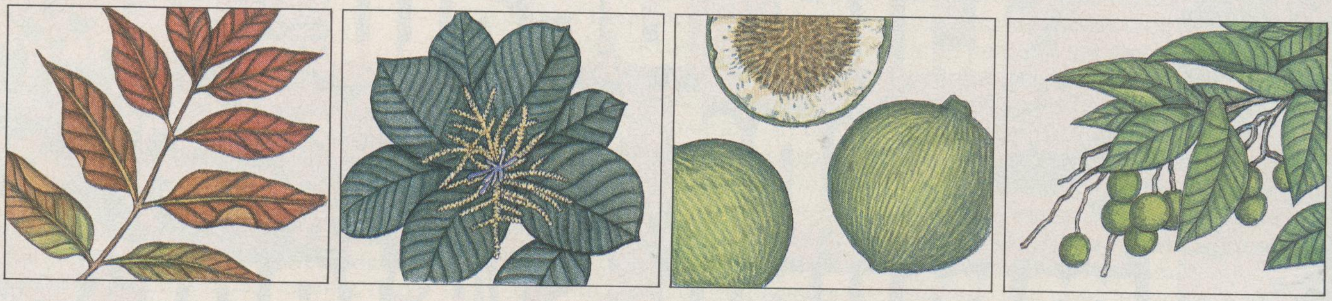
Diet and Primate Evolution

Many characteristics of modern primates, including our own species, derive from an early ancestor's practice of taking most of its food from the tropical canopy

by Katharine Milton



As recently as 20 years ago, the canopy of the tropical forest was regarded as an easy place for apes, monkeys and prosimians to find food. Extending an arm, it seemed, was virtually all our primate relatives had to do to acquire a ready supply of edibles in the form of leaves, flowers, fruits and other components of trees and vines. Since then, efforts to understand the reality of life for tree dwellers have helped overturn that misconception.

My own field studies have provided considerable evidence that obtaining adequate nutrition in the canopy—where primates evolved—is, in fact, quite difficult. This research, combined with complementary work by others, has led to another realization as well: the strategies early primates adopted to cope with the dietary challenges of the arboreal environment profoundly influenced the evolutionary trajectory of the primate order, particularly that of the anthropoids (monkeys, apes and humans).

Follow-up investigations indicate as well that foods eaten by humans today, especially those consumed in industrially advanced nations, bear little resemblance to the plant-based diets anthropoids have favored since their emergence. Such findings lend support to the suspicion that many health problems common in technologically advanced nations may result, at least in part, from a mismatch between the diets we now eat and those to which our bodies became adapted over millions of years. Overall, I would say that the collected evidence justifiably casts the evolutionary history of primates in largely dietary terms.

The story begins more than 55 million years ago, after angiosperm forests spread across the earth during the late Cretaceous (94 to 64 million years ago). At that time, some small, insect-eating mammal, which may have resembled a tree shrew, climbed into the trees, presumably in search of pollen-distributing insects. But its descendants came to rely substantially on edible plant parts from the canopy, a change that set the stage for the emergence of the primate order.

Natural selection strongly favors traits that enhance the efficiency of foraging. Hence, as plant foods assumed increasing importance over evolutionary time (thousands, indeed millions, of years), selection gradually gave rise to the suite of traits now regarded as characteristic of primates. Most of these traits facilitate movement and foraging in trees. For instance, selection yielded hands well suited for grasping slender branches and manipulating found delicacies.

Selective pressures also favored considerable enhancement of the visual apparatus (including depth perception, sharpened acuity and color vision), thereby helping primates travel rapidly through the three-dimensional space of the forest canopy and easily discern the presence of ripe fruits or tiny, young leaves. And such pressures favored increased behavioral flexibility as well as the ability to learn and remember the identity and locations of edible plant parts. Foraging benefits conferred by the enhancement of visual and cognitive skills, in turn, promoted development of an unusually large brain, a characteristic of primates since their inception.

As time passed, primates diverged into various lineages: first prosimians, most of which later went extinct, and then monkeys and apes. Each lineage arose initially in response to the pressures of a somewhat different dietary niche; distinct skills are required to become an efficient forager on a particular subset of foods in the forest canopy. Then new dietary pressures placed on some precursor of humans paved the way for the development of modern humans. To a great extent, then, we are truly what we eat.

My interest in the role of diet in primate evolution grew out of research I began in 1974. While trying to decide on a topic for my doctoral dissertation in physical anthropology, I visited the tropical forest on Barro Colorado Island in the Republic of Panama. Studies done on mantled howler monkeys (*Alouatta palliata*) in

KATHARINE MILTON is professor of anthropology at the University of California, Berkeley. After earning her doctorate from New York University in 1977, she spent three years conducting field studies on the foraging behavior of howler and spider monkeys. She joined the Berkeley faculty in 1980. Milton is now studying the dietary behavior and diseases of indigenous human populations living in the tropical forests of Brazil.

the 1930s at that very locale had inadvertently helped foster the impression that primates enjoyed the "life of Riley" in the canopy.

Yet, during my early weeks of following howlers, I realized they were not behaving as expected. Instead of sitting in a tree and eating whatever happened to be growing nearby, they went out of their way to seek specific foods, meanwhile rejecting any number of seemingly promising candidates. Having found a preferred food, they did not sate themselves. Instead they seemed driven to obtain a mixture of leaves and fruits, drawn from many plant species.

The old easy-living dogma was clearly far too simplistic. I decided on the spot to learn more about the problems howlers and other anthropoids face meeting their nutritional needs in the tropical forest. I hoped, too, to discern some of the strategies they had evolved to cope with these dietary difficulties.

The challenges take many forms. Because plants cannot run from hungry predators, they have developed other defenses to avoid the loss of their edible components. These protections include a vast array of chemicals known as secondary compounds (such as tannins, alkaloids and terpenoids). At best, these chemicals taste awful; at worst, they are lethal.

