A Hypothesis to Explain the Role of Meat-Eating in Human Evolution

KATHARINE MILTON

> "In the mammalian gut . . . the inherited element dominates the structure."
>
> (Mitchell[1])

Primates, particularly humans, are noted for their relatively large brains and considerable behavioral plasticity.[2–4] In contrast to behavior, morphological structures tend to alter only slowly over time, generally in response to particular selective pressures. Furthermore, though each evolutionary lineage represents a long history of morphological change, such changes are not changes sui generis, but rather arise out of the "basic physiological design"[5] bequeathed to that lineage by its ancestors.

Here I will argue that the pattern of gut anatomy and digestive kinetics characteristic of ancestral Hominoidea imposed certain constraints on their descendents in terms of diet. Meat-eating in the human lineage (*Homo* spp.) appears to be one way of circumventing these constraints.

SUMMARY OF THE ARGUMENT

Extant apes and humans are descended from a common plant-eating ancestor. Great apes and humans also show similarities in many features of gut anatomy and a similar pattern of digestive kinetics, passing ingesta at a relatively slow rate. This kinetic pattern appears to be a conservative feature of the lineage. In mammalian herbivores, an increase in body size is generally associated with a decrease in dietary quality. Thus, any hominoid increasing in body size and continuing to focus largely on plant foods is likely to show lowered dietary quality and decreased energetic input per unit of food consumed.

Extant apes and humans show various dietary strategies for dealing with the limitations set by their common pattern of gut anatomy and digestive kinetics. Over their evolutionary history, orangutans and gorillas appear to have followed a dietary strategy associated with increased body size and lowered dietary quality. Because of their large size, both species can and often do subsist on fairly low quality foods such as mature foliage, bark, and unripe fruits. But they have paid for this compromise in dietary quality. For example, relative to many other anthropoids, orangutans, mountain gorillas, and most lowland gorillas are rather passive primates that lack notable sociality, probably because they lack the energy required for a more active life.

Chimpanzees, on the other hand, have followed a different dietary strategy. Though they have fairly large bodies, chimpanzees, like many cercopithecine monkeys, eat a high-energy diet consisting in large part of ripe fruits. In this manner, though often only with considerable effort, including extensive travel and the occupation of large home ranges, chimpanzees generally are able to secure sufficient high-quality food to maintain their active and highly social lives.

Humans, who are believed to have evolved in a more arid and seasonal environment than did extant apes, illustrate a third dietary strategy in the hominoid line. By routinely including animal protein in their diet, they were able to reap some nutritional advantages enjoyed by carnivores, even though they have features of gut anatomy and digestive kinetics of herbivores. Using meat to supply essential amino acids and many required micronutrients frees space in the gut for plant foods. In addition, because these essential dietary requirements are now being met by other means, evolving humans would have been able select plant foods primarily for energy rather than relying on them for most or all nutritional requirements. This dietary strategy is compatible with hominoid gut anatomy and digestive kinetics and would have permitted ancestral humans to increase their body size without losing mobility, agility, or sociality. This dietary strategy could also have provided the energy required for cerebral expansion.

HOMINOID GUT STRUCTURE

All extant apes eat strongly plant-based diets composed of the fruits, leaves, flowers, and bark of tropical forest trees and vines.[6–15] Most apes also consume some invertebrates and, less commonly, vertebrates.[10,13–15] Not surprisingly, in view of their close relationship and similar diets, all extant apes, both greater and lesser, show the same basic gut anatomy: a simple acid stomach, a small intestine, a small cecum terminating in a vermiform appendix, and a capacious, markedly sacculated colon.[1] Mitchell[1] discussed minor differences in gut morphology between ape taxa such as the degree of twisting of the appendix or the looping pattern of the colon. Similarly, Scott[15]

Katharine Milton, Department of Environmental Science, Policy & Management, Division of Insect Biology, University of California, Berkeley, Ca 94720-3112.

kmilton@socrates.berkeley.edu

Key words: Primates; evolution; hominoids; apes; humans; gut anatomy; digestive kinetics; diet; animal prey; meat

discussed comparative features of the cecum of chimpanzees and orangutans. In general, however, the gut anatomy of all extant apes is quite similar.

Human gut anatomy is quite similar to that of other extant hominoids.[1,16] Mitchell[1] remarked that primitive humans were probably omnivorous with a tendency toward carnivory, but pointed out that "the result has not yet been any marked adaptive change in the character of the gut as compared with that of the Anthropoid Apes, although in the latter the diet is omnivorous with the strongest leaning toward the vegetable side." In 1904, based on study of the comparative anatomy of the hominoid gut, Elliott and Barclay-Smith[17] suggested that the structure of the human gut actually appeared to be closer to that of a herbivore than an omnivore.

The marked sacculations characteristic of the human and ape colon also support the view that the ancestral line giving rise to all extant hominoids was strongly herbivorous.[5,18,19] Further evidence of a plant-based diet for ancestral hominoids comes from the study of dentition, which suggests that many fossil hominoids were largely frugivorous.[20] The importance of plants in the diets of hominoids, both extant and ancestral, is reinforced by the fact that no anthropoid, including humans, can synthesize vitamin C.[21] The inability to synthesize vitamin C is known to occur in a only a few mammalian lineages, all of which are strongly herbivorous.[21] Thus, using data from various lines of evidence, there seems to be general consensus that humans come from an ancestral lineage that was strongly dependent on plant foods, and that human gut anatomy is very similar to that of other extant hominoids.

Despite this basic similarity, there is one striking difference between the gut anatomy of humans and apes. This difference is in the size relationship of different sections of the gut. In all apes, the greatest gut volume is in the colon (>45% of total), with only about 14 to 29% of the total gut volume in the small intestine. For humans, the greatest gut volume is in the small intestine (>56%); only about 17 to 23% of the total gut volume is in the colon.[18,19,22] Compared to apes, modern humans also have a relatively small total gut for their body size.[22,23] These size relationships make it clear that among extant Hominoidea, humans are the outlier taxon. This suggests that humans rather than apes have deviated most markedly from the ancestral condition in terms of gut proportions and diet.[18,19]

PLASTICITY OF GUT PROPORTIONS

Gut proportions are one feature of vertebrate digestive anatomy known to show a fair degree of intraspecific plasticity.[24–32] When faced with reduced dietary quality or changes in diet type or energetic demands some rodent and bird species are able to significantly alter the length of the total digestive tract and the volume of some sections of it.[24–32] In such species, the most notable increase in volume occurs in the hindgut.[25,26] In contrast, an increase in energetic demands with no change in dietary quality is associated most strongly with an increase in the size of the small intestine.[25,26] These modifications in gut size occur in response to changes in the immediate environment, including the dietary environment, and represent an inherent plasticity already present in the genome of these species.

Despite this basic similarity, there is one striking difference between the gut anatomy of humans and apes. This difference is in the size relationship of different sections of the gut.

