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SPECIAL ARTICLE

PALEOLITHIC NUTRITION

A Consideration of Its Nature and Current Implications

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HUMANITY has existed as a genus for about 2 million years, and our prehuman hominid ancestors, the australopithecines, appeared at least 4 million years ago (Table 1). This phase of evolutionary history made definitive contributions to our current genetic composition, partly in response to dietary influences at that time. The foods available to evolving hominids varied widely according to the paleontological period, geographical location, and seasonal conditions, so that our ancestral line maintained the versatility of the omnivore that typifies most primates. Natural selection has provided us with nutritional adaptability; however, human beings today are confronted with diet-related health problems that were previously of minor importance and for which prior genetic adaptation has poorly prepared us. Chronic illnesses affecting older, postreproductive persons could have had little selective influence during evolution, yet such conditions are now the paramount cause of morbidity and mortality in Western nations.

The human genetic constitution has changed relatively little since the appearance of truly modern human beings, *Homo sapiens sapiens*, about 40,000 years ago.[2,3] Even the development of agriculture 10,000 years ago has apparently had a minimal influence on our genes. Certain hemoglobinopathies and retention of intestinal lactase into adulthood are "recent" genetic evolutionary trends, but very few other examples are known. Such developments as the Industrial Revolution, agribusiness, and modern food-processing techniques have occurred too recently to have had any evolutionary effect at all. Accordingly, the range of diets available to preagricultural human beings determines the range that still exists for men and women living in the 20th century — the nutrition for which human beings are in essence genetically programmed.[4]

Differences between the dietary patterns of our remote ancestors and the patterns now prevalent in industrialized countries appear to have important implications for health, and the specific pattern of nutritional disease is a function of the stage of civilization.[5] Physicians and nutritionists are increasingly convinced that the dietary habits adopted by Western society over the past 100 years make an important etiologic contribution to coronary heart disease, hypertension, diabetes, and some types of cancer. These conditions have emerged as dominant health problems only in the past century and are virtually unknown among the few surviving hunter-gatherer populations whose way of life and eating habits most closely resemble those of preagricultural human beings.[6] The longer life expectancy of people in industrialized countries is not the only reason that chronic illnesses have assumed new importance. Young people in the Western world commonly have developing asymptomatic forms of these conditions, but hunter-gatherer youths do not.[7-10] Furthermore, the members of technologically primitive cultures who survive to the age of 60 years or more remain relatively free from these disorders, unlike their "civilized" counterparts.[9,11,12]

Nutritional Evolution

The ancestral mammals were insectivores, and invertebrate predation was thus the basis from which primate feeding behavior evolved.[13] However, as the primate order expanded and body size increased,

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Table 1. The Main Events of Human Evolution.*

Millions of Years Ago	Epoch	Development	
0.0002		Industrial revolution	
	Holocene		
0.01		Agricultural revolution	
	Latest Pleistocene		Paleolithic period (from first manufacture of stone tools to shortly before the development of agriculture)
0.045		*Homo sapiens sapiens* (anatomically modern) appears	
	Late Pleistocene		
0.080		*H. sapiens neanderthalensis* appears	
	Middle Pleistocene		
0.400		Archaic *H. sapiens* appears	
1.6	Early Pleistocene	*H. erectus* present	
2.0		*H. habilis* present	
	Pliocene	Australopithecine divergence	
4.5		Bipedal *Australopithecus afarensis* present	
	Late Miocene		
7.5		Hominid–pongid divergence (inferred from molecular data)	
11			
	Middle Miocene	African and Asian hominoids diverge	
17			
	Early Miocene	Hominoid radiation begins	
24			

