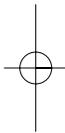


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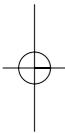
## Implications of Plio-Pleistocene Hominin Diets for Modern Humans

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LOREN CORDAIN



### Introduction



Within the anthropology community, there has been a long and sustained interest in the diets and eating patterns of Plio and Pleistocene hominins, primarily because these nutritional practices provide a glimpse into their varied and distinctive lifeways, activities, and cultural patterns. In contrast, until relatively recent times, the nutritional and medical communities have largely ignored anthropological dietary information for a variety of reasons, not the least of which is its perceived lack of immediate relevance to their respective disciplines. Beginning in the mid 1980s, a series of key publications in mainstream medical and nutrition journals (Eaton and Konner, 1985; Eaton, Konner, and Shostak, 1988; Eaton and Nelson, 1991; Eaton, 1992) triggered an increased awareness of the relevance of ancestral diets to the health and well being of modern peoples. Because of that insight as well as others gleaned from a variety of medical branches of learning, an entirely new academic discipline was born, dubbed “evolutionary medicine” (Williams and Neese, 1991), or sometimes “Darwinian medicine” (Williams and Neese, 1991). The primary tenet of evolutionary medicine is that the profound changes in the environment (e.g., in diet and other lifestyle conditions), which began with the introduction of agriculture and animal husbandry approximately 10,000 years ago, occurred too recently on an evolutionary timescale for natural selection to adjust the human genome (Eaton and Konner, 1985; Williams and Neese, 1991). In conjunction with this discordance between our ancient (millions of years ago), genetically determined biology and the nutritional, cultural, and activity patterns of contemporary western populations, many of the so-called diseases of civilization have emerged (Eaton, Konner, and Shostak, , 1988; Williams and Neese, 1991).

With regard to diet and health, food staples and food-processing procedures introduced during the Neolithic and Industrial era have fundamentally altered seven crucial nutritional characteristics of ancestral hominin diets: (1) glycemic load, (2) fatty acid composition, (3) macronutrient composition, (4) micronutrient density, (5) acid/base loads, (6) sodium/potassium ratio, and (7) fiber content. Each of these nutritional factors either alone or combined with some, or all, of the remaining factors underlie the pathogenesis of a wide variety of chronic diseases and maladies that almost universally afflict people living in western, industrialized societies. Increasingly, dietary interventions and clinical trials have demonstrated the therapeutic potential of contemporary diets, which emulate one or more of the seven universal characteristics common to preagricultural diets.

## Plio-Pleistocene Hominin Diets: The Known

### An Omnivorous Diet: The Evidence

Figure 19.1 demonstrates that since the evolutionary emergence of hominins twenty or more species may have existed (Wood, 2002). Similar to historically studied hunter-gatherers (Cordain et al., 2000; Cordain et al., 2002b), there would have been no single, universal diet consumed by all extinct hominin species. Rather, diets would have varied by geographic locale, climate, and specific ecologic niche. However, a number of universal dietary characteristics and trends within preagricultural hominins have emerged, which have important health ramifications for contemporary humans.

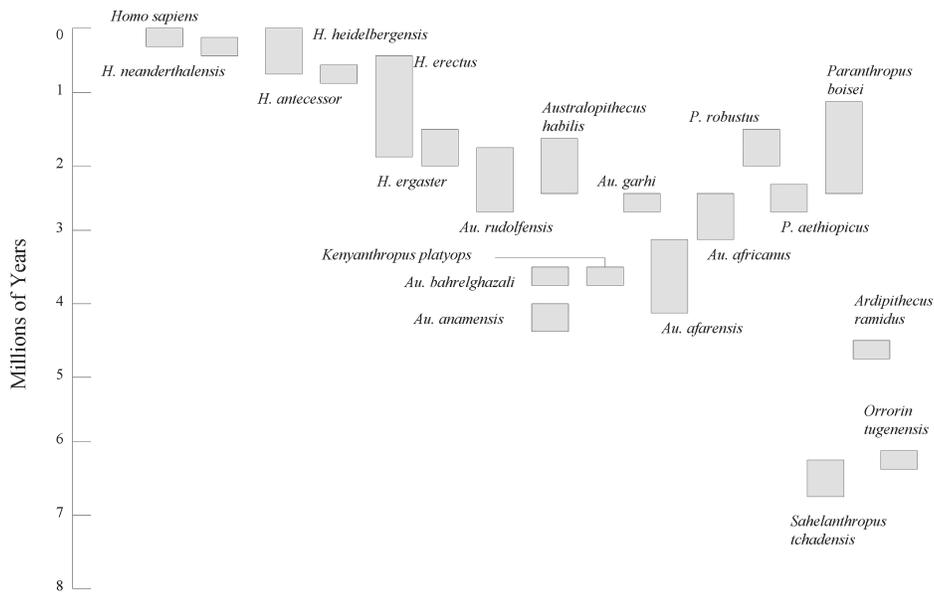


Figure 19.1 The hominin fossil record. Species are indicated with the dates of the earliest and latest fossil record. Adapted from Wood (2002).

