

# *Phytochemicals*

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## Nutrient–Gene Interactions

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## CHAPTER 8

# Saturated Fat Consumption in Ancestral Human Diets: Implications for Contemporary Intakes

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## INTRODUCTION

### Genetic Discordance

Nutritional requirements for all organisms are ultimately determined by the expression of specific genes within an organism's genome. These genes, in turn, are created and shaped by an ongoing interaction between the genome and its envi-

ronment via evolution acting through natural selection over many generations. Genetic traits may be positively or negatively selected relative to their concordance or discordance with environmental selective pressures.<sup>1</sup> When the environment remains relatively constant over a long period of time, stabilizing selection tends to maintain genetic traits that represent the optimal average for a population.<sup>2</sup> On the other hand, when environmental conditions change over long periods of time, evolutionary discordance arises between a species' genome and its environment, and stabilizing selection is replaced by directional selection, moving the average population genome to a new set point.<sup>1,2</sup> Initially, when long term environmental changes occur in a population, individuals bearing the previous average status-quo genome experience evolutionary discordance.<sup>2,3</sup> In the affected genotype, this evolutionary discordance manifests itself phenotypically as disease, increased morbidity and mortality, and reduced reproductive success.<sup>1–3</sup>

Since the introduction of agriculture and animal husbandry 10,000 years ago, and more recently with the beginning of the Industrial Revolution 200 years ago, crucial changes have occurred in both diet and lifestyle conditions that are vastly different than the prevailing environmental conditions during which the human genome adapted. Numerous Neolithic and Industrial era food introductions have been identified that promote the development of chronic disease in contemporary western populations.<sup>4–10</sup> In most cases, a dose response exists between these novel foods and the emergence of disease. For instance, occasional seasonal exposure to honey (a refined sugar) results in negligible dental caries rates in hunter-gatherers,<sup>11</sup> whereas daily consumption of refined sucrose in Western diets almost universally causes a high incidence of caries and dental decay.<sup>12</sup> In many cases (such as with dental caries) the proximate physiological and biochemical causes for the diseases are well understood. Despite this knowledge, it is frequently less well appreciated that the ultimate basis for most diet-related diseases results from the evolutionary discordance between our ancient and conservative genome and recently introduced foods.<sup>2,3,13</sup> By examining pre-agricultural diets and their nutritional characteristics and comparing them to contemporary diets, insight can be gained into complex questions regarding diet and disease in existing populations.

### **Dietary Saturated Fats**

A diet–disease question that has become contentious in recent years is saturated fats and the role they might play in the pathogenesis of coronary heart disease.<sup>14–17</sup> The traditional view has been that certain saturated fats (12:0, 14:0, and 16:0) downregulate the LDL receptor and thereby increase plasma concentrations of LDL cholesterol, which in turn increases the risk for coronary artery disease (CAD).<sup>18,19</sup> It is increasingly being recognized that this traditional model of atherosclerosis and CAD is overly simplistic, primarily because CAD is a multifactorial disease involving numerous dietary and genetic factors acting in concert with one another.<sup>17</sup> The dietary glycemic load, the n6/n3 fatty acid balance, chronic inflammation, trans fatty acids, homocysteine, alcohol intake, exercise, smoking, and numerous other dietary and lifestyle factors play key roles in the

pathogenesis of CAD.<sup>17</sup> Nevertheless, the molecular<sup>20</sup> and clinical<sup>21</sup> basis for the elevation of plasma LDL by saturated fatty acids cannot be ignored, nor can the continuous and graded risk for CAD mortality with increasing LDL and total cholesterol concentrations,<sup>22,23</sup> despite suggestions otherwise.<sup>14-16</sup>