Likewise, within an individual animal's lifetime, the intestine responds to many conditions associated with increased nutrient requirements, among them pregnancy, lactation, diabetes, intestinal resection, and possibly reduced environmental temperatures, by proliferation of mucosal surface per unit of intestinal length.[33] Such mucosal proliferation has the same result as lengthening the gut: increased rate of uptake of nutrients.[33]

Though it is probable that most or all mammal species show some degree of plasticity in terms of gut size[24] and extent of mucosal proliferation,[31,33] I predict that for most mammals immediate gut plasticity is likely to be limited in scope. Because voles are among the smallest of all mammalian herbivores, they might be expected to show extreme strategies for the digestion of low-quality plant material if found in environments of fluctuating dietary quality.[25] In environments where dietary fluctuation is not marked, the gastrointestinal tract size of vole species shows little to no response to changes in dietary quality.[25] Similarly, small passarines have high metabolic demands and often face quite dramatic dietary changes and fluctuating environments.[33]

In anthropoids as a class, gut plasticity is predicted to be less pronounced in comparison with that in vole and bird species, partly because of the anthropoids' generally larger body size. In addition, most primates live in tropical environments, which do not show the same degree of fluctuation in food supply or the climatic extremes that can occur in the environments of these vole and bird species. However, it is clear that some gut plasticity occurs in anthropoids. Martin and coworkers[23] found that intraspecific dimensions of the gastrointestinal tract in six of twelve primate species differed notably when the guts of captive animals were compared with those of wild conspecifics. In at least three species, no change was detected, suggesting that "for many species the gut may be modified very little by artificial diets" (p. 84). The authors noted that even the differences that were observed are difficult to interpret and should be treated with caution.

Modern humans show both intra- and interpopulational differences in features of the gut such as colon length.[34] Western humans show considerable inter-individual difference in the length of the small intestine.[35] A study of 1,000 Egyptian mummies indicated that their cecums were larger than those of present-day humans.[17]

These comparative data indicate that particular sections of the digestive tract of modern *Homo sapiens* can differ notably in size though such differences say little about the immediate capacity for gut plasticity in any individual.

However, in comparing gut proportions of apes and humans, I am not concerned with the potential for some degree of plasticity in overall size or the size of some gut sections because, as noted, it is probable that some degree of gut plasticity characterizes most animal species. Rather, my concern is with the inherited pattern of gut proportions characteristic of all extant apes on the one hand and all modern humans on the other—a proportional relationship that I hypothesize is found in all apes regardless of their environmental circumstances or genetic background and one characteristic of all humans regardless of their environmental circumstances or genetic background.

The dominance of the small intestine in humans suggests adaptation to a high-quality diet composed of foods that are nutritionally dense, volumetrically concentrated, and amenable to digestion in the small intestine.[18,19] In contrast, dominance of the colon in extant apes suggests adaptation to a diet with considerable refractory plant material that cannot be digested in the small intestine and that passes into the voluminous hindgut, where it is retained while certain essential functions such as fermentation of refractory materials are carried out.[18,19] Because guts do not tend to fossilize, it is difficult to state when the change in gut proportions between humans and apes originated. My prediction that the dominance of the small intestine is characteristic of all modern humans suggests that such proportions were characteristic of the ancestral lineage that gave rise to modern humans 200,000 years ago. However, similar gut proportions could have characterized *Homo erectus* or even earlier hominids.

KINETICS OF THE HOMINOID GUT

> "The primary significance of gut structure is that of its influence upon digesta movement."
> (Clemens and Phillips[36])

Gut proportions are one factor that can influence digestive parameters and food choices in the natural environment, but another important factor that needs consideration is gut kinetics. Gut kinetics refers to the pattern of movement of ingesta, both particulate and liquid, through the digestive tract.[36–41] 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 on dietary breadth.[31,32,36–44]

Milton and Demment[22] examined the pattern of digestive kinetics of common chimpanzees (*Pan troglodytes*) fed diets of two fiber levels. One diet contained 14% neutral detergent fiber; the other contained 34%

My prediction that the dominance of the small intestine is characteristic of all modern humans suggests that such proportions were characteristic of the ancestral lineage that gave rise to modern humans 200,000 years ago. However, similar gut proportions could have characterized *Homo erectus* or even earlier hominids.

neutral detergent fiber. Ingesta passed more rapidly on the high fiber diet (mean transit time = 38 hours on the high-fiber diet and 48 hours on the low-fiber diet. Mean transit time is an estimate of the average time "particles" of marker take to pass through a system of unknown or undefinable compartments[45]).[22,45–48] Because ingesta passed more rapidly when dietary quality was low (high-fiber diet), the chimp gastrointestinal tract had less time to process ingesta flowing through it. However, because this lower-quality food passed more rapidly, chimpanzees could eat more food per unit of time.

With only moderate alterations in dietary quality in the natural environment, the end result of both passage rates in chimpanzees would probably be about the same; that is, chimpanzees would be able to meet their daily requirements for energy and nutrients on both diets. It is important to note, however, that in neither case was mean transit time in chimpanzees particularly rapid: 48 hours for the higher-quality diet versus 38 hours for the lower-quality diet. Thus, it appears that the kinetics of the chimpanzee gut are such that food tends to be retained in the tract for a fairly lengthy period regardless of quality. Similar data on mean transit time of gorillas and orangutans have recently been obtained by Caton.[48] Results of her work indicate that the pattern of gut kinetics of gorillas and orangutans is similar to that of common chimpanzees[48] (Table I).

Extensive work has been carried out on the passage kinetics of humans.[37,45,47,49–52] For example, a detailed study of human passage kinetics at Cornell University showed a mean transit time of 62.4 hours for subjects on a 0% fiber diet and 40.9 hours for human subjects on a 17.3% fiber diet[47] (Table 1). Studies show that mean transit time in humans can vary considerably from population to population, from person to person, and even within a given individual.[50,52] However, an extensive body of data supports the view that in humans higher-quality diets tend to pass more slowly than do fibrous, lower-quality diets.[50,52]

In feeding trials, using wheat bran of identical particle size, both humans and chimpanzees displayed similar mean total gut transit times and hindgut transit times.[22,46] This is remarkable because this similarity in transit occurred despite the fact that the chimpanzee has a total gut, as well as hindgut region, that is considerably larger than is the case for humans.[22,23] The similarity of mean transit times in both humans and chimpanzees supports the view that passage kinetics in hominoids are a conservative feature relative to other features such as gut proportions or overall gut size. Using equations derived from the study of digestive kinetics in a large number of

TABLE 1. Comparative Data on Mean Transit Time (MTT*) in Hours of Markers in Chimpanzees (*Pan troglodytes*),[22] Orangutans (*Pongo pygmaeus*),[48] Gorillas (*Gorilla gorilla*),[48] and Humans (*Homo sapiens*)[22,45,47]

Source (ref #)	Species	MTT Liquid (Co-EDTA)	MTT Particulate (Cr-CWC)	Time of 1st Appearance
22	Chimpanzee n = 6			
	Low fiber (14% NDF)	47.7 ± 3.2	48.0 ± 3.4	24.9 ± 3.6-Liq. 27.4 ± 7.5-Part.
	High fiber (34% NDF)	35.1 ± 2.3	37.7 ± 2.2	23.7 ± 2.6-Liq. 23.3 ± 2.5-Part.
48	Orangutan n = 3	70.6 ± 9.5	73.7 ± 15.5	24.2 ± 0.8**
48	Gorilla n = 4	45.4 ± 13.7	57.2 ± 15.4	23.4 ± 0.6**
47	Western human n = 24			
	Low fiber 0% NDF	61.6***	62.4	26.0 ± 1.0****
	High fiber 17.3% NDF	38.9***	40.9	

* Mean transit time (MTT) = estimate of the average amount of time "particles" of marker take to pass through the total digestive tract. The estimate of MTT represents the integrated average of a marker excretion curve; see Wrick[45] and Wrick and coworkers[47] for discussion of the method of calculation.

