

# FOOD AND EVOLUTION

Toward a Theory of Human Food Habits

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## Primate Diets and Gut Morphology: Implications for Hominid Evolution

THERE IS CURRENTLY STRONG INTEREST IN DEVELOPING A BETTER understanding of the probable food habits and dietary niche of early humans (Isaac 1978; Peters and O'Brian 1981; Stahl 1984). Without such information, we are handicapped in our ability to interpret the significance of many features of human morphology and to construct viable models of early human ecology (Isaac 1978; Sussman 1978). Further, it is increasingly obvious that many of the major health problems faced today by more modern technological societies stem from factors related to diet. This strongly suggests that the average diet in such societies is not entirely suitable for human nutritional needs (Burkitt, Walker, and Painter, 1972; Trowell 1978; Truswell 1977). In this paper, I review information about dietary choice in primates, paying particular attention to members of the Hominoidea. I then examine features of the human gut, comparing it with the guts of other mammals, both primates and non-primates, to distinguish any features that appear to set humans apart. I conclude by speculating on the probable diet of early humans, using the behavior of extant pongids as a partial foundation for my speculations.

### Omnivory

Humans are generally viewed as omnivores (Fischler 1981; Harding 1981). By definition, an omnivore is any animal that takes food from more than one trophic level. Most mammals are in fact omnivorous (Landry 1970; Morris and Rogers 1983a, 1983b), including such diverse forms as pigs, tayras, dogs, pandas, bears, primates, skunks, some bats, and dozens of rodents. Though all omnivorous mammals appear to have basically similar nutritional requirements, different species satisfy these needs in different ways, using a tremendous

range and variety of foods. Describing a given species as omnivorous, therefore, does little to clarify what foods it may depend on, or how its digestive capabilities may differ from those of other omnivores, or why it may show decided preferences for some food types over others.

Both pure herbivores, such as bovids, and pure carnivores, such as felids, show highly characteristic metabolic specializations to the peculiar end products of their respective and specialized diets (Morris and Rogers 1983b). In bovids, microbial fermentation results in little glucose being absorbed from the gut. Ruminant metabolism is adapted toward the use of acetate rather than glucose for fatty acid synthesis and a constant high rate of gluconeogenesis (Morris and Rogers 1982; Van Soest 1982). Further, because bovids typically obtain all essential amino acids and most vitamins from gut flora, they do not have to choose foods to meet these needs. Similarly, pure carnivores, with strict adherence to a diet of animal tissue, absorb little glucose as a result of digestive processes and show a pattern of carbohydrate metabolism differing from that of omnivores (Morris and Rogers 1982). Pure carnivores have lost the ability to synthesize certain proteins (enzymes) that appear to be of no advantage to them because of their highly specialized diets. Adult cats, for example, require a dietary source of arginine, an amino acid typically synthesized by adult omnivores in sufficient amounts to meet maintenance requirements (Morris and Rogers 1982, 1983a, 1983b). In general, the pure carnivore appears intolerant of diets adequate for the adult omnivore (*ibid.*).

Humans are not ruminants; nor do they possess the suite of specialized metabolic adaptations to diet that distinguishes the pure carnivore. Thus, in terms of metabolic adaptations to diet, humans fall in with other omnivorous mammals. To clarify more precisely what type of omnivory may have characterized ancestral hominids, it is useful to examine certain broad characteristics of the primate diet, paying special attention to hominoids.

## The Primate Diet

The adaptive radiation and eventual dominance of angiosperms during the Cretaceous opened up a variety of new dietary opportunities (Regal 1977). Potential foods included not only insects that pollinated angiosperm flowers but also the pollen, nectar, fruits, seeds, and foliage of the angiosperms themselves. The primate line is believed to have differentiated by the Middle Paleocene, arising from some type of terrestrial insectivorous stock (Eisenberg 1981).

If present-day primates are any indication, early primates appear to have taken strong advantage of arboreal plant foods. All extant primates take food

from the first trophic level, but not all primates take food from the second, at least not intentionally. A very few prosimians (e.g., *Galago demidovi*) take the bulk (wet weight) of their diet from animal matter (Charles-Dominique 1977), but the overwhelming majority of primates take the bulk (wet weight) of the diet from plants, eating only small amounts of animal matter (Gaulin and Konner 1977; Harding 1981; Hladik 1977). This indicates that the adaptive radiation of primates, particularly the anthropoids, occurred by virtue of their ability to penetrate the as yet unfilled arboreal plant food niche and radiate to the point where they came to dominate a strong subset of the available arboreal dietary resources.

