

# Animal Source Foods to Improve Micronutrient Nutrition and Human Function in Developing Countries



## The Critical Role Played by Animal Source Foods in Human (*Homo*) Evolution<sup>1,2</sup>

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**ABSTRACT** Wild primates take most of the daily diet from plant sources, eating moderate to small amounts of animal source foods (ASF). Plant materials make up from 87% to >99% of the annual diet of great apes, the closest living relatives of modern humans (*Homo sapiens sapiens*). Reflecting their close genetic relationship, gut form and nutrient requirements of apes and humans (*Hominoidea*) are very similar, as is their pattern of digestive kinetics—one predicated on a relatively slow turnover of ingesta. In plant-eating mammals, in contrast to carnivorous mammals, greater body size is associated with lower dietary quality. Turning to ASF as a routine rather than occasional dietary component would have permitted the evolving human lineage to evade the nutritional constraints placed on body size increases in apes. Without routine access to ASF, it is highly unlikely that evolving humans could have achieved their unusually large and complex brain while simultaneously continuing their evolutionary trajectory as large, active and highly social primates. As human evolution progressed, young children in particular, with their rapidly expanding large brain and high metabolic and nutritional demands relative to adults would have benefited from volumetrically concentrated, high quality foods such as meat. Today, many humans, particularly those in high income nations, have a variety of high quality, non-ASF dietary alternatives, but such foods were not generally available to paleolithic human ancestors nor to many people today in low income nations. *J. Nutr.* 133: 3886S–3892S, 2003.

**KEY WORDS:** • animal source foods • primates • human evolution • meat eating • childhood nutrition

Humans are placed in the order Primates, suborder Anthrozoidea, superfamily Hominoidea, a classification that reflects the close evolutionary relationship between humans and apes. Genetic data suggest that chimpanzees and humans may have diverged from a common ancestor as recently as 7–6 million years ago (mya)<sup>4</sup> (1), which is not a long time evolutionarily. To appreciate the role played by animal source foods (ASF) in human evolution, it is important to consider the dietary behavior of extant wild primates and their predecessors. Primates are generally described as omnivores but they are omnivores of a very particular type in that the great majority of their foods each day come from plant sources (2,3).

Primates are believed to have evolved in tropical forests some 65 mya and even today this is where most primate species

are found (2,3). Recent paleontological evidence suggests that the earliest known hominid<sup>5</sup>, *Ardipithecus ramidus*—a taxon estimated to be some 4.4 million years (my) old—lived in a closed wooded rather than more open savanna environment (4,5). As forest and woodland inhabitants, the plant foods available to most primates for their entire evolutionary history have been the leaves, fruits and flowers of tropical trees and vines (largely dicotyledonous, woody angiosperm species) (2,3).

It is popularly believed that smaller monkeys eat largely ASF but this is not correct. Even the smallest extant monkey, *Cebuella*, takes ≥65% of its daily diet from plant sources, e.g., nectars, gums and sweet fruit pulp, supplemented with animal matter, largely insects. All great apes are markedly herbivorous (plant eating) (6–8). (As great apes are the closest living relatives of modern humans, this examination will focus largely on ape diet and morphology but much of it is also applicable to monkeys.) Gorillas and orangutans are estimated to take some 99% of their annual diet from plant sources whereas for chimpanzees this figure is placed at >87–98% (9,10). The strongly plant-based dietary focus of all living apes appears evolutionarily quite

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<sup>4</sup> Abbreviations used: ASF, animal source foods; MTT, mean transit time; mya, million years ago; NDF, neutral detergent fiber.

<sup>5</sup> Approximately 7–6 mya, humans shared a common ancestor from which one line led to the two modern chimpanzee (*Pan*) species and the other led to hominids. The term “hominid” refers to a family of primates on the human side of this split. Modern humans are hominids, as are earlier species of the genus *Homo* (including *H. erectus*), a line thought to have arisen around 2.5 mya. Small-brained but bipedal species in genera such as *Ardipithecus* (5.8–4.4 mya) and *Australopithecus* (4.0–1.2 mya), are also hominids.

ancient. The dentition of fossil apes >15 my old indicates a plant-eating, primarily frugivorous, way of life (11).

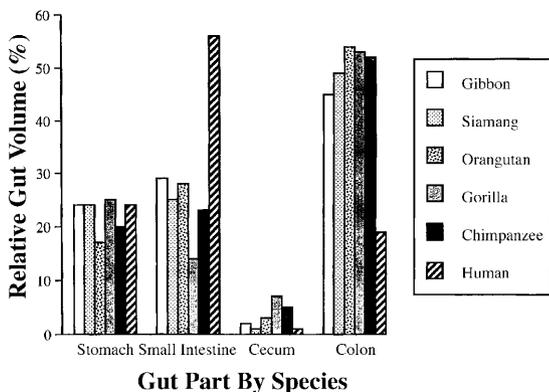
All apes consume some insect matter, often inadvertently when eating plant parts. Small quantities of animal source foods (ASF) provide apes with important trace nutrients. Some communities of chimpanzees eat termites and ants and, at times, hunt, kill and eat vertebrates. However, only the most dominant male chimpanzees typically consume any notable amount of vertebrate prey (12) and the typical chimpanzee diet is composed largely of ripe fruits (8,12).