** Approximately the same time of first appearance (TFA) was shown for liquid and particulate markers.[48] (Also Caton, personal communication).

*** Using polyethylene glycol as a soluble marker; see Wrick and coworkers.[47]

**** TFA for three adult human subjects calculated by Milton using a particulate marker composed of small strips of soft, nonsoluble plastic. Fiber content of diet not recorded, but low.[44]

herbivorous species, Milton and Demment[22] generated values to make comparisons among hominoids. The mean transit time of chimpanzees and humans in feeding trials was considerably longer than that predicted by the general equation for nonruminants based on body weight.[19] Chimpanzees in the wild eating their natural diet might well show values close to predicted ones.

Relative to wild apes, most human populations eat foods that are amazingly refined, digestible, and calorie-rich, as well as low in plant fiber.[18,19,53] In humans, much food preparation (nonsomatic digestion) occurs before a food item is ever brought into contact with the mouth and gastrointestinal tract,[22] a behavior that could ultimately have affected human gut proportions. However, as noted (see also Table 1), turnover of this high-quality ingesta in humans typically is quite slow. Even with a dietary fiber content of 17.3%, the mean transit time for humans in the Cornell trials was still almost 41 hours.[22,47] There clearly is plasticity in mean transit time in hominoids. However, depending on dietary quality and perhaps factors such as the fat content of the diet, with the evidence in hand there seems no way that either humans or chimpanzees could suddenly begin to turn over ingesta very rapidly (the "power" approach).[43] Rather, as noted, the pattern of passage kinetics within a given lineage appears to be a conservative feature.[22] Further evidence to support this view is found in examination of the gut anatomy and passage kinetics of extant Carnivora.

GUT ANATOMY AND PASSAGE KINETICS OF CARNIVORA

> "The terrestrial Carnivora, from the Lion to the smallest Suricate, display a pattern of intestinal tract essentially similar. And yet, although we give the name Carnivora to the group, almost every possible kind of diet is found amongst them—purely carnivorous, piscivorous, omnivorous, frugivorous."
>
> (Mitchell[1])

As Mitchell[1] and Stevens,[54] discussed, all 284 species of Carnivora have essentially the same pattern of gut anatomy. This consists of a simple stomach and a short total gastrointestinal tract; the colon is not sacculated.[1,54] In some lineages there is some development of a cecum, but in the Ursidae, Procyonidae, and Mustelidae no cecum is present. The distal segment of the small intestine is marked only by a sudden change in the mucosa.[1] 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, koalas).[1,54]

In Carnivora, the transit time of food is rapid. For example, average transit time (here, time of first appearance of ingesta) in the mink, a pure carnivore, is 2.4 hours (range, 1.03 to 3.6 hrs).[55] A 370-kg (814-pound) polar bear showed a bimodal mode of defecation after a meal of seal meat, with the first defecation of the meal occurring about 17 to 18 hours after ingestion and the second between 23 and 26 hours.[56] Contrast this with mean transit times for human subjects at Cornell (Table 1): In 26 hours, the average ingesta particle of a meal is still in passage through the human gastrointestinal tract and will remain there for an additional 15 to 35 hours or more before it is excreted. And humans weigh far less than polar bears.

At some point in the past, many lineages of one superfamily of Carnivora, the Canoidea, began to depend on plant as well as animal matter in the diet.[57] Foxes, bears, raccoons, pandas, and some other Canoidea eat fruits or other plant material such as leaves, often in quantity but this dietary shift is not well reflected in either their gut anatomy or their pattern of digestive kinetics.[19] For example, in the wild greater pandas eat a diet primarily of bamboo.[58,59] Their gut seems poorly adapted to a bulky, fibrous bamboo diet. Furthermore, study of the gut morphology of pandas does not suggest a herbivorous diet.[19] Not surprisingly, as Carnivora, pandas show a rapid transit rate of food.[60,61] Given their gut structure (no cecum and lack of colon sacculations), pandas apparently are able to live on bamboo by passing masses of it rapidly through the gastrointestinal tract each day, digesting only the more available, higher-quality fraction.[61]

The large body size of the greater panda should facilitate use of a low-quality diet because in homeotherms increased body size is associated with lowered metabolic costs per unit of mass,[62] as well as lowered requirements per unit of mass for nutrients such as protein.[63] The panda example might seem to contradict my initial statement that gut anatomy and the pattern of digestive kinetics can set limits on diet breadth in a given lineage. However, pandas apparently have found a way to work with their inherited gut characteristics, particularly their rapid passage kinetics, so that they can exploit bamboo rather than live prey. This dietary compromise, however, at least in the case of greater pandas, seems to have resulted in selection for a large, ponderous animal that now is poorly adapted to hunting mobile prey.

HOMINOID EVOLUTION

Like the Carnivora, extant Hominoidea seem "stuck" with their ancestral pattern of digestive kinetics and basic features of gut anatomy. The fossil record shows that during the early to middle Miocene, hominoids reached their greatest level of diversity.[64] In the early Miocene, eight to ten species of apes belonging to the Dryopithecinae lived in Africa and Arabia; these ranged in size from that of the smallest extant Old World monkeys to that of female gorillas.[64] Various Miocene ape species appeared to live sympatrically and must have filled a range of niches. In general, Miocene apes were characterized by a frugivorous pattern of molar morphology,[20] though some evidence suggests that larger middle-Miocene apes may have had omnivorous tendencies.[64]

It is hypothesized that by the late Miocene, some competitive advantages of cercopithecines may gradually have displaced most apes from their niches, leading to their extinction.[64,65] As Andrews[64,65] pointed out, the few ape species alive today are adapted to somewhat unusual ecological niches, in part through the evolution of highly specialized forms of locomotion.[64,65] Large body size also appears to have facilitated survival, for extant hominoids as a class are considerably larger than extant monkeys are as a class. I will compare the dietary niches of extant pongids to illustrate how meat-eating may have permitted human ancestors to overcome the energetic constraints imposed by increasing body size in the hominoid lineage.

LOWER DIETARY QUALITY IN GORILLAS AND ORANGUTANS

Gorillas are the largest extant Primates: adult males weigh approximately 160 kg (352 pounds) and females 93 kg (205 pounds).[66] Orangutans are next in size, with males weighing about 69 kg (152 pounds) and females 37 kg (81 pounds).[66] Not surprisingly, in view of their size and strongly plant-based diet, gorillas (particularly mountain gorillas) and orangutans are often forced to turn to lower quality plant foods—mature leaves, bark, pith, and unripe fruits—when sufficient ripe fruits and high-quality young leaves are not available. A capacious cecum could be useful in processing fibrous plant foods. Indeed, many plant-eating lineages among them atelines, equids, and lagomorphs show marked development of the cecum. But gorillas and orangutans, like other hominoids, characteristically have a small cecum (7% of total gut volume in gorillas and 3% in orangutans).[18,19] This fact emphasizes the point made earlier that, in its evolution, a given lineage must work with its inherited features. But many such features appear to be resistant to changes that, at least theoretically, might seem useful.

Like the Carnivora, extant Hominoidea seem "stuck" with their ancestral pattern of digestive kinetics and basic features of gut anatomy.

