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Diet-dependent acid load, Paleolithic nutrition, and evolutionary health promotion[1,2]

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The article by Ströhle et al (1) in this issue of the Journal significantly furthers appreciation of our remote ancestors' nutritional milieu. Such insight has potential biomedical significance because nearly all the genes and epigenetic regulatory mechanisms we carry today were originally selected for behaviorally modern humans who appeared in Africa between 100,000 and 50,000 y ago. Genetic evolution during subsequent millennia has continued, as shown by pigmentation changes (hair, eyes, skin), intestinal lactase retention beyond infancy, and adaptive defenses against microorganisms (eg, hemoglobinopathies and immune system adaptations). However, core biochemical and physiologic processes have been preserved (2). Accordingly, it can be argued that the typical diet, physical activity patterns, and body composition of late Paleolithic humans remain normative for contemporary humans—and models for disease-prevention recommendations.

As Ströhle et al (1) rightly note, recently studied hunter-gatherers (HGs) exhibited a wide range of nutritional patterns that varied according to local availability of animals and edible plants. Information on all HG diets is interesting; however, data from East Africa are especially valuable because of their relevance to health promotion. Conditions on humanity's mother continent most nearly match the ancestral paradigm and therefore accord best with our underlying genetic and epigenetic makeup. In this part of the world, the Stone Age plant-to-animal subsistence ratio is retrodicted to have been ≈1:1, with fish and shellfish providing a significant proportion of the animal component (3, 4). Estimates of dietary composition for humans just before the "out of Africa" diaspora (eg, references 3 and 5 and RS Kuipers et al, unpublished manuscript, 2010) vary in detail but converge on important cardinal features (**Table 1**).

As humans migrated over the globe and cultures changed, nutrition increasingly diverged from the ancestral pattern. Genetic evolution was unable to keep pace, and, consequently, various pathologies developed (6). In contemporary affluent nations, complex degenerative diseases such as atherosclerosis, numerous cancers, and hypertension reflect discordance between ancient genes and current diets, whereas the "epidemics" of obesity and diabetes can be largely attributed to our unholy (and unpaleolithic) alliance of sedentism and hypernutrition (7).

The striking prevalence of osteoporosis in Inuit skeletal remains from the early contact period (8) is especially pertinent to the observations of Ströhle et al (1) because plant foods are necessarily scarce in circumpolar environments. In East Africa, late Paleolithic plant-to-animal energy intake ratios would have approximated 50:50, and diet-dependent net endogenous acid production (NEAP) would have been alkaline—the norm for human biochemistry, physiology, and bone health. In contrast, for traditional Inuit HGs, whose subsistence derived overwhelmingly from aquatic and animal sources, NEAP would have been acidic, contributing to their osteoporosis.

Unbiased observers would agree that nutritional advice from conventional sources, whether based on epidemiologic or mechanistic findings, has not affected complex degenerative disease incidence/prevalence as much as might be wished. Gradually, such recommendations (and some biomarker goals) are shifting toward the ancestral exemplar (**Table 2**).

This shift toward humanity's biological baseline will probably continue as more studies like that of Ströhle et al (1) are published. However, the process might be accelerated, and its investigative expense reduced, if the health research community came to organize its terms, concepts, observations, and arguments in accord with paleoanthropologic insights. To achieve a paradigm shift of this magnitude will require the mental agility to integrate ideas and data from widely separate disciplines—heretofore an uncommon characteristic of our much-fragmented academic community.

Groups whose way of life tends to continue the Stone Age pattern have low rates of complex degenerative diseases; however, predictions arising from the ancestral health concept have only just begun to be rigorously evaluated (5, 19). For the present, therefore, the theory that deviation from our ancestral lifestyle increases, while reversion toward the basics of Stone Age existence reduces, chronic disease risk must be judged by its simplicity, intrinsic elegance, and conceptual economy. The Paleolithic health paradigm readily withstands such scrutiny, heightening expectations with regard to its potential as an investigative guide

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TABLE 1
Nutritional comparisons[1]

	Ancestral	Contemporary Western
Total energy intake	More	Less
Caloric concentration	Very little	Much
Dietary bulk	More	Less
Total carbohydrate intake	Less	More
Added sugar and refined carbohydrate	Very little	Much more
Glycemic load	Relatively low	High
Fruit and vegetables	Twice as much	Half as much
Antioxidant capacity	Greater	Lesser
Fiber	More	Less
Soluble:insoluble	Closer to equal	Far more insoluble
Protein intake	More	Less
Total fat intake	Equivalent	
Serum cholesterol–raising fat	Less	More
Total polyunsaturated fat	More	Less
ω–6:ω–3	Closer to equal	Far more ω–6
Long-chain essential fatty acids	More	Less
Cholesterol intake	More	Less
Micronutrient intake	More	Less
Electrolytes	Much more potassium	More sodium
Acid-base effect (NEAP)	Alkaline	Acidic
"Dairy" products	Mother's milk only	Considerable
Cereal grains	Very little	A great deal
Free water intake	More	Less

[1] NEAP, net endogenous acid production.

and, perhaps, as a psychologically powerful influence on future health-related public behavior.

As recently observed in *Nature*, "It is difficult to refute the assertion that if modern populations returned to a hunter-gatherer state then obesity and diabetes would not be the major public health threats that they now are" (20). Proponents of evolutionary health promotion maintain that this principle applies to all the complex degenerative "diseases of civilization" and that an appreciation of

TABLE 2
Comparative recommendations[1]

	Recommendations		
	Pre-1990	Current (reference no.)	Estimated ancestral intake
Nutrients			
Carbohydrate (% daily energy)	55–60[2]	45–65 (9)	35–40
Added sugar (% daily energy)	12	<25 (9)	2
Fiber (g/d)	—	38 for males, 25 for females (9)	>70
Protein (% daily energy)	10–15	10–35 (9)	25–30
Fat (% daily energy)	30	20–35 (9)	30–40
Saturated fat (% daily energy)	<10	<7 (10)	7.5–12
Cholesterol (mg/d)	<300	<300 (10)	≥500
EPA+DHA (g/d)	—	1.6 for males, 1.1 for females (9)	5–6
Vitamin C (mg/d)	60	90 for males, 75 for females (9)	500
Vitamin D (IU/d)	400	1000 (11)	4000 (sunlight)
Calcium (mg/d)	800	1000 (12)	1000–1500
Sodium (mg/d)	2400	1500 (13)	<1000
Potassium (mg/d)	2500	4700 (13)	7000
Biomarkers			
Blood pressure (mm Hg)	<140/90	115/75 (14)	110/70
Serum cholesterol (mm/dL)	200–240	115–165 (15)	125
Body composition (%lean:%fat)			
Females	—	<31% fat (16)	35–40:20–25
Males	—	<26% fat (16)	45–50:10–15
Physical activity (kcal/d)	—	150–490 (17, 18)	>1000

[1] EPA+DHA, eicosapentaenoic acid + docosahexaenoic acid.
[2] Range (all such values).

human experience during the late Paleolithic will eventually become the foundation for preventive research and recommendations.

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