### Comparative morphology of human and ape guts

When the human gut is compared with those of extant apes, many similarities and some differences can be detected. All extant hominoids (apes and humans), in keeping with their descent from a common ancestor, show the same basic gut anatomy: a simple acid stomach, a small intestine, a small cecum terminating in an appendix and a markedly sacculated colon (13). However, humans stand apart from all apes in some features of the gut proportions (Fig. 1). In humans, more than half (56%) of the total gut volume is found in the small intestine whereas all apes have by far the greatest total gut volume (>45%) in the colon (9,10). In addition, the overall size of the human gut in relation to body size is small in comparison to that of apes (9,10).

Hindgut dominance in apes suggests adaptation to a diet lower in quality than that consumed by humans, a diet containing considerable bulky plant material, such as insoluble fiber and seeds. In contrast, the proportions of the human gut, dominated as it is by the small intestine, the principal site of nutrient digestion and absorption, suggests adaptation to a high quality diet, one that is nutritionally dense and highly digestible relative to that of any wild ape (9,10).

Total gut size and the size of some gut sections are known to alter significantly within the space of a few weeks in some small mammal and avian species in response to fluctuations in dietary quality (14,15). Humans and apes are not known to exhibit such dramatic gut plasticity. Humans do show some degree of gut plasticity and there are both intra- and interpopulation differences in features of the human gut such as the colon



**FIGURE 1** Relative gut proportions for extant hominoids (percentage of total gut volume). Lesser apes: gibbon (*Hylobates pileatus*), siamang (*Hylobates syndactylus*); great apes: orangutan (*Pongo pygmaeus*), gorilla (*Gorilla gorilla*), chimpanzee (*Pan troglodytes*); Western humans (*Homo sapiens sapiens*). All calculations of relative volume by K. Milton. See Milton (10) for sources of raw data. Reprinted from *Nutrition* Vol. 15(6), K. Milton, Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us?, pp. 488-498, 1999, with permission from Elsevier Science.

length, length of the small intestine and the size of the cecum (16,17). However, all living humans have a gut dominated by the small intestine whereas all living apes have a gut dominated by the colon, a difference that appears to be genetically mediated in both cases. It is difficult to state when the change in gut proportions between humans and apes originated. Such gut proportions must have characterized the ancestral lineage giving rise to all modern humans (*Homo sapiens*) some 160,000 y ago; however, such gut proportions could also have characterized earlier *H. erectus* or even *H. habilis*.

### Comparative kinetics of human and ape guts

Gut proportions are one factor affecting food choices in the natural environment, but another important factor that needs to be considered is gut kinetics. Gut kinetics refers to the pattern of movement of ingesta, both particulate and liquid, through the digestive tract (18,19). Study of the pattern of gut kinetics of a given species can often provide insight into factors underlying its choice of foods as well as indicate limitations to its dietary breadth (18-21)

Milton and Demment (22) examined the pattern of digestive kinetics of common chimpanzees (*Pan troglodytes*) fed diets containing either 14% neutral detergent fiber (NDF) or 34% NDF (Table 1). Ingesta passed more rapidly with the high fiber diet, with a mean transit time (MTT) of 38 h with the high fiber diet and 48 h with the low fiber diet. MTT is an estimate of the average time "particles" of marker take to pass through a system of unknown or indefinable compartments (18,22). Because ingesta passed more rapidly in chimpanzee subjects when dietary quality was low (as with the high fiber diet), the chimp gastrointestinal tract had less time to process ingesta flowing through it. However, because the lower quality food passed more rapidly, chimpanzees could process a greater volume of food per day. This kinetic pattern would prove beneficial in the natural environment when seasonal or other environmental fluctuations reduced the availability of higher quality foods. Similar data on MTT of gorillas and orangutans have been obtained by Caton (23). Her results indicate that the gut kinetics of gorillas and orangutans are similar to those of common chimpanzees (23). It should be noted, however, that in all great apes, even the more rapid transit of food particles is not particularly fast.

Extensive work has been carried out on the passage kinetics of humans (18,19,24,25). For example, a detailed study of human passage kinetics at Cornell University showed an MTT of 62.4 h for subjects fed a 0% fiber diet and 40.9 h for those fed a 17.3% fiber diet (19) (Table 1). Studies show that MTT in humans can vary considerably from population to population, from person to person and even within a given individual (24,25). However, an extensive body of data supports the view that in humans, higher quality diets pass more slowly than lower quality diets and that most adult humans require  $\geq 36$  h to turn over the average particle of ingesta, even on unrefined diets (24,25).

In feeding trials, both humans and chimpanzees displayed similar MTT and  $T$  ( $T$  = the average time "particles" of marker take to pass through the hindgut region only) in digestion trials using wheat bran diets of similar particle size (22,26). This remarkable similarity in transit time occurred despite the fact that the chimpanzee has a total gut, as well as a hindgut region, considerably larger than that of humans (22).

The similarity of MTT and  $T$  in humans and chimpanzees supports the view that the passage kinetics of extant hominoids is a conservative trait genetically, relative to a trait such as gut proportions. With evidence in hand, there seems no way that either humans or chimpanzees could suddenly begin to turn over ingesta very rapidly (22). Rather, as noted above, the

TABLE 1

Time of first appearance (TFA), mean transit time (MTT) and lower gut turnover time (T) of liquid (CoEDTA) and fiber (Cr) markers in response to fiber level of the diet for chimpanzees and Western humans