Also, plant cells are encased by walls made up of materials collectively referred to as fiber or roughage: substances that resist breakdown by mammalian digestive enzymes. Among the fibrous constituents of the cell wall are the structural carbohydrates—cellulose and hemicellulose—and a substance called lignin; together these materials give plant cell walls their shape, hardness and strength. Excessive intake of fiber is troublesome, because when fiber goes undigested, it provides no energy for the feeder. It also takes up space in the gut. Hence, until it can be excreted, it prevents intake of more nourishing items. As will be seen, many primates, including humans, manage to extract a certain amount of energy, or calories, from fiber despite their lack of fiber-degrading enzymes. But the process is time-consuming and thus potentially problematic.

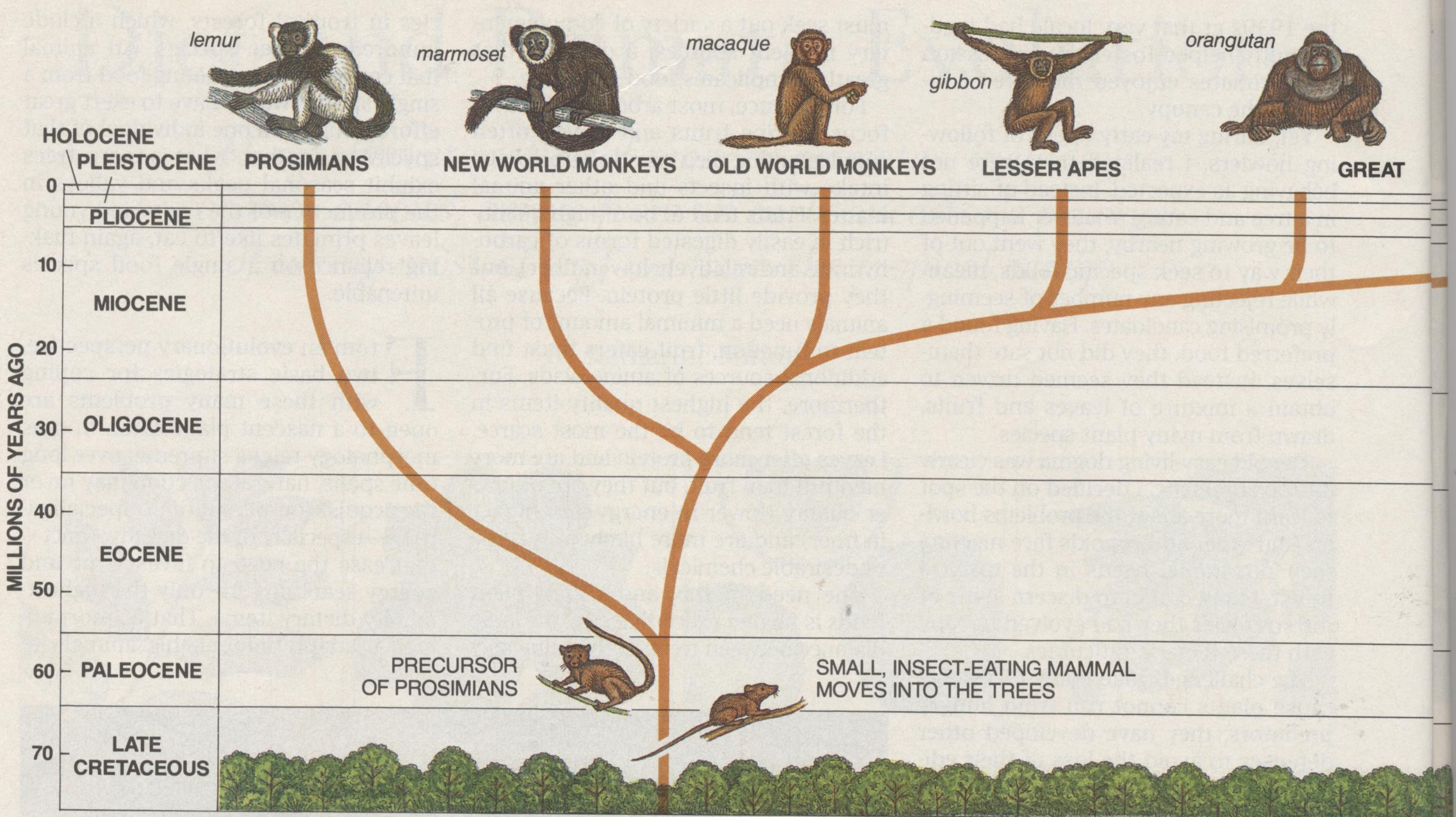
The dietary challenges trees and vines pose do not end there. Many plant foods lack one or more nutrients required by animals, such as particular vitamins or amino acids (the building blocks of protein), or else they are low in readily digestible carbohydrates (starch and sugar), which provide glucose and therefore energy. Usually, then, animals that depend primarily on plants for meeting their daily nutritional requirements must seek out a variety of complementary nutrient sources, a demand that greatly complicates food gathering.

For instance, most arboreal primates focus on ripe fruits and leaves, often supplementing their mostly herbivorous intake with insects and other animal matter. Fruits tend to be of high quality (rich in easily digested forms of carbohydrate and relatively low in fiber), but they provide little protein. Because all animals need a minimal amount of protein to function, fruit eaters must find additional sources of amino acids. Furthermore, the highest-quality items in the forest tend to be the most scarce. Leaves offer more protein and are more plentiful than fruit, but they are of lower quality (lower in energy and higher in fiber) and are more likely to include undesirable chemicals.

The need to mix and match plant foods is further exacerbated by the large distance between trees of the same species in tropical forests, which include hundreds of tree species. An animal that concentrated on eating food from a single species would have to exert great effort going from one individual of that species to another. What is more, trees exhibit seasonal peaks and valleys in the production of the fruits and young leaves primates like to eat, again making reliance on a single food species untenable.