In the tropical forest, almost all potential plant food comes from dicotyledonous species using the  $C_3$  carbon pathway. In sharp contrast, many potential plant foods in the savannas come from monocotyledonous species using the  $C_4$  carbon pathway. I do not know whether these differences in plant food types are reflected to any degree in the digestive physiology of primates. Certainly, if extant primates are any indication, the primate gut was initially adapted for both the nutritive and the defensive components of dicotyledonous  $C_3$  rather than monocotyledonous  $C_4$  plant foods. Recent experimental work on human fiber digestion shows that human microflora are very sensitive to different fiber sources. As a group, humans are very efficient at degrading the relatively unlignified hemicelluloses and cellulose of dicot vegetable fibers such as cabbage or carrots but are less efficient on monocot cereal fibers such as wheat bran or monocot plant fibers such as alfalfa, with a high cellulose to hemicellulose ratio and considerable lignification (Van Soest et al. 1983). Though most extant primates eat primarily dicotyledonous plant species, a few species (e.g., *Papio* spp., *Theropithecus gelada*) eat quantities of grass blades and presumably are able to degrade the dietary fiber of grasses with some degree of efficiency. The current dependence of most large human populations on quantities of monocotyledonous plant foods, particularly cereal grains, is a notable departure from the traditional plant foods consumed by the majority of primates, both in the past and today. Monocot cereal grains also tend to be high in phytate, which, because of its high anionic character, is ideal for forming complexes with mineral elements, particularly transitional elements such as zinc, iron, and manganese (Lloyd, McDonald, and Crompton 1978). Any primate turning to phytate-rich plant foods as a major dietary staple may require other special foods in the diet to avoid potential mineral deficiencies due to complexing of phytates with essential minerals. Animal foods, for example, are a good source of zinc, which could help to augment losses due to binding of this element in cereal foods by phytates.

In choosing foods, small primates, because of the increase in the ratio of metabolic requirements to gut capacity (Demment and Van Soest 1985), tend

to select rapidly digestible plant foods with little bulk, such as sugary fruit or gum (Gaulin and Konner 1977; Hladik 1977). These high-quality plant foods are supplemented to a greater or lesser extent by animal matter, typically insects. Larger-bodied primates generally include some foliage in the diet, eating leaves and buds as well as fruits, seeds, gum, flowers, and cambium. When eating foliage, most primates focus their attention on young rather than mature leaves in spite of the fact that mature leaves are far more abundant. Younger leaves generally show a higher protein-to-fiber ratio than mature leaves and tend to be less lignified, thus offering greater nutritive returns to the feeder (Milton 1979). Some larger-bodied primates routinely seek out foods from the second trophic level, particularly insects, but occasionally vertebrates (e.g., *Cebus* spp., *Papio* spp., *Pan troglodytes*), whereas others rarely appear to ingest animal matter intentionally (e.g., *Alouatta* spp.).

A wealth of available data indicates that primates, particularly anthropoids, typically include a number of different plant parts and plant species in the daily diet. Over an annual cycle, for example, howler monkeys (*Alouatta palliata*) living in lowland tropical forest on Barro Colorado Island, Republic of Panama, take foods from more than 109 plant species (Milton 1980). Further, on any given day, howlers may take foods from 10 to 20 or more different plant species. Two other primate species sympatric with howlers in this same forest, the black-handed spider monkey (*Ateles geoffroyi*) and the capuchin monkey (*Cebus capucinus*), also take foods from well over a hundred plant species per annum, using 10 or more plant species per day (Hladik and Hladik 1969; Oppenheimer 1968; Milton, unpublished data). Arboreal and semi-arboreal animals of some other orders do not appear to include as many plant species in the diet either per annum or per day. For example, the Barro Colorado forest has also been the site of detailed study of the dietary ecology of the red-tailed tree squirrel (*Sciurus granatensis*), two-toed sloth (*Choloepus hoffmanni*), three-toed sloth (*Bradypus variegatus*), and coati (*Nasua narica*) (Glanz et al. 1982; Montgomery and Sunquist 1978; Russell 1979). These species range from purely herbivorous (the two sloth species) to omnivorous (squirrel and coati); in no case do individuals of any of these species even begin to approach the dietary diversity reported for the monkey species in this forest. The large number of plant species eaten by most primate species is an interesting and perhaps unique characteristic of the primate diet (but see Sussman 1978 for a contrasting view).

Conversely, scant data suggest that primate species routinely including animal prey in the diet tend to show strong prey specificity within particular habitats (see, e.g., the work of Charles-Dominique [1977] on the Gabon lorises). The broad plant food niche of primates and the apparently more narrow and specialized animal food niche are an aspect of primate food choice that warrants further study and quantification.