Since the evolutionary split between hominins and pongids approximately 7 million years ago, the available evidence shows that all species of hominins ate an omnivorous diet composed of minimally processed, wild-plant, and animal foods. In support of this view is the omnivorous nature of chimpanzees, the closest living pongid link to hominins. Although chimpanzees (*Pan paniscus* and *Pan troglodytes*), our genetically closest nonhuman relatives, primarily consume a frugivorous diet, they still eat a substantial amount of meat obtained throughout the year from hunting and scavenging (Teleki, 1973; Stanford, 1996; Schoeninger, Moore, and Sept, 1999). Observational studies of wild chimpanzees demonstrate that during the dry season meat intake is about 65 g per day for adults (Stanford, 1996). Accordingly, it is likely that the very earliest hominins would have been capable of obtaining animal food through hunting and scavenging in a manner similar to chimpanzees.

Carbon isotope data also support the notion that early hominins were omnivorous. By about 3 million years ago (Mya), *Australopithecus africanus* obtained a significant portion of food from C<sub>4</sub> sources (grasses, particularly seeds and rhizomes; sedges; invertebrates, including locusts and termites; grazing mammals; and perhaps even insectivores and carnivores; van der Merwe et al., 2003). Other fossils of early African hominins, including *Australopithecus robustus* and *Homo ergaster*, maintain carbon isotope signatures characteristic of omnivores (Lee-Thorp, Thackeray, and van der Merwe, 2000; Sponheimer and Lee-Thorp, 2003). The finding of C<sub>4</sub> in *A. robustus* fossils refutes the earlier view that this hominin was vegetarian (Lee-Thorp, Thackeray, and van der Merwe, 2000).

#### Secular Increase in Animal Food: The Evidence

Beginning approximately 2.6 Mya, the hominin species that eventually led to *Homo* began to include more animal food in their diet. A number of lines of evidence support this viewpoint. First, Oldowan lithic technology appears in the fossil record 2.6 Mya (Semaw et al., 2003), and there is clear cut evidence to show that these tools were used to butcher and disarticulate animal carcasses (Bunn and Kroll, 1986; de Heinzelin et al., 1999). Stone tool cut marks on the bones of prey animals and evidence for marrow extraction appear concurrently in the fossil record with the development of Oldowan lithic technology by at least 2.5 Mya (de Heinzelin et al., 1999). It is not entirely clear which specific early hominin species or group of species manufactured and used these earliest of stone tools; however, *Australopithecus garhi* may have been a likely candidate (Asfaw et al., 1999; de Heinzelin et al., 1999).

The development of stone tools and the increased dietary reliance on animal foods allowed early African hominins to colonize northern latitudes outside of Africa where plant foods would have been seasonally restricted. Early *Homo* skeletal remains and Oldowan lithic technology appear at the Dmanisi site in the Republic of Georgia (40° N) by 1.75 Mya (Vekua et al., 2002), and more recently Oldowan tools dating to 1.66 Mya have been discovered at the Majuangou site in North China (40° N; Zhu et al., 2004). Both of these tool-producing hominins would likely have consumed considerably more animal food than prelithic hominins living in more temperate African climates.

In addition to the fossil evidence suggesting a trend for increased animal food consumption, hominins may have experienced a number of genetic adaptations to

animal-based diets early on in our genus's evolution analogous to those of obligate carnivores such as felines. Carnivorous diets reduce evolutionary selective pressures that act to maintain certain anatomical and physiological characteristics needed to process and metabolize high amounts of plant foods. In this regard, hominins, like felines, have experienced a reduction in gut size and metabolic activity along with a concurrent expansion of brain size and metabolic activity as they included more energetically dense animal food into their diets (Leonard and Robertson, 1994; Aiello and Wheeler, 1995; Cordain, Watkins, and Mann, 2001). Further, similar to obligate carnivores (Pawlosky, Barnes, and Salem, 1994), humans maintain an inefficient ability to chain elongate and desaturate 18 carbon fatty acids to their product 20 and 22 carbon fatty acids (Emken et al., 1992). Since 20 and 22 carbon fatty acids are essential cellular lipids, then evolutionary reductions in desaturase and elongase activity in hominins indicate that preformed dietary 20 and 22 carbon fatty acids (found only in animal foods) were increasingly incorporated in lieu of their endogenously synthesized counterparts derived from 18 carbon plant fatty acids. Finally, our species has a limited ability to synthesize the biologically important amino acid, taurine, from precursor amino acids (Sturman et al., 1975; Chesney et al., 1998), and vegetarian diets in humans result in lowered plasma and urinary concentrations of taurine (Laidlaw et al., 1988). Like felines (Knopf et al., 1978; MacDonald, Rogers, and Morris, 1984), the need to endogenously synthesize taurine may have been evolutionarily reduced in humans because exogenous dietary sources of preformed taurine (found only in animal food) had relaxed the selective pressure formerly requiring the need to synthesize this conditionally essential amino acid.

### **Plio-Pleistocene Hominin Diets: The Uncertain**

#### **The Uncertain: How Much Plant Food, How Much Animal Food?**

There is little evidence to the contrary that animal foods have always played a significant role in the diets of all hominin species. Increased reliance on animal foods not only allowed for enhanced encephalization and its concomitant behavioral sophistication (Leonard and Robertson, 1994; Aiello and Wheeler, 1995; Cordain, Watkins, and Mann, , 2001), but this dietary practice also permitted colonization of the world outside of Africa. An unresolved issue surrounding Plio-Pleistocene diets is the relative amounts of plant and animal foods that were typically consumed.