From an evolutionary perspective, two basic strategies for coping with these many problems are open to a nascent plant eater. In one, morphology reigns supreme: over long time spans, natural selection may favor the acquisition of anatomic specializations—especially of the digestive tract—that ease the need to invest time and energy searching for only the highest-quality dietary items. That is, morphological adaptations enable animals to

YOUNG CHIMPANZEES SEEK FRUIT as part of a diet that consists primarily of ripe fruits supplemented by leaves and some animal prey. Obtaining the foods needed for adequate nutrition in the tropical forest turns out to be significantly more difficult for primates than was once believed. The author contends that the solutions adopted by primates millions of years ago strongly influenced the subsequent evolution of the primate order. The drawings on the opposite page depict some typical plant foods available to arboreal animals in the tropical forest.



EVOLUTIONARY TREE of the primate order is rooted in the late Cretaceous, when a small, insect-eating mammal climbed into the trees to take advantage of feeding opportunities presented by the spread of angiosperm forests. As the descendants of this mammal (*artist's representation to left of tree*) adapted to a new dietary niche in the canopy, they developed traits now regarded as characteristic of primates, such as a rounded snout and nails (instead of claws). These descendants

depend on plant parts that are ubiquitous, such as on mature leaves (which are readily available but not of particularly high quality).

Colobine monkeys, one of the Old World primate groups in Africa and Asia, offer an excellent example of this strategy. Unlike the typical primate digestive tract (including that of humans), with its simple acid stomach, that of colobines includes a compartmentalized, or sacculated, stomach functionally analogous to that of cows and other ruminants. This anatomic specialization enables colobines to process fiber extremely efficiently.

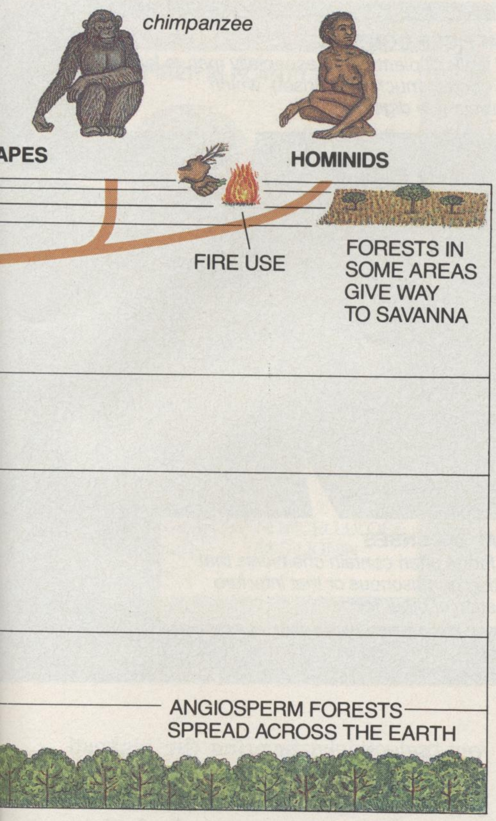
Chewed leaves flow through the esophagus into the forestomach, one of the two stomach compartments in colobines. In this alkaline forestomach, microbes known as cellulolytic bacteria do what digestive enzymes of the monkeys cannot do: degrade fiber. In a process known as fermentation, the bacteria break down the cellulose and hemicellulose in plant cell walls, using those substances as an energy source to fuel their own activities. As the bacteria consume the fiber, they release gases called volatile fatty acids. These gases pass through the stomach wall into the colobine bloodstream, where they provide energy for body tissues or are delivered to the liver for conversion into glucose. Some researchers think the colobine forestomach may also aid in the detoxification of harmful secondary compounds in plant foods.

Efficiency of nutrient extraction from fibrous foods is enhanced in another way in colobine monkeys. As cellulolytic bacteria die, they pass out of the forestomach into the second compartment, a simple acid stomach similar to our own. Here special enzymes (lysozymes) cleave the bacterial cell walls. In consequence, protein and other nutritious materials that compose the cellulolytic bacteria become available for digestion by the monkeys. (In a sense, then, once leaves are chewed and swallowed, colobine monkeys do not interact directly with their food; they live on products of the fermentation process and on the nutrients provided by the fermenters.)

In contrast to colobines, humans and most other primates pass fiber basically unchanged through their acid stomach and their small intestine (where most nutrients are absorbed) and into the hindgut (the cecum and colon). Once fiber reaches the hindgut, cellulolytic bacteria may be able to degrade some of it. But, for most primates, eating copious amounts of fiber does not confer the same benefits as it does for the digestively specialized colobines.

Another morphological change that can facilitate survival on lower-quality plant parts is to grow larger over time. Compared with small animals, big ones must consume greater absolute amounts of food to nourish their more extensive tissue mass. But, for reasons that are imperfectly understood, the bigger animals can actually attain adequate nourishment by taking in less energy per unit of body mass. This relatively lower energy demand means larger animals can meet their energy requirements with lower-quality foods. Growing bigger has been only a limited option for most primates, however. If arboreal animals grow too massive, they risk breaking the branches underneath their feet and falling to the ground.

The second basic strategy open to plant eaters is more behavioral than morphological. Species can opt to feed selectively on only the highest-quality plant foods. But because quality items are rare and very patchily distributed in tropical forests, this strategy requires the adoption of behaviors that help to minimize the costs of pro-



gave way to true primates, beginning with the prosimians. Our own genus, *Homo,* emerged during the Pliocene. Exact dates of radiations are debatable.

curing these resources. The strategy would be greatly enhanced by a good memory. For example, an ability to remember the exact locations of trees that produce desirable fruits and to recall the shortest routes to those trees would enhance foraging efficiency by lowering search and travel costs. So would knowledge of when these trees were likely to bear ripe fruits. Reliance on memory, with its attendant benefits, might then select for bigger brains having more area for storing information.

