The Western Lowland Gorilla Diet Has Implications for the Health of Humans and Other Hominoids[1,2]

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ABSTRACT We studied the western lowland gorilla diet as a possible model for human nutrient requirements with implications for colonic function. Gorillas in the Central African Republic were identified as consuming over 200 species and varieties of plants and 100 species and varieties of fruit. Thirty-one of the most commonly consumed foods were collected and dried locally before shipping for macronutrient and fiber analysis. The mean macronutrient concentrations were (mean ± SD, g/100 g dry basis) fat 0.5 ± 0.4, protein 11.8 ± 8.2, available carbohydrate 7.7 ± 6.3 and dietary fiber 74.0 ± 12.9. Assuming that the macronutrient profile of these foods was reflective of the whole gorilla diet and that dietary fiber contributed 6.28 kJ/g (1.5 kcal/g), then the gorilla diet would provide 810 kJ (194 kcal) metabolizable energy per 100 g dry weight. The macronutrient profile of this diet would be as follows: 2.5% energy as fat, 24.3% protein, 15.8% available carbohydrate, with potentially 57.3% of metabolizable energy from short-chain fatty acids (SCFA) derived from colonic fermentation of fiber. Gorillas would therefore obtain considerable energy through fiber fermentation. We suggest that humans also evolved consuming similar high foliage, high fiber diets, which were low in fat and dietary cholesterol. The macronutrient and fiber profile of the gorilla diet is one in which the colon is likely to play a major role in overall nutrition. Both the nutrient and fiber components of such a diet and the functional capacity of the hominoid colon may have important dietary implications for contemporary human health. J. Nutr. 127: 2000–2005, 1997.

KEY WORDS: • *western lowland gorilla* • *dietary fiber* • *short-chain fatty acids* • *dietary evolution* • *coronary heart disease* • *cancer*

Although much is known of the chemical composition of foods eaten by the great apes (Rogers et al. 1990, Tutin and Fernandez 1993, Watts 1984), no attempt has been made to express their macronutrient intakes in terms that allow comparison with human diets. We believe that an understanding of the diets eaten by the great apes might provide insights into the diet eaten by a common ancestor, which thus influenced the evolution of the human genome. Such knowledge may be valuable in understanding human dietary requirements. Anatomically, the digestive tracts of humans and great apes are very similar (Stevens and Hume 1995). It has also been estimated that the great apes differ in genetic makeup by <3% among themselves and that the difference between humans and the great apes is of the same magnitude (Sibley and Ahlquist 1984 and 1987). In addition, the great apes have many dietary factors in common, namely, largely vegetarian diets with high foliage and fruit consumption (MacKinnon 1971, McGrew et al. 1988, Tutin and Fernandez 1993). These conclusions are based on tracking and direct observation of feeding practices and fecal analysis. This dietary characteristic of high foliage consumption has been developed still further in certain old world monkeys (colobus monkeys) who have evolved foregut fermentation chambers analogous to herbivorous ungulates (Waterman et al. 1980). In terms of high levels of plant consumption, great apes differ from humans, and western humans in particular, at a time when, ironically, health recommendations all point to the increased consumption of fruit and vegetables (Health Canada 1992, Suber et al. 1992).

Therefore, to assess the gorilla diet and compare the macronutrient profile with human diets, we studied food selection by the western lowland gorilla (*Gorilla gorilla gorilla*). We collected commonly consumed foods, which were analyzed by the same methods as those used for human diets. From these data, we derived a macronutrient profile of the western lowland gorilla diet using energy values for fiber (Livesey and Elia 1995) that have been applied to humans.