A PARADOX

In herbivorous mammals, an increase in body size has far different dietary implications than does an increase in body size in a strongly carnivorous lineage. A pure carnivore (Feloidea) can increase in size over evolutionary time with no decrease in dietary quality. Compare, for example, the foods of a mink with those of a polar bear. This situation does not prevail in the case of herbivores. As herbivores increase in body size in the natural environment, invariably their dietary quality must decrease. Compare, for example, the foods of a dik dik and those of an elephant. Demment[67] and Demment and Van Soest[68] postulated that changing body size is a mechanism for differentiating the feeding requirements of herbivores, noting that the fiber content of the diet rises with increasing body size.

As discussed, there seems general consensus that extant hominoids come from a strongly herbivorous ancestral lineage. Presumably, selection for increased body size in gorillas and orangutans was initially associated with environmental conditions in which, for whatever reason—competition with other primate species, seasonality, mast fruiting, or distribution patterns—high-quality plant foods simply were not available or accessible in sufficient quantity to exploit efficiently throughout the year. Increasing body size would have permitted these apes to survive on lower-quality plant foods than otherwise would be possible, as well as to use foods that would not support most smaller-bodied primates.

Large body size appears to be the single most important adaptation to diet shown by both of these great apes. However, this increased body size has carried with it certain consequences, particularly the diminution of some traits generally viewed as being highly characteristic of anthropoids, including a high degree of mobility and sociality.[6,7,18,19,69] Although some western lowland gorilla groups at times eat a considerable amount of fruit[12,70] and may range as far as 2.3km/day,[12] it seems to be generally accepted that lowland gorillas eat more vegetative plant parts than do chimpanzees[9,10,70] and fall in an intermediate ecological position between chimpanzees and bonobos on the one hand and mountain gorillas on the other.[12] In short, even lowland gorillas do not appear to be as active, agile, and socially complex as are members of the genus *Pan*.

I hypothesize that, due to features of their almost exclusively plant-based diet, in combination with features of their common hominoid digestive tracts, energy input in these great apes may often be sufficiently limited such that nonessential behaviors are not favored. In other words, I do not believe that orangutans and gorillas have sufficient "extra" energy to be more active and social.[19,71]

HOLDING DIETARY QUALITY CONSTANT: CHIMPANZEES

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 this lineage if, in spite of environmental pressures, a taxon is able to maintain dietary quality while continuing to feed largely on plant foods? Extant chimpanzees and bonobos, as well as the considerably smaller gibbons and siamangs, demonstrate this dietary strategy. Members of the genus *Pan* eat a specialized diet composed, in large part, of succulent ripe fruits. They supplement this basic fruit diet with select protein-rich young leaves, buds, and flowers, as well as animal matter (particularly invertebrates but also some vertebrates).[9–11,14,70,72]

The *Pan* ancestor may have been somewhat smaller than extant species and perhaps not such an extreme ripe-fruit specialist. By becoming somewhat larger over evolutionary time—extant male chimpanzees weigh some 49 kg (108 pounds) and females some 41 kg (90 pounds)[66]— as well as increasingly specialized on ripe fruits, an unusually high-energy food, common chimpanzees and bonobos persist today as highly active and social apes. Larger bodies would have permitted chimpanzees to reap some of the metabolic benefits discussed earlier, as well as facilitated preferred access to fruit crops and provided some degree of predator protection when traveling on the ground.

WHERE DO WILD CHIMPANZEES GET PROTEIN?

The fact that the chimpanzee diet is heavily dominated by fruits raises the question of how these apes obtain the protein they require each day. Although wild fruits as a class are low in protein, fruits average 6.5 ± 2.6% protein dry weight (range, 3.2% to 12.6% (Milton, unpublished data). An 8-kg wild howler monkey is estimated to take in about 300 gm dry weight of plant foods (leaves, fruits, and flowers) per day.[64] Let us assume that a 41-kg adult chimp, which is about five times larger than an adult howler monkey, takes in an absolutely greater amount of food, or 1,500 gm dry weight per day. This is a crude approximation, but it will serve to make my point.

If this food were all fruits with a protein content of 3.2% per gm dry weight, which is the single lowest protein content in a sample of 18 fruit species from Panama (Milton, unpublished data), this chimpanzee would be taking in approximately 48 g of protein per day. That amount, given an estimated requirement of approximately 1 g of protein per kg of body weight per day, could, at face value, cover its estimated protein needs if the protein was of sufficiently high quality. Fleshy fruits as a class tend to be low in the sulfur-containing amino acid methionine[53] but, given the amount of fruit a chimpanzee can eat per day, low methionine content might not pose a problem. If low methionine did pose a problem, chimpanzees would be forced to supplement fruits with methionine-rich foods.

> **Increased body size has carried with it certain consequences, particularly the diminution of some traits generally viewed as being highly characteristic of anthropoids including a high degree of mobility and sociality.**

In addition, it is certain that fruit protein is not digested with 100% efficiency; ca. 50% efficiency is probably more realistic. But most wild fruits have protein contents higher than 3%. Also, there are other protein-rich foods in the forest, including young leaves, some mature leaves, some nuts and seeds, and some flowers, that could help make up any amino acid deficits.[39] Common chimpanzees, particularly females, also often "fish" for termites and ants,[3,10,15] sometimes devoting hours per day to this activity. This suggests that although termites and ants are small, the nutritive benefits they provide are worth this considerable investment of time.

Chimpanzees have a capacious hindgut; they apparently can pack in sufficient ripe fruits and other plant matter each day to satisfy most nutritional requirements even though their predicted mean transit time on a high-fiber diet is around 33 hours.[22] Gastric (stomach) emptying time in human subjects fed bread diets is 4 to 5 hours.[73] If a similar gastric emptying rate prevails in wild chimpanzees, they should be able to fill the stomach several times each day, retaining refractory materials (seeds, seed coats, pectic substances, cellulose, hemicelluloses) in the cecum and proximal colon for fermentation activities.

Because fruits, the foods chimpanzees specialize on, tend to be high in energy, one might wonder why they need a capacious hindgut at all. Why don't the gut proportions of chimpanzees, as well as lesser apes, more closely approximate those of modern humans? We need to remember that as a hominoid, chimpanzees have both a small cecum and a slow turnover rate of ingesta. They must be able to take in enough plant food each day to meet or almost meet their protein and other nutrient requirements. Woody seeds and plant fiber are an inevitable component of fruit-eating. An animal with a slow transit time needs somewhere to retain this indigestible material. In addition, the availability of ripe fruit in tropical forests varies in space and time.[4,70] Volatile fatty acids produced by fermentation in the cecum and colon may be essential to chimpanzees' survival during periods when ripe fruits are in low supply.

We now have two examples: one, extant hominoids that appear to represent an evolutionary trajectory associated with enlarged body size and lowered dietary quality, and another, extant hominoids of somewhat smaller body size and an evolutionary trajectory predicated on "holding the line" regarding dietary quality. In my view, early humans represent an example of the only other possibility, which is what can happen in Hominoidea when, for whatever reason, energetic needs increase and dietary quality not only remains constant but actually improves.