Diet & marker	TFA <sup>1</sup>		MTT <sup>2</sup>		T <sup>2</sup>	
	Chimpanzees <sup>3</sup>	Humans <sup>1</sup>	Chimpanzees <sup>3,5</sup>	Humans <sup>4</sup>	Chimpanzees <sup>3,5</sup>	Humans <sup>4</sup>
Low fiber						
Liquid	24.9 ± 3.6	—	47.7 ± 3.2 <sup>a</sup>	61.6	—	—
Particulate	27.4 ± 7.5	26.0 ± 1.0	48.0 ± 3.4 <sup>b</sup>	62.4	17.2 ± 2.6 <sup>a</sup>	17.5
High fiber						
Liquid	23.7 ± 2.6	—	35.1 ± 2.3 <sup>b</sup>	38.9	—	—
Particulate	23.3 ± 2.5	—	37.7 ± 2.2 <sup>c</sup>	40.9	12.3 ± 3.7 <sup>b</sup>	11.7

<sup>1</sup> Time of first appearance (TFA) represents the first appearance of liquid or particulate marker materials in fecal matter. TFA for human subjects calculated by K. Milton using a particulate marker composed of small strips of soft, nonsoluble plastic;  $n = 3$ .

<sup>2</sup> Mean transit time (MTT) and lower gut turnover times (T) (in hours) of chimpanzees and humans calculated with the technique described in Wrick et al. (19) and Van Soest et al. (61).

<sup>3</sup> Chimpanzee data from Milton & Demment (22);  $n = 6$ ; low fiber diet, 14% NDF; high fiber diet, 34% NDF.

<sup>4</sup> Human data from Wrick et al. (19);  $n = 24$ ; low fiber diet, 0% fiber; high fiber diet, 10–15% neutral detergent fiber (NDF)

<sup>5</sup> Values are means ± SEM for MTT in chimpanzees. Different superscript letters within a column indicate differences due to treatments for chimpanzee data [ $P < 0.01$ ; see Milton & Demment (22) for details of chimpanzee passage trials].

pattern of passage kinetics within a given lineage appears to be a genetically conservative trait (22). Further evidence to support this statement is found from examination of the gut anatomy and passage kinetics of all extant members of the order Carnivora.

### Gut proportions and passage kinetics of Carnivora

All 284 extant species of Carnivora show essentially the same pattern of gut anatomy—a simple stomach and a short total gastrointestinal tract; the colon is not sacculated (13,27). In some lineages there is some development of a cecum but in others, as, for example, the Ursidae, Procyonidae and Mustelidae, the distal segment of the small intestine is marked only by a sudden change of the mucosa with no cecum present (13). The gut of all Carnivora is amazingly simple in form when compared to the guts of most omnivores (e.g., pigs) and herbivores (e.g., cattle, kangaroos) (13,27).

In all Carnivora, transit time of food appears to be rapid. For example, average transit time (here, time of first appearance of ingesta) in the mink, a pure carnivore, is 2.4 h (range 1.03–3.6 h) (28). A 370-kg polar bear showed a bimodal mode of defecation after a meal of seal meat with the first defecation of the meal occurring some 17–18 h after ingestion and the second between 23 and 26 h (29). In contrast, the data above on MTT for Western humans subjects at Cornell University showed that after 26 h, the average food particle is still in passage through the Western human gastrointestinal tract and will remain there for at least an additional 15–35 h before it is excreted (19). Like Carnivora, all extant Hominoidea (apes and humans) seem “stuck” with their ancestral pattern of digestive kinetics, i.e., such patterns appear resistant to evolutionary modification.

### Hominoid evolution

The fossil record shows that during the early to mid-Miocene Epoch (~25–15 mya), there was a proliferation of ape species. These ranged in size from extant small monkeys to female gorillas (11,30). In general, Miocene apes are characterized by a frugivorous pattern of molar morphology although some evidence suggests that larger apes may have had omnivorous tendencies (11,30). By the late Miocene Epoch, it is hypothe-

sized that some competitive advantage(s) possessed by monkeys may gradually have displaced most apes from their niches, leading to their extinction (11,30). As pointed out by Andrews, all hominoids alive today are adapted to somewhat unusual ecological niches in part through the evolution of highly specialized forms of locomotion (30,31). Increasingly large body size also appears to have facilitated ape survival for extant hominoids as a class (apes and humans) are considerably larger than extant monkeys as a class. A brief examination of the dietary behavior of extant great apes illustrates the important role meat eating may have played in permitting members of what became the human lineage to overcome the energetic constraints imposed by increasing body size in the hominoid lineage without a concomitant increase in dietary quality.

### Effects of lowered dietary quality in Hominoidea: gorillas and orangutans as modern examples

Gorillas are the largest extant Primates with adult males weighing some 160 kg and females 93 kg (32). Orangutans are next in size with males weighing some 69 kg and females 37 kg (32). Not surprisingly, in view of their large size and strongly plant-based diet, gorillas, particularly mountain gorillas, as well as orangutans are often forced to turn to lower quality plant foods—mature leaves, bark, unripe fruits—when sufficient higher quality plant sources such as ripe fruits and young leaves are not available.

In plant-eating mammals, an increase in body size has far different dietary implications than an increase in body size in strongly carnivorous mammals. A pure carnivore, such as a cat, can increase in size over evolutionary time with no decrease in dietary quality. This can be seen by comparing, for example, the foods of a lynx with those of a tiger; the only difference is the size of the prey. This situation does not prevail in the case of plant-eating mammals. As plant-eating mammals increase in body size, invariably their dietary quality must decrease, as can be seen by comparing, for example, the foods of a tiny forest antelope with those of an elephant. Demment (33) and Demment and Van Soest (34) have postulated that changing body size is a mechanism for differentiating the feeding requirements of herbivores and note that with larger body size, the fiber content of the diet invariably rises (i.e., dietary quality decreases).