## The Hominoid Diet

An examination of the food choices of hylobatids and pongids shows that all species conform to the general primate trend just described in that they eat considerable plant material, supplementing it with some animal matter, typically eaten in small or even trace amounts. Mountain gorillas are almost exclusively herbivorous (Fossey and Harcourt 1977; Goodall 1977), followed by orangutans (Rodman 1977, 1984) and siamangs (Chivers 1977; Gittins and Raemaekers 1980), both of which eat notable amounts of leaves, shoots, stems, and/or bark as well as fruit and some insect matter (Table 3.1). Gibbons and chimpanzees focus very strongly on fruit in the diet, eating some foliage and from 4 percent to 13 percent animal matter (Gittins and Raemakers 1980; Rodman 1984; Wrangham 1977). The diet of the pygmy chimpanzee is not as yet well documented, but it appears to feed partially on fruit and partially on fibrous vegetable matter, particularly that of ground cover species, supplemented by some animal matter (Kano 1983).

As a dietary category, ripe fruit tends to be relatively high in soluble carbohydrates but low in protein, whereas leaves tend to be relatively high in protein but low in soluble carbohydrates (Milton 1979, 1981). Primate species routinely including large quantities of foliage in the diet each day would not be expected to take foods from the second trophic level unless such foods were required for some essential trace nutrient such as vitamin B<sub>12</sub>.

## The Primate Digestive Tract

The above data show that primates are omnivores of a particular type in that the great majority show a clear focus on plant foods, eating only modest amounts of animal matter. Generally, however, when we think of plant-eating animals, primates do not come to mind; rather, we think of cows, sheep, horses, koalas, kangaroos, and the like. All of these highly herbivorous forms routinely eat the photosynthetic tissues of plants as their staple item of diet, and all show digestive tracts that are amazingly specialized in form when compared with those of most primates. As an order, primates show a digestive tract that, in its general form, is not greatly modified from the primitive mammalian pattern (Mitchell 1905). In many respects the anthropoid gut is simpler in form than that of prosimians, and it has been suggested that their respective gut forms may have been independently derived from the primitive mammalian pattern (Mitchell 1905). The relatively unspecialized form of the normative primate gut supports the view that, as an order, primates, particularly the

TABLE 3.1. Food Choices of Hominoids (Percentage of Feeding Time)<sup>a</sup>

Species	Fruit	Leaves, Shoots, and Stems	Other Plant Foods	Animal Matter	Source
<i>Gorilla gorilla</i> <i>beringei</i> (mountain gorilla)	2	86	2 flowers 7 wood 3 roots	Negligible— "grubs"	<i>a</i>
<i>Pongo pygmaeus</i> (orangutan)	53 (often unripe)	25	15 bark	<1 insects	<i>b</i>
<i>Pan troglodytes</i> (common chimpanzee)	63 (ripe) 68	20 28	— gum	3 insects 4 insects, eggs, fledglings <sup>b</sup>	<i>b</i> <i>c</i>
<i>Pan paniscus</i> (pygmy chimpanzee)	—	—	—	termites(?)	<i>d</i>
<i>Hylobates</i> <i>syndactylus</i> (siamang)	36	43	6 flowers	15	<i>e</i>
<i>Hylobates lar</i> (lar gibbon)	50	29	7 flowers	13	<i>e</i>
<i>Hylobates agilis</i> (agile gibbon)	58	39	3 flowers	1	<i>e</i>
<i>Homo sapiens</i> (modern hunt- er-gatherers, excluding high- est latitudes)	Plant foods, ≥60			ca. 30–40	<i>f</i>

SOURCES: *a*, Fossey and Harcourt (1977); *b*, Rodman (1984); *c*, Hladik (1977); *d*, Kano (1983); *e*, Gittins and Raemaekers (1980); *f*, Lee (1968).

<sup>a</sup>Values should not necessarily sum to 100 percent as different sources may not present data on all food types eaten by their study subjects.

<sup>b</sup>Chimpanzees were also observed to hunt mammals at Gombe site (Teleki 1981).

anthropoids, have traditionally focused on very high-quality plant foods that are not extensively fibrous or lignified and supplemented them with some second-trophic-level foods. Primates deviating from this pattern of gut morphology appear to represent special radiations that have turned heavily to foliage as a dietary staple (i.e., Colobinae, Indridae).

