Proceedings of the British Academy, 77, 247–264

Light Stable Isotopes and the Reconstruction of Prehistoric Diets

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Summary. Several stable isotope ratios have been measured in human skeletons to determine prehistoric diet. These include the isotopes of nitrogen, sulphur and strontium, which have been used to assess the importance of marine foods in human diets. The systematics of these isotopes in food chains are imperfectly understood, whereas that of carbon is quite well-known. Stable carbon isotope ratios (i.e., $^{13}C/^{12}C$ ratios, reported as $\delta^{13}C$ values) are of particular relevance to terrestrial foodwebs because of the characteristic isotope signatures of plants with different photosynthetic chemistry. The two dominant photosynthetic pathways produce C_3 plants (all trees and woody shrubs; temperate and shaded grasses) and C_4 plants (subtropical and tropical grasses, except those in shaded forests). The carbon isotope ratios of the two plant groups are distinctive and are passed along the food chain to herbivores and carnivores. This fact has been used to trace the spread of, for example, maize agriculture in the woodlands of North America and in the tropical forests of South America, as well as rice agriculture in China. Such applications have invariably made use of bone collagen as sample material, which has restricted their use to the last 10,000 years or so. The alternative is to use substituted carbonates in biological apatite, particularly in tooth enamel, after appropriate chemical cleaning to remove diagenetic carbonates. Although still controversial, this method is being used with success to study the diets of early hominids of more than two million years ago.

Read 14 February 1991.

1. Introduction

During the past fifteen years, measurements of light stable isotope ratios in bone have been convincingly shown to provide useful indicators of animal and human diets. From the first application in archaeology (Vogel and van der Merwe 1977), this procedure has been expanded to solve problems of prehistoric subsistence world-wide. In certain circumstances—particularly those surrounding the spread of maize agriculture in the Americas—isotopic analysis has become a routine research technique. This application is closely followed by situations where marine and terrestrial foods were involved in a prehistoric subsistence strategy. On a wider screen, isotopic tracing techniques have developed as powerful tools in the life and environmental sciences, from studies of the feeding habits of sardines to evaluations of atmospheric and climatic conditions of the distant past.

This paper is concerned with dietary tracing in archaeology by means of isotopic bone chemistry, specifically the stable isotope ratios of nitrogen and carbon (with emphasis on the latter). Early developments in this field have been reviewed in some detail (van der Merwe 1982; DeNiro 1987) and will not be repeated here. In recent years, as the number of researchers in this field has grown and the applications have multiplied, several seminars and conference panels have produced compilations of work in progress. Of particular significance have been the Advanced Seminars on Dietary Bone Chemistry, which first met in 1986 in Santa Fe, and produced a volume of edited papers (Price 1989). The seminar met again in 1988 at the University of Cape Town; the proceedings, edited by Andrew Sillen and George Armelagos, have appeared as a special issue of the *Journal of Archaeological Science* (volume 18 part 3) and again in Bad Hamburg, Germany, in 1991 (proceedings in preparation).

My involvement with isotopic dietary tracing took place at the University of Cape Town from the mid-1970's on, and more recently at Harvard. In the course of unravelling prehistoric diets in Africa, the Americas, and the Middle East, I have collaborated with many archaeologists and other isotope specialists. Some of them will be mentioned in this article, but this is not a review of the major contributions to this varied field of research. It is, instead, a selected and personal view of some of the highlights I have seen.

2. Bone and light stable isotopes

2.1 Composition of bone

Bone consists of two phases: organic and mineral. The organic phase consists primarily of collagen fibres, which provide a matrix for bone growth. The mineral phase is biological apatite, consisting mostly of calcium phosphate, but with a variety of ions (e.g., fluorine, strontium, carbonate) substituted in the apatite crystals as impurities (Lee-Thorp 1989). Since bone is constructed from the food an animal eats, it encodes information about the diet. Exactly which components of the diet contribute to the organic and mineral phases of bone is a subject of considerable debate and active research. The simplest model holds that dietary proteins build collagen, while carbohydrates and fats build apatite (Krueger and Sullivan 1984). Since humans cannot synthesise certain amino acids (so-called essential amino acids), it is clear that at least these building blocks of collagen must be obtained from dietary proteins. Even here, though, it can be shown that only the carbon skeletons of essential amino acids (excepting threonine and lysine, which are incorporated unchanged) pass directly from food to collagen, while nitrogen is obtained from a pool of glutamic acid in the body which derives from all the nitrogen in the diet (Hare *et al.* 1991). The non-essential amino acids in collagen may be taken directly from dietary proteins or synthesised from the energy portion of the diet. The carbon in apatite-carbonate comes from blood carbonate, which is most likely to derive from the energy portion of the diet. These relationships have not been conclusively demonstrated, which affects the interpretation of carbon and nitrogen isotope signals in bone.

Research on these topics is under way at several centres, but until the models are refined it will be difficult to obtain unequivocal quantitative interpretations of the contribution of major food groups to the building of bone. Qualitative interpretation of the relative importance of certain foods is, of course, possible and is widely applied in archaeology.