MATERIALS AND METHODS

Lowland gorillas of the Bai Hokou study area, Haute Sangh Prefecture, Dzanga-Ndoki National Park in the southwestern part of the Central African Republic (**Fig. 1**) were tracked for 10 mo, from July 1988 to April 1989, and found to eat >200 species and varieties of

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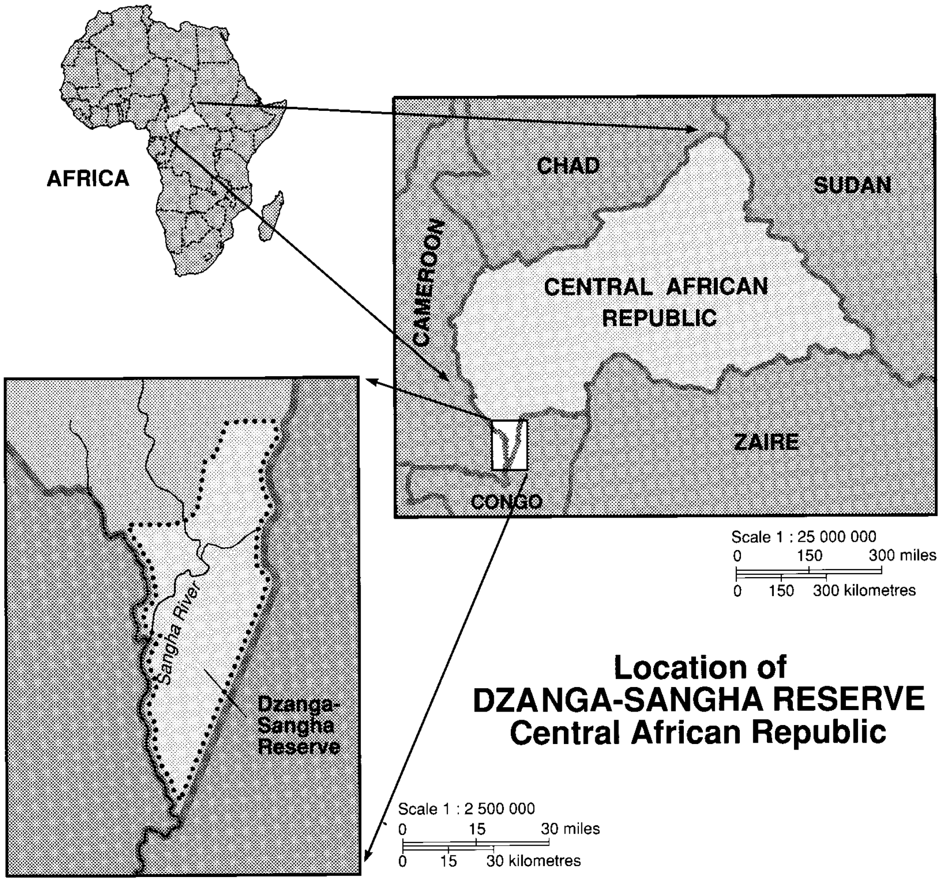

FIGURE 1 Study site for food consumption by lowland gorillas in Dzanga-Ndoki National Park, Central African Republic.

vegetation and 100 species and varieties of fruit. Identification of foods eaten was based on standard methods, a combination of direct observation and fecal analysis (Goodall 1977, Moreno-Black 1978). Gorilla fecal samples were collected from nest sites and feeding trails throughout the study area, placed in polyethylene bags and labeled. Each sample was sorted through by one investigator (R.W.C.) and a team of two to five Aka botanists. All identifiable components of each sample were separated, given an Aka name if known, listed in a notebook, and saved as voucher specimens. Later this information was entered into a computer and assessed using the Paradox data base program (Borland International, Scotts Valley, CA). Fruit, seeds and hulls, leaf fragments, fibers, stems, bark and vines and invertebrate remains could be identified. No attempt was made to quantify the volume of foods ingested by extrapolation from fecal remains. Vouchers of each item were stored in polyethylene bags, labeled and compared with herbarium vouchers of each species. Identification of all plant vouchers is being undertaken by the Missouri Botanical Gardens and Kew Gardens. Until in-depth comparison of the remains collected from fecal samples with properly identified herbarium samples can be made, many of these observations from fecal material will remain tentative.