*Modified slightly from the "1984 consensus" of paleontologists, as presented by Pilbeam.[1]

vegetable foods became increasingly important for most species. During the Miocene era (from about 24 to about 5 million years ago) fruits appear to have been the main dietary constituent for hominids,[14] but their fossilized dental remains seem suitable for mastication of both animal and vegetable material.[15] After the divergence of the human and ape lines (now thought to have occurred between 7.5 and 4.5 million years ago)[1] our ancestral feeding pattern included increasing amounts of meat, although it is uncertain whether this change reflects hunting, scavenging, or both.[16,17] It is now thought that *Homo habilis* began to manufacture stone tools about 2 million years ago and that the succeeding species, *Homo erectus*, began to consume a much larger amount of meat between 1.8 and 1.6 million years ago.[18-20] It is clear that thereafter early human beings consumed a considerable amount of meat: large accumulations of animal remains are found where they lived, the tools they used were mainly geared toward processing game, and their living sites were selectively located in areas where there was a relatively substantial biomass of large grazing animals. The importance of vegetable foods is harder to assess, since plant remains are poorly preserved. Fossilized fruit pits and nuts are commonly found, but tools for processing plant foods are conspicuously absent in comparison with their widespread proliferation in later prehistory.[21] Shells and fish bones are unknown in archaeological material dating from before 130,000 years ago[22] and are found infrequently in material dating from before 20,000 years ago, so that, in paleontological terms, widespread use of aquatic foods is a recent phenomenon.[23]

Several authorities have estimated that *Homo erectus* and early *Homo sapiens* obtained over 50 per cent of their diet from plant sources.[24,25] However, when the Cro-Magnons and other truly modern human beings appeared, concentration on big-game hunting increased; techniques and equipment were fully developed while the human population was still small in relation to the biomass of available fauna.[26] In some areas during this time meat probably provided over 50 per cent of the diet.[27] But because of overhunting, climate changes, and population growth, the period shortly before the inception of agriculture and animal husbandry was marked by a shift away from big-game hunting and toward a broader spectrum of subsistence activities. Remains of fish, shellfish, and small game are all more common at sites dating from this period, as well as tools that are useful for processing plant foods, such as grindstones, mortars, and pestles.[23] In at least two Middle Eastern sites, trace-element analysis for strontium levels in bone reveals a definite increase in the amount of vegetable material in the diet together with decreased meat consumption at this time.[28] Modern hunter-gatherers most closely resemble the human beings of this relatively recent period.

Agriculture markedly altered human nutritional patterns: over the course of a few millenia the proportion of meat declined drastically while vegetable foods came to make up as much as 90 per cent of the diet.[27] This shift had prominent morphologic consequences: early European *Homo sapiens sapiens*, who enjoyed an abundance of animal protein 30,000 years ago, were an average of six inches taller than their descendants who lived after the development of farming.[29] The same pattern was repeated later in the New World: the Paleoindians were big-game hunters 10,000 years ago, but their descendants in the period just before European contact practiced intensive food production, ate little meat, were considerably shorter,[30] and had skeletal manifestations of suboptimal nutrition,[31-34] which apparently reflect both the direct effects of protein–calorie deficiency and the synergistic interaction between malnutrition and infection.[35] Since the Industrial Revolution, the animal-protein content of Western diets has become more nearly adequate, as indicated by increased average height: we are now nearly as tall as were the first biologically modern human beings. However, our diets still differ markedly from theirs, and these differences lie at the heart of what has been termed "affluent malnutrition."[6]

Recent Hunter-Gatherer Nutrition

Over 50 hunter-gatherer societies have been studied extensively enough to justify some nutritional generalizations about them,[36-38] but only a handful have survived into the second half of the 20th century and have had their diets thoroughly analyzed. In general, groups of hunter-gatherers who, like the earliest human beings, live in an inland, semitropical habitat derive between 50 and 80 per cent of their food (by weight) from plants, with animal sources providing between 20 and 50 per cent.[38] These generalizations hold true for the Hadza of Tanzania[39] (who obtain 20 per cent of their diet from animals), the !Kung[37] (37 per cent) and ≠Kade[40] (20 per cent) San (Bushmen) of the Kalahari, and the Philippine Tasaday[41] (42 per cent), though before contact with Western civilization, the Tasaday were probably less successful hunters. The recently investigated Aché of Paraguay[42] (80 per cent) represent a possible exception, but their setting is so unusual and so affected by contact with more modern economies that they are very unlikely to be representative. Coastal and riverine peoples derive from 10 to 50 per cent of their food from fishing; for example, the Australian Aborigines of Arnhem Land get about 40 per cent of their total intake from fish and shellfish, whereas only a quarter comes from plants.[43,44] Because of their harsh environment, Arctic hunters, such as the aboriginal Eskimos, obtain less than 10 per cent of their food from vegetation.[45] In comparison with the majority of paleolithic human beings, existing hunter-gatherers occupy marginal habitats,[26] and their lives differ in many ways from those of people living before the advent of agriculture. Nevertheless, the range and content of foods they consume are similar (in the sense that they represent wild game and uncultivated vegetable foods) to those that our ancestors ate for up to 4 million years. Thus, an analysis of the nutritional content of these foods can provide a rational basis for estimating what human beings are genetically "programmed" to eat, digest, and metabolize.