Of course, these two basic evolutionary strategies—the morphological and behavioral—are not mutually exclusive, and species vary in the extent to which they favor one or the other. As a group, however, primates have generally depended most strongly on selective feeding and on having the brain size, and thus the wit, to carry off this strategy successfully. Other plant-eating orders, in contrast, have tended to focus heavily on morphological adaptations.

I gained my first insights into the evolutionary consequences of selective feeding in primates in the mid-1970s, when I noticed that howler monkeys and black-handed spider monkeys (*Ateles geoffroyi*)—two New World primate species—favored markedly different diets. Howler and spider monkeys, which diverged from a common ancestor, are alike in that they are about the same size, have a simple, unsacculated stomach, are totally arboreal and eat an almost exclusively plant-based diet, consisting for the most part of fruits and leaves. But my fieldwork showed that the foundation of the howler diet in the Barro Colorado forest was immature leaves, whereas the foundation of the spider monkey diet was ripe fruits.

Most of the year howlers divided their daily feeding time about equally between new leaves and fruits. But during seasonal low points in overall fruit availability, they ate virtually nothing but leaves. In contrast, spider monkeys consumed ripe fruits most of the year, eating only small amounts of leaves. When fruits became scarce, spider monkeys did not simply fill up on leaves as the howlers did. Their leaf intake did increase, but they nonetheless managed to include considerable quantities of fruit in the diet. They succeeded by carefully seeking out all fruit sources in the forest; they even resorted to consuming palm nuts that had not yet ripened.

These observations raised a number of questions. I wanted to know how howlers obtained enough energy during months when they lived exclusively on leaves. As already discussed, much of the energy in leaves is bound up in fiber that is inaccessible to the digestive enzymes of primates. Further, why did howlers eat considerable foliage even when they had abundant access to ripe fruits? By the same token, why did spider monkeys go out of their way to find fruit during periods of scarcity; what stopped them from simply switching to leaves, as howlers did? And how did spider monkeys meet daily protein needs with their fruit-rich diet? (Recall that fruits are a poor source of protein.)

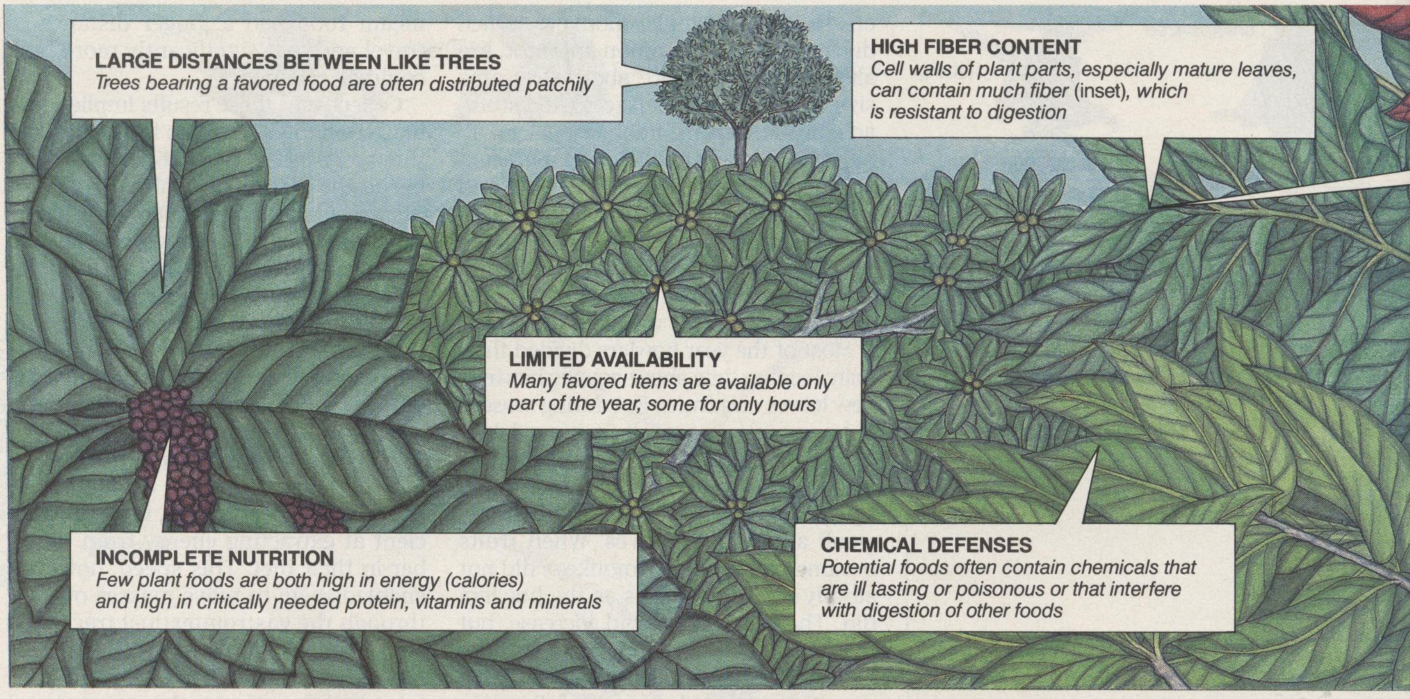
Because howler and spider monkeys are much alike externally, I speculated that some internal feature of the two species—perhaps the structure of the gut or the efficiency of digestion—might be influencing these behaviors. And, indeed, studies in which I fed fruits and leaves to temporarily caged subjects revealed that howler monkeys digested food more slowly than did spider monkeys. Howlers began eliminating colored plastic markers embedded in foods an average of 20 hours after eating. In contrast, spider monkeys began eliminating these harmless markers after only four hours. Examining the size of the digestive tract in the two species then revealed how these different passage rates were attained. In howler monkeys the colon was considerably wider and longer than in spider monkeys, which meant food had a longer distance to travel and that significantly more bulk could be retained.