It should be noted that within lineages the ancestral pattern tends to dominate gut form (Mitchell 1905). Gut form, therefore, cannot in itself be used to predict diet. For example, a well-developed cecum is generally associated with diets high in plant fiber. All extant prosimians have a cecum, in most cases capacious, but have not been noted to eat any great amount of plant fiber. In many cases the prosimian cecum appears to function as a fermentation chamber for plant exudates and/or chitin of insect exoskeletons (Clemans 1980; Sheine 1979). Conversely, if one examines animals from other orders, the hippopotamus and the giant panda are both strongly herbivorous, and both lack a cecum (Hill and Rewell 1948; P. J. Van Soest, pers. comm.). The bear, a decided omnivore, has a gut as simple in form as that of the mink, a strong carnivore (Hill and Rewell 1948). A sacculated stomach and the strong development of both the cecum and colon are generally good predictors of diets high in plant fiber. But the absence of such features does not mean that a given species is

TABLE 3.2. Relative Gut Volume Proportions for Some Hominoid Species (Percentage of Total Volume)

Species	Stomach	Small Intestine	Cecum	Colon	Source of Raw Data
<i>Gorilla gorilla</i> (gorilla)	25	14	7	53	<i>a</i>
<i>Pongo pygmaeus</i> (orangutan)	17	28	3	54	<i>a</i>
<i>Pan troglodytes</i> (chimpanzee)	20	23	5	52	<i>a</i>
<i>Hylobates syndactylus</i> (siamang)	24	25	1	49	<i>a</i>
<i>Hylobates pileatus</i> (pillated gibbon)	24	29	2	45	<i>a</i>
<i>Homo sapiens</i> (human)	17	67	n.a.	17	<i>b</i>
<i>Homo sapiens</i>	24	56	1	19	<i>c</i>
<i>Homo sapiens</i>	10	63	3	23	<i>d</i>

SOURCES: *a*, Chivers and Hladik (1979); *b*, Maynard and Loosli (1969); *c*, D. J. Chivers, pers. comm.; *d*, R. W. Sussman, pers. comm. All calculations of relative volumes by the author.

NOTE: These figures are not scaled with respect to inter-specific differences in body size and as such should only be used inter-specifically as an indication of the pattern of gut proportions of the different species. As data are often taken from immature specimens or single specimens, all of these data, perhaps excluding those for *Homo sapiens*, should be regarded as rough estimates.

not strongly herbivorous, nor does it mean that a given species is strongly carnivorous. Staple items of diet or even trophic levels may alter within members of a particular family or genus, but, very broadly, phylogeny appears to dominate function in terms of gut form (Mitchell 1905). This is not to imply that all members of a particular lineage share the same gut scale or proportions, for such is most emphatically not the case. Within lineages, many features of the gut can show modification, particularly in the volume or length of particular sections (see Table 3.2). Work on a number of bird and mammal species likewise shows that within species, between individuals, and perhaps even in the same individual, the nature of the diet can affect gut scale and proportions (Gentle and Savory 1975; Gross, Wang, and Wunder, in press; Koong et al. 1982; Miller 1975; Moss 1972; Murray, Tulloch, and Winter 1977). There are also presumed to be a number of more subtle differences within lineages and intra-specifically in terms of morphological and physiological features of the gut such as mucosa thickness, villi length, and the like (Hill 1949; Hladik 1967; Karasov and Diamond 1983; Sonntag 1924).

### The Hominoid Digestive Tract

In keeping with the above observation, all members of the Hominoidea show the same basic gut pattern. Hominoids have a simple acid stomach, a small cecum terminating in a true appendix, and a well-sacculated colon. The hominoid appendix represents a shared trait of this superfamily not found in other extant primates. The night monkey (*Aotus* spp.) is reported to show some development of an appendix, though not to the same extent as hominoids (Hill and Rewell 1948). The hominoid appendix appears to represent the culmination of a strong trend in primates for lymphoid tissue to collect in the cecal apex (Berry 1900; Hill and Rewell 1948). In hominoids, this lymphoid tissue has migrated from the cecal apex into a discrete structure. The functions of the hominoid appendix are not known, but it is clearly an active, functioning organ (Hill and Rewell 1948). In humans, the appendix secretes an alkaline fluid containing amylase, eripin, and mucin. Davenport (1971) suggests that the human appendix is an especially lively site of antibody production. In rabbits, the appendix has been found to serve immunological functions, producing antibodies against certain protein antigens (Draper and Sussdorf 1965; Hanaoka, Nomoto, and Waksman 1970; Konda and Harris 1966). Other species with an appendix are the capybara (*Hydrochoerus hydrochaeris*) and the wombat (*Lasiorninus latifrons*). The rabbit, capybara, and wombat, like all hominoids, are strongly herbivorous.