Before the advent of Oldowan lithic technology about 2.6 Mya, quantitative estimates of hominin energy intake from animal food sources are unclear, other than they were likely similar to, or greater than, estimated values (4%–8.5% total energy) for chimpanzees (Sussman, 1978; Stanford, 1996). Although all available data point to increasing animal food consumption following the arrival of lithic technology, the precise contribution of either animal or plant food energy to Plio-Pleistocene hominin diets is not known. Obviously, then as now, no single (animal/plant) subsistence ratio would have been necessarily representative of all populations or species of hominins. However, there are a number of lines of evidence which suggest more than half (>50%) of the average daily energy intake for most

Paleolithic hominin species and populations of species was obtained from animal foods.

Richards, Pettitt, and colleagues (2000) have examined stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in two Neanderthal specimens (~28,000—29,000 years BP) from Vindija Cave in northern Croatia and contrasted these isotopic signatures to those in fossils of herbivorous and carnivorous mammals from the same ecosystem. The analysis demonstrated that Neanderthals, similar to wolves and arctic foxes, behaved as top-level carnivores, obtaining all of their protein from animal sources (Richards, Pettitt, et al., 2000). A similar analysis was made of five Upper Paleolithic *Homo sapiens* specimens dated to the Upper Paleolithic (~11,700–12,380 years BP) from Gough’s and Sun Hole Caves in Britain (Richards, Hedges, et al. 2000). The data indicated these hunter-gatherers were consuming animal protein year-round at a higher trophic level than the arctic fox.

Both studies by Richards, Hedges, and colleagues (2000) and Richards, Pettitt, and colleagues (2000) could be criticized as not being representative of typical hominin diets, as these two species lived in climates and ecosystems that fostered an abundance of large, huntable mammals, which were preyed on preferentially. Additional clues to the typical plant-to-animal subsistence ratio in Paleolithic hominin diets can be found in the foraging practices of historically studied hunter-gatherers.

Our analysis (fig. 19.2) of the *Ethnographic Atlas* data (Gray, 1999) showed that the dominant foods in the majority of historically studied hunter-gatherer diets were derived from animal food sources (Cordain et al., 2000). Most (73%) of the world’s hunters-gatherers obtained >50 percent of their subsistence from hunted and fished animal foods, whereas only 14 percent of worldwide hunter gatherers obtained >50

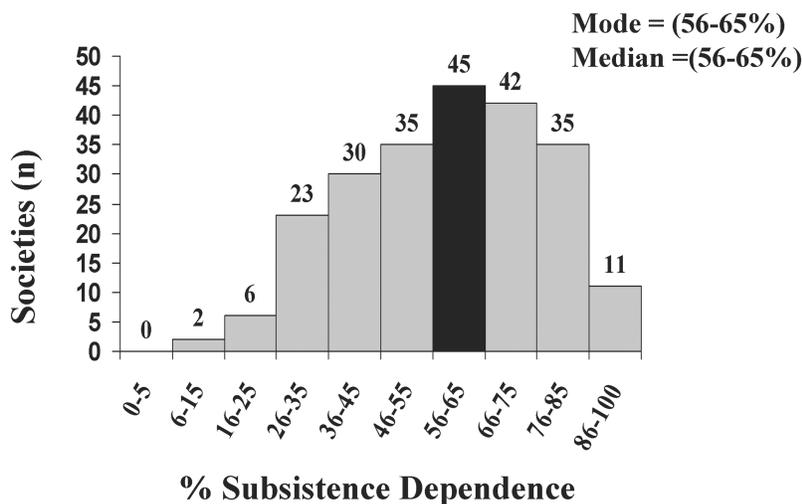


Figure 19.2 Frequency distribution of subsistence dependence upon total (fished + hunted) animal foods in worldwide hunter-gatherer societies ( $n = 229$ ). Adapted from Cordain et al. (2000).

percent of their subsistence from gathered plant foods. For all 229 hunter-gatherer societies, the median subsistence dependence on animal foods was 56 percent to 65 percent. In contrast, the median subsistence dependence on gathered plant foods was 26 percent to 35 percent (Cordain et al., 2000).

The major limitation of ethnographic data is that the preponderance of it is subjective in nature, and the assigned scores for the five basic subsistence economies in the *Ethnographic Atlas* are not precise, but rather are approximations (Hayden, 1981). Fortunately, more exact, quantitative dietary studies were carried out on a small percentage of the world's hunter-gatherer societies. Table 19.1 lists these studies and shows the plant-to-animal subsistence ratios by energy. The average score for animal food subsistence is 65 percent, while that for plant-food subsistence is 35 percent. These values are similar to our analysis of the entire ( $n = 229$ ) sample of hunter-gatherer societies listed in the *Ethnographic Atlas* in which the mean score for animal food subsistence was 68 percent and that for plant food was 32 percent. When the two polar hunter-gatherer populations, who have no choice but to eat animal food because of the inaccessibility of plant foods, are excluded from table 19.1, the mean score for animal subsistence is 59 percent and that for plant-food subsistence is 41 percent. These animal-to-plant subsistence values fall within the same respective class intervals (56%–65% for animal food; 26%–35% for plant food) as those we estimated from the ethnographic data when the confounding influence of latitude was eliminated (Cordain et al., 2000). Consequently, there is remarkably close agreement between the quantitative data in table 19.1 and the ethnographic data that animal food comprised more than half of the energy in historically studied hunter-gatherer diets.