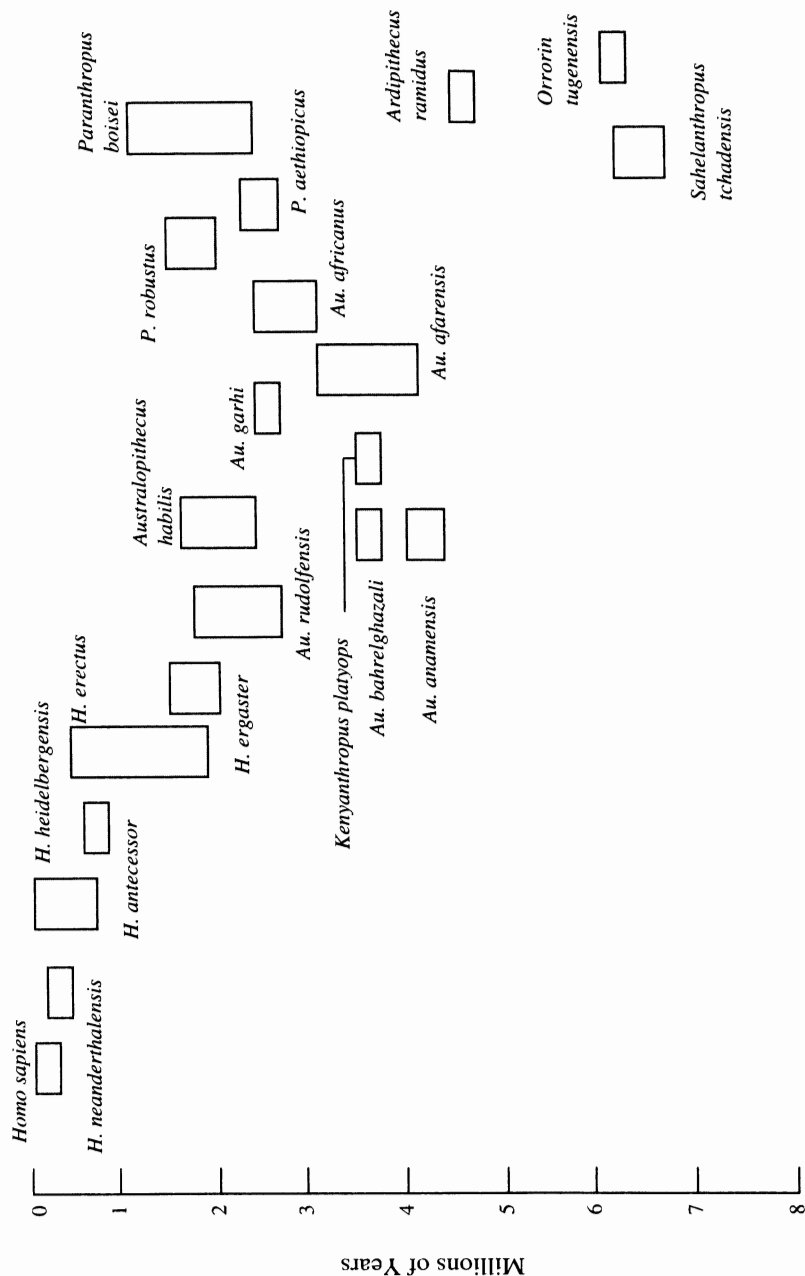
The relative contribution that dietary saturated fats may make to the overall development and progression of CAD under the backdrop of the typical Western diet and lifestyle is unclear, particularly given that individual genetic differences may modulate the cholesterol-raising effects of saturated fats.<sup>17</sup> However, this lack of precise evidence by no means exonerates dietary saturated fats. Rather, they represent a known risk factor for CAD that should be recognized and considered similar to other known dietary risk factors. In the current U.S. diet, an average of 11% of the daily energy is derived from saturated fat,<sup>24</sup> a figure slightly higher than the 10% or less recommended by the American Heart Association.<sup>25</sup> By examining the amounts of saturated fats in pre-agricultural hominin diets, an evolutionary baseline can be established regarding the normal range and limits of saturated fats that would have conditioned the human genome.

## SATURATED FATS IN PRE-AGRICULTURAL DIETS

Figure 8.1 demonstrates that since the evolutionary emergence of hominins, 20 or more species may have existed.<sup>26</sup> Similar to historically studied hunter-gatherers,<sup>27,28</sup> 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 lines of evidence indicate that all hominin species and populations were omnivorous; consequently, dietary saturated fats would have always been a component in hominin diets.