Though the basic form of the hominoid gut is similar throughout the super-

family, there are notable differences between humans and other hominoids when relative gut proportions are compared (Table 3.2). Humans concentrate by far the greatest gut volume in the small intestine ( $\geq 56$  percent), whereas gibbons and orangutans show the greatest gut volume in the colon. In addition, the size of the human gut relative to body mass is small in comparison with most other anthropoids (R. D. Martin, pers. comm.). A variety of animal studies indicate that increases in energy requirements without a decrease in dietary quality will increase the size of the small intestine and decrease the colon (Cripps and Williams 1975; Fell, Smith, and Campbell 1963; Gross, Wang, and Wunder, in press). Certainly the present-day gut proportions of humans in modern technological societies indicate utilization of nutritionally dense, energetically concentrated foods. At the present time, however, it is difficult to evaluate the implications of differences in gut proportions between humans and other hominoids. As noted, many animal species are able to respond rapidly to changes in dietary quality in terms of modification of gut proportions. The size of the present-day human small intestine could be an ancient or a relatively recent trait. Indeed, it is not known whether all modern human populations show such gut proportions. On average, for example, individuals in Western societies are estimated to take in no more than 10 grams of fiber per day, whereas members of some rural African populations may take in more than 170. A difference of this magnitude, in view of the gut plasticity demonstrated for animals of some other orders, suggests that there may be some differences in gut proportions between extant human populations. Of interest would be data on the gut proportions of human populations on different dietary substrates as well as data on the plasticity of the hominoid gut in terms of its responses to changes in diet.

Burkitt, Walker, and Painter (1972), in observing defecation patterns of rural Ugandans eating unrefined, fibrous diets, commented that they showed transit times two to five times as rapid as those of British navy personnel eating refined Western diets and produced some four to five times more fecal matter. A number of other studies of human fiber digestion likewise show that increasing the fiber level of the diet (which generally implies lowered dietary quality) significantly decreases mean transit time (e.g., Wruck et al. 1983). A similar response was found in chimpanzees fed trial diets of different fiber levels (Milton and Demment, in prep.). Extrapolating to the natural environment, this pattern of digestive kinetics indicates that when dietary quality in the natural environment declines, both humans and chimps respond by increasing intake, which results in a more rapid turnover rate of ingesta. This kinetic response could help to ensure that individuals of both species continue to supply energy and nutrients to body tissue at an optimal rate in spite of some fluctuations in the availability of higher-quality foods in the natural environment.

The relatively small size of the human colon appears to represent the de-

rived rather than ancestral condition of Hominoidea. The colon of human neonates is more similar to that of pongids than is the case for mature individuals (Hill 1949). Humans show regression of the colon as they mature, whereas pongids show elongation, particularly of the left colon. Hill (1949) points out that in the arrangement of the colon, as in many other features of anatomy, pongids appear to have a gerontomorphic status as compared with humans. The marked sacculcation of the human colon can also be viewed as a possible retention feature.

When compared with those of most other mammals, the relative proportions of the human gut are unusual (my calculations, using data from Chivers and Hladik 1980 and Hladik 1967). Pure carnivores, such as felids, or more omnivorous carnivora, such as canids, do not have gut proportions similar to humans'. Rather, more carnivorous animals tend to show considerable volume in the stomach or in the stomach and small intestine. For example, 70 percent of the gut volume of the adult cat occurs in the stomach, whereas for dogs this figure is 62 percent. Highly herbivorous forms also differ from humans. Ruminants tend to show the greatest volume in the region of the stomach, whereas non-ruminant herbivores such as equines show tremendous volume in the cecum and colon. Swine, often regarded as good omnivore analogues for humans, in fact differ considerably. Some swine have a specialized area in the stomach near the pyloric region that is totally lacking in humans; further, swine are characterized by a large cecum relative to that of humans and a tremendous proportion of gut volume in the lower tract (Ehle et al. 1982; Stanogias and Pearce 1985a, 1985b). Work by Ehle et al. (1982) suggests that pigs may also have a somewhat different pattern of lower-gut turnover than humans as a result of cecal pulsing.

When the relative proportions of the human gut are compared with those of other primates, it is still difficult to find a good match. Most anthropoids show notable volume in the cecum and/or colon or have a highly specialized stomach (e.g., Colobinae). Prosimians show gut proportions somewhat similar to those of humans in that the small intestine tends to dominate the gut. However, like some carnivora, some prosimians show greater relative volume in the stomach than is the case for humans; further, most prosimians have a notable cecum that in some cases is highly specialized (Clemens 1980).

One primate whose gut proportions are strikingly similar to those of humans is the New World capuchin monkey (*Cebus* spp.). Like humans, capuchins concentrate most gut volume in the small intestine. The ratio of gut mass to body mass in capuchins is also small in comparison with other non-human anthropoids (R. D. Martin, pers. comm.). Capuchin monkeys eat a high-quality diet made up of unusually rich wild foods, both sugary fruits and protein- and oil-rich seeds. Capuchins also routinely devote 40 to 50 percent of their daily foraging time to seeking out second-trophic-level foods, including soft-bodied

grubs, cicadas, and small vertebrates (Oppenheimer 1968; Parker and Gibson 1977; Terborgh 1983; Milton, unpublished data).