Samples of identified foods were collected, oven dried in the field, packaged and shipped to the Wildlife Conservation Society (New York, NY) and ground through a 20-mesh screen (2 mm) in a Wiley mill. Twenty-six samples of leaves, stems and vines, and five fruit from different plant species, the most common foods eaten by gorillas, were then analyzed for neutral detergent fiber (NDF)[4] and acid detergent fiber (ADF) (Van Soest et al. 1991) in New York; total dietary fiber and macronutrient content were determined in Toronto by AOAC methods for fat, protein and fiber (AOAC 1980, Prosky et al. 1988). Available carbohydrate was determined by difference. Data are expressed as a percentage of dry weight. To assess the possible relative contribution of each macronutrient as a percentage of total energy intake, we used a conservative conversion factor of 6.28 kJ/g (1.5 kcal/g) for dietary fiber (Cummings 1981, Livesey and Elia 1995, McBurney 1994, McNeil 1984).

Results are presented as mean ± SD; the significance of differences in macronutrients between the main classes of foods (leaves, stems, vine and fruit) was analyzed by ANOVA and Student-Newman-Keuls test (Fleiss 1986, Searle, 1971) using SAS (SAS Institute 1985).

RESULTS

Foods were low in fat (g/100 g dry matter) (0.5 ± 0.4; range 0.1–1.8) and available carbohydrate (7.7 ± 6.3; range 0–22.4), varied in protein (11.8 ± 8.2; range 1.7–30.0), high in total dietary fiber (74.0 ± 12.9; range 52.0–96.5), NDF (71.7 ± 13.2, range 49.6–94.2) and ADF (53.3 ± 16.4, range 17.5–83.8) and had a mean ash concentration of 6.1 ± 2.6 (range 2.3–13.9) (**Table 1**). Vines contained higher concentrations of ash than leaves and stems ($P < 0.05$), and both leaves and vines were higher in protein than stems and fruit ($P < 0.05$). Stems and fruit contained more total dietary fiber than leaves and vines ($P < 0.05$) (Table 1). The overall correlation between total dietary fiber and neutral detergent fiber in these foods was significant ($r = 0.75$, $n = 27$, $P < 0.001$). Assuming that the 31 foods selected as commonly consumed were representative of the diet as a whole, the metabolizable energy value per 100 g dry weight would be 346 kJ (83 kcal), and the theoretical macronutrient profile of the gorilla diet in terms of metabolizable energy, without accounting for colonic fiber fer-

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[4] Abbreviations used: ADF, acid dergent fiber; NDF, neutral detergent fiber; SCFA, short-chain fatty acids.

TABLE 1

Macronutrient composition of 31 foods commonly consumed by the western lowland gorilla