As discussed, there is general consensus that extant hominoids, both apes and humans, come from a strongly plant-eating ancestry. Presumably selection for increased body size in gorillas and orangutans was initially associated with environmental conditions in which higher quality plant foods, for whatever reason—competition with monkeys, seasonal shortages, or other factors—simply were not available and/or accessible in sufficient quantity throughout the year. Or, conversely, it could also have been the case that lower quality plant foods were abundant and could easily and efficiently be used by a larger-bodied hominoid. Increasing body size over evolutionary time would permit these apes to survive on lower quality plant foods than otherwise would be possible, and to utilize plant sources that would not support smaller primates, thus getting around the postulated competition with monkeys. Large body size appears to be the single most important adaptation to diet shown by both gorillas and orangutans (6,7,9).

However, this increase in body size and dependence on lower quality plant foods carries with it certain negative consequences, namely, the diminution of some traits generally viewed as highly characteristic of higher primates, and in particular, a high degree of mobility and sociality (3,6,7,9,10). Neither gorillas nor orangutans are as active, agile and behaviorally complex as members of the genus *Pan* (chimpanzees) nor do they show the high degree of sociality that characterizes chimpanzees. In fact, orangutans are the only extant anthropoids that live solitarily, a social regression apparently dictated by their large size and the distribution patterns of their wild plant foods. Due to features of their almost exclusively plant-based diet in combination with their pattern of gut kinetics, energy input in these two great apes may often be sufficiently limited such that nonessential behaviors are not favored by selection—in other words, orangutans and gorillas may not have sufficient “extra” energy to be more active and social (3,10).

#### ***Holding the line in Hominoidea: chimpanzees as modern examples***

Gorillas and orangutans illustrate what can occur in the hominoid lineage on an evolutionary trajectory of increased body size and lowered dietary quality. What happens in a hominoid if, despite environmental pressures, a species is able to maintain dietary quality while continuing to feed largely on plant foods? Extant chimpanzees and bonobos (genus *Pan*) illustrate this dietary strategy. They eat a high quality diet composed largely of ripe fruits, and supplement this basic fruit diet with select protein-rich young leaves, buds and flowers as well as some animal matter, largely invertebrates but occasionally smaller vertebrates (8,12,35).

The *Pan* ancestor may have been somewhat smaller than extant chimpanzees and perhaps not such an extreme ripe fruit specialist. By becoming larger in body size over evolutionary time—extant male chimpanzees weigh some 49 kg and females 41 kg (32)—and increasingly specialized on ripe fruits, which are an unusually high energy food, chimpanzees and bonobos persist today as highly active and social apes. Somewhat larger body size permits chimpanzees to reap some of the metabolic benefits discussed above for the other two great apes. It also ensures access to fruit crops (chimps can displace smaller-bodied competitors from fruiting trees) and offers some degree of predator protection when traveling on the ground (chimpanzees generally travel through the forest on the ground, climbing into fruiting trees to feed).

Because the foods on which chimpanzees specialize (ripe fruits) are high in energy, one might wonder why they retain

a capacious hindgut. Why don't gut proportions of extant chimpanzees more closely approximate those of modern humans? As hominoids, chimpanzees have both a small cecum and a slow turnover rate of ingesta. They also must be able to take in sufficient plant material each day to meet or almost meet their protein and other required nutrients. Woody seeds, pectic substances, cellulose and hemicellulose are inevitable components of fruit eating. The large colon enables chimps to retain such plant materials for sufficient time to allow gut bacteria to ferment pectin and some dietary fiber (22). Volatile fatty acids produced in fermentation provide chimpanzees with energy and such energy may be essential to their survival during periods of the year when ripe fruit is in short supply.

We now have two examples. One is that of extant hominoids (gorillas and orangutans) that represents an evolutionary trajectory associated with enlarged body size and lowered dietary quality. The other example is that of extant hominoids of somewhat smaller body size (chimpanzees), and an evolutionary trajectory predicated on “holding the line” regarding dietary quality. Early humans appear to represent an example of the only other possibility—that is, what can happen in the hominoid line when, for whatever reason, energy needs gradually begin to increase and dietary quality does not decline or remain constant but actually improves.

#### ***Enhanced dietary quality in Hominoidea: emergence of the human lineage***

Imagine a potential human ancestor weighing 35–45 kg (the size range of some *Australopithecus* and *Paranthropus* species), living in Africa during the Plio-Pleistocene. This prehuman ancestor has a gut anatomy and a pattern of digestive kinetics similar to those of extant apes. Furthermore, it has the typical hominoid diet of fruits and seeds supplemented with young leaves, flowers and other plant parts as well as occasional animal matter. A climatic change occurs such that areas of wet lowland rainforest gradually became both cooler and drier (36). As a result of this climatic shift and its effects on vegetation, higher quality plant foods become more difficult to procure (more seasonal and more diffuse in space as well as less diverse).