Scant data on one specimen of *Papio papio* suggest that this species may be somewhat similar to humans in relative gut proportions (Chivers and Hladik 1980; Hladik 1969). Here too there appears to be an emphasis on the volume of the small intestine relative to other sections of the gut. Savanna baboons, like capuchin monkeys, are unusually selective feeders who specialize in high-quality foods. Baboons at times may devote almost all of their daylight hours to painstakingly seeking out small, nutritious food items such as corns, acacia gum, grass seeds, flowers, fruits, and animal matter, including copious quantities of insects when these are available (DeVore and Hall 1965; Hamilton, Buskirk, and Buskirk 1978). Baboons also feed opportunistically on small vertebrates, particularly immature animals (DeVore and Hall 1965; Harding 1973; Strum 1981).

Capuchin monkeys and savanna baboons are also unusual primates in that both use the hand to a considerable degree both to find and to prepare food items for consumption (Beck 1975; Parker and Gibson 1977). Capuchins are noted for their manual dexterity. They routinely use the hand to crack hard-shelled fruits, to unroll dead leaves in search of insect prey, and to pry among palm fronds for insects and small vertebrates (Parker and Gibson 1977). Baboons rely heavily on the hand when feeding, particularly to remove dirt from food items, to peel, husk, and open food items, and to grasp live prey. M. W. Demment (pers. comm.) points out that an adult male baboon (*Papio cynocephalus*) may pick up as many as 3,000 individual food items in a single day of feeding, each weighing no more than one-tenth of a gram dry weight. Thus, savanna baboons are heavily committed to the use of the hand in feeding. The frequent modification of a dietary item before ingestion in effect buffers the teeth and digestive tract of these species from the physical effects of many items in their diet. The similarity in relative gut proportions of humans, capuchin monkeys, and perhaps savanna baboons is not derived from a close common ancestor. Rather, it appears to represent similar adaptive trends in gut morphology in response to diets made up of unusually high-quality dietary items that are capable of being digested and absorbed primarily in the small intestine.

### Food Choices of Early Humans

As discussed above, the comparative anatomy of the hominoid digestive tract indicates that modern human gut proportions and scale represent the derived rather than the ancestral condition for the superfamily Hominoidea. There can

be little doubt that the ancestral line giving rise to this superfamily and ultimately to hominids was markedly herbivorous. Kliks (1978) has presented evidence from analyses of human coprolites to document the fact that until quite recently, many human populations took in an impressive amount of plant fiber in the diet, estimated from rehydration at perhaps some 130 grams of fiber per day. In addition, human coprolites also contain undigested residues of animal tissue, including such materials as bones, teeth, hair, feathers, keratinized skin, fish scales, and insect cuticle that at times contribute more than 10 percent of the total weight of undigested residues (Kliks 1978). Without more data on the comparative gut proportions of modern human populations and the degree of short-term gut plasticity characteristic of humans and apes, it is difficult to state whether the gut proportions and scale of modern humans as reported in this paper in fact characterized early humans. However, my prediction is that all extant humans will be found to have a gastrointestinal tract dominated by the small intestine, though considerable variation may be recorded for the size of the colon region.

Examination of the diets and activity patterns of extant pongids, in combination with evidence from the hominid fossil record, suggests that early humans focused feeding on energy-rich, high-quality foods. With an adult body weight of 93 kilograms (female) to 160 kilograms (male), gorillas are by far the largest anthropoids (Clutton-Brock and Harvey 1977). Gorillas typically feed on quantities of leafy material, a dietary category that is low in soluble carbohydrates. On such a diet, large body size confers decided energetic and nutritional advantages. In mammalian herbivores and omnivores, relative gut capacity and body mass show a linear relationship, whereas maintenance metabolism and body mass show an exponential relationship (Demment and Van Soest 1985; Parra 1978). In effect, a larger herbivore has proportionately more room in the gut and can exploit foods with a lower protein/fiber ratio than its smaller-sized counterparts (Demment and Van Soest 1985; Janis 1976; Nuzum 1985; Parra 1978). The large body size of the gorilla facilitates exploitation of a fibrous dietary matrix, but on such a diet energy appears to be in short supply. Gorillas are relatively inactive for terrestrial anthropoids and also show low levels of social interaction. This suggests that energy may be limited, so that behaviors that conserve energy are favored.