Vegetation[1,2]								
Common name	Species name	Ash	Protein	Fat	Available carbohydrate	Total dietary fiber[3]	Neutral detergent fiber	Acid detergent fiber
					g/100 g dry weight			
Leaves								
Baturro	*	10.1	30.0	0.4	5.0	54.6	51.9	29.0
Demelle	*	6.0	14.5	1.3	18.0	60.1	50.3	31.1
Ebandja	*Diospyros bipindensis* Gurke	3.8	11.6	0.7	22.4	61.5	66.8	59.0
Egumdu	*	7.6	15.4	0.9	12.7	63.5	71.4	58.1
Gima	*	7.8	22.2	0.1	0.6	69.3	76.5	61.0
Gombe	*Deltis* sp.	9.8	14.9	0.2	4.8	70.4	80.1	64.4
Indolu	*Whitfieldra elongata*	13.9	26.8	0.5	6.6	52.3	51.6	29.59
Koko	*Gnetum africanum*	4.6	7.2	0.3	0.2	87.8	58.9	40.1
Mogombagumba	*	7.1	17.0	1.1	15.3	59.6	—	—
Molindu	*	4.1	13.7	0.2	19.0	63.1	60.0	47.7
Mosarakosarako	*	5.5	18.3	0.7	4.3	71.2	77.1	55.6
Mopusupusu	*	7.5	15.1	0.7	6.9	69.7	70.9	55.0
Ngala	*Deilschimiedi*	6.0	14.7	0.5	1.0	77.8	76.5	61.0
Ngambe	*Cananum schwan*	3.1	10.9	0.6	16.8	68.6	57.6	45.3
Ngombegombe	*	8.5	15.5	0.9	9.5	65.7	—	—
Boyo	*Entrandrophragma cylindricum*	9.5	28.7	0.4	9.4	52.0	49.6	30.2
Mean ± SD		$7.2^{ab} \pm 2.8$	$17.3^{a} \pm 6.5$	0.6 ± 0.3	9.5 ± 7.1	$65.5^{a} \pm 9.4$	64.2 ± 11.2	47.7 ± 13.3
Stems								
Bokoko	*Klainedoxa oabonensis*	2.3	2.7	0.5	5.5	88.9	—	—
Dembelembe	*	6.0	2.9	0.3	4.5	86.4	87.2	66.6
Djombo	*	6.6	2.1	0.2	7.9	83.3	85.3	63.5
Njokoko 14	*Aframonum* sp.	4.5	1.9	0.3	3.9	89.4	72.9	17.5
Nuokoko 8	*Aframonum* sp.	2.4	1.7	0.1	0.0	96.5	86.5	69.5
Njokoko 9	*Aframonum* sp.	3.9	2.1	0.2	5.9	87.9	87.9	68.8
Nojombo 5	*Aframonum* sp.	6.4	4.0	0.2	5.7	83.7	87.3	67.5
Nzilgi	*Haumania anedelmaniana*	5.3	10.0	0.3	5.3	79.1	56.0	28.3
Vines								
Mean (± SD)		$4.7^{b} \pm 1.7$	$3.4^{b} \pm 2.8$	0.3 ± 0.1	4.8 ± 2.3	$86.9^{b} \pm 5.2$	80.4 ± 12.0	54.5 ± 21.9
Koko	*Gnetum africanum*	8.7	21.5	0.6	10.1	59.3		
Mongenje	*Orthopichonia*	8.6	10.2	0.6	6.9	73.6	79.5	64.6
Mean ± SD		$8.7^{a} \pm 0.1$	$15.9^{a} \pm 8.0$	0.6 ± 0.0	8.5 ± 2.3	$66.5^{a} \pm 10.1$	79.5	64.6
Fruit								
Gumu	*Psidium guajava*	5.2	6.9	1.8	5.3	80.7	76.6	67.8
Guruma	*Duboscia macrocarpa*	3.4	5.3	1.1	19.7	70.5	65.5	54.5
Mokandja	*Synsepalum stipulatum*	2.8	4.2	0.2	0.0	93.4	94.2	83.8
Payo	*Irvingia excelsa*	4.9	4.5	0.6	4.2	85.7	75.0	58.8
Ekombolo	*Tetraplaura teraptera*	4.4	8.3	0.3	0.0	88.9	82.4	61.9
Mean ± SD		$4.1^{b} \pm 1.0$	$5.8^{b} \pm 1.7$	0.8 ± 0.7	5.8 ± 8.1	$83.8^{b} \pm 8.8$	78.7 ± 10.6	65.4 ± 1.4
Overall mean ± SD		6.1 ± 2.6	11.8 ± 8.2	0.5 ± 0.4	7.7 ± 6.3	74.0 ± 12.9	71.7 ± 13.3	53.3
Overall energy,[4] *kJ* (kcal)			197.0 (47.1)	20.3 (4.9)	128.2 (30.6)	464.5 (111.0)		

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[1] Local Aka pygmies' vegetation name.

[2] *Not classified.

[3] Total dietary fiber analyzed by method of Prosky et al. (1988), fat and protein by AOAC methods (1980); available carbohydrate determined by difference; neutral and acid detergent fiber by method of Van Soest et al. (1991).

[4] Overall mean total energy is 810.1 kJ (193.6 kcal) per 100 g dry weight, using Atwater factors for macronutrients and assuming 6.3 kJ (1.5 kcal) per gram dietary fiber.

