anthropol.* 39, 375–394.
- Wood, A.E., 1985. The relationships, origin and dispersal of the hystricognathous rodents. In: Lockett, W.P., Hartenberger, J.-L. (Eds.), *Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis*. Plenum Press, New York, pp. 475–513.
- Wood, B., Strait, D.S., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *J. Hum. Evol.* 46, 119–162.
- Wrangham, R., Pilbeam, D., 2001. African apes as time machines. In: Galdikas, B., Briggs, N., Sheeran, L., Shapiro, G., Goodall, J. (Eds.), *All Apes Great and Small*. Plenum Publishers, New York, pp. 5–17.
- Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P., Isabirye-Basuta, G., 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 45–57.
- Wrangham, R.W., Conklin-Brittain, N.L., Hunt, K., 1998. Dietary response of chimpanzees and cercopithecines to



- seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* 19, 949–970.
- Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.* 40, 567–594.
- Wrangham, R.W., Peterson, D., 1996. *Demonic Males: Apes and the Origins of Human Violence*. Houghton Mifflin, Boston.
- Yamagiwa, J., Maruhashi, T., Yumoto, T., Mwanza, N., 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 82–98.
- Yamashita, N., 1998. Functional dental correlates of food properties in five Malagasy lemur species. *Am. J. Phys. Anthropol.* 106, 169–188.
- Zihlman, A.L., 1978. Interpretations of early hominid locomotion. In: Jolly, C.J. (Ed.), *Early Hominids of Africa*. St. Martin's Press, New York, pp. 361–377.