Taking the path of least resistance and turning to lower quality plant foods, a dietary approach that actually was adapted by some hominid species in this environment during the Plio-Pleistocene (i.e., *Paranthropus* spp.) was not successful. Fossil evidence shows that by ~1.2 mya, all such species, popularly referred to as the “robust australopithecines,” became extinct (11). If a hominoid in this environment is to persist through time as a mobile, active and social species, all data suggest it must at least hold the line on dietary quality regardless of these environmental changes. But if higher quality plant foods, particularly fruits, are becoming more scattered and seasonal, at the very least this implies higher travel costs to obtain a sufficiency. So even though our hypothetical ancestor is, for the time being, still the same size and eating the same quality diet, the energetic costs associated with the procurement of this diet are increasing. This hypothetical ancestor will have to eat more of its normal plant foods per unit time or become more efficient at extracting nutrients from these foods just to “stay in place” dietarily. Furthermore, conflicting demands are gradually being placed on its hominoid digestive tract. If this ancestor is to process sufficient plant material each day to satisfy its nutrient as well as energy requirements, the standard large hominoid colon would prove useful; but if it has increasing energetic demands with no decrease in dietary

quality, evidence from studies of voles and birds suggest that such pressures will increase the size of the small intestine and decrease the size of the colon (14,15,22). This ancestral species thus appears to be approaching an evolutionary crossroads in terms of diet.

### *The role played by animal source foods*

Options for diet in any mammal are limited. Food has to consist either of plant or animal matter or a mix of both, and it has to supply all nutrients (or their precursors) regarded as essential for that particular animal's needs. What spells the difference between animal species in terms of diet are the types and proportions of foods from each of these two basic dietary categories that each species can most efficiently exploit. In terms of gut anatomy and digestive kinetics, meat and other ASF, at least up to some maximum percentage of diet, pose no digestive problems for a hominoid. In captivity, for example, boned meat (raw beef and cooked chicken) was so well digested by common chimpanzees that it typically produced no visible residue in feces (37). Data suggest that most monkeys and all great apes can digest ASF, and that many primates appear to relish them (38, 39). But ASF are not eaten in quantity by most wild primates (39), largely because such foods are rare, generally small in size and difficult to procure, particularly in the tropical forest canopy. This is not to say that ASF are not important, indeed essential, dietary components, for many primate species (39). But because only small amounts typically can be secured each day, anthropoids typically fill up on higher quality plant foods and supplement this plant-based diet with as much ASF as can be secured without undue cost or effort.

The earliest humans (members of the genus *Homo*) appear to have evolved in a woodland-savanna environment in Africa where ripe fruits and other high quality plant sources showed strong seasonal fluctuation. Fossil evidence suggests there may have been three or more different species of *Homo* living in Africa approximately two million years ago (11). These *Homo* species differed morphologically from other hominids (e.g., *Australopithecus*, *Paranthropus*) in that their cheek tooth size was smaller and somewhat more refined and their brain size was notably larger. The first stone tools found in association with a hominid are found with the fossilized remains of *Homo habilis*, one of the earliest *Homo* species (11). This association indicates that stone tool technology now plays a role in human dietary behavior (11). At one site, dated at 2.5 mya, the fossilized bones of large mammals have been recovered with definitive evidence of fracture by stone tools for marrow acquisition (40). As yet, it is uncertain which hominid species carried out these butchering activities but this evidence shows that stone implements are now being used by at least one hominid species to process animal carcasses to obtain meat, marrow and other ASF.

Meat and other ASF provide all amino acids required for human protein synthesis; animal protein is also more bioavailable than plant protein (41,42). For these reasons, a plant-eating hominoid turning to ASF would need to eat a smaller amount of ASF to satisfy all protein requirements each day than would be the case if protein requirements were being met exclusively from plant parts, even very high quality plant parts. Perhaps equally important, ASF also supply many minerals and vitamins that humans require as well as essential fatty acids (41–43).

Evolution humans able to satisfy their protein and many mineral and vitamin requirements with ASF rather than plant foods, would free space in the gut for energy-rich plant foods such as fruits, nuts, starchy roots or honey. It is popularly

believed that plant starches need to be cooked before they can be digested by humans, but this is not necessarily the case (44).

## DISCUSSION

### *Benefits of the dual dietary strategy*

Using animal matter primarily to satisfy requirements for essential nutrients other than energy, and plant sources primarily for energy, is a dietary strategy compatible with hominoid gut anatomy and digestive kinetics. Such a diet, because of its high quality, would permit evolving humans to avoid the constraints imposed by body size increases in the apes (i.e., lowered dietary quality along with lowered mobility and sociality). This dietary breakthrough in the human lineage presumably was achieved through both technological and social innovations that enabled these earliest humans to greatly improve their net returns from foraging by efficiently exploiting foods from two trophic levels simultaneously, both animal and plant foods, while simultaneously greatly lowering dietary bulk (2,3,10,22).

One critical aspect of this novel dietary trajectory is the fact that once ASF enter the human diet as a dependable staple, the overall nutritional quality of the plant food portion of the diet can drop drastically if necessary, so long as digestible energy is present. This would permit intensified use by human ancestors of formerly unacceptable or marginal plant foods, including cyanogenic plant foods. Many underground storage organs are a rich source of energy but low in nutrients; some, such as manioc, contain potentially harmful chemical compounds such as cyanogenic glycosides (45). But with animal matter in the diet to supply many essential nutrients (including the sulfur-containing amino acids, essential in the detoxification of cyanogenic compounds), the low nutritional value of plant foods or some degree of potential toxicity should not pose a barrier to the human feeder, as long as digestible energy can be obtained and potentially harmful secondary compounds adequately detoxified.

This change in dietary focus in early *Homo*, which is a clear departure from known diets of other members of the Hominoidea, both fossil and extant, was gradually reflected both in the human brain size (substantial increase) and in the form of the human gut (a shift in gut proportions and overall gut size) as well as features of the dentition (smaller teeth, jaws and muscles of mastication) (3,22). Evidence from the human fossil record, and the archaeological record, suggests a process involving increased dependence on technology and learned skills (manufacture and use of stone tools and hunting implements, techniques of food preparation) as well as social skills (cooperative hunting, division of labor, food sharing, a long period of offspring provisioning) that probably took place over a period of 2.5 million or more years (3).