Collectively, these results implied that howlers could survive on leaves because they were more adept at fermenting fiber in the cecum and colon. They processed food slowly, which gave bacteria in the capacious hindgut a chance to produce volatile fatty acids in quantity. Experiments I later carried out with Richard McBee of Montana State University confirmed that howlers may obtain as much as 31 percent of their required daily energy from volatile fatty acids produced during fermentation.

In contrast, spider monkeys, by passing food more quickly through their shorter, narrower colons, were less efficient at extracting energy from the fiber in their diet. This speed, however, enabled them to move masses of food through the gastrointestinal tract each day. By choosing fruits, which are highly digestible and rich in energy, they attained all the calories they needed and some of the protein. They then supplemented their basic fruit-pulp diet with a few very select young leaves that supplied the rest of the protein they required, without an excess of fiber.

Hence, howler monkeys never devote themselves exclusively to fruit, in part because their slow passage rates would probably prevent them from processing all the fruit they would need to meet their daily energy requirement. And the amount of fruit they could consume certainly would not provide enough protein. Conversely, spider monkeys must eat fruit because their digestive tract is ill equipped to provide great amounts of energy from fermenting leaves; efficient fermentation requires that plant matter be held in the gut for some time.

By luck, I had chosen to study two species that fell at opposite ends of the continuum between slow and rapid passage of food. It is now clear that most primate species can be ranked somewhere along this continuum, depending on whether they tend to maximize the efficiency with which they digest a given meal or maximize the volume of food processed in a day. This research further shows that even without major changes in the design of the digestive tract, subtle adjustments in the size of different segments of the gut can help compensate for nutritional problems posed by an animal's dietary choices. Morphological compensations in the digestive tract can have their drawbacks, however, because they may make it difficult for a species to alter its dietary habits should environmental conditions change suddenly.



These digestive findings fascinated me, but a comparison of brain size in the two species yielded one of those "eurekas" of which every scientist dreams. I examined information on the brain sizes of howler and spider monkeys because the spider monkeys in Panama seemed "smarter" than the howlers—almost human. Actually, some of them reminded me of my friends. I began to wonder whether spider monkeys behaved differently because their brains were more like our own. My investigations showed that, indeed, the brains of howler and spider monkeys do differ, even though the animals are about the same size. (Same-sized animals generally have like-sized brains.) The spider monkey brain weighs about twice that of howlers.

Now, the brain is an expensive organ to maintain; it usurps a disproportionate amount of the energy (glucose) extracted from food. So I knew natural selection would not have favored development of a large brain in spider monkeys unless the animals gained a rather pronounced benefit from the enlargement. Considering that the most striking difference between howler and spider monkeys is their diets, I proposed that the bigger brain of spider monkeys may have been favored because it facilitated the development of mental skills that enhanced success in maintaining a diet centered on ripe fruit.

A large brain would certainly have helped spider monkeys to learn and, most important, to remember, where certain patchily distributed fruit-bearing trees were located and when the fruit would be ready to eat. Also, spider monkeys comb the forest for fruit by dividing into small, changeable groups. Expanded mental capacity would have helped them to recognize members of their particular social unit and to learn the meaning of the different food-related calls through which troop members convey over large distances news of palatable items. Howler monkeys, in contrast, would not need such an extensive memory, nor would they need so complex a recognition and communication system. They forage for food as a cohesive social unit, following well-known arboreal pathways over a much smaller home range.

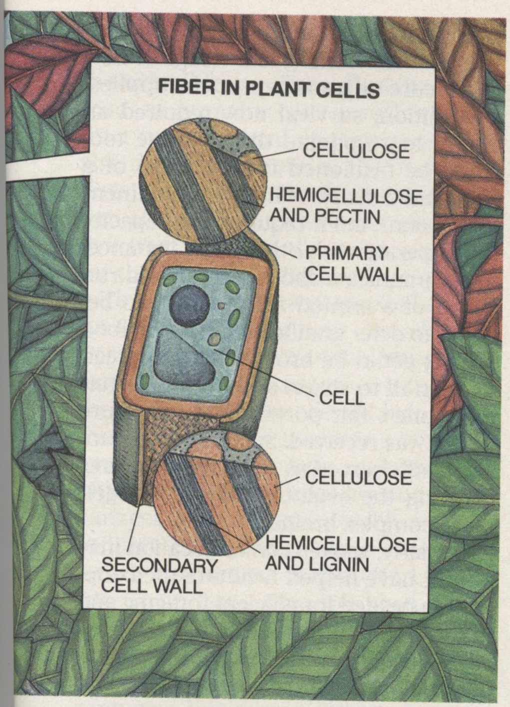
If I was correct that the pressure to obtain relatively difficult-to-find, high-quality plant foods encourages the development of mental complexity (which is paid for by greater foraging efficiency), I would expect to find similar differences in brain size in other primates. That is, monkeys and apes who concentrated on ripe fruits would have larger brains than those of their leaf-eating counterparts of equal body size. To pursue this idea, I turned to estimates of comparative brain sizes published by Harry J. Jerison of the University of California at Los Angeles. To my excitement, I found that those primate species that eat higher-quality, more widely dispersed foods generally have a larger brain than do their similar-sized counterparts that feed on lower-quality, more uniformly distributed resources.

As I noted earlier, primates typically have larger brains than do other mammals of their size. I believe the difference arose because primates feed very selectively, favoring the highest-quality plant parts—for instance, even primates that eat leaves tend to choose very immature leaves or only the low-fiber tips of those leaves.