Table 19.1 Quantitatively Determined Proportions of Plant and Animal Food in Hunter-gatherer Diets.

Population	Location	Latitude	% Animal Food	% Plant Food	Reference
Aborigines					
(Arhem Land)	Australia	12°S	77	23	McArthur, 1960
Ache	Paraguay	25°S	78	22	Hill et al., 1984
Anbarra	Australia	12°S	75	25	Meehan, 1982
Efe	Africa	2°N	44	56	Dietz et al., 1989
Eskimo	Greenland	69°N	96	4	Sinclair, 1953; Krogh and Krogh, 1914
Gwi	Africa	23°S	26	74	Silberbauer, 1981; Tanaka, 1980
Hadza	Africa	3°S	48	52	Blurton Jones et al., 1997; Hawkes et al., 1989
Hiwi	Venezuela	6°N	75	25	Hurtado and Hill, 1986, 1990
!Kung	Africa	20°S	33	67	Lee, 1968
!Kung	Africa	20°S	68	32	Yellen, 1977
Nukak	Columbia	2°N	41	59	Politis, 1996
Nunamiut	Alaska	68°N	99	1	Binford, 1978
Onge	Andaman Islands	12°N	79	21	Rao et al., 1989; Bose, 1964

Source: Adapted from Kaplan et al. (2000).

### Differences between Postagricultural and Plio-Pleistocene Diets: The Known

In contrasting pre- and postagricultural diets, it is important to consider not only the nutrient qualities and categories of foods that were consumed by preagricultural hominins but also to recognize the categories of foods and their nutrient qualities that could not have been regularly consumed before the development of agriculture, industrialization, and advanced technology. Table 19.2 lists the food categories that would have generally been unavailable to preagricultural hominins. Tables 19.3–19.5 show when these novel Neolithic and Industrial era food introductions occurred.

Although dairy products, cereals, refined sugars, refined vegetable oils, and alcohol make up 72.1 percent of the total daily energy consumed by all people in the United States, these types of foods would have contributed little or no energy in the archetypal preagricultural hominin diet (Cordain et al., 2000). Furthermore, mixtures of foods shown in table 19.2 encompass the ubiquitous processed foods (e.g.,

Table 19.2 Food and Food Types Found in Western Diets Generally Unavailable to Preagricultural Hominins.

Food or Food Group	% Total Energy in U.S. Diet
Dairy products	
Whole milk	1.6
Low-fat milks	2.1
Cheese	3.2
Butter	1.1
Other	2.6
Total	10.6
Cereal grains	
Whole grains	3.5
Refined grains	20.4
Total	23.9
Refined sugars	
Sucrose	8.0
High-fructose corn syrup	7.8
Glucose	2.6
Syrups	0.1
Other	0.1
Total	18.6
Refined vegetable oils	
Salad, cooking oils	8.8
Shortening	6.6
Margarine	2.2
Total	17.6
Alcohol	1.4
Total energy	72.1
Added daily salt (NaCl)	9.6 g

Sources: Data adapted from Gerrior and Bente (2002), United States Department of Agriculture (1997), United States Department of Agriculture (2002).

Table 19.3 Neolithic Food Introductions

Food	Date	Reference
Domesticated Meats		
Sheep	~11,000 BP	Hiendleder et al., 2002
Goats	~10,000 BP	Luikart et al., 2001
Cows	~10,000 BP	Loftus et al., 1999
Pigs	~9,000 BP	Giuffra et al., 2000
Chickens	~8,000 BP	Fumihito et al., 1996
Dairy products	6,100–5,500 BP	Copley et al., 2003
Cereal grains		
Wheat	10,000–11,000 BP	Salamini et al., 2003
Barley	~10,000 BP	Badr et al., 2000
Rice	~10,000 BP	Vitte et al., 2004
Maize	~9,000 BP	Matsuoka et al., 2002
Wine	7,100–7,400 BP	McGovern et al., 1996
Salt	5,600–6,200 BP	Weller, 2002
Vegetable oils	5,000–6,000 BP	O'Keefe, 2000; Liphshitz et al., 1991
Beer	~4,000 B.C.	Rudolph et al., 1992

cookies, cake, bakery foods, breakfast cereals, bagels, rolls, muffins, crackers, chips, snack foods, pizza, soft drinks, candy, ice cream, condiments, salad dressings, etc.) that dominate the typical U.S. diet.