### *Childhood nutrition*

Another important aspect of ASF in the diet of human ancestors concerns the increasing importance, as human evolution progressed, of high quality, volumetrically concentrated foods for small children. E. O. Wilson has hypothesized that for more than two million years (until ~250,000 y ago), the human brain grew by a tablespoon every 100,000 y (47). The brain currently makes up 17% of a newborn human infant's weight and 75% of the weight of the four major organs combined (brain, liver, heart, kidney) (48). During the first year of life, while traditionally an infant is breastfed, the brain grows rapidly, after which its growth rate decreases (48).

Eighty-seven percent of basal metabolic rate (BMR) in a 3.5 kg newborn is due to energetic demands of the brain alone. By 5 y of age, this figure has decreased to 44% and by adulthood, it is 23%. Thus, by age 5 y, human brain weight is near adult size but body weight is only one-third of adult size (48). A small child has to take in enough energy each day to fuel an almost-adult-sized brain, as well as meet high nutritional and other energetic requirements. In our evolutionary past, breast milk was the major food source for very young infants, and likely continued to be an important food for children up to the age of  $\geq 4$  y. But supplementary foods are needed after  $\sim 6$  mo of age, and these must be compatible with a glucose-demanding, unusually large brain, a gut size that scales to body mass, energetic requirements that scale to the three-fourth power, a slow rate of food turnover, and a high demand for energy and nutrients by the growing and active young child (33,34,48–50).

Because of the increase in the ratio of metabolic requirements to gut capacity in homeotherms, (33,34,49), a diet high in fibrous plant material could pose virtually insurmountable problems for small children. Meat, organs, brains, viscera and marrow are highly digestible, concentrated sources of iron, calcium, iodine, sodium and zinc as well as vitamins A, B-1, niacin, B-6, B-12, folate, vitamin K and other micronutrients, as well as high quality protein and essential fatty acids (3,42,46,51).

If the dietary trajectory described above was characteristic of human ancestors, the routine, that is, daily, inclusion of ASF in the diets of children seems mandatory as most wild plant foods would not be capable of supplying the protein and micronutrients children require for optimal development and growth, nor could the gut of the child likely provide enough space, in combination with the slow food turnover rate characteristic of the human species, to secure adequate nutrition from wild plant foods alone. Wild plant foods, though somewhat higher in protein and some vitamins and minerals than their cultivated counterparts (52), are also high in fiber and other indigestible components and most would have to be consumed in very large quantity to meet the nutritional and energetic demands of a growing and active child.

Given the postulated body and brain size of the earliest humans and the anatomy and kinetic pattern characteristics of the hominoid gut, turning increasingly to the intentional consumption of ASF on a routine rather than fortuitous basis seems the most expedient, indeed the only, dietary avenue open to the emerging human lineage (2,3,10,53). Early humans might have been able to utilize technological innovations to raise the quality of some wild plant foods through fermentation, grinding or (eventually) cooking activities. They might also have been able to secure access to physically defended, but abundant, high quality wild plant foods (using stones to open mongongo nuts, for example). Such dietary innovations require implements such as containers and grinding stones as well as the continuous availability of these unusual plant resources. For these reasons as well as those discussed above, it seems most parsimonious to view the earliest humans and their descendants as turning increasingly to animal prey to supply required amino acids and many essential micronutrients in the diet, and using plant foods primarily as an energy source. Both in quantity and composition, the fat content of wild game differs in many important respects from that of domesticated livestock (54) and is unlikely to have posed health problems to human consumers.

### Pregnancy aversion to ASF

Meat is noted to be a principal target of food aversion in early pregnancy, for many Westernized and non-Westernized

women (55). It is hypothesized that meat aversion, particularly during the first trimester of pregnancy, may represent an adaptive response evolved to protect the fetus from harmful effects of meat-borne pathogens (55–57). Such pathogens occur in a wide variety of foods other than meat, and food aversions in pregnant women encompass a wide variety of nonmeat dietary items as well (55–57). In the temperate regions eventually occupied by Paleolithic hunter-gatherers, it is difficult to imagine what foods other than ASF might have been consumed by pregnant women for many months of the year and, until quite recently, many circumpolar peoples lived exclusively on ASF for almost the entire annual cycle (58–60). Freezing temperatures would likely have eliminated most pathogens in such environments for most of the year, making a meat aversion in pregnancy largely unnecessary or even detrimental. The suggestion that human females have evolved an aversion response to meat due to its potential pathogenic properties in pregnancy seems unlikely, although this continues to be a topic of lively debate.

Over evolutionary time, each animal species builds on the genetic template inherited from its ancestors. Given the probable diet, gut form and pattern of digestive kinetics characteristic of prehuman ancestors, it is hypothesized that the routine inclusion of animal source foods in the diet was mandatory for emergence of the human lineage. As human evolution progressed, ASF likely achieved particular importance for small children due to the energetic demands of their rapidly expanding large brain and generally high metabolic and nutritional demands relative to adults. Species discussed in this context were *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus* and *Homo sapiens*.