Having uncovered these links between dietary pressures and evolution in nonhuman primates, I became curious about the role of such pressures in human evolution. A review of the fossil record for the hominid family—humans and their precursors—provided some intriguing clues.

Australopithecus, the first genus in our family, emerged in Africa more than 4.5 million years ago, during the Pliocene. As is true of later hominids, they were bipedal, but their brains were not appreciably larger than those of today's apes. Hence, selection had not yet begun to favor a greatly enlarged brain in our family. The fossil record also indicates *Australopithecus* had massive molar teeth that would have been well suited to a diet consisting largely of tough plant material. Toward the end of the Pliocene, climate conditions began to change. The next epoch, the Pleistocene (lasting from about two million to 10,000 years ago), was marked by repeated glaciations of the Northern Hemisphere. Over both epochs, tropical forests shrank and were replaced in many areas by savanna woodlands.

As the diversity of tree species decreased and the climate became more seasonal, primates in the expanding savanna areas must have faced many new dietary challenges. In the Pleistocene the last species of *Australopithecus*—which



	READILY ACCESSIBLE CALORIES	PROTEIN	FIBER	CHEMICAL DEFENSES	AVAILABILITY ON A GIVEN TREE
FLOWERS	Moderate	Moderate to high	Low to moderate	Variable	Fewer than three months
FRUITS	High	Low	Moderate	Low	Fewer than three months
YOUNG LEAVES	Low	High	Moderate	Moderate	Half the year
MATURE LEAVES	Low	Moderate	High	Moderate	Almost year-round

MANY CHALLENGES can deter primates in the tropical forest from obtaining the calories and mix of nutrients they need from plant foods (*left*). Because most such foods are inadequate in one way or another, animals must choose a variety of items each day. The chart at the right loosely reflects the relative abundance of desirable (*green*) and problematic (*yellow*) components in a mouthful of common foods. It also indicates the typical availability of these foods on any given tree.

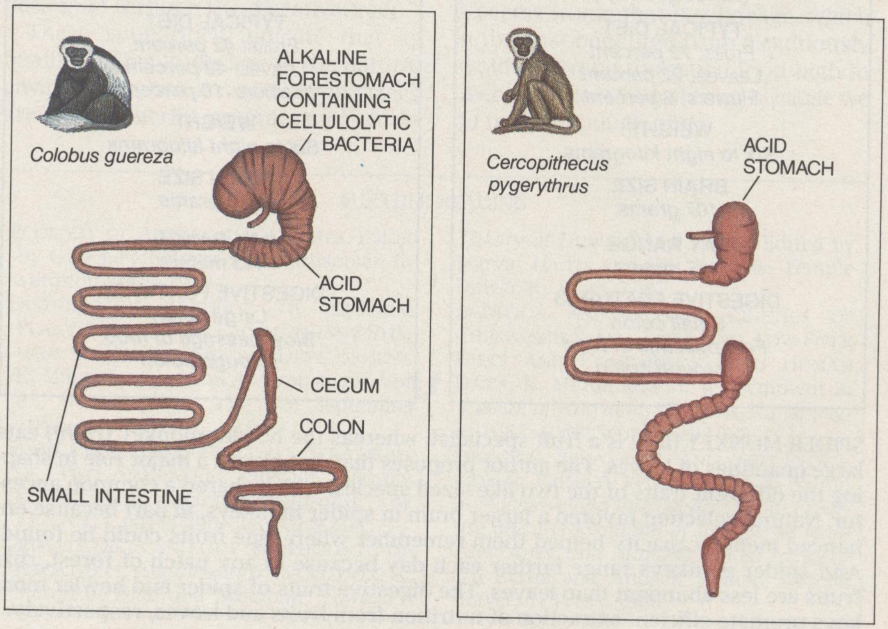
by then had truly massive jaws and molars—went extinct. Perhaps those species did so, as my colleague Montague W. Demment of the University of California at Davis speculates, because they were outcompeted by the digestively specialized ungulates (hoofed animals).

The human, or *Homo,* genus emerged during the Pliocene. The first species of the genus, *H. habilis,* was similar in body size to *Australopithecus* but had a notably larger brain. This species was replaced by the even larger-brained *H. erectus* and then, in the Pleistocene, by *H. sapiens,* which has the biggest brain of all. In parallel with the increases in brain size in the *Homo* genus, other anatomic changes were also occurring. The molar and premolar teeth became smaller, and stature increased.

To me, the striking expansion of brain size in our genus indicates that we became so successful because selection amplified a tendency inherent in the primate order since its inception: that of using brain power, or behavior, to solve dietary problems. Coupled with the anatomic changes—and with the associations in living primates between larger brains and a high-quality diet—this increase also points to the conclusion that the behavioral solution was to concentrate on high-quality foods. In fact, I suspect early humans not only maintained dietary quality in the face of changing environmental conditions but even improved it.

Expansion of the brain in combination with growth in body size and a reduction in the dentition supports the notion of a high-quality diet for a couple of reasons. When one examines present-day orangutans and gorillas, it becomes clear that in our superfamily, Hominoidea (apes and humans), an increase in body size combined with *decreased* dietary quality leads to a slow-moving, fairly sedentary and unsociable ape. Yet our *Homo* ancestors apparently were mobile and sociable—more resembling the lively, social and communicative chimpanzee. Unlike orangutans and gorillas, chimpanzees feed preferentially on high-quality, energy-rich ripe fruits.

Likewise, the reduction in the molars and premolars shows that the texture of foods we ate had somehow been altered such that the dentition no longer had so much work to do. In other words, either these early humans were eating differ-



DIGESTIVE TRACT of colobine monkeys, such as that in *Colobus guereza* (*left*), is specialized: the stomach consists of two distinct compartments instead of the single chamber found in vervet monkeys (*right*) and most other primates. One of those compartments—the forestomach—is designed to extract more energy from fiber than would normally be obtainable. Colobine monkeys can thus survive on a more fibrous diet than can other primates of similar size.

ent (less fibrous, easier-to-chew) foods than was *Australopithecus,* or they were somehow processing foods to remove material that would be hard to chew and digest. Indeed, stone tools found with fossil remains of *H. habilis* indicate that even the earliest members of our genus were turning to technology to aid in the preparation of dietary items.