### Health Ramifications of Neolithic and Industrial Era Foods

The novel foods (dairy products, cereals, refined cereals, refined sugars, refined vegetable oils, fatty meats, salt and combinations of these foods) introduced as staples during the Neolithic and Industrial eras fundamentally changed a number of major nutritional characteristics of ancestral hominin diets and ultimately had far-reaching effects on health and well being. As these foods gradually displaced the minimally

Table 19.4 Historical and Industrial Era Food-type Introductions

Food	Date	Reference
Refined sugar (sucrose)	500 B.C.	Galloway, 2000
Distilled alcoholic beverages	800–1300 AD	Comer, 2000
Refined sugar (widely available)	1800 AD	Ziegler, 1967
Fatty, feedlot-produced meats	~1860 AD	Whitaker, 1975
Refined grains (widely available)	~1880 AD	Storck and Teague, 1952
Hydrogenated vegetable fats	1897 AD	Emken, 1984
Vegetable oils (widely available)	~1910 AD	Gerrior and Bente, 2002
High-fructose corn syrup	~1970s AD	Hanover and White, 1993

Table 19.5 Assorted Processed Food Introductions

Food	Date	Food	Date
Saltine crackers	1876	Processed cheese	1915
Pillsbury white flour	1881	Orange Crush soda	1916
Coca-Cola	1886	Moon Pie	1917
Log Cabin syrup	1888	Baby Ruth candy bar	1920
Fig Newton	1891	Wonder Bread	1921
Triscuits	1895	Milky Way™ candy bar	1923
Tootsie Rolls	1896	Wheaties cereal	1924
Graham crackers	1898	Kool Aid	1927
Wesson oil	1899	Rice Krispies cereal	1928
Chiclets chewing gum	1900	Birds Eye frozen vegetables	1930
Hershey's chocolate bar	1900	Hostess Twinkies	1930
Karo corn syrup	1902	Frito Corn chips™	1932
Pepsi soft drink	1902	Kraft Macaroni & Cheese	1937
Canned tuna fish	1903	Kit Kat candy bar	1937
Campbell's pork and beans	1904	M&M'S candy	1941
Peanut butter	1904	Cheerios cereal	1945
Kellogg's corn flakes	1906	Frozen orange juice	1946
Hershey's kisses	1907	Instant mashed potatoes	1946
Quaker puffed wheat 1	1909	Cheetos	1948
Crisco	1911	Kellogg's Frosted Flakes	1952
Mazola corn oil	1911	Kentucky Fried Chicken	1952
Hamburger buns	1912	M&M'S Peanut Candy	1954
Hellmann's mayonnaise	1912	Fruit Loops cereal	1963
Lifesavers	1912	Doritos	1966
Oreo cookies	1913	Pringles chips	1969

Source: Adapted from <http://www.geocities.com/foodedge/timeline.htm>

processed wild-plant and animal foods in hunter-gatherer diets, they adversely affected the following dietary parameters: (1) glycemic load, (2) fatty acid composition, (3) macronutrient composition, (4) micronutrient density, (5) acid/base load, (6) sodium/potassium ratio, and (7) fiber content.

### The Glycemic Load

The glycemic index, originally developed in 1981, is a relative comparison of the blood-glucose-raising potential of various foods or combination of foods based on equal amounts of carbohydrate in the food (Jenkins et al., 1981). In 1997, the concept of glycemic load (glycemic index  $\times$  the carbohydrate content per serving size) was introduced to assess blood-glucose-raising potential of a food based on both the quality and quantity of dietary carbohydrate (Liu and Willett, 2002). Refined grain and sugar products nearly always maintain much higher glycemic loads than unprocessed fruits and vegetables (Foster-Powell, Holt, and Brand-Miller, 2002). Unrefined wild-plant foods, like those available to contemporary hunter-gatherers, typically exhibit low glycemic indices (Thorburn, Brand, and Truswell, 1987).

Within the past two decades, substantial information has accumulated showing that long-term consumption of high glycemic load carbohydrates can adversely affect

metabolism and health (Liu and Willett, 2002; Ludwig, 2002; Cordain, Eades, and Eades, 2003). Specifically, chronic hyperglycemia and hyperinsulinemia, induced by high glycemic load carbohydrates may elicit a number of hormonal and physiological changes that promote insulin resistance (Liu and Willett, 2002; Ludwig, 2002; Cordain, Eades, and Eades, 2003). Diseases of insulin resistance are frequently referred to as “diseases of civilization” (Eaton, Konner, and Shostak, 1988; Reaven, 1995) and include obesity, coronary heart disease, type 2 diabetes, hypertension, and dyslipidemia (elevated serum triacylglycerols; small-dense, low-density lipoprotein cholesterol; and reduced high-density lipoprotein cholesterol). It is likely that the metabolic syndrome may extend to other chronic illnesses and conditions that are widely prevalent in western societies, including myopia, acne, gout, polycystic ovary syndrome, epithelial cell cancers (breast, colon, and prostate), male vertex balding, skin tags, and acanthosis nigricans (Cordain, Eades, and Eades, 2003). Diseases of insulin resistance are rare or absent in hunter-gatherer and other less-westernized societies living and eating in their traditional manner (Schaeffer, 1971; Trowell, 1980; Eaton, Konner, and Shostak, 1988).

In addition to high glycemic load carbohydrates, other elements of Neolithic and Industrial era foods may contribute to the insulin resistance underlying metabolic syndrome diseases. Milk, yogurt, and ice cream, despite having relatively low glycemic loads are highly insulinotropic, with insulin indices comparable to white bread (Ostman, Liljeberg Elmsthal, and Bjorck, 2001). Fructose is a major constituent in high fructose corn syrup (table 19.2) and maintains a low glycemic index of 23 but paradoxically may worsen insulin sensitivity (Reiser et al., 1989) and cause acute insulin resistance in humans (Dirlewanger et al., 2000).