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### LITERATURE CITED

- Gagneux, P., Wills, C., Gerloff, U., Tautz, D., Morin, P. A., Boesch, C., Fruth, B., Hohmann, G., Ryder, O. A. & Woodruff, D. S. (1996) Mitochondrial sequences show diverse evolutionary histories of African hominoids. *Proc. Natl. Acad. Sci. U.S.A.* 88: 1570–1574.
- Milton, K. (1981) Diversity of plant foods in tropical forests as a stimulus to mental development in primates. *Am. Anthropol.* 83: 534–548.
- Milton, K. (1993) Diet and primate evolution. *Sci. Am.* 269: 86–93.
- Wolde-Gabriel, G., White, T. D., Suwa, G., Renne, P., deHeinzellin, J., Hart, W. K. & Haiken, G. (1994) Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371: 330–333.
- White, T. D., Suwa, G. & Asfaw, B. (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371: 306–331.
- Rodman, P. S. (1977) Feeding behaviour of orangutans of the Kutai Nature Reserve, East Kalimantan. In: *Primate Ecology*. (Clutton-Brock, T. H., ed.), pp. 384–413. Academic Press, London, UK.
- Fossey, D. & Harcourt, A. H. (1977) Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: *Primate Ecology*. (Clutton-Brock, T. H., ed.), pp. 415–447. Academic Press, London, UK.
- Goodall, J. (1986) *The Chimpanzees of Gombe: Patterns of Behaviour*. Belknap Press of Harvard University Press, Cambridge, MA.
- Milton, K. (1999) A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol.* 8: 11–21.
- Milton, K. (1987) Primate diets and gut morphology: implications for human evolution. In: *Food and Evolution: Toward a Theory of Human Food Habits*. (Harris, M. & Ross, E. B., eds.), pp. 93–116. Temple University Press, Philadelphia, PA.
- Fleagle, J. G. (1999) *Primate Adaptation and Evolution*, 2<sup>nd</sup> ed. Academic Press, New York, New York.
- Stanford, C. B. (1998) *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Harvard University Press, Cambridge, MA.
- Mitchell, P. (1905) C.V. On the intestinal tract of mammals. *Trans. Zool. Soc. Lond.* XVII: 437–536.