Similarly, orangutans, though often described as fruit-eaters, in fact concentrate much of their feeding on unripe fruit, leaves, and bark (Rodman 1977). Like gorillas, orangutans tend toward a fibrous dietary substrate that is often presumed to be low in soluble carbohydrates, and, again like gorillas, they are relatively immobile. Ninety percent of their travel takes place at a slow pace through the trees; the average day range is only some 300 meters (Rodman 1977). Further, orangutans are relatively unsocial and are one of the few anthropoid species not associating in any type of relatively permanent social group.

In contrast to gorillas and orangutans, chimpanzees focus their feeding primarily on high-quality foods. The keystone of the chimpanzee diet is ripe fruit, and individuals are very active, often traveling three to four kilometers a day in search of sufficient ripe fruit to meet nutritional requirements. Over 70 percent of chimpanzee travel takes place on the ground. Chimps use smaller, more dispersed food sources than orangutans and show longer median interpatch distances between food sources in  $\geq 10$ -minute feeding bouts (Rodman 1984). They supplement their basic ripe fruit diet with young leaves of unusually high quality (Hladik 1977) as well as insect and mammal prey. Male chimpanzees have been observed to hunt monkeys and pigs, and meat resulting from communal kills may be shared. (However, it should be noted that no more than 6 percent of the total annual diet of chimpanzees is estimated to come from second-trophic-level foods; see Table 3.1.) Chimpanzees are also extremely social and have a rich repertoire of facial gestures and calls. When feeding, chimpanzees make use of stones to crack hard-shelled fruits (Boesch and Boesch 1981) and use twigs and grasses to harvest termites (McGrew 1974). Thus, like capuchin monkeys and savanna baboons, chimpanzees rely on the hand for many fine-level manipulations with respect to food preparation, and in their case tools may also be employed (see e.g., Parker and Gibson 1977).

In summary, these comparative data on the dietary foci and behaviors of extant pongids strongly suggest that in the hominoid line, a focus on lower-quality, more fibrous plant foods leads to selection for a larger-bodied and relatively inactive and unsocial primate. In pongids, there is a clear pattern toward increasing the relative size of the hindgut and increasing the fiber content of the diet with increasing body size (Milton and Demment, in prep.).

Early humans are believed to have evolved in a savanna-mosaic setting. High-quality foods, both plant and animal, are more patchily distributed in both space and time in a savanna environment than in tropical forests (Milton 1981; Milton and May 1976; D. Olson, pers. comm.). This implies that early hominids in such a setting may have had both large day ranges and large home ranges if they concentrated on higher-quality, more digestible foods. In the hominid line, bipedalism is a more energetically efficient terrestrial locomotor mode than quadrupedalism (Rodman and McHenry 1980). Rodman and McHenry (1980) have hypothesized that selective pressures related to increased travel efficiency between widely dispersed food sources in a savanna setting may underlie the adaptation of bipedalism in the hominid line.

One way to lower foraging costs when moving from the tropical forest into a savanna-mosaic setting is simply to lower dietary quality. The "robust" australopithecines may have opted for this type of dietary strategy. Their relatively large post-canine teeth and massive skull bones suggest that they fed on tough, fibrous, and/or hard plant foods (Grine 1981). M. Demment (pers. comm.) suggests that dietary competition between the digestively specialized ungulates and the robust australopithecines may have contributed to the



eventual extinction of the robust forms. However, another way to lower foraging costs when moving into a patchy savanna environment is to continue to specialize in high-quality foods and to cover increased foraging costs both by improving food-search efficiency and by eating even higher-quality foods (Milton 1980, 1981). This may have been the dietary strategy of the "gracile" australopithecines. Ultimately, however, an adaptive peak should be reached, such that no further improvement on this basic foraging strategy can occur, because there are a finite number of ways to locate a finite number of high-quality dietary items efficiently in the savanna.

All australopithecines, both robust and gracile, are characterized by thick molar enamel and large cheek teeth. Australopithecines show somewhat more cranial expansion than extant pongids, but the difference is slight (Holloway 1973; Leutenegger 1973). In contrast, members of the genus *Homo* show thinner molar enamel, a dramatic reduction in cheek tooth size, and considerable cranial expansion (Grine 1981; McHenry 1982; S. Ambrose, pers. comm.). In combination, these dental and cranial features, as well as an increase in body size, apparently with no loss of mobility or sociality, strongly imply that early members of the genus *Homo* made a dramatic breakthrough with respect to diet—a breakthrough that enabled them to circumvent the nutritional constraints imposed on body size increases in the apes. It would appear that early humans were able in some manner to greatly improve their intake and uptake of energy, apparently without any decrease in dietary quality.