### Saturated Fat in Early Pliocene Hominin Diets

Our closest living primate relative, the chimpanzee (*Pan paniscus* and *Pan troglodytes*) is omnivorous and consumes a substantial amount of meat throughout the year obtained from hunting and scavenging.<sup>29-31</sup> Observational studies of wild chimpanzees demonstrate that during the dry season, meat intake is about 65 g per day for adults.<sup>30</sup> Accordingly, it is likely that the very earliest Pliocene hominins would have been capable of obtaining animal food through hunting and scavenging in a manner similar to chimpanzees. Additionally, fossils of early African hominins including *Australopithecus africanus*, and *Australopithecus robustus* maintain carbon isotope signatures characteristic of omnivores.<sup>32,33</sup> Quantitative estimates of energy intake from animal food sources in these early hominins are unclear, other than that they were likely similar to, or greater than, estimated values (4 to 8.5% total energy) for chimpanzees.<sup>30,34</sup> Consequently, the amount of dietary saturated in the earliest hominin diets would have been substantially lower than later hominins whose diet became more dependent upon animal food energy sources.



**Figure 8.1** The hominin fossil record. Species are indicated with the dates of the earliest and latest fossil record. (Adapted from Wood, B., *Nature*, 418, 133, 2002.)

### Saturated Fat in Pliocene/Pleistocene Hominin Diets

Approximately 2.6 million years ago (MYA), the hominin species that eventually led to *Homo* began to include more and 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,<sup>35</sup> and there is clear cut evidence to show that these tools were used to butcher and disarticulate animal carcasses.<sup>36–37</sup> 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.<sup>37</sup> It is not entirely clear which specific early hominin species or species manufactured and used these earliest stone tools, however *Australopithecus garhi* might have been a likely candidate.<sup>37,38</sup>

The development of stone tools and the increased dietary reliance upon animal foods allowed early African hominins to colonize northern latitudes outside 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,<sup>39</sup> and more recently Oldowan tools dating to 1.66 MYA have been discovered at the Majuangou site in North China (40°N).<sup>40</sup> Both of these tool-producing hominins would likely have consumed considerably more animal food than pre-lithic hominins living in more temperate African climates because of reduced availability of plant foods during winter and early spring. Hence, the consumption of saturated fat would have, accordingly, been higher. Once again, quantitative estimates of the saturated fat content in early *Homo* species are speculative because of the uncertain plant–animal subsistence ratio. However, there is suggestive isotopic data indicating that the majority of the energy in more northerly living *Homo* species may have been obtained from animal foods.

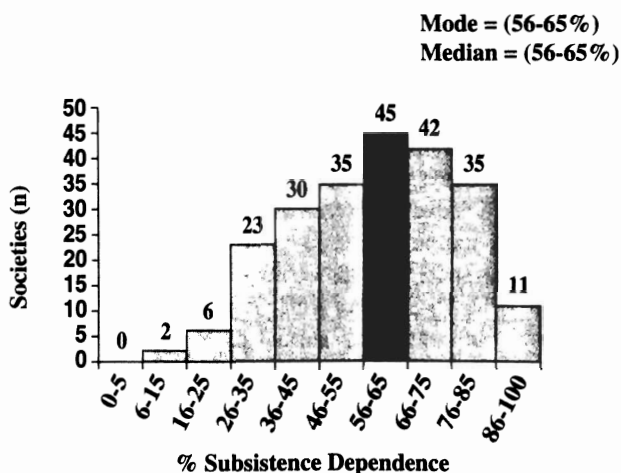
### Saturated Fat in Late Pleistocene Hominin Diets

Richards et al.<sup>41</sup> have examined stable isotopes (<sup>13</sup>C and <sup>15</sup>N) in two Neanderthal specimens (~28,000 to 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. A comparable analysis was made of five Upper Paleolithic *Homo sapiens* specimens dated to the Upper Paleolithic (~11,700 to 12,380 years BP) from Gough's and Sun Hole Caves in Britain.<sup>42</sup> The data indicated these hunter-gatherers were consuming animal protein on a year-round basis at a higher trophic level than the arctic fox. Although precise quantitative estimates of saturated fat intake are not possible, the saturated fat intake in both Neanderthal and Upper Paleolithic *Homo sapiens* would have been substantial because of their great dependence upon animal food sources for daily energy.