In the typical U.S. diet, high glycemic load sugars now supply 18.6 percent of total energy, whereas high glycemic load, refined cereal grains supply 20.4 percent of energy (table 19.2). Hence, at least 39 percent of the total energy in the typical U.S. diet is supplied by foods that may promote insulin resistance. Although high glycemic load sugars and grains now represent a dominant element of the modern urban diet, these foods were rarely or never consumed by average citizens as recently as 200 years ago (tables 19.3–19.5).

### The Fatty Acid Composition

Chemically, fats are defined as acylglycerols, compounds in which a fatty acid molecule (acyl group) is linked to a glycerol molecule by an ester bond. Almost all dietary and storage fats are triacylglycerols, compounds in which three fatty acid molecules are bound to a single glycerol molecule. Fatty acids fall into one of three major categories: (1) saturated fatty acids (SFA), (2) monounsaturated fatty acids (MUFA), and (3) polyunsaturated fatty acids (PUFA). Additionally, essential PUFA occur in two biologically important families, the n-6 PUFA and the n-3 PUFA. Substantial evidence now indicates that for preventing the risk of chronic disease the absolute amount of dietary fat is less important than the type of fat (Institute of Medicine of the National Academies, 2003). Beneficial, health-promoting fats are MUFA and some PUFA, whereas most SFA and *trans* fatty acids are detrimental when consumed in excessive quantities (Institute of Medicine of the National Academies, 2003). Further, the balance of dietary n-6 and n-3 PUFA is integral in preventing the

risk of chronic disease and promoting health (Kris-Etherton, Harris, and Appel, 2002; Simopoulos, 2002).

The western diet frequently contains excessive saturated and *trans* fatty acids and has too little n-3 PUFA relative to its n-6 PUFA (Simopoulos, 2002; Institute of Medicine of the National Academies, 2003). High dietary intakes of SFA and *trans* fatty acids increase the risk of cardiovascular disease by elevating blood levels of total and LDL cholesterol (97, 100–102). N-3 PUFA may reduce the risk for cardiovascular disease via a number of mechanisms, including reductions in ventricular arrhythmias, blood clotting, serum triacylglycerol concentrations, growth of atherosclerotic plaques, and blood pressure (Kris-Etherton et al., 2002).

The six major sources of SFA in the U.S. diet are fatty meats, baked goods, cheese, milk, margarine, and butter (Subar et al., 1998). Five of these six foods would not have been components of hominin diets before the advent of animal husbandry or the Industrial Revolution. Because of the inherently lean nature of wild-animal tissues throughout most of the year and the dominance of MUFA + PUFA in their muscle and organ tissues (Cordain et al., 2002a), high dietary levels of SFA on a year-round basis would have been infrequently encountered in preagricultural diets (O'Keefe and Cordain, 2004).

The advent of the oil seed processing industry at the beginning of the twentieth century significantly raised the total intake of vegetable fat (Gerrior and Bente, 2002), which directly increased the dietary level of n-6 PUFA at the expense of a lowered n-3 PUFA because of the inherently higher concentrations of n-6 PUFA and lower concentrations of n-3 PUFA in most vegetable oils (Simopoulos, 2002). The trend toward a higher n-6/n-3 PUFA ratio was exacerbated as meat from grain-fed cattle and livestock became the norm in the U.S. diet over the past one hundred years (Whitaker, 1975; Cordain et al., 2002a). In the current U.S. diet, the ratio of n-6/n-3 PUFA has risen to 10 : 1 (Kris-Etherton et al., 2000), whereas in wild-animal-food dominated, hunter-gatherer diets it has been estimated between 2 : 1 and 3 : 1 (Cordain et al., 2002a).

The invention of the hydrogenation process in 1897 (Emken, 1984) allowed vegetable oils to become solidified and marketed as shortening or margarine and as foods containing hydrogenated vegetable oils. The hydrogenation process introduced a novel *trans* fatty acid (*trans* elaidic acid) into the human diet, which elevates blood cholesterol levels and leads to an increased risk of cardiovascular disease (Ascherio et al., 1994). *Trans* fatty acids in the U.S. diet now are estimated to constitute 7.4 percent of the total fatty acid intake (Allison et al., 1999).

### The Macronutrient Composition

In the present U.S. diet, the percentage of total food energy derived from the three major macronutrients is as follows: carbohydrate (51.8%), fat (32.8%), and protein (15.4%). Current advice for reducing the risk of cardiovascular and other chronic diseases is to limit fat intake to 30 percent of total energy, to maintain protein at 15 percent of total energy and to increase complex carbohydrates to 55 percent 60 percent of total energy (Krauss, et al., 2000). Both the current U.S. macronutrient intakes and suggested healthful levels differ considerably from average levels obtained from ethnographic (Cordain et al., 2000) and quantitative studies (Cordain et al.,

2002b) of hunter-gatherers in which dietary protein is characteristically elevated (19%–35% energy) at the expense of carbohydrate (22%–40% energy; Cordain et al., 2000).

An increasing body of evidence indicates high-protein diets may improve blood lipid profiles (Cordain et al., 2002b) and thereby lessen the risk for cardiovascular disease. A four-week dietary intervention of hypertensive subjects has demonstrated that a high-protein diet (25% energy) was effective in significantly lowering blood pressure (Burke et al., 2001). Further, high-protein diets have been shown to improve metabolic control in type 2 diabetes patients (O’Dea, 1984; O’Dea, et al., 1989).