ENHANCING DIETARY QUALITY: HUMANS

Imagine a human ancestor weighing perhaps >30 kg, living in Africa in the Pliocene, having gut anatomy and a pattern of digestive kinetics similar to those of modern apes. Because dental studies suggest that some australopithecines may have been fruit eaters,[74,75] this ancestral form can be viewed as being partially frugivorous, but also eating some young leaves, flowers, and other plant parts, as well as small amounts of animal matter. A climatic change causes areas that annually produced wet lowland rainforest to become both cooler and drier:

> "East African vegetation shifted from closed canopy to open savanna vegetation starting in the mid-Pliocene, marking a progression toward reduced and seasonally contrasted precipitation. . . . The expansion of arid-adapted flora and fauna near 2.8 Ma may have occurred rapidly or more gradually."
>
> (de Menocal[76])

As a result of this climatic shift and its effects on vegetation, high-quality plant parts in such environments presumably become more difficult to procure,[75] particularly during some months.

Taking the path of least resistance and eating coarse, tough plant foods, the dietary trajectory presumably adopted by "robust" australopithecines, ultimately did not work in this environment,[69,70] perhaps because such dietary niches were filling up with specialist herbivores[67,68] or because a lower-quality diet spelled limitations on mobility and increased risks of predation. Nor is reduced body size an option: This hypothetical human ancestor is already fairly large.[77,78] For various reasons, including predation and possible competition with other species,[67] let us assume that size reversal is not an option.

If this ancestral form is to persist through time as a large, mobile, active, and social hominoid, all data suggest it must at least hold the line with respect to dietary quality regardless of environmental conditions. But if high-quality plant foods, particularly fruits, are becoming more patchily distributed, at the very least this will mean increased travel costs to obtain them. So even though this postulated ancestor is, for the time being, still the same size and eating the same quality diet, the energetic costs associated with procuring this diet are now increasing. So this ancestor will have to eat more of its normal diet per unit of time or become more efficient at extracting nutrients from the same quantity of food just to "stay in place" dietarily.

Up to a point, providing sufficient high-quality plant food is available and the ancestral form can process a sufficient quantity each day, this strategy should work. But there are potential problems because our hypothetical ancestor is not living in a moist tropical forest environment but in one that is becoming increasingly arid and more seasonal.[76,79,80] Furthermore, conflicting demands are gradually being placed on its digestive tract. If this ancestor is to process sufficient plant foods each day to satisfy its protein as well as energy requirements, the standard large hominoid colon would prove useful. But if our ancestor faces increasing energetic demands with no decrease in dietary quality, evidence from studies of voles and birds suggests that these pressures should increase the size of the small intestine at the expense of the colon.[22] This species thus appears to be approaching an evolutionary crossroad in terms of diet.

WHY NOT EAT MEAT?

Options for any mammal's diet are limited. Food has to be either plants or animals or a mix of both, and has to supply all nutrients or their precursors that are essential for that particular animal. What spells the difference between species in terms of diet are the types and proportions of foods from each of these two basic dietary categories that can be efficiently exploited. In terms of gut anatomy and digestive kinetics, meat, at least up to some maximum percentage of diet, should pose no problem 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 residues in feces.[81]

However, hominoids are not carnivores and have neither the gut anatomy nor digestive physiology of Carnivora. A pure carnivore (Feloidea) obtains all of its required daily energy, as well as protein and other essential nutrients, from the digestion of animal matter.[57] Pure carnivores show a range of quite specific metabolic anomalies that are related to their all-flesh diets, including an inability to synthesize vitamin A and niacin from dietary precursors; the need for a dietary source of taurine; an unusually high requirement, relative to other mammals, for protein for maintenance and growth; and an unusual pattern of gluconeogenesis.[57] In addition, as discussed earlier, Carnivora have a rapid pattern of ingesta turnover.

A fair amount of data exists on the effects of high-protein diets on noncarnivorous mammals. For example, high protein diets produce acute, subacute, and chronic nephritis in rabbits. Rats fed a diet in which about 70% of daily calories came from protein sustain no deleterious effects if fed the diet for only one-third of their lifetime, but develop mild to severe chronic nephritis if the diet is maintained for all of their life.[82] In some animal species such as trout and rotifers, a decrease in dietary protein greatly increases life span.[82] As Speth and Speilman[83] and Speth[84] discussed, healthy humans are not known to derive any particular benefit from eating excessive amounts of protein; indeed, some evidence suggests that excessive protein consumption is unhealthy for humans.[82-86] Excessive protein consumption "idles" the body engine faster while producing no demonstrably favorable metabolic effects.[82]

In addition to these concerns, catabolizing protein for energy is not practical for mammals such as hominoids if other energy substrates are available, the reason being that the metabolic costs of protein conversion greatly exceed those of converting carbohydrates and fat.[82,84] Perhaps most important, adult humans apparently cannot catabolize sufficient protein to meet more than 50% of their daily energetic requirements.[87] If sufficient fat were available with meat, as it is for circumpolar peoples, early humans presumably could have used fat as an energy source.[19,83,84] But African mammals, unlike those in the Arctic, generally do not have thick deposits of fat.[53,84]

SOME MEAT IS THE SOLUTION

Though animal matter presumably did not serve as a primary source of calories for evolving humans, there is no reason why moderate amounts of animal matter could not have been used as an important dietary component if it could be secured.[4,19,71,88,89] I depart from those who suggest that meat may have been only a marginal food for early humans.[84] I have come to believe that the incorporation of animal matter into the diet played an absolutely essential role in human evolution, though I leave it to others to determine prey types and sizes, means of procurement,[88,89] and the like.

Human ancestors appear to have evolved in a somewhat arid, seasonal, and fairly open environment where ripe fruits and young leaves probably were not available throughout the year. Animal protein not only provides all of the amino acids humans require in the proper complements and proportions for human protein synthesis, but also is more efficiently digested than plant protein.[4,70,86] A hominoid would thus need to eat fewer grams of meat to satisfy all protein requirements than it would if protein requirements were being met from plant parts even of very high quality. Perhaps equally important, animal tissues also supply many essential minerals and vitamins that humans require.[86,90]

We need to bear in mind that carnivores and omnivores do not eat only muscle tissue or only muscle and fat but instead eat brains, viscera, bone marrow, the liver, and other organs. These different animal tissues provide different types and proportions of particular essential nutrients.[90] In this sense, the eating of different body parts by a carnivore resembles the feeding behavior of a herbivore, which consumes plant foods of different types to obtain a better dietary mix and thereby improve overall dietary quality.[91,92]

Humans able to satisfy their total protein and much of their essential mineral and vitamin requirements with animal matter rather than plants would free space in their gut for energy-rich plant foods such as fruits, nuts, starchy roots, other plant parts, or honey. It is popularly believed that plant starches need to be cooked before humans can digest them, but this is not necessarily the case. Raw corn and wheat starches fed to human subjects were found to be completely assimilated; no trace of them could be found in feces. These subjects also digested 62.3 to 95.2% of raw potato starch (average, 78.2%).[93] Furthermore, subjects suffered no discomfort as a result of ingesting high amounts of raw starch, which was taken in as a pudding with other dietary constituents.

I depart from those who suggest that meat may have been only a marginal food for early humans. I have come to believe that the incorporation of animal matter into the diet played an absolutely essential role in human evolution.

In addition, the digestibility of other dietary constituents was not affected by large amounts of raw starch.[93]

In terms of energy-rich plant foods, Jones[94] has pointed out that a disproportionately large number of the major food plants domesticated by humans are cyanogenic. If this is an ancient trend in human food habits, the incorporation of animal protein, with its high methionine content, in the diet of early humans could have had considerably utility. An adequate supply of sulfur-containing amino acids is essential in the detoxification of cyanogenic plant foods.[94] Animal protein may therefore have permitted early humans to use, or to use more heavily, such cyanogenic but energy-rich foods.