## Saturated Fat in Historically Studied Hunter-Gatherer Diets

Because reasonable estimates exist for the average plant-to-animal subsistence ratio for historically studied hunter-gatherers, it is possible to estimate the amount of saturated fat in their diet. Our analysis (Figure 8.2) of the *Ethnographic Atlas* data<sup>43</sup> showed that the dominant foods in the majority of historically studied hunter-gatherer diets were derived from animal food sources.<sup>27</sup> Most (73%) of the world's hunter-gatherers obtained >50% of their subsistence from hunted and fished animal foods, whereas only 14% of worldwide hunter-gatherers obtained >50% of their subsistence from gathered plant foods. For all 229 hunter-gatherer societies, the median subsistence dependence upon animal foods was 56 to 65%. In contrast, the median subsistence dependence upon gathered plant foods was 26 to 35%.<sup>27</sup>

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.<sup>44</sup> Fortunately, more exact, quantitative dietary studies were carried out on a small percentage of the world's hunter-gatherer societies. Table 8.1 lists these studies and shows the plant to animal subsistence ratios by energy.<sup>28</sup> The average score for animal food subsistence is 65%, while that for plant food subsistence is 35%. When the two polar hunter-gatherer populations, who have no choice but to eat animal food because of the inaccessibility of plant food, are excluded from Table 8.1, the mean score for animal subsistence is 59% and that for plant food subsistence is 41%. These animal-to-plant subsistence values fall within the same respective class intervals (56 to 65% for animal food; 26 to 35% for plant food) as those we estimated from the ethnographic data when the confounding influence of latitude was eliminated.<sup>27</sup> Consequently, there is remarkably close agreement between the quantitative data in Table



**Figure 8.2** Frequency distribution of subsistence dependence upon total (fished + hunted) animal foods in world wide hunter-gatherer societies (n = 229). (Adapted from Cordain, L. et al., *Am. J. Clin. Nutr.*, 71, 682, 2000.)

**Table 8.1 Quantitatively Determined Proportions of Plant and Animal Food in Hunter-Gatherer Diets**

Population	Location	Latitude	% animal food	% plant food
Aborigines (Arhem Land)	Australia	12S	77	23
Ache	Paraguay	25S	78	22
Anbarra	Australia	12S	75	25
Efe	Africa	2N	44	56
Eskimo	Greenland	69N	96	4
Gwi	Africa	23S	26	74
Hadza	Africa	3S	48	52
Hiwi	Venezuela	6N	75	25
!Kung	Africa	20S	33	67
!Kung	Africa	20S	68	32
Nukak	Columbia	2N	41	59
Nunamiut	Alaska	68N	99	1
Onge	Andaman Islands	12N	79	21

Source: Cordain, L. et al., *Eur. J. Nutr.*, 56 (Suppl 1), S42, 2002.

8.1 and the ethnographic data that animal food comprised more than half of the energy in historically studied hunter-gatherer diets.

## THE ESTIMATION OF DAILY DIETARY SATURATED FATS

Using the same model we developed for estimating the macronutrient content in hunter-gatherer diets,<sup>27</sup> it is possible to estimate the dietary saturated fat content, provided saturated fat values in the plant and animal food databases are known. Similar to our previous model, a range of plant-to-animal subsistence ratios are utilized to estimate the most likely range for dietary saturated fat.

### Saturated Fat in Plant Foods

In the current model, fat contributed 24% of the total energy derived from all wild plant food (n = 768), whereas carbohydrate (62% energy) and protein (14%) comprised the balance of plant food energy. The mean fatty acid breakdown for 64 cultivated equivalent category plant foods was 22.4% saturated fatty acids, 28.6% monounsaturated fatty acids, and 49% polyunsaturated fatty acids.<sup>45</sup> Accordingly, in our model, 5.4% of plant food energy was derived from saturated fat.