Meat

Paleolithic populations obtained their animal protein from wild game, especially gregarious ungulate herbivores, such as deer, bison, horses, and mammoths. The nutritional quality of such meat differs considerably from that of meat available in the modern American supermarket; the latter has much more fat — in subcutaneous tissue, in fascial planes, and as marbling within the muscle itself.[46] Domesticated animals have always been fatter than their wild ancestors because of their steady food supply and reduced physical activity, but recent breeding and feeding practices have further increased the proportion of fat to satisfy our desire for tender meat.[47-49] These efforts have succeeded: modern high-fat carcasses are 25 to 30 per cent fat or even more.[47] In contrast, a survey of 15 different species of free-living African herbivores revealed a mean carcass fat content of only 3.9 per cent.[50] Not only is there more fat in domesticated animals, its composition is different; wild game contains over five times more polyunsaturated fat per gram than is found in domestic livestock.[51,52] Furthermore, the fat of wild animals contains an appreciable amount (approximately 4 per cent) of eicosapentaenoic acid (C20:5), a long-chain, polyunsaturated, ω3 fatty acid currently under investigation because of its apparent antiatherosclerotic properties.[53,54] Domestic beef contains almost undetectable amounts of this nutrient.[53]

Meat from free-living animals has fewer calories and more protein per unit of weight than meat from domesticated animals,[40,51,55,56] but the amino acid composition of muscle tissue from each source is similar.[51] Since the cholesterol content of fat is roughly equivalent to that of lean tissue,[57] the cholesterol content of game would not be expected to differ substantially from that of commercially available meat. A detailed list of selected nutritional characteristics of 25 wild animal species is available from us.

Vegetable Foods

Except for Eskimos and other high-latitude peoples, hunter-gatherers typically use many species of wild plants for food.[36,39,40] Roots, beans, nuts, tubers, and fruits are the most common major dietary constituents, but others, ranging from flowers to edible gums, are occasionally consumed. Small cereal grains, which have been staples for "civilized" peoples since the Agricultural Revolution, make a surprisingly minor contribution overall; however, the wide range of vegetable foods eaten by foragers contrasts with the relatively narrow variety of crops produced by horticulturists and traditional agriculturists. Furthermore, many domesticated food plants have higher ratios of starch to protein than do their wild forms.[58] The nutrient composition of the wild vegetable foods most commonly consumed by the !Kung,[59] and ≠Kade[40] San, Hadza,[60] Australian Aborigines,[61-63] and Tasaday[41] has been determined. A detailed list of the individual nutritional contents of all 44 items is available from us; average values of selected nutrients are shown in Table 2.

Table 2. Nutritional Values (Mean ±S.E.) of 44 Wild Vegetable Foods* Consumed by the !Kung[59] and ≠Kade[40] San, Hadza,[60] Tasaday,[41] and Australian Aborigines.[61-63]

Content	Nutritional Value
Protein (g/100 g)	4.13±1.04
Fat (g/100 g)	2.84±1.54
Carbohydrate (g/100 g)	22.79±3.15
Fiber (g/100 g)	3.12±0.62
Energy (kcal)	128.76±21.17

*The foods include 2 beans, 2 nuts, 11 roots, 1 rhizome, 2 leaf buds, 1 stalk, 2 melons, 1 seed pod, 2 berries, 1 truffle, 7 tubers, 11 fruits, and 1 corm.

Probable Daily Nutrition for Paleolithic Human Beings

Representative nutrient values for wild game and vegetable foods consumed by recent hunter-gatherers can be derived from the literature.[40,41,50,51,55,56,59-71] In turn, these figures can be used to estimate the daily nutrient intake for paleolithic human beings. Estimates of energy intake and various animal:vegetable ratios in subsistence patterns can be generated. Although the specific dietary constituents used by any particular group of preagricultural human beings must have varied with ambient conditions, average nutrient values should reflect central tendencies transcending these effects.