BENEFITS OF THIS STRATEGY

Using animal matter primarily to satisfy requirements for essential nutrients and plant foods primarily for energy is a dietary strategy that is compatible with hominoid gut anatomy and digestive kinetics as well as evidence from the human fossil and archeological record.[22] Such a diet, because of its high quality, would have permitted evolving humans to avoid the constraints gorillas and orangutans suffered as a result of body size increases (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 permitted early humans to greatly improve their net returns from foraging by simultaneously exploiting foods from two trophic levels while, at the same time, lowering dietary bulk.[4,19,22,70,95]

One critical aspect of this dietary trajectory is that once animal matter entered the human diet as a dependable staple, the overall nutrient content of plant foods could drop drastically, if need be, so long as the digestible calories were present. This permitted human ancestors to intensify their use of formerly unacceptable or marginal plant foods, including cyanogenic plant parts. Many underground storage organs, for example, are a rich source of calories but are almost devoid of nutrients; some contain cyanogenic glycosides.[94] Grains, too, are a rich source of calories but most species lack some essential nutrients humans require[96,97] and many contain cyanogenic glycosides.[94] But with animal matter in the diet to supply many essential nutrients, including sulfur-containing amino acids, the low nutritional value of some plant foods should not pose a barrier to human feeders as long as the digestible energy is there and any harmful secondary compounds can be detoxified.

CHILDHOOD NUTRITION

Another important aspect of meat-eating concerns the increasing importance, as evolution progressed, of higher-quality, volumetrically concentrated foods for infants and children. As the World Health Organization states:

> "A newborn infant needs dietary protein that contains 37% of its weight in the form of essential amino acids, whereas for adults the figure is less than half—about 15%. This has led many to suspect that protein quality is of limited relevance to adults. . . . Protein quality is of great importance in rapidly growing young animals which are actively depositing new body protein."
>
> (Lozy and coworkers[90])

Current evidence offers strong support for the critical role of micronutrients in the proper development and growth of human infants.[97] The high nutritional value of animal matter, not only as a source of essential amino acids, but also as a concentrated supply of micronutrients, seems particularly critical. Because of the increase in the ratio of metabolic requirements to gut capacity in homeotherms,[62,68,98] eating a diet high in bulky plant material could pose virtually insurmountable problems for small children, with their high energetic and nutrient demands,[53,97] as well as large brain relative to body size. Raw meat, organs, brains, viscera, and bones are concentrated sources of iron, calcium, iodine, sodium, and zinc, vitamin A, many B vitamins, vitamin C and other essential micronutrients, not to mention high-quality protein and fat.[53,86,89,95,96]

A recent study of factors associated with inadequate childhood growth, size, and health in several third-world nations identified inadequate amounts of particular micronutrients including iron, zinc, calcium, and vitamin B_{12}, rather than an inadequate supply of protein or particular amino acids, as the likely culprits.[97] Due to their content of available minerals and vitamins, animal foods were recommended to help improve the nutritional status of such children.[97] If the evolutionary trajectory I have hypothesized was characteristic of human ancestors, the routine inclusion of animal foods in the diets of weaned children seems mandatory. Plant foods selected largely for energy content would not be capable of supplying the essential micronutrients or protein children require for optimal mental development and growth.

CONCLUSIONS

Many anthropoids appear to regard invertebrates as highly desirable foods and will heavily exploit them when possible.[9–11,14,70,72,99,100] For example, Hamilton and coworkers[100] discussed two instances in which chacma baboons largely abandoned the plant component of their diet for days to feed on insect outbreaks.[100] Ayres reported that red howler monkeys in Brazil focused on eating caterpillars when a huge number of them occurred in their forested environment (personal communication). These and other accounts suggest that many anthropoid species like invertebrates and will eat more of them when they can.

If the evolutionary trajectory I have hypothesized was characteristic of human ancestors, the routine inclusion of animal foods in the diets of weaned children seems mandatory.

As noted, some chimpanzees commit a fair degree of daily foraging time to termite fishing and ant dipping.[11,72] Apes in general have been noted to eat small amounts of invertebrate matter.[9–11,70,72,99] However, it has been suggested that heavy reliance on invertebrates as a protein source may not be a viable strategy for most larger-bodied anthropoids.[101,102] Such foods may, however, provide apes with particular essential nutrients that are inadequately supplied by their particular plant-based diets.

Utami and Van Hooff[103] have recently reviewed the consumption of vertebrate prey by Old World anthropoids. Their summary indicates that meat-eating is not a common feature of Old World anthropoid dietary behavior. One exception is the hunting behavior of some common chimpanzees. Stanford[14] reports that during peak periods of meat eating by chimpanzees at Gombe, some adult male hunters may ingest as much as 500 g of meat per week—a substantial amount. To date, factors contributing to the hunting behavior of chimpanzees are not well understood, but it has been suggested that social factors may be more important than nutritional ones.[14] One key point is that chimpanzees at Gombe rarely appear to set out with the intention of hunting, but typically attacked prey when they fortuitously encounter it during routine foraging excursions.[14]

Most monkeys and apes do not live in an environment similar to that in which humans are believed to have evolved. Also, most anthropoids are not terrestrial. Given the postulated body and brain size of the earliest humans and the anatomy and kinetic characteristics of the extant hominoid gut, the most expedient dietary avenue open to protohumans seems to have been to turn increasingly to the intentional consumption of animal matter on a routine rather than a fortuitous basis.[4,19,88,89,95]

Early humans might have been able to transform a lower-quality plant food into a higher-quality one through technological innovations such as grinding or cooking. They might also have gained access to well-protected but abundant high-quality foods, using stones, for example, to crack mongongo nuts. However, such dietary innovations require considerable planning and forethought, and implements such as containers, grinding stones, and the like, as well as continuous availability of the plant resource. For these reasons as well as those discussed earlier, it seems most expedient to view the earliest humans (*Homo*) as initially having turned to animal prey to supply the amino acids and many micronutrients they required, using plant foods primarily as an energy source. Future paleontological and archaeological research, together with closer examination of features of comparative gut anatomy and digestive physiology of Hominoidea and other anthropoids should help to clarify the costs and benefits that were involved in the adaptation of this dietary strategy in the human lineage and to determine how this strategy may initially have been implemented.

ACKNOWLEDGEMENTS

My particular thanks to Dr. Ganga Deo, Staff Research Assistant, Department of Agronomy and Range Sciences, University of California at Davis, for his meticulous dietary analyses and record keeping over the years. Were it not for his unusual skills and attention to detail, many vital pieces of information would not have been preserved and available years after the fact, when their utility gradually became apparent to me. I also thank Dr. Montague Demment, who always finds time to answer my questions.

REFERENCES

1 Mitchell PCV. 1905. On the intestinal tract of mammals. Trans Zool Soc Lond. XVII:437–536.

2 Napier J. 1970. The roots of mankind. Washington DC: Smithsonian Press.

3 Eisenberg JF. 1973. Mammalian social systems: are primate social systems unique? In: Menzel EW Jr, editor. Precultural primate behavior. Basel: Karger. p 232–249.

4 Milton K. 1981. Diversity of plant foods in tropical forests as a stimulus to mental development in primates. Am Anthropol 83:534–548.