### Saturated Fat in Animal Foods

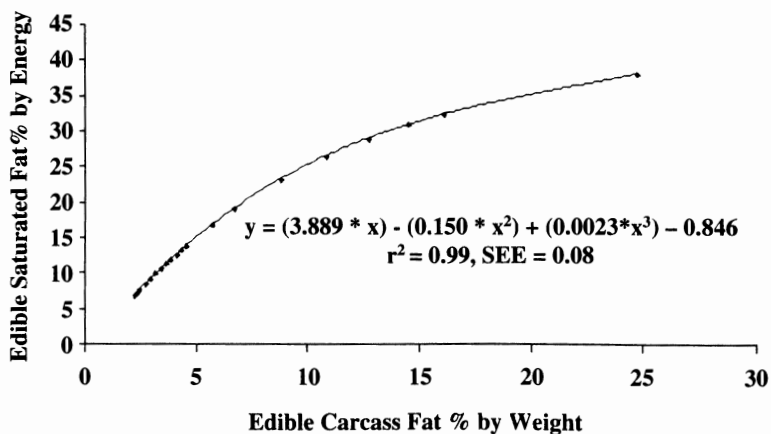
The estimation of saturated fat from animal sources is more complex because hunter-gatherers typically ate the entire edible carcass of most vertebrates,<sup>46,47</sup> thereby necessitating the calculation of the total edible carcass saturated fatty acid content. In mammals and most vertebrates, organ and tissue mass scales closely with body



mass. Consequently, the mass of individual edible organs can be calculated from body mass using allometric equations.<sup>48-51</sup> The edible carcass mass can then be determined by subtracting the mass of the bones (minus marrow), hide, hooves, antlers, blood, urine, and gastrointestinal contents from the total live weight. Edible carcass saturated fatty acid mass can be computed by multiplying individual tissue and organ mass by their respective saturated fatty acid compositions (% mass) and then summing these values. Finally, the edible carcass saturated fatty acid content by energy can be calculated from values by mass using the cubic regression equations developed by Cordain et al.<sup>27</sup> Figure 8.3 shows the cubic relationship between edible body fat percent by mass and edible body saturated fat percent by energy in mammals. Application of this equation along with the saturated fat content of plant and fish foods, as previously described,<sup>27</sup> allows for the estimation of total dietary saturated fat when the relative plant-to-animal subsistence values are known (Table 8.2). In the current model, a range of likely plant-to-animal subsistence values in hunter-gatherer diets have been employed as previously outlined.<sup>27</sup> Note that in the current model, saturated fat content for fish was derived from the mean value (26.1% of total fat energy) from 20 species of fish.<sup>45</sup>

## DISCUSSION

In Table 8.2 the mean dietary saturated fat as a percentage of total energy is  $11.0 \pm 3.9$  (S.D.). However, it is likely that a number of the projected values are physiologically unrealistic because they encroach upon or exceed the physiologic protein ceiling.<sup>27,52</sup> If those values whose protein intake exceeds 35.1% of total energy are excluded from the analysis, the mean dietary saturated fat as a percentage of total energy is  $13.2 \pm 2.8$ . In the typical hunter-gatherer diet, the animal subsistence falls between 55 to 65% of total energy; consequently, in this group, the mean dietary



**Figure 8.3** Regression of whole edible carcass fat percentage by weight on edible carcass saturated fat % by energy.

**Table 8.2 Dietary Macronutrient (% energy) and Saturated Fat (SAT) (% Energy) Estimates in Worldwide Hunter-Gatherer Societies (n = 229) with Varying Plant:Animal Subsistence Ratios and with Varying Animal (Hunted + Fished) Body Compositions**