Because protein has more than three times the thermic effect of either fat or carbohydrate (Crovetti et al., 1998) and because it has a greater satiety value than fat or carbohydrate (Crovetti, et al., 1998), increased dietary protein may represent an effective weight-loss strategy for the overweight or obese. Recent clinical trials have demonstrated that calorie-restricted high-protein diets are more effective than calorie-restricted high-carbohydrate diets in promoting (Skov et al., 1999) and maintaining (Westerterp-Plantenga et al., 2004) weight loss in overweight subjects, while producing less hunger and more satisfaction (Johnston, Tjonn, and Swan, 2004).

#### The Micronutrient Density

Refined sugars are essentially devoid of any vitamin or mineral. Accordingly the consumption of refined sugar or foods containing refined sugar reduces the total vitamin, mineral (micronutrient) density of the diet by displacing more nutrient dense foods. A similar situation exists for refined vegetable oils, except that they contain two fat-soluble vitamins (vitamin E and vitamin K). Because vegetable oils and refined sugars contribute at least 36.2 percent of the energy in a typical U.S. diet (table 19.2), the widespread consumption of these substances—or food made with them—has considerable potential to influence the risk of vitamin and mineral deficiencies.

At least half the U.S. population fails to meet the recommended daily allowances (RDA) for vitamin B6, vitamin A, magnesium, calcium, and zinc, and 33 percent of the population does not meet the RDA for folate (United States Department of Agriculture, Agricultural Research Service, 1997). Adequate dietary intake of both folate and vitamin B6 prevent the accumulation of homocysteine in the bloodstream. Elevated blood concentrations of homocysteine represent an independent risk factor for development of cardiovascular disease, stroke, and deep-vein thrombosis (Wald, Law, and Morris, 2002).

Displacement of fruits, vegetables, lean meats, and seafood by whole grains and milk lowers the overall dietary micronutrient density because whole grains and milk maintain lower-nutrient densities than these other foods (Cordain, 2002). Additionally, wild-plant foods, known to be consumed by hunter-gatherers, generally maintain higher micronutrient concentrations than their domesticated counterparts (Brand-Miller and Holt, 1998), as does the muscle meat of wild animals (First Data Bank, 2000). Consequently, the Neolithic introduction of dairy foods and cereal grains as staples would have caused the average micronutrient content of the diet to decline. This situation worsened as cereal milling techniques developed in the Industrial era allowed for the production of bread flour devoid of the more nutrient dense bran and germ (Storck and Teague, 1952). The displacement of more nutrient-dense items

(fruits, vegetables, lean meats, and seafood) by less dense foods (refined sugars, grains, vegetable oils, and dairy products) and the subsequent decline in dietary vitamin and mineral density has far-reaching health implications; consequences that not only promote the development of vitamin deficiency diseases but also numerous infectious and chronic diseases (Cordain, 1999).

### Acid/Base Balance

After digestion, absorption, and metabolism, nearly all foods release either acid or bicarbonate (base) into the systemic circulation (Frassetto et al., 1998). Table 19.6 shows that fish, meat, poultry, eggs, cheese, milk, and cereal grains are net acid producing, whereas fresh fruits, vegetables, tubers, roots, and nuts are net-base producing. Legumes yield near-zero mean acid values, reflecting an overlapping distribution from slightly net acid producing to slightly net-base producing. Not shown in table 19.6 are energy-dense, nutrient-poor foods, such as separated fats and refined sugars, that contribute neither to the acid nor base load. Additionally, salt (NaCl) is net acid producing because of the chloride ion (Frassetto et al., 1998).

The typical western diet yields a net acid load estimated to be + 50 meq/day (Lemann, 1999). As a result, normal adults consuming the standard U.S. diet sustain a chronic, low-grade pathogenic metabolic acidosis that worsens with age as kidney function declines (Frassetto, Morris, and Sebastian, 1996). Virtually all preagricultural

Table 19.6 Potential Net Acid (or Base) Loads of 17 Food Groups

	<i>n</i>	Net Acid Load (meq/418 kJ)	Net Acid Load (meq/10,460 kJ)	Potassium (meq/418 kJ)	Protein (g/418 kJ)	Protein g/100 meq Potassium
<b>Acid-producing foods</b>						
Fish	8	+14.6	+398	8.1	16.8	207
Meat	3	+12.4	+342	7.6	18.4	242
Poultry	2	+7.8	+227	4.7	13.4	287
Egg	1	+7.3	+215	2.4	8.3	339
Shellfish	3	+7.3	+215	18.4	18.0	159
Cheese	9	+3.3	+115	0.8	7.1	982
Milk	4	+1.3	+64	6.4	5.7	90
Cereal grains	7	+1.1	+60	2.6	3.2	153
<b>Near-neutral foods</b>						
Legumes	6	-0.4	+24	12.6	10.6	100
<b>Base-Producing Foods</b>						
Nut	6	-1.1	+6	3.8	2.5	86
Fresh fruit	11	-5.2	-98	9.4	1.6	16
Tuber	2	-5.4	-102	11.8	2.2	18
Mushroom	1	-11.2	-247	62.3	25.7	41
Root	5	-17.1	-395	34.3	6.8	21
Vegetable fruit	1	-17.5	-404	35.5	5.6	15
Leafy greens	6	-23.4	-553	43.5	10.0	24
Plant stalks	1	-24.9	-590	54.8	4.6	8