The probability that hominids persisted in seeking energy-rich foods throughout their evolution suggests an interesting scenario. As obtaining certain types of plant foods presumably became more problematic, early humans are thought to have turned increasingly to meat to satisfy their protein demands. One can readily envision their using sharp stone flakes to cut through tough hides and to break bones for marrow. To incorporate meat into the diet on a steady basis and also to amass energy-rich plant foods, our ancestors eventually developed a truly novel dietary approach. They adopted a division of labor, in which some individuals specialized in the acquisition of meat by hunting or scavenging and other individuals specialized in gathering plants. The foods thus acquired were saved instead of being eaten on the spot; they were later shared among the entire social unit to assure all members of a balanced diet.

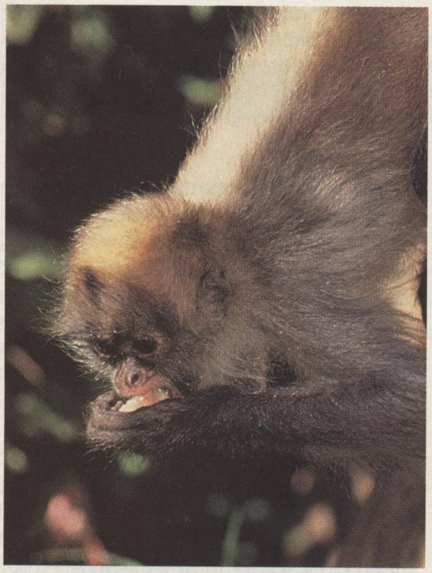
Survival of the individual thus came to depend on a number of technological and social skills. It demanded not only having a brain able to form and retain a mental map of plant food supplies but also having knowledge of how to procure or transform such supplies. In addition, survival now required an ability to recognize that a stone tool could be fashioned from a piece of a rock and a sense of how to implement that vision. And it required the capacity to cooperate with others (for instance, to communicate about who should run ahead of a hunted zebra and who behind), to defer gratification (to save food until it could be brought to an agreed site for all to share) and both to determine one's fair portion and to ensure that it was received. Such demands undoubtedly served as selective pressures favoring the evolution of even larger, more complex brains.

Similarly, spoken communication may at first have helped facilitate the cooperation needed for efficient foraging and other essential tasks. Gradually, it became elaborated to smooth the course of social interactions.

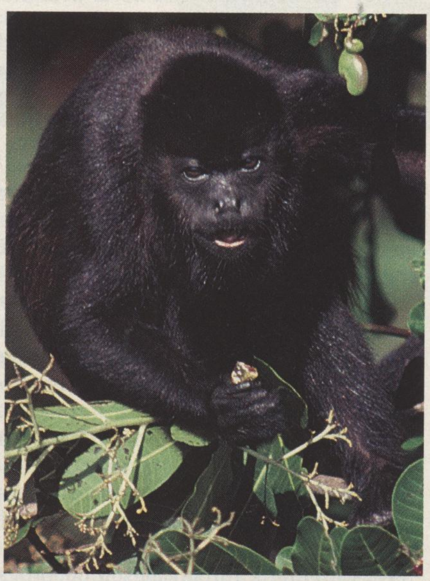
In other words, I see the emergence and evolution of the human line as stemming initially from pressures to acquire a steady and dependable supply of very high quality foods under environmental conditions in which new dietary challenges made former foraging behaviors somehow inadequate. Specialized carnivores and herbivores that abound in the African savannas were evolving at the same time as early humans, perhaps forcing them to become a new type of omnivore, one ultimately dependent on social and technological innovation and thus, to a great extent, on brain power. Edward O. Wilson of Harvard University has estimated that for more than two million years (until about 250,000 years ago), the human brain grew by about a tablespoon every 100,000 years. Apparently each tablespoonful of brain matter added in the genus *Homo* brought rewards that favored intensification of the trend toward social and technological advancement.

Although the practice of adding some amount of meat to the regular daily intake became a pivotal force in the emergence of modern humans, this behavior does not mean that people today are biologically suited to the virtually fiber-free diet many of us now consume. In fact, in its general form, our digestive tract does not seem to be greatly modified from that of the common ancestor of apes and humans, which was undoubtedly a strongly herbivorous animal.

Yet as of the mid-1980s no studies had been done to find out whether the gut functions of modern humans were in fact similar to those of apes. It was possible that some functional differenc-



SPIDER MONKEY
(*Ateles geoffroyi*)
TYPICAL DIET
Fruits: ***72 percent***
Leaves: ***22 percent***
Flowers: ***6 percent***
WEIGHT
Six to eight kilograms
BRAIN SIZE
107 grams
DAY RANGE
915 meters
DIGESTIVE FEATURES
Small colon
Fast passage of food through colon



HOWLER MONKEY
(*Alouatta palliata*)
TYPICAL DIET
Fruits: ***42 percent***
Leaves: ***48 percent***
Flowers: ***10 percent***
WEIGHT
Six to eight kilograms
BRAIN SIZE
50.3 grams
DAY RANGE
443 meters
DIGESTIVE FEATURES
Large colon
Slow passage of food through colon

SPIDER MONKEY (*left*) is a fruit specialist, whereas the howler monkey (*right*) eats large quantities of leaves. The author proposes that diet played a major role in shaping the different traits of the two like-sized species, which shared a common ancestor. Natural selection favored a larger brain in spider monkeys, in part because enhanced mental capacity helped them remember where ripe fruits could be found. And spider monkeys range farther each day because in any patch of forest, ripe fruits are less abundant than leaves. The digestive traits of spider and howler monkeys promote efficient extraction of nutrition from fruits and leaves, respectively.

es existed, because anatomic evidence had shown that despite similarity in the overall form of the digestive tract, modern humans have a rather small tract for an animal of their size. They also differ from apes in that the small intestine accounts for the greatest fraction of the volume of the human digestive tract; in apes the colon accounts for the greatest volume.