Energy Sources

Game and wild plants yield an average of 1.41 and 1.29 kcal per gram, respectively.[40,41,50,51,55,56,59-71] We can estimate the weight of animal and plant food consumed by assuming a daily energy intake of, say, 3000 kcal,[72] and a subsistence pattern of 35 per cent meat[36,73] and calculating as follows. The daily weight of animal food, in grams, multiplied by 1.41 kcal per gram plus the daily weight of plant food multiplied by 1.29 kcal per gram must equal 3000 kcal. In this model, animal food is 35 per cent and plant food is 65 per cent of the total weight of food eaten. If x is the total weight of food, then:

$$1.41(0.35x) + 1.29(0.65x) = 3000$$
$$x = 2252 \text{ g.}$$

(These figures suggest a degree of precision that is of course unwarranted. They are presented simply as the results generated by this particular model.) Under these idealized and probably intermittent isocaloric conditions, the total daily food intake of 2252 g would have been provided by 788.2 g of game and 1463.8 g of vegetable food. On the basis of these calculations and mean nutrient values, the average daily nutrient intake for paleolithic human beings can be reconstructed as shown in Table 3.

Fat and Fatty Acids

The fat from Cape buffalo is 30 per cent polyunsaturated, 32 per cent monounsaturated, and 38 per cent saturated.[51] Assuming a similar ratio for wild game in general, the animal fat in a reconstructed paleolithic diet would provide 8.91 g of polyunsaturated fatty acids and 11.29 g of saturated fatty acids. The fat in 36 wild vegetable foods used by the Hadza,[60] San (Bushmen),[74] and other African tribal groups[75] is 38.7 per cent polyunsaturated, on average. If a similar figure can be assumed for wild vegetable fat generally, then the plant foods in this paleolithic dietary example would yield 16.1 g of polyunsaturated fatty acids. In 24 American vegetable foods saturated fatty acids constitute 15.6 per cent of total fat.[56] If the proportion in wild plants is similar, then a paleolithic diet containing 35 per cent meat and 65 per cent vegetables would contribute 6.49 g of saturated vegetable fat, and the overall ratio of polyunsaturated to saturated fats for a day's total (animal and vegetable) fat intake would be 1.41.

Table 3. Proposed Average Daily Macronutrient Intake for Late Paleolithic Human Beings Consuming a 3000-kcal Diet Containing 35 per Cent Meat and 65 per Cent Vegetable Foods.

	Intake (g)
Protein	**251.1**
Animal	190.7
Vegetable	60.4
Fat	**71.3**
Animal	29.7
Vegetable	41.6
Carbohydrate	**333.6**
Fiber	**45.7**

Cholesterol

Meat from modern domesticated animals has an average of 75 mg of cholesterol in each 100-g portion.[56] The cholesterol content of meat from wild game should be similar, since the proportion of cholesterol in meat is surprisingly unaffected by the fat content.[57] Thus, paleolithic human beings consuming 788.2 g of meat in a day would have ingested 591.2 mg of cholesterol.

Sodium and Potassium

The sodium and potassium content for 14 vegetable foods used by recent hunter-gatherers is known.[40,41,59] These foods have an average of 10.1 mg of sodium and 550 mg of potassium, respectively, for each 100-g portion. If these values are representative, the daily average of 1463.8 mg of paleolithic vegetable food would have yielded 147.8 mg of sodium. Data on the sodium and potassium content of wild game are unavailable, but if the average values for beef, lamb, pork, and veal (68.75 mg of sodium and 387.5 mg of potassium per 100 g)[56] are assumed to be comparable to those for meat from wild animals, then the 788.2 g of meat in a 35:65 (meat:vegetable) paleolithic diet would have provided 541.9 mg of sodium, for a daily total of 689.7 mg. The overall ratio of dietary potassium to sodium would have been 16.1 to 1.0.

Calcium

The calcium content of 37 plant foods consumed by recent foragers averages 102.5 mg for each 100 g,[40,59,61,62] so the daily provision of calcium from vegetable sources would have been 1500.4 mg in the paleolithic diet. Venison and the meat of most domesticated animals contain about 10 mg of calcium per 100 g of tissue,[56] so meat in a 35:65 paleolithic diet would have yielded an additional 78.8 mg, for a daily grand total of 1579.2 mg of calcium.