Such a dietary breakthrough had to go beyond improved food search efficiency or simple utilization of available high-quality foods, for I think that the gracile australopithecines were probably already at the apex of possibilities in this respect. There had to be some type of novel innovation—either technological or social or both—that altered the dietary potential of proto-humans (see, e.g., Lancaster 1968, 1975). A technological innovation could somehow make a low-quality but available and abundant food into a high-quality food. A social innovation, such as cooperative hunting and food sharing, could make formerly inaccessible or restricted high-quality food accessible and relatively dependable. An innovation such as language could help to coordinate foraging activities and thereby greatly enhance foraging efficiency (see, e.g., Lancaster 1968, 1975). I cannot state what this innovation was, but perhaps it was both technological and social, for certainly we see the strong development of both trends in human evolution. I can, however, speculate on possible selective pressures.

For most of its evolutionary history, the ancestral line leading to hominoids presumably lived in a forested environment. Plant foods are presumed to have composed the bulk of the diet, complemented perhaps by a modest amount of second-trophic-level food (Kliks 1978; Milton 1981, 1984). Data from extant hunter-gatherer societies suggest that this basic pattern of primate omnivory may also have been practiced by most hunter-gatherer groups living in tropical

areas (Lee 1968). It is only in temperate to Arctic latitudes that second-trophic-level foods are noted at times to compose the bulk of the diet (Lee 1968). Early hominids and humans are believed to have evolved in the tropics. If this assumption is correct, it is doubtful, by analogy with both the diets of extant primates and what is known of the diets of extant tropical hunter-gatherer societies, that animal protein in itself composed the bulk of the early human diet (Hayden 1981; Speth and Spielmann 1983). Indeed, research suggests that for most modern humans large quantities of animal protein may actually be detrimental to both normal growth and good health (Edozien and Switzer 1978; Nelson 1975). Human populations such as the Arctic Eskimo, whose diet is composed primarily of animal matter, show special adaptations for energy and nitrogen metabolism, and it is speculated that some of their dietary adaptations may be under some degree of genetic control (Draper 1977). Further, Arctic Eskimos do not eat a diet of pure animal protein but rather eat a mixture of animal protein and animal fat. Animal protein seems most appropriate in the human diet when it is eaten in combination with notable amounts of either fat or carbohydrates and used primarily to meet demands for amino acids and nitrogen (Edozien and Switzer 1978; Maynard and Loosli 1969; Nelson 1975). It seems unlikely that animal protein has ever served as the principal item of diet for the majority of tropical-living human populations.

Given the patchy nature of higher-quality foods in a savanna environment, however, I would suggest that both animal protein and animal fat may have been important dietary resources for early humans. Though relatively few non-human primate species live in the savannas, those that do frequently include animal matter in the diet, at times in considerable amounts (Hamilton, Buskirk, and Buskirk 1978). This suggests that in a savanna environment, animal matter may be somewhat more available for larger-bodied primates than it is in a tropical forest. If early humans were able to depend on protein-rich animal foods to fulfill their daily amino acid requirements, this would buffer the digestive tract from selective pressures related to the need to efficiently process large quantities of proteinacious plant matter—typically leaves. A larger body mass could perhaps be supported with less gut mass, as is suggested to be the case for some carnivores as well as capuchin monkeys and modern humans (Chivers and Hladik 1979; R. D. Martin, pers. comm.). Routinely using some animal matter in the diet would make proportionately more room available in the gut to process carbohydrate-rich plant foods, the traditional energy source for the great majority of primate species.

Plant foods differ in many important respects from animal foods, placing the plant-eating animal under somewhat different selective pressures than carnivores with respect to features of foraging success (Milton 1984; Westoby 1974). Plant foods are sessile and tend to be buffered from consumption by internal, chemical characteristics such as low nutrient content, high cell wall



matter, or secondary compounds. In contrast, animal prey is typically highly mobile and protected from predation by external defenses such as speed, spines, teeth, or claws (Milton 1984). If early humans devoted some foraging effort each day to the procurement of second- as well as first-trophic-level foods, their foraging strategy, necessarily focused for most of their past evolutionary history on the efficient exploitation of sessile plant foods, must have undergone some rather radical modifications. The pressures to become efficient at procuring foods from two rather than one trophic level may have set in motion a new suite of behaviors (see, e.g., Strum 1981), leading eventually to what we recognize as the *Homo* grade of development. Like some other researchers (e.g., Isaac 1978; Lancaster 1968, 1975), I see a division of labor with respect to food procurement in combination with food sharing as a pivotal adaptation in human evolution. Indeed, I think that the implications of this type of dietary innovation have not been fully appreciated, for, in effect, a division of labor and food sharing provide a means whereby individuals of a given species can efficiently utilize foods from two trophic levels simultaneously—a foraging strategy that appears to be truly unique among mammals.

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