5 Stahl WR. 1965. Organ weights in Primates and other mammals. Science 150:1039–1041.

6 Rodman PS. 1977. Feeding behaviour of orangutans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p 384–413.

7 Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p 415–447.

8 Curtin SH, Chivers DJ. 1978. Leaf-eating primates of peninsular Malaysia: the siamang and the dusky leaf monkey. In: Montgomery GG, editor. Ecology of arboreal folivores. Washington, DC: Smithsonian Press. p 441–464.

9 Kuroda S, Nishihara T, Suzuki S, Oko RA. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In McGrew WC, Marchant LF, Nishida T, (editors). Great ape societies. Cambridge: Cambridge University Press. p 71–81.

10 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 WC, Marchant LF, Nishida T, (editors). Great ape societies. Cambridge: Cambridge University Press. p 82–98.

11 Goodall J. 1986. The chimpanzees of Gombe: patterns of behaviour. Cambridge: Blaknap Press of Harvard University Press.

12 Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. Am J Primatol 43:87–110.

13 Wrangham RW, Conklin NL, Chapman CA, Hunt KD. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. Philos Trans R Soc Lond 334:171–178.

14 Stanford CB. 1998. Chimpanzee and red colobus: the ecology of predator and prey. Cambridge: Harvard University Press.

15 Scott GBD. 1980. The primate caecum and appendix vermiformis: a comparative study. J Anat 131:549–563.

16 Floch MH, Van Noorden S, Spiro HM. 1967. Histochemical localization of gastric and small bowel mucosal enzymes of man, monkey and chimpanzee. Gastroenterology 52:230–238.

17 Elliott TR, Barclay-Smith MA. 1904. Antiperistalsis and other muscular activities of the colon. J Physiol 31:272–304.

18 Milton K. 1986. Features of digestive physiology in primates. News Physiol Sci 1:76–79.

19 Milton K. 1987. Primate diets and gut morphology: implications for human evolution. In: Harris M, Ross EB, editors. Food and evolution: toward a theory of human food habits. Philadelphia: Temple University Press. p 93–116.

20 Kay RF. 1977. Diet of early Miocene hominoids. Nature 268:628–630.

21 Milton K, Jenness R. 1987. Ascorbic acid content of neotropical plant parts available to wild monkeys and bats. Experientia 43:339–342.

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 Martin RD, Chivers DJ, MacLarnon AM, Hladik CM. 1985. Gastrointestinal allometry in Primates and other mammals. In: Jungers WL, editor. Size and scaling in primate biology. New York: Plenum Press. p 61–139.

24 Sibly RM. 1981. Strategies of digestion and defectation. In: Townsend CR, Calow P, editors. Physiological ecology. Oxford: Blackwell Scientific. p 109–139.

25 Gross JE, 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.

26 Wunder BA. 1990. Effects of increased energy need on gut morphology of two small herbivores, *Microtus ochrogaster* and *Dictostonyx groenlandicus*. In: Digestive strategies of animals. Proceedings of the Symposium on the Relationships Between Diet Composition, Feed Intake, Digestive Processes, Nutritional Absorption and Their Ecological Consequences, Washington, DC: Center for Biological Research, National Zoological Park. p 90–91.

27 Lee WB, Houston DC. 1993. The effect of diet quality on gut anatomy in British voles. J Comp Physiol 163B:337–339.

28 Lee WB, Houston DC. 1995. The rate of change of gut anatomy in voles in relation to dietary quality. J Zool Lond 236:341–345.

29 Savory C, Gentle MJ. 1976. Changes in food intake and gut size in Japanese quail in response to manipulation of dietary fiber content. Br Poultry Sci 17:571–580.

30 Piersma T, Gill RE. 1998. Guts don't fly: small digestive organs in obese bar-tailed godwits. Awk 115:196–203.

31 Karasov WH. 1993. In the belly of the bird. Nat Hist 11:33–36.

32 Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7:8–20.

33 Karasov WH, Diamond JM. 1985. Digestive adaptations for fueling the costs of endothermy. Science 228:202–204.

34 Miloslavich EL. 1925. 1. Racial studies on the large intestine. Am J Phys Anthropol VIII:11–22.

35 Gray H. 1901. Anatomy, descriptive and surgical. New York: Bounty Books, revised from the 15th English edition.

36 Clemens E, Phillips B. 1980. Organic acid production and digesta movement in the gastrointestinal tract of the baboon and Sykes monkey. Comp Biochem Physiol 66A:529–532.

37 Heller SN, Hackler LR, Rivers JM, Van Soest PJ, Roe DA, Lewis BA, Robertson JB. 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.

38 Van Soest P. 1982. Nutritional ecology of the ruminant. Corvallis, OR: O & B Books.

39 Uden P, Van Soest PJ. 1982. The determination of digesta particle size in some herbivores. Anim Feed Sci Tech 7:35–44.

40 Phillips B, Clemens E. 1981. Nutritional implications of ad libitum versus limited feeding in baboons. Lab Anim Sci 31:192–193.

41 Bjornhag G. 1972. Separation and delay of contents in the rabbit colon. Swed J Agric Res 2:125–136.

42 Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am Nat 114:362–378.

43 Milton K. 1981. Food choice and digestive strategies of two sympatric primate species. Am Nat 117:476–495.

44 Milton K. 1984. The role of food processing factors in primate food choice. In: Rodman P, Cant J, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 249–279.

45 Wrick KL. 1979. The influence of dietary fibers on intestinal passage, laxation and stool characteristics in humans. Unpublished doctoral dissertation. Ithaca: Cornell University.

46 Ehle RR, Jeraci JJ, Robertson JB, Van Soest PJ. 1982. The influence of dietary fiber on digestibility, rate of passage and gastrointestinal fermentation in pigs. J Anim Sci 55:1071–1080.

47 Wrick KL, Robertson JB, Van Soest PJ, Lewis BA, Rivers JM, Roe DA, Hackler LR. 1983. The influence of dietary fiber source on human intestinal transit and stool output. J Nutr 113:1464–1479.

48 Caton J. 1997. Digestive strategies of nonhuman primates. Doctoral Dissertation. Canberra: The Australian National University.

49 Kelsay JL, Behall KM, Prather ES. 1978. Effects of fiber from fruits and vegetables on metabolic responses of human subjects. Am J Clin Nutr 31:1149–1153.

50 Mitchell WD, Eastwood MA. 1976. Dietary fiber and colon function. In: Spiller GA, Amen RJ, editors. Fiber in human nutrition. New York: Plenum Press. p 185–206.

51 Van Soest PJ. 1981. Some factors influencing the ecology of gut fermentation in man. Reprinted from Banbury Report 7: Gastrointestinal cancer: endogenous factors. Cold Spring Harbor: Cold Springs Harbor Laboratory.

52 Burkitt DP, Walker ARP, Painter NS. 1972. Effect of dietary fibre on stools and transit times and its role in the causation of disease. Lancet 2:1408–1411.

53 Liebermann LS. 1987. Biological consequences of animals versus plants as sources of fats, protein and other nutrients. In: Harris M, Ross EB, editors. Diet and human evolution. Philadelphia: Temple University Press. p 225–260.