Ascorbic Acid

The mean ascorbic acid content of 27 vegetables eaten[40,59-62] by recent hunter-gatherers is 26.8 mg per 100 g, so that the average vitamin C intake would have been 392.3 mg each day in paleolithic diets conforming to this pattern. (This calculation excludes the Australian green plum,[62] which has the highest known vitamin C content [3150 mg per 100 g] and would tend to inflate the estimate.)

Other Nutrients

Even at the lowest estimate of the ratio of meat to plant food (20:80), by modern standards, the estimated paleolithic diet would have been adequate in animal protein, iron, vitamin B_{12}, and folate, whereas agricultural populations of the underdeveloped world in the 20th century have widespread deficiencies in these nutrients.

Because of seasonal and local variation, among other factors, populations that subsist by collecting food invariably have a greater variety of plant foods than is typical for agricultural populations.[13] This variety would have ensured a gradual accumulation of most of the necessary trace elements found in plant foods, despite differing concentrations in different sources. However, the possibility of geographically limited deficiencies in certain nutrients (e.g., iodine) cannot be ruled out.

Fiber

Because of the relatively high proportion of vegetable foods and the primitive character of food processing, paleolithic diets must have included substantially more nondigestible fiber than do typical Western diets. The average fiber content of 37 wild plant foods for which information on fiber content is available is 3.12±0.62 g per 100 g (mean ±S.E.). For a paleolithic diet containing 65 per cent vegetable foods, the estimated fiber content would have been 45.7 g.

Shortages

The majority of preindustrial societies, including those based on hunting and gathering, experience seasonal nutritional stress and occasional (less frequent than annual) severe shortages. Although the paleolithic period was almost certainly characterized by conditions of greater abundance, both in game and plant foods, than those experienced by recent hunter-gatherers,[26] it is nevertheless likely that paleolithic populations experienced infrequent shortages sufficient to produce weight loss and to threaten survival in persons with inadequate adipose reserves. It would have been adaptive to consume more calories than the minimal daily requirement and to store fat during periods of relative abundance. This pattern is in fact observed among recent hunter-gatherers,[76,77] although its magnitude is not known.[37]

Subsistence data from 58 technologically primitive societies reveal that the mean, median, and mode for recent foragers converge on a dietary ratio of 35 per cent meat and 65 per cent vegetable foods.[36,73] Of course, the paleolithic diet was not fixed; it varied in its individual components, as well as in its relative proportions of animal and vegetable foodstuffs. For these reasons, the use of average nutrient values derived from items used by different groups of contemporary hunter-gatherers is more helpful than an analysis of any one group's diet. The mean values can be used to estimate nutritional characteristics for widely varying subsistence patterns (Table 4).

Table 4. Estimated Nutritional Characteristics for Various Animal:Vegetable Subsistence Patterns

	Animal:Vegetable Ratio			
	20:80	*40:60*	*60:40*	*80:20**
Total dietary energy (%)				
Protein	24.5	37	49	61
Carbohydrate	55	41	28	14
Fat	20.5	22	23	25
P:S ratio †	1.72	1.33	1.08	0.91
Cholesterol (mg)	343	673	991	1299

*For a 3000-kcal diet, an 80:20 subsistence pattern would require an intake of 437 g of protein per day. Urea synthesis and its accompanying obligate water loss place an approximate upper limit of about 400 g of protein per day for a steady diet. This suggests that with animal:vegetable subsistence patterns of this magnitude, the animals eaten were probably fatter (e.g., for hibernation or cold insulation) than those described in the text. This inference, in turn, is consistent with high proportions of meat consumed only by hunter-gatherers in the higher latitudes.

†P:S denotes polyunsaturated:saturated fats.