	% PRO%	% CHO	% FAT	% SAT FAT
<b>(Plant:Animal) Subsistence Ratio</b>				
35:65 – 20% animal fat	21	22	58	17.6
35:65 – 15% animal fat	28 <sup>a</sup>	22	50	16.3
35:65 – 10% animal fat	35 <sup>a</sup>	22	43	14.1
35:65 – 5% animal fat	47 <sup>a,b,c</sup>	22	32	10.6
35:65 – 2.5% animal fat	56 <sup>a,b,c</sup>	22	23	8.1
45:55 – 20% animal fat	20	28	52	15.8
45:55 – 15% animal fat	26	28	46	14.5
45:55 – 10% animal fat	32 <sup>a</sup>	28	40	12.3
45:55 – 5% animal fat	42 <sup>a,b,c</sup>	28	30	8.7
45:55 – 2.5% animal fat	49 <sup>a,b,c</sup>	28	23	6.3
50:50 – 20% animal fat	20	31	49	15.1
50:50 – 15% animal fat	25	31	44	13.8
50:50 – 10% animal fat	31 <sup>a</sup>	31	38	11.6
50:50 – 5% animal fat	39 <sup>a,b</sup>	31	30	8.1
50:50 – 2.5% animal fat	46 <sup>a,b,c</sup>	31	23	5.6
55:45 – 20% animal fat	19	34	47	14.5
55:45 – 15% animal fat	24	34	42	13.1
55:45 – 10% animal fat	29 <sup>a</sup>	34	37	11.0
55:45 – 5% animal fat	37 <sup>a,b</sup>	34	29	7.4
55:45 – 2.5% animal fat	43 <sup>a,b,c</sup>	34	23	4.9
65:35 – 20% animal fat	19	40	41	13.1
65:35 – 15% animal fat	22	40	37	11.8
65:35 – 10% animal fat	26	40	34	9.6
65:35 – 5% animal fat	32 <sup>a</sup>	40	28	6.1
65:35 – 2.5% animal fat	37 <sup>a,b</sup>	40	23	3.6

<sup>a</sup> Exceeds low value (27.6% protein energy) for the range of maximal hepatic urea synthesis

<sup>b</sup> Exceeds mean value (35.1% protein energy) for the range of maximal hepatic urea synthesis

<sup>c</sup> Exceeds high value (40.9% protein energy) for the range of maximal hepatic urea synthesis

saturated fat as a percentage of total energy is higher still ( $15.1 \pm 1.9$ ). Even in plant dominated (>50% energy from plant foods) hunter-gatherer diets, the mean dietary saturated fat as a percentage of total energy is slightly higher ( $11.3 \pm 2.8$ ) than recommended healthful values of <10%.<sup>25</sup>

The present data suggests that the normal dietary intake of saturated fatty acids that conditioned our species genome likely fell between 10 to 15% of total energy, and that values lower than 10% or higher than 15% would have been the exception rather than the rule. Consequently, population-wide recommendations to lower

dietary saturated fat below 10% to reduce the risk of CAD<sup>25</sup> have little or no evolutionary foundation in pre-agricultural *Homo sapiens*. Because no randomized clinical trials of low saturated fat diets of sufficient duration have been carried out,<sup>53</sup> there is a lack of knowledge how low saturated fat intake can be without the risk of potentially deleterious health consequences.<sup>17</sup> Hence, extremely low, or conversely, high, lifelong consumption of dietary saturated fatty acids is likely to be discordant with the human genome.