*Note:* Acid load calculations were made using previously described procedures (Sebastian et al., 2002). Positive (+) and negative (-) values represent acid-producing and base-producing equivalents, respectively.

diets were net-base yielding because of the absence of cereals and energy-dense, nutrient-poor foods—foods that were introduced during the Neolithic and Industrial eras and which displaced base-yielding fruits and vegetables (Sebastian et al., 2002). Consequently, a net-base-producing diet was the norm throughout most of hominin evolution (Sebastian et al., 2002). The known health benefits of a net-base-yielding diet include preventing and treating osteoporosis (Sebastian et al., 1994), age-related muscle wasting (Frassetto, Morris, and Sebastian, 1997), calcium kidney stones (Pak et al., 1985), hypertension (Morris et al., 1999), exercise-induced asthma (Mickleborough et al., 2001), as well as slowing the progression of age- and disease-related chronic renal insufficiency (Alpern and Sakhaee, 1997).

### Sodium/Potassium Ratio

The average sodium content (3,271 mg/day) of the typical U.S. diet is substantially higher than its potassium content (2,620 mg/day; United States Department of Agriculture, Agricultural Research Service, 1997). Three dietary factors are primarily responsible for the dietary ratio of Na/K, which is greater than 1.0. First, 90 percent of the sodium in western diets comes from manufactured salt (NaCl); hence, the sodium content of naturally occurring foods in the average U.S. diet (~330 mg) is quite low. Second, vegetable oils and refined sugars, which are essentially devoid of potassium, make up 36 percent of the total food energy. The inclusion of these two foods into the diet displaces other foods with higher potassium concentrations and thereby reduces the total dietary potassium. Third, the displacement of vegetables and fruits by whole grains and milk products may further reduce the potassium intake because potassium concentrations in vegetables are four and twelve times higher than in milk and whole grains, respectively, whereas in fruits the potassium concentration is two and five times higher than in milk and whole grains (First Data Bank, 2000). Taken together, the addition of manufactured salt to the food supply and the displacement of traditional potassium-rich foods by foods introduced during the Neolithic and Industrial periods caused a 400 percent decline in the potassium intake while simultaneously initiating a 400 percent increase in sodium ingestion (Frassetto et al., 2001).

The inversion of potassium and sodium concentrations in hominin diets had no evolutionary precedent and now plays an integral role in eliciting and contributing to numerous diseases of civilization. Diets low in potassium and high in sodium may partially or directly underlie or exacerbate a variety of maladies and chronic illnesses including: hypertension (Morris et al., 1999), stroke (Antonios and MacGregor, 1996), kidney stones (Pak et al., 1985), osteoporosis (Devine et al., 1995), gastrointestinal tract cancers (Tuyns, 1988), asthma (Carey, Locke, and Cookson, 1993), exercise-induced asthma (Mickleborough et al., 2001), insomnia (Miller, 1945), airsickness (Lindseth and Lindseth, 1995), high-altitude sickness (Porcelli and Gugelchuk, 1995), and Menière's syndrome (ear ringing; Thai-Van, Bounaix, and Fraysse, 2001).

### The Fiber Content

The fiber content (15.1 g/day; United States Department of Agriculture, Agricultural Research Service, 1997) of the typical U.S. diet is considerably lower than recommended values (25–30 g; Krauss et al., 2000). Refined sugars, vegetable oils, dairy

products, and alcohol are devoid of fiber and compose an average of 48.2 percent of the energy in the typical U.S. diet (table 19.2). Further, fiber-depleted, refined grains represent 85 percent of the grains consumed in the United States (table 19.2), and because refined grains contain 400 percent less fiber than whole grains (by energy), they further dilute the total dietary fiber intake. Fresh fruits typically contain twice the fiber of whole grains, and nonstarchy vegetables contain almost eight times more fiber than whole grains on an energy basis (First Data Bank, 2000). Fruits and vegetables known to be consumed by hunter-gatherers also maintain considerably more fiber than their domestic counterparts (Brand-Miller and Holt, 1998). Contemporary diets devoid of cereal grains, dairy products, refined oils, and sugars and processed foods have been shown to contain significantly more fiber (42.5 g/day) than either current or recommended values (Cordain, 2002).

Once again, the displacement of fiber-rich plant foods by novel dietary staples, introduced during the Neolithic and Industrial periods, was instrumental in changing the diets our species had traditionally consumed—a diet that would have almost always been high in fiber. Soluble fibers (those found primarily in fruits and vegetables) modestly reduce LDL and total cholesterol concentrations beyond those achieved by a diet low in saturated fat, and fiber, by slowing gastric emptying, may reduce appetite and help to control caloric intake (Anderson, Smith, and Gustafson, 1994). Diets low in dietary fiber may underlie or exacerbate constipation, appendicitis, hemorrhoids, deep-vein thrombosis, varicose veins, diverticulitis, hiatal hernia, and gastroesophageal reflux (Trowell, 1985).

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