54 Stevens CE. 1988. Comparative physiology of the vertebrate digestive system. Cambridge: Cambridge University Press.

55 Sibbald IR, Sinclair DG, Evans EV, Smith DLT. 1962. The rate of passage of feed through the digestive tract of the mink. Comp J Biochem Physiol 40:1391–1394.

56 Best RC. 1977. Ecological aspects of polar bear nutrition. In Phillips RL, Jonkel C, editors. Proceedings of the 1975 Predator Symposium. Missoula: Montana Forest and Conservation Experimental Station, University of Montana. p 203–211.

57 Morris JG, Rodgers QR. 1989. Comparative aspects of nutrition and metabolism of dogs and cats. In: Burger IH, Rivers JPW, editors. Waltham Symposium #7. Nutrition of dog and cat. Cambridge: Cambridge University Press. p 35–66.

58 Schaller GB, Hu J, Pan W, Jhu J. 1985. The giant pandas of Wolong. Chicago: University of Chicago Press.

59 Johnson KG, Schaller GB, Hu J. 1988. Comparative behavior of red and giant pandas in the Wolong Reserve, China. J Mammal 69:552–564.

60 Dierenfeld ES, Hintz HF, Robertson JB, Van Soest PJ, Oftedal OT. 1982. Utilization of bamboo by the giant panda. J Nutrit 112:636–341.

61 Oftedal OT, Fulton KJ, Crissey SD, Roberts MS. 1990. Bamboos as a source of digestible energy for red pandas. In: Digestive strategies of animals. Proceedings of the Symposium on the Relationships Between Diet Composition, Feed Intake, Digestive Processes, Nutritional Absorption and Their Ecological Consequences. Washington, DC: Center for Biological Research, National Zoological Park. p 77–79.

62 Klieber M. 1975. The fire of life. Huntington, NY: Krieger.

63 Janis C. 1976. The evolutionary strategy of the Equidae and origins of rumen and cecal digestion. Evolution 30:757–774.

64 Andrews P. 1981. Species diversity and diet in monkeys and apes during the Miocene. In: Stringer CB, editors. Aspects of human evolution. London: Taylor and Francis. p 25–61.

65 Andrews P. 1995. Ecological apes and ancestors. Nature 376:555–556.

66 Clutton-Brock TH, Harvey PH. 1977. Species differences in feeding and ranging behaviours in Primates. In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p 557–584.

67 Demment MW. 1983. Feeding ecology and the evolution of body size in baboons. Afr J Ecol 21:219–233.

68 Demment MW, Van Soest PJ. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. Am Nat 125: 641–672.

69 Milton K. 1980. The guts of the matter: a look at the comparative anatomy of the hominid digestive tract. Presented at Plenary Session on Diet, Annual Meeting of the American Association of Physical Anthropologists, April 1980, Niagara Falls, NY.

70 Milton K. 1988. Foraging behavior and the evolution of primate cognition. In: Whiten A, Byrne R, editors. Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Oxford: Oxford University Press. p 285–305.

71 McGrew WC. 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg DA, McCown ER, editors. The great apes. Menlo Park: Benjamin/Cummings. p 441–464.

72 Tutin CEG, Fernandez M, Rogers ME, Williamson ES, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. Philos Trans R Soc Lond B 334:179–186.

73 McCance RA, Prior KM, Widdowson EM. 1953. A radiological study of the rate of passage of brown and white bread through the digestive tract of man. Br J Nutrit 7:98–104.

74 Walker A. 1981. Diet and teeth. Philos Trans R Soc 292:57–64.

75 Andrews P, Aiello L. 1984. An evolutionary model for feeding and positional behaviour. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 429–465.

76 de Menocal PB. 1995. Plio-Pleistocene African climate. Science 270:53–59.

77 McHenry H. 1992. Body size and proportions in early hominids. Am J Phys Anthropol 37:407–431.

78 Wood B. 1992. Origin and evolution of the genus *Homo*. Nature 355:785–790.

79 Vrba ES. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. Paleoclimate and evolution, with emphasis on human origins. New Haven: Yale University Press. p 385–424.

80 Sept J. 1998. Shadows on a changing landscape: comparing nesting patterns of hominids and chimpanzees since their last common ancestor. Am J Primatol 46:85–101.

81 Milton K, Demment M. 1989. Features of meat digestion by captive chimpanzees, *Pan troglodytes*. Am J Primatol 18:45–52.

82 Nelson RA. 1975. Implications of excessive protein. In: White PL, Selvey N, editors. Proceedings of the Western Hemisphere Nutrition Congress IV. Acton, Mass: Publishing Sciences Group. p 71–76.

83 Speth JD, Speilmann KA. 1983. Energy source, protein metabolism and hunter-gatherer subsistence strategies. J Anthropol Archeol 2:1–31.

84 Speth JD. 1989. Early hominid hunting and scavenging: the role of meat as an energy source. J Hum Evol 18:329–343.

85 Carpenter KJ. 1986. The history of enthusiasm for protein. J Nutri 116:1364–1370.

86 Carpenter KJ. 1994. Protein and energy: a study of changing ideas in nutrition. Cambridge: Cambridge University Press.

87 Draper HH. 1977. The aboriginal eskimo diet. Am Anthropol 79:309–316.

88 Blumenschine RJ, Cavallo JA. 1992. Scavenging and human evolution. Sci Am 276:90–96.

89 Aiello LC, Wheeler P. 1995. The expensive tissue hypothesis. Curr Anthropol 36:199–211.

90 Lozy M, Herrera MG, Latham MC, McGandy RB, McCann MB, Stare FJ. 1980. Nutrition: a scope publication. Kalamazoo: The Upjohn Company.

91 Westoby M. 1974. An analysis of diet selection by large generalist herbivores. Am Nat 108:290–304.

92 Nagy K, Milton K. 1979. Aspects of dietary quality, nutrient assimilation and water balance in wild howler monkeys. Oecologia 30:249–258.

93 Langworthy CF, Deuel HJ Jr. 1920. Digestibility of raw corn, potato and wheat starches. J Biol Chem 42:27–40.

94 Jones DA. 1998. Why are so many plant foods cyanogenic? Phytochemistry 47:155–162.

95 Milton K. 1993. Diet and primate evolution. Sci Am 269:86–93.

96 Nutritive Value of Foods. 1981. USDA, Science and Education Administration. Home & Garden Bulletin #72. Washington DC.

97 Calloway DH, Murphy S, Balderston J, Receveur O, Lein D, Hudes M. 1992. Village nutrition in Egypt, Kenya and Mexico: looking across CRSP projects. U.S. Agency for International Development. Final Report.

98 Parra R. 1978. Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington, DC: Smithsonian Press. p 205–230.

99 Harding RSO. 1981. An order of omnivores: nonhuman primate diets in the wild. In Harding RSO, Teleki G, editors. Omnivorous primates. New York: Columbia University Press. p 191–214.

100 Hamilton WJ III, Buskirk RE, Buskirk WH. 1978. Omnivory and utilization of food resources by chacma baboons. Am Nat 112:911–924.

101 Kay RF, Hylander WL. 1978. The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In Montgomery GG, editor. The ecology of arboreal folivores. Washington DC: Smithsonian Press. p 173–196.

102 Hamilton WJ III. 1987. Omnivorous primate diets and human overconsumption of meat. In Harris M, Ross EB, editors. Food and evolution. Philadelphia: Temple University Press. p 117–132.

103 Utami SS, van Hooff JARAM. 1997. Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). Am J Primatol 43:159–166.