[a,b] Means for particular components bearing different superscripts differ significantly ($P < 0.05$) by Student-Neuman-Keuls multiple range test.

mentation, would be as follows: fat 5.9%, protein 57.0% and available carbohydrate 37.1% (**Fig. 2**). However, if dietary fiber provides at least 6.28 kJ/g (1.5 kcal/g) (Cummings 1981, Livesey and Elia 1995, McBurney 1994, McNeil 1984), the resulting energy value would be 810 kJ/100 g dry matter (194 kcal) and the macronutrient profile of the western lowland gorilla diet, as a percentage of daily energy intake, would be fat 2.5%, protein 24.3%, carbohydrate 15.8% and short-chain fatty acids (SCFA) 57.3% as shown in Figure 2. If a higher energy value was attributed to fiber, on the basis that leafy vegetable fibers are among the more readily fermentable (Cummings 1982, McNeil 1984), then the increased energy retrieved from colonic fermentation of fiber would further reduce the relative contribution of the macronutrients, fat, protein and carbohydrate as a percentage of total energy (Fig. 2).

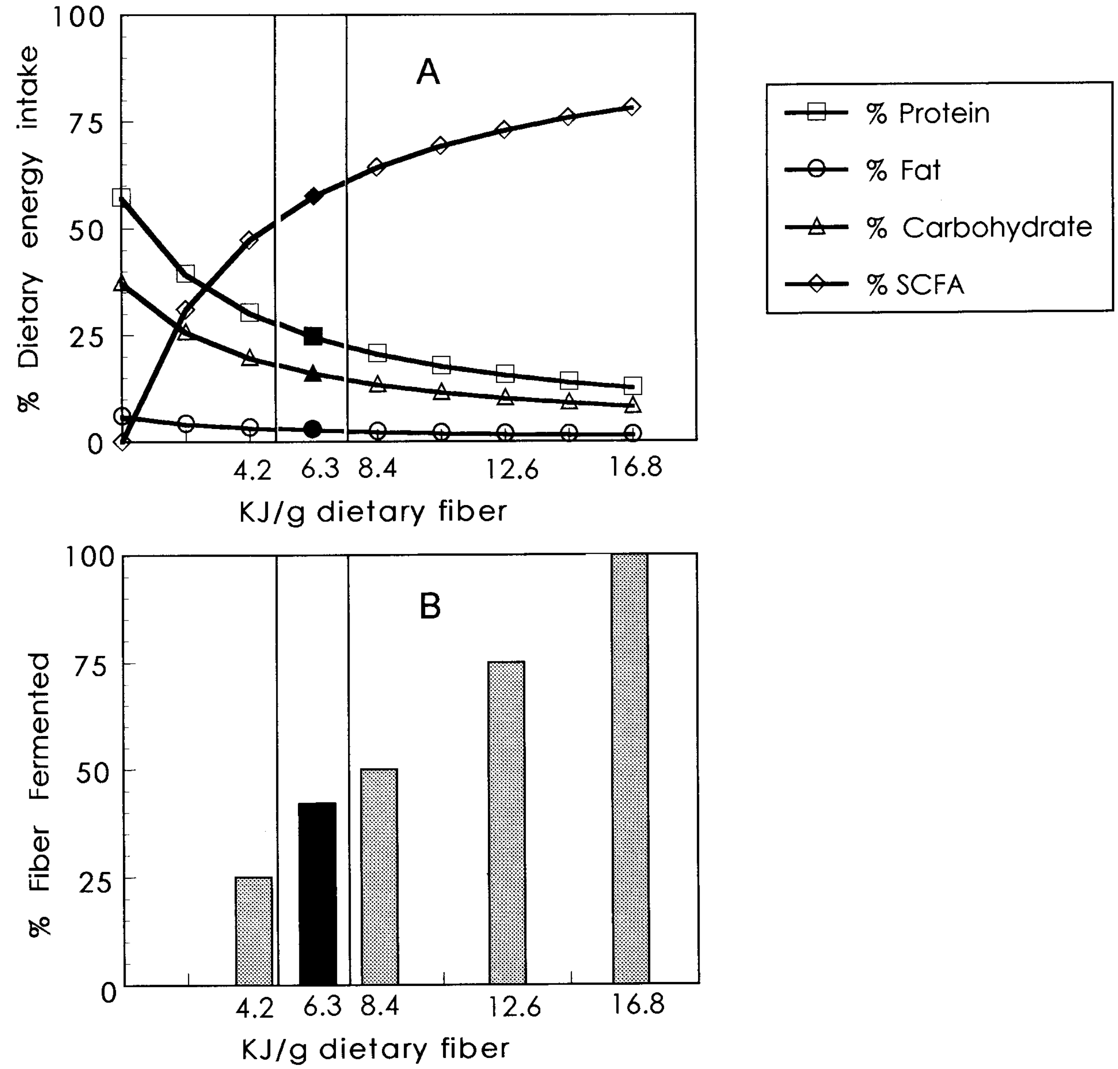

FIGURE 2 The theoretical effect of different levels of fiber fermentation on the macronutrient profile of the gorilla diet. The points trace the theoretical reduction in energy contribution from protein, fat and carbohydrate as increasing amounts of energy are derived from fiber through the production of short-chain fatty acids (SCFA) (*top panel*). The bars in the *bottom panel* indicate the theoretical increase in energy value per gram of fiber, dependent on the degree to which fiber is fermented. At zero fermentation of fiber, the energy intake from fat, protein and carbohydrate (*top panel*) reflects the proportion of these nutrients in the gorilla diet (0.5 g fat, 11.8 g protein and 7.7 g available carbohydrate per 100 g dry weight). Values are then calculated for the macronutrient profile, assuming that an increasing proportion of the 74.0 g fiber per 100 g dry weight is fermented to SCFA with increasing energy available from SCFA (up to 100% fermented, i.e., 16.8 kJ/g fiber). The black bar (*bottom panel*) and solid symbols (*top panel*) represent our suggested level of fermentation and macronutrient profile, respectively, for the gorilla diet on the assumption that 6.3 kJ (1.5 kcal) per gram of fiber is a conservative figure for the energy value of fiber (1 kcal = 4.18 kJ).

DISCUSSION