14. Gross, J. E., Wang, Z. & Wunder, B. (1985) Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus orchrogaster*. *J. Mammal.* 66: 661–667.
15. Savory, C. & Gentle, M. J. (1976) Changes in food intake and gut size in Japanese quail in response to manipulation of dietary fiber content. *Br. Poult. Sci.* 17: 571–580.
16. Miloslavich, E. L. (1925) 1. Racial studies on the large intestine. *Am. J. Phys. Anthropol.* VIII: 11–22.
17. Underhill, B. M. L. (1955) Intestinal length in man. *Br. Med. J.* ii: 1243–1246.
18. Wrick, K. L. (1979) The Influence of Dietary Fibers on Intestinal Passage, Laxation and Stool Characteristics in Humans. Doctoral thesis, Cornell University, Ithaca, New York.
19. Wrick, K. L., Robertson, J. B., Van Soest, P. J., Lewis, B. A., Rivers, J. M., Roe, D. A. & Hackler, L. R. (1983) The influence of dietary fiber source on human intestinal transit and stool output. *J. Nutr.* 113: 1464–1479.
20. Heller, S. N., Hackler, L. R., Rivers, J. M., Van Soest, P. J., Roe, D. A., Lewis, B. A. & Robertson, J. B. (1980) Dietary fiber: the effects of particle size of wheat bran on colonic function in young adult men. *Am. J. Clin. Nutr.* 33: 1734–1744.
21. Milton, K. (1981) Food choice and digestive strategies of two sympatric primate species. *Am. Nat.* 117: 476–495.
22. Milton, K. & Demment, M. (1988) Digestive and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. *J. Nutr.* 118: 1–7.
23. Caton, J. (1997) Digestive Strategies of Nonhuman Primates. Doctoral thesis, The Australian National University, Canberra, AU
24. Mitchell, W. D. & Eastwood, M. A. (1976) Dietary fiber and colon function. In: *Fiber in Human Nutrition* (Spiller, G. & Amen, R. J., eds.), pp. 185–206. Plenum Press, New York, New York.
25. Burkitt, D. P., Walker, A. R. P. & Painter, N. S. (1972) Effect of dietary fibre on stools and transit times and its role in the causation of disease. *Lancet* 2: 1408–1411.
26. Ehle, R. R., Jeraci, J. J., Robertson, J. B. & Van Soest, P. J. (1982) The influence of dietary fiber on digestibility, rate of passage and gastrointestinal fermentation in pigs. *J. Anim. Sci.* 55: 1071–1078.
27. Stevens, C. E. (1988) Comparative Physiology of the Vertebrate Digestive System. Cambridge University Press, Cambridge, UK.
28. Sibbald, I. R., Sinclair, D. G., Evans, E. V. & Smith, D. L. T. (1962) The rate of passage of feed through the digestive tract of the mink. *J. Biochem. Physiol.* 40: 1391–1394.
29. Best, R. C. (1977) Ecological aspects of polar bear nutrition. In: *Proceedings of the 1975 Predator Symposium*. (Phillips, R. L. & Jonkel, C., eds.), pp. 203–211. Montana Forest and Conservation Experimental Station, University of Montana, Missoula, MT.
30. Andrews, P. (1981) Species diversity and diet in monkeys and apes during the Miocene. In: *Aspects of Human Evolution*. (Stringer, C. B., ed.), pp. 25–61. Taylor and Francis, London, UK.
31. Andrews, P. (1995) Ecological apes and ancestors. *Nature* 376: 555–556.
32. Clutton-Brock, T. H. & Harvey, P. H. (1977) Species differences in feeding and ranging behaviours in Primates. In: *Primate Ecology*. (Clutton-Brock, T. H., ed.), pp. 557–584. Academic Press, London, UK.
33. Demment, M. W. (1983) Feeding ecology and the evolution of body size in baboons. *Afr. J. Ecol.* 21: 219–233.
34. Demment, M. W. & Van Soest, P. J. (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* 125: 641–672.
35. McGrew, W. C. (1979) Evolutionary implications of sex differences in chimpanzee predation and tool use. In: *The Great Apes*. (Hamburg, D. A. & McCown, E. R., eds.), pp. 441–464. Benjamin/Cummings Publishing Co., Menlo Park, CA.
36. de Menocal, P. B. (1995) Plio-Pleistocene African climate. *Science* 270: 53–59.
37. Milton, K. & Demment, M. (1989) Features of meat digestion by captive chimpanzees, *Pan troglodytes*. *Am. J. Primatol.* 18: 45–52.
38. Utami, S. S. & van Hooff, J. A. (1997) Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). *Am. J. Primatol.* 43: 159–166.
39. Harding, R. S. O. (1981) An order of omnivores: nonhuman primate diets in the wild. In: *Omnivorous Primates*. (Harding, R. S. O & Teleki, G., eds.), pp. 191–214. Columbia University Press, New York, NY.
40. de Heinzelin, J., Clark, J. D., White, T., Hart, W., Renne, P., Wolde-Gabrial, G., Beyene, Y. & Vrba, E. (1999) Environment and behavior of 2.5 million-year-old Bouri hominids. *Science* 284: 625–629.
41. Carpenter, K. J. (1986) The History of Enthusiasm for Protein. American Institute of Nutrition publication. Presented as part of the History of Nutrition symposium given by the American Institute of Nutrition at the 69th Annual Meeting of the Federation of American Societies for Experimental Biology, Anaheim, CA.
42. Carpenter, K. J. (1994) Protein and Energy: A Study of Changing Ideas in Nutrition. Cambridge University Press, Cambridge, UK.
43. Lozy, M., Herrera, M. G., Latham, M. C., McGandy, R. B., McCann, M. B. & Stare, F. J. (1980) Nutrition: A Scope Publication. The Upjohn Company, Kalamazoo, MI.
44. Langworthy, C. F. & Deuel, H. J., Jr. (1920) Digestibility of raw corn, potato and wheat starches. *J. Biol. Chem.* 42: 27–40.
45. Jones, D. A. (1998) Why are so many plant foods cyanogenic? *Phytochemistry*. 47: 155–162.
46. Nutritive Value of Foods. (1981) USDA, Science and Education Administration. Home & Garden Bulletin #2. Washington, DC.
47. Wilson, E. O. (1978) On Human Nature. Harvard University Press, Cambridge, MA.
48. Holliday, M. A. (1978) Body composition and energy needs during growth. In: *Human Growth*, 2<sup>nd</sup> ed. (Faulkner, F. & Tanner, G. M., eds.), pp. 101–117. Plenum Press, New York, NY.
49. Parra, R. (1978) Comparison of foregut and hindgut fermentation in herbivores. In: *The Ecology of Arboreal Folivores*. (Montgomery G. G., ed.), pp. 205–230. Smithsonian Press, Washington, DC.
50. Foley, R. A. & Lee, P. E. (1991) Ecology and energetics of encephalization in hominid evolution. *Philos. Trans. R. Soc. Lond. B* 334: 223–232.
51. Liebermann, L. S. (1987) Biological consequences of animals versus plants as sources of fats, protein and other nutrients. In: *Diet and Human Evolution*. (Harris, M. & Ross, E. B., eds.), pp. 225–260. Temple University Press, Philadelphia, PA.
52. Milton, K. (1999) Do the diets of our closest living relatives have lessons for us? *Nutrition* 15: 488–498.
53. Blumenschine, R. J. & Cavallo, J. A. (1992) Scavenging and human evolution. *Sci. Am.* 276: 90–96.
54. O'Dea, K. (1991) Traditional diet and food preferences of Australian aboriginal hunter-gatherers. *Philos. Trans. Royal Soc. Lond.* 334: 233–241.
55. Fessler, D. M. (2002) Reproductive immunosuppression and diet; an evolutionary perspective on pregnancy sickness and meat consumption. *Curr. Anthropol.* 43: 19–61.
56. Wiley, A. S. (2002) Response to reproductive immunosuppression and diet. *Curr. Anthropol.* 43: 47.
57. Tepper, B. J. & Crystal-Mansour, S. (2002) Response to reproductive immunosuppression and diet. *Curr. Anthropol.* 43: 46–47.
58. Draper, H. H. (1977) The aboriginal Eskimo diet. *Am. Anthropol.* 79: 309–316.
59. Ho, K. J., Mikkelsen, B., Lewis, L. A., Feldman, S. A. & Taylor, C. B. (1972) Alaskan arctic Eskimos: response to a customary high fat diet. *Am. J. Clin. Nutr.* 25: 737–745.
60. Stefansson, V. (1960) Food and food habits in Alaska and northern Canada. In: *Human Nutrition Historic and Scientific*. (Galdston, I., ed.), pp. 23–60. International Universities Press, Inc., New York, NY.
61. Van Soest, P. J., Uden, P. & Wrick, K. L. (1983) Critique and evaluation of markers for use in nutrition of humans and farm and laboratory animals. *Nutr. Rep. Int.* 27: 17–28.