## REFERENCES

1. Gould, S.J., *The Structure Of Evolutionary Theory*, Harvard University Press, Cambridge, MA, 2002.
2. Boaz, N.T., *Evolving Health: The Origins Of Illness and How the Modern World Is Making Us Sick*, John Wiley & Sons, Inc., New York, 2002.
3. Nesse, R.M. and Williams G.C., *Why We Get Sick. The New Science of Darwinian Medicine*, Times Books, New York, 1994.
4. Eaton, S.B., Konner, M., and Shostak, M., Stone agers in the fast lane: chronic degenerative diseases in evolutionary perspective, *Am. J. Med.*, 84, 739, 1988.
5. Eaton, S.B., Eaton, S.B., III., and Konner, M.J., Paleolithic nutrition revisited: a twelve-year retrospective on its nature and implications, *Eur. J. Clin. Nutr.*, 51, 207, 1997.
6. O'Keefe, J.H., Jr. and Cordain, L., Cardiovascular disease resulting from a diet and lifestyle at odds with our Paleolithic genome: how to become a 21st-century hunter-gatherer, *Mayo Clin. Proc.*, 79, 101, 2004.
7. Cordain, L., The nutritional characteristics of a contemporary diet based upon Paleolithic food groups, *J. Am. Nutraceut. Assoc.*, 5, 15, 2002.
8. Sebastian, A., et al., Estimation of the net acid load of the diet of ancestral preagricultural *Homo sapiens* and their hominid ancestors, *Am. J. Clin. Nutr.*, 76, 1308, 2002.
9. Frassetto, L., et al., Diet, evolution and aging — the pathophysiologic effects of the post-agricultural inversion of the potassium-to-sodium and base-to-chloride ratios in the human diet, *Eur. J. Nutr.*, 40, 200, 2001.
10. Colagiuri, S. and Brand Miller, J., The “carnivore connection” — evolutionary aspects of insulin resistance, *Eur. J. Clin. Nutr.*, 56 Suppl 1, S30, 2002.
11. Turner, C.G., Dental anthropological indications of agriculture among the Jomon people of central Japan, *Am. J. Phys. Anthropol.*, 51, 619, 1979.
12. Zero, D.T., Sugars — the arch criminal? *Caries Res.*, 38, 277, 2004.
13. Eaton, S.B., et al., Evolutionary health promotion, *Prev. Med.*, 34, 109, 2002.
14. Ravnskov, U., et al., Studies of dietary fat and heart disease, *Science*, 295, 1464, 2002.
15. Ravnskov, U., The questionable role of saturated and polyunsaturated fatty acids in cardiovascular disease, *J. Clin. Epidemiol.*, 51, 443, 1998.
16. Taubes, G., The soft science of dietary fat, *Science*, 291, 2535, 2001.
17. German, J.B. and Dillard, C.J., Saturated fats: what dietary intake? *Am. J. Clin. Nutr.*, 80, 550, 2004.
18. Grundy, S.M., Dietary fat: at the heart of the matter, *Science*, 293, 801, 2001.
19. Katan, M.B., Zock, P.L., and Mensink, R.P., Dietary oils, serum lipoproteins, and coronary heart disease, *Am. J. Clin. Nutr.*, 61 (6 Suppl), 1368S, 1995.
20. Horton, J.D., Cuthbert, J.A., and Spady, D.K. Dietary fatty acids regulate hepatic low density lipoprotein (LDL) transport by altering LDL receptor protein and mRNA levels, *J. Clin. Invest.*, 92, 743, 1993.

