

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

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"In the mammalian gut . . . the inherited element dominates the structure."

(Mitchell¹)

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 to 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 Mitchell¹ 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, Scott¹⁵

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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} Mitchell¹ 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-Smith¹⁷ 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 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, mod-

ern 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 spe-

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ies, 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.

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 tempera-

tures, 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 size²⁴ 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 passerines 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 coworkers²³ 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 Phillips³⁶)

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 Demment²² 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%

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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 compartments⁴⁵).^{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 rap-

idly, 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 chimpanzees⁴⁸ (Table 1).

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 diet⁴⁷ (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 Wick⁴⁵ and Wick and coworkers⁴⁷ 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 Wick 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 Dement²² 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."

(Mitchell¹)

As Mitchell¹ 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

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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.

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. Demment⁶⁷ and Demment and Van Soest⁶⁸ 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 2.3 km/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 be-

lieve 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 $6.5 \pm 2.6\%$ 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 flow-

ers) 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

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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 methionine⁵³ 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.

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 defi-

cits.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 Menocal⁷⁶)

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, ac-

tive, 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 Spielman⁸³ and Speth⁸⁴ 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.³⁷ If sufficient fat were available with meat, as it is for circumpolar peoples, early humans presumably could have used fat as an energy source.^{19,33,34} But African mammals, unlike those in the Arctic, generally do not have thick deposits of fat.^{53,34}

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,^{38,39} 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.^{4,70,36} 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.

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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, Jones⁹⁴ 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 sociability). 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 coworkers⁹⁰)

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 B₁₂, 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 micro-

nutrients 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 coworkers¹⁰⁰ 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 Hooff¹⁰³ 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 be-

havior. One exception is the hunting behavior of some common chimpanzees. Stanford¹⁴ 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 proto-humans seems to have been to turn increasingly to the intentional consumption of animal matter on a routine rather than a fortuitous basis.^{4,19,38,39,95}

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 deter-

mine how this strategy may initially have been implemented.

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