The Paleolithic Diet in Modern Perspective

Whether based on as much as 80 per cent or as little as 20 per cent meat, the paleolithic diet differed substantially from the typical diet in the United States today, and it also differed, although much less so, from that currently advocated by nutritionists and by the U.S. government[78] (Table 5). The foods we eat are usually divided into four basic groups; meat and fish, vegetables and fruit, milk and milk products, and breads and cereals. Two or more daily servings from each are now considered necessary for a balanced diet, but adults living before the development of agriculture and animal husbandry derived all their nutrients from the first two food groups; they apparently consumed cereal grains rarely, if at all, and they had no dairy foods whatsoever. Nevertheless, with a diet containing 35 per cent meat, their calcium intake would have far exceeded the highest estimate of the minimal daily requirement. Neanderthals and Cro-Magnons who inhabited subarctic Eurasia and whose diet is considered to have been most like that of the Eskimos, among recent populations, had massive bones, indicating that they obtained sufficient calcium. The probable paleolithic intake of dietary fiber was much higher than ours and approached that common in rural Africa, where disease conditions linked with deficient dietary fiber rarely occur,[79] although paleolithic human beings obtained their fiber predominantly from fruits and vegetables rather than grain. A paleolithic diet consisting of 35 per cent meat would have contained only a sixth of the sodium in the typical American diet — a third of the level most recently recommended.[80] Even in a diet with 80 per cent meat, the sodium intake would have just reached the lowest recommended level and would have been markedly below the lowest estimate of current intake. Given the typically wide variety of collected plant foods and assuming ascorbic acid to be representative, the vitamin intake of paleolithic human beings would have substantially exceeded ours, irrespective of the proportion of meat in the diet.

In the hunting society of our ancestors meat provided a large fraction of each day's food, ensuring high iron and folate levels. Protein contributed twice to nearly five times the proportion of total calories that it does for Americans. Their high-meat diet contained a high level of cholesterol — similar to or even higher than the level in our diet; most paleolithic human beings must have greatly exceeded the U.S. Senate Select Committee's recommended cholesterol level.[78] Conversely, they ate much less fat than we do, and the fat they ate was substantially different from ours. Whether subsistence was based predominantly on meat or on vegetable foods, the paleolithic diet had less total fat, more essential fatty acids, and a much higher ratio of polyunsaturated to saturated fats than ours does. In comparison with us, our paleolithic ancestors consumed more structural and less depot fat.

The extent to which some of the major chronic diseases of industrialized society are related to the typical Western diet is controversial, but evidence for an important linkage is steadily accumulating. Medical researchers in diverse fields are beginning to define a generally preventive diet — one of benefit against conditions ranging from atherosclerosis to cancer. Such investigations are converging in several ways with the studies of paleontologists and anthropologists. Ultimately, of course, only experimental and clinical studies can confirm hypotheses about the medical consequences of dietary choices. Nevertheless, it is both intellectually satisfying and heuristically valuable to estimate the typical diet that human beings were adapted to consume during the long course of our evolution. Points of convergence between this estimate and modern recommendations are encouraging, and points of divergence suggest new lines of research. The diet of our remote ancestors may be a reference standard for modern human nutrition and a model for defense against certain "diseases of civilization."

Table 5. Comparison of the Late Paleolithic Diet,* the Current American Diet, and U.S. Dietary Recommendations.

	Late Paleolithic Diet*	Current American Diet[78]	U.S. Senate Select Committee Recommendations[78]
Total dietary energy (%)			
Protein	34	12	12
Carbohydrate	45	46	58
Fat	21	42	30
P:S ratio †	1.41	0.44	1.00
Cholesterol (mg)	591	600	300
Fiber (g)	45.7	19.7 ‡	30–60[79]
Sodium (mg)	690	2300–6900[80]	1100–3300[80]
Calcium (mg)	1580	740 §	800–1200 ¶
Ascorbic acid (mg)	392.3	87.7 §	45 ¶

*Assuming the diet contained 35 per cent meat and 65 per cent vegetables.

†P:S denotes polyunsaturated: saturated fats.

‡British National Food Survey, 1976.

§U.S. Department of Agriculture Food Consumption Survey, 1977–1978.

¶Recommended Daily Dietary Allowance, Food and Nutrition Board, National Academy of Sciences–National Research Council.

We are indebted to Denis Burkitt, George Cahill, Irven DeVore, Richard Lee, John R.K. Robson, Margaret J. Schoeninger, Pat Shipman, Marjorie Shostak, and Alan Walker for helpful comments, and to Debra Fey for assistance in preparing it.

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