21. Phinney, S.D., et al., The human metabolic response to chronic ketosis without caloric restriction: physical and biochemical adaptation, *Metabolism*, 32, 757, 1983.
22. Stamler, J., Wentworth, D., and Neaton, J.D., Is relationship between serum cholesterol and risk of premature death from coronary heart disease continuous and graded? Findings in 356,222 primary screenees of the Multiple Risk Factor Intervention Trial (MRFIT), *JAMA*, 256, 2823, 1986.
23. Stamler, J., et al., Relationship of baseline serum cholesterol levels in 3 large cohorts of younger men to long-term coronary, cardiovascular, and all-cause mortality and to longevity, *JAMA*, 284, 311, 2000.
24. Popkin, B.M., et al., Where's the fat? Trends in U.S. diets 1965–1996, *Prev. Med.*, 32, 245, 2001.
25. Krauss, R.M., et al., AHA Dietary Guidelines: revision 2000: a statement for health-care professionals from the Nutrition Committee of the American Heart Association, *Circulation*, 102, 2284, 2000.
26. Wood, B., Palaeoanthropology: hominid revelations from Chad, *Nature*, 418, 133, 2002.
27. Cordain, L., et al., Plant to animal subsistence ratios and macronutrient energy estimations in world wide hunter-gatherer diets, *Am. J. Clin. Nutr.*, 71, 682, 2000.
28. Cordain, L., et al., The paradoxical nature of hunter-gatherer diets: Meat based, yet non-atherogenic, *Eur. J. Clin. Nutr.*, 56 (suppl 1), S42, 2002.
29. Schoeninger, M.J., Moore, J., and Sept, J.M., Subsistence strategies of two “savanna” chimpanzee populations: the stable isotope evidence, *Am. J. Primatol.*, 49, 297, 1999.
30. Stanford, C.B., The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids, *Am. Anthropol.*, 98, 96, 1996.
31. Teleki, G., The omnivorous chimpanzee, *Sci. Am.*, 228, 33, 1973.
32. Lee-Thorp, J., Thackeray, J.F., and van der Merwe, N., The hunters and the hunted revisited, *J. Hum. Evol.*, 39, 565, 2000.
33. Sponheimer, M. and Lee-Thorp, J.A., 2003. Differential resource utilization by extant great apes and australopithecines: towards solving the C4 conundrum, *Comp. Biochem. Physiol. A Mol. Integr. Physiol.*, 136, 27, 2003.
34. Sussman, R.W., Foraging patterns of nonhuman primates and the nature of food preferences in man, *Fed. Proc.*, 37, 55, 1978.
35. Semaw, S., et al., 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia, *J. Hum. Evol.*, 45, 169, 2003.
36. Bunn, H.T. and Kroll, E.M., Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania, *Curr. Anthropol.*, 17, 431, 1986.
37. de Heinzelin, J., et al., Environment and behavior of 2.5-million-year-old Bouri hominids, *Science*, 284, 625, 1999.
38. Asfaw, B., et al., Australopithecus garhi: a new species of early hominid from Ethiopia, *Science*, 284, 629, 1999.
39. Vekua, A., et al., A new skull of early Homo from Dmanisi, Georgia, *Science*, 297, 85, 2002.
40. Zhu, R.X., et al., New evidence on the earliest human presence at high northern latitudes in northeast Asia, *Nature*, 431, 559, 2004.
41. Richards, M.P., et al., Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes, *Proc. Natl. Acad. Sci.*, 97, 7663, 2000.
42. Richards, M.P., et al., Focus: Gough's Cave and Sun Hole Cave human stable isotope values indicate a high animal protein diet in the British Upper Palaeolithic, *J. Archaeol. Sci.*, 27, 1, 2000.
43. Gray, J.P., A corrected ethnographic atlas, *World Cultures J.*, 10, 24, 1999.

44. Hayden, B., Subsistence and ecological adaptations of modern hunter/gatherers, in *Omnivorous Primates*, Harding, R.S.O. and Teleki, G., Eds., Columbia University Press, New York, 1981, 344.
45. Nutritionist V Nutrition Software (Version 2.3), N-Squared Computing, San Bruno, CA, 2000.
46. Thomas, E.M., *The Harmless People*, New York, Knopf, 1959.
47. McArthur, M., Food consumption and dietary levels of groups of aborigines living on naturally occurring foods, in *Records of the American-Australian Scientific Expedition to Arnhem Land*, Mountford C.P., Ed, Melbourne University Press, Melbourne, 1960, 90.
48. Stahl, W.R., Organ weights in primates and other mammals, *Science*, 150, 1039, 1965.
49. Calder, W.A., *Size, Function and Life History*, Harvard University Press, Cambridge, 1984.
50. Meadows, S.D. and Hakonson, T.E., Contributions of tissues to body mass in elk, *J. Wildl. Manage.*, 46, 838, 1982.
51. Hakonson, T.E. and Whicker, F.W., The contribution of various tissues and organs to total body mass in mule deer, *J. Mammal.*, 52, 628, 1971.
52. Rudman, D., et al., Maximal rates of excretion and synthesis of urea in normal and cirrhotic subjects, *J. Clin. Invest.*, 52, 2241, 1973.
53. Sacks, F.M. and Katan, M., Randomized clinical trials on the effects of dietary fat and carbohydrate on plasma lipoproteins and cardiovascular disease, *Am. J. Med.*, 113 Suppl 9B, 13S, 2002.