These data indicate that the macronutrient profile of the gorilla diet is likely to be very low in fat and high in dietary fiber. Because there is a virtual absence of foods of animal origin, dietary cholesterol intake is likely to be negligible. The macronutrient profile of this diet therefore far exceeds current guidelines for the management of serum lipids in western populations (Expert Panel, National Cholesterol Education Program 1993).

The high level of consumption of plant foods by gorillas is shared by other great apes (MacKinnon 1971, Tutin and Fernandez 1993), and the macronutrient profile of their diets is likely to be similar to that of gorillas. Only chimpanzees consume and occasionally hunt vertebrates. Despite this omnivorous behavior, which more clearly resembles *Homo sapiens* than the other great apes, the intake of food of animal origin is still at a very low level (de Waal 1995) with only 1.7% of chimpanzee feces providing evidence of animal food consumption (Tutin and Fernandez 1993).

The data also suggest an important nutritional role for the hominoid colon. The high fiber content of the foods eaten provide a substrate for bacterial fermentation in the colon with SCFA generation. This process in turn increases the energy value of the diet and reduces the relative contribution of the three macronutrients.

Although no data have been available for the gorilla until now, other great apes are very effective hindgut fermentors (Milton and Demment 1988, Van Soest 1994). The sacculated colon of humans led Elliot and Barclay-Smith (1904) to conclude that the colonic structure of humans is closer to that of a herbivore than to an omnivore. Studies in humans have indicated that dietary fiber is 35–100% fermentable, depending on the fiber type, with 80% fermentation of leafy vegetables (e.g., cabbage) (Cummings 1982). Approximately

75% of the energy resulting from fermentation can be used by the host in the form of absorbed SCFA: acetate, propionate and butyrate (Cummings 1981, McNeil 1984). On the basis of human feeding studies, including those involving fermentation of ileostomy effluent, we selected 6.28 kJ/g (1.5 kcal/g) as a conservative energy value for dietary fiber that might be applied to gorilla diets (McBurney 1994, Livesey and Elia 1995). In view of the very high fiber content of gorilla foods, the gorilla colon thus becomes a potentially important organ for dietary energy retrieval.