To better understand the kind of diet for which the human gut was adapted, Demment and I decided to compare human digestive processes with those of the chimpanzee, our closest living relative. We hoped to determine whether, over the course of their respective evolutionary histories, humans and chimpanzees had diverged notably in their abilities to deal with fiber. (We were greatly encouraged in this effort by the late Glynn Isaac, who was then at the University of California at Berkeley.)

The feeding habits of chimpanzees are well known. Despite their skill in capturing live prey (particularly monkeys), these apes actually obtain an estimated 94 percent of their annual diet from plants, primarily ripe fruits. Even though the fruits chimpanzees eat tend to be rich in sugar, they contain far less pulp and considerably more fiber and seeds than do the domesticated fruits sold in our supermarkets. Hence, I calculated that wild chimpanzees take in hundreds of grams of fiber each day, much more than the 10 grams or less the average American is estimated to consume.

Various excellent studies, including a fiber project at Cornell University, had already provided much information about fiber digestion by humans. At one time, it was believed that the human digestive tract did not possess microbes capable of degrading fiber. Yet bacteria in the colons of 24 male college students at Cornell proved quite efficient at fermenting fiber found in a variety of fruits and vegetables. At their most effective, the microbial populations broke down as much as three quarters of the cell-wall material that the subjects ingested; about 90 percent of the volatile fatty acids that resulted were delivered to the bloodstream.

Following the example of the Cornell study, Demment and I assessed the efficiency of fiber breakdown in chimpanzees fed nutritious diets containing varying amounts of fiber. Demment handled the statistical analyses, and I collected raw data. How dry that sounds in comparison to the reality of the experience! At the Yerkes Primate Center in Atlanta, I whiled away the summer with six extremely cross chimpanzees that never missed an opportunity to pull my hair, throw fecal matter and generally let me know they were underwhelmed by our experimental cuisine.

BURGER AND FRIES, like many popular foods eaten in the U.S., bear little resemblance to the fruits and leaves most primates have emphasized since the inception of our order. Early humans, too, are thought to have consumed large quantities of plant foods. Hence, modern diets often diverge greatly from those to which the human body may be adapted.

Our results showed that the chimpanzee gut is strikingly similar to the human gut in the efficiency with which it processes fiber. Moreover, as the fraction of fiber in the diet rises (as would occur in the wild during seasonal lulls in the production of fruits or immature leaves), chimpanzees and humans speed the rate at which they pass food through the digestive tract.

These similarities indicate that as quality begins to decline in the natural environment, humans and chimpanzees are evolutionarily programmed to respond to this decrease by increasing the rate at which food moves through the tract. This response permits a greater quantity of food to be processed in a given unit of time; in so doing, it enables the feeder to make up for reduced quality by taking in a larger volume of food each day. (Medical research has uncovered another benefit of fast passage. By speeding the flow of food through the gut, fiber seems to prevent carcinogens from lurking in the colon so long that they cause problems.)

If the human digestive tract is indeed adapted to a plant-rich, fibrous diet, then this discovery lends added credence to the commonly heard assertion that people in highly technological societies eat too much refined carbohydrate and too little fiber. My work offers no prescription for how much fiber we need. But certainly the small amount many of us consume is far less than was ingested by our closest human ancestors.

More recently, my colleagues and I have analyzed plant parts routinely eaten by wild primates for their content of various constituents, including vitamin C and pectin. Pectin, a highly fermentable component of cell walls, is thought to have health benefits for humans. Our results suggest that diets eaten by early humans were extremely rich in vitamin C and contained notable pectin. Again, I do not know whether we need to take in the same proportions of these substances as wild primates do, but these discoveries are provocative.

To a major extent, the emergence of modern humans occurred because natural selection favored adaptations in our order that permitted primates to focus their feeding on the most energy-dense, low-fiber diets they could find. It seems ironic that our lineage, which in the past benefited from assiduously avoiding eating too much food high in fiber, may now be suffering because we do not eat enough of it.

FURTHER READING

ECOLOGY OF ARBOREAL FOLIVORES. Edited by G. Gene Montgomery. Smithsonian Institution Press, 1978.

DISTRIBUTION PATTERNS OF TROPICAL PLANT FOODS AS AN EVOLUTIONARY STIMULUS TO PRIMATE MENTAL DEVELOPMENT. K. Milton in *American Anthropologist*, Vol. 83, No. 3, pages 534–548; September 1981.

FOOD CHOICE AND DIGESTIVE STRATEGIES OF TWO SYMPATRIC PRIMATE SPECIES. K. Milton in *American Naturalist*, Vol. 117, No. 4, pages 496–505; April 1981.

PRIMATE DIETS AND GUT MORPHOLOGY: IMPLICATIONS FOR HOMINID EVOLUTION. K. Milton in *Food and Evolution: Toward a Theory of Human Food Habits.* Edited by Marvin Harris and Eric B. Ross. Temple University Press, 1987.

DIGESTION AND PASSAGE KINETICS OF CHIMPANZEES FED HIGH AND LOW-FIBER DIETS AND COMPARISON WITH HUMAN DATA. K. Milton and M. W. Demment in *Journal of Nutrition*, Vol. 118, No. 9, pages 1082–1088; September 1988.

FORAGING BEHAVIOUR AND THE EVOLUTION OF PRIMATE INTELLIGENCE. K. Milton in *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans.* Edited by Richard Byrne and Andrew Whiten. Oxford University Press, 1988.