Mountain gorillas (*Gorilla gorilla beringei*) (Fossey 1974, Watts 1984) eat foliage throughout the year, whereas the western lowland gorillas (e.g., in Gabon) consume less foliage and more fruit in the wet season (Williamson et al. 1988) as do sympatric chimpanzees (Tutin and Fernandez 1993). Geographic and seasonal variation may influence the extent to which hindgut fermentation is likely to play a part in colonic retrieval of dietary energy by the great apes, depending on variation in fiber intake. Nevertheless, these variations are relatively small compared with the difference between the diets of modern western man and the western lowland gorilla. Despite a genetic difference of as little as 2% between humans and gorillas (Sibley and Ahlquist 1984), the human colon may contribute as little as 2–9% to total energy (Livesey and Elia 1995, McBurney 1994, McNeil 1984) compared with possibly 30–60% for the gorilla. Assuming that the diets of the great apes are closer to the diet on which our common ancestor evolved before the clade split 4.5–7.5 million years ago (Pilbeam 1984), the high fiber folifrugivorous diet may have important implications for both human health and the health of captive great apes.

High ADF and lignin levels have been found in the forage of topical ruminant herbivores including the rhinoceros. Our data are in agreement with the protein (mean 11.8 ± 8.2 g/100 g dry weight) and available carbohydrate concentrations (mean 7.7 ± 6.3 g/100 g dry weight) documented by Waterman et al. (1980) for the leaves and shoots consumed in Uganda and Cameroon rainforests by colobus monkeys. However, the colobus monkey has a ruminant forestomach from which only foods that have been relatively highly digested by the enzymes of the resident microflora are allowed to pass to the rest of the gut (Hungate 1975). What fermentation takes place in the gorilla must do so in the colon. The concentrations of condensed tannins and to a lesser extent total phenolics have been shown to be predictors of digestibility possibly related to inactivation of microbial enzymes by tannins (Waterman et al. 1980). We did not measure tannins, but these may be important determinants of fiber utilization by both fore- and hindgut fermentors.

Low fat diets, high in fiber, vegetable protein and plant sterols are all associated with reduced serum cholesterol levels in humans (Carroll 1983, Howard and Kritchevsky 1997, Jenkins et al. 1993, Kritchevsky 1979, Miettinen et al. 1995). Captive gorillas have high serum cholesterol levels, 281–311 mg/dL, (7.27–8.04 mmol/L) (McGuire et al. 1989) and suffer premature cardiovascular disease when they consume low fiber diets that often contain meat and eggs (Cousins 1979). It has been suggested that ulcerative colitis in humans is due to a lack of energy normally provided by SCFA for colonic mucosal repair (Roediger 1982). The fiber-derived SCFA, butyrate, is a preferred energy substrate for colonic mucosal cells and may have antineoplastic properties (Roediger 1982, Weaver et al. 1988). It is relevant that ulcerative colitis figures prominently among the intestinal disorders of great apes in captivity consuming relatively low fiber diets (Scott and Kemer 1975). High fiber diets may also improve colonic health by increasing fecal bulk and water-holding capacity, shortening transit time and decreasing concentrations of toxic substances including bile acids (McKeigue et al. 1989) and free ammonia (Visek 1978). Leafy vegetables are also rich sources of antioxidants including β-carotene, vitamin C, lignans and flavonoids, some of which have been associated with reduced rates of cardiovascular disease in humans (Hertog et al. 1993). High folate intakes, derived from leafy vegetation by the great apes, may have implications in the prevention of cardiovascular disease (Selhub et al. 1995), colon cancer (Kim and Mason 1995) and spina bifida (Wald et al. 1991) in humans. Natural gorilla feeding patterns of "foraging" throughout the day may also have health benefits because increased feeding frequency, "nibbling," has been shown in human studies to reduce LDL cholesterol and the postprandial insulin response (Jenkins et al. 1989).

In conclusion, we believe that the diets of the great apes in the wild may provide insights into the nature of the foods that hominoids evolved to eat and that have shaped human nutrient requirements for health and the function of the hominoid gut.

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