2.2 Measurement of isotope ratios

Isotopic dietary tracing is possible because of the uneven distribution in nature of ^{13}C and ^{15}N (the heavy stable isotopes of these elements). Certain categories of food have distinctive ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. These ratios are passed along the foodchain and are recorded in the bone of the consumers. Measurement of these isotopic signals in archaeological bone makes it possible to reconstruct particular elements of the diet. In the case of nitrogen and carbon, isotopic ratios are usually measured in bone collagen after the mineral phase has been dissolved away. The collagen is combusted to form nitrogen and carbon dioxide, which are cryogenically purified. The isotopic ratios of these gases are compared with the known ratio of a standard in a ratio mass spectrometer. The difference between the two ratios is given in parts per mil ($^0/_{00}$) in the delta notation, e.g.;

$$\delta^{13}C = \frac{^{13}C/^{12}C \text{ sample} - {}^{13}C/^{12}C \text{ standard}}{^{13}C/^{12}C \text{ standard}} \times 1000$$

For carbon isotope ratios, the standard is a marine carbonate called PDB with a value of zero. Most $\delta^{13}C$ values in nature are negative compared to PDB. For nitrogen the standard is air, and most $\delta^{15}N$ values are positive.

2.3 Nitrogen isotopes

$^{15}N/^{14}N$ ratios are strongly fractionated by metabolic processes; i.e., the ratios are altered. Each trophic level may increase the $\delta^{15}N$ value. A typical terrestrial biotic community in, say, England will have air with a $\delta^{15}N$ value of zero (the standard). Plants which can fix nitrogen in their tissues directly from the air (legumes) will have values near zero. Other plants may have values around (+)3 $^0/_{00}$, herbivores 4–7 $^0/_{00}$, and carnivores 7–9 $^0/_{00}$. In the ocean, the foodchain is much longer, and the spread of values can range from zero (for air-fixing blue-green algae) at one extreme to values as high as 15–20 $^0/_{00}$ for swordfish and seals (Schoeninger *et al.* 1983). If an Arctic hunter could stand to live on polar bear meat, he would be so high on the foodchain that his $\delta^{15}N$ value would be above 20 $^0/_{00}$. This information can be used to determine the relative amount of seafood in prehistoric diets, provided that the archaeologist has a fair idea of where in the foodchain the people got their food. Seals and killer whales will yield results quite different from oysters.

Marine/terrestrial contrasts only work for nitrogen isotopes in areas with good rainfall. In dry regions, animals have $\delta^{15}N$ values above 10 $^0/_{00}$, and the top of the foodchain may approach 20 $^0/_{00}$ (Heaton *et al.* 1986; Ambrose and DeNiro 1986; Sealy *et al.* 1987). The relationship between annual rainfall and $\delta^{15}N$ values in herbivore bone appears to be inversely linear, with the value going above 10 $^0/_{00}$ as the rainfall drops below 400 mm/year. These values come from empirical field studies, and the phenomenon has not yet been completely explained (Ambrose 1991). High $\delta^{15}N$ values in drought-stressed animals result from the excretion of urea that is depleted in ^{15}N (Ambrose and DeNiro 1986) and also of similarly depleted ammonia. Part of this depletion may be due to urea recycling and intestinal microbial action in the animal (Sealy *et al.* 1987), which is necessary to extract scarce protein from arid region plants. The animal's metabolism effectively moves it several trophic levels up the foodchain. As a result of these high $\delta^{15}N$ values, it is not possible to tell marine and terrestrial foods apart in dry coastal regions by means of nitrogen isotope analysis. Conversely, however, aridity in the past can be established under certain circumstances.

Our understanding of the distribution of ^{15}N in nature is still in the developmental stages. Recent measurements of nitrogen isotopes in elephant bone from different African habitats (van der Merwe *et al.* 1990) show that tropical forest animals have relatively high $\delta^{15}N$ values (around 8 $^0/_{00}$), thus refuting the simple relationship with rainfall that had seemed to be established earlier. Archaeological interpretations cannot, as yet, be argued from first principles (as is the case for carbon), but need to be arrived at empirically by measuring the nitrogen isotopes in the natural environment of each case study.

2.4 Carbon isotopes

Dietary tracing in archaeology has been particularly successful with carbon isotopes. This method has been extensively used to trace the spread of maize agriculture in the Americas (some examples are described here), the prehistoric use of African cereals in Europe (Murray and Schoeninger 1988), the the start of rice agriculture in China (Cai and Qiu 1984), and the like. It has also been utilised to study the exploitation of marine foods by coastal people of British Columbia (Chisholm *et al.* 1982), Japan (Minegawa and Akazawa, in press), Australia (Hobson and Collier 1984), mesolithic Europe (Tauber 1981), and of South Africa (Sealy and van der Merwe 1985).

Stable carbon isotope ratios are fractionated by various natural processes, the most important in this context being different systems of photosynthesis (reviewed in van der Merwe 1982). Plants with C_3 photosynthesis (all trees and woody shrubs, grasses from temperate and shaded forest environments) have foliage with average $\delta^{13}C$ values of $-26.5\,^0/_{00}$. C_4 plants (grasses from the subtropics) have average $\delta^{13}C$ values of $-12.5\,^0/_{00}$. These values have been arrived at from cumulative assessments by many researchers in different parts of the world, and are particularly well demonstrated by the C_3 and C_4 grasses of South Africa (Vogel *et al.* 1978; Figure 1). The stability of such values depends on an average $\delta^{13}C$ value of about $-7\,^0/_{00}$ for atmospheric carbon dioxide, the source carbon for photosynthesis; it varies with the concentration of carbon dioxide in the atmosphere. Fossil fuel burning is slowly altering this value to about $-8\,^0/_{00}$, for example, while rotting leaf litter in the Amazonian forests produces air near the ground with values as low as $-15\,^0/_{00}$ (van der Merwe and Medina 1989).

When animals eat plants, enrichment in ^{13}C of about $+5\,^0/_{00}$ occurs during the formation of collagen (Figure 2). In savannahs with C_3 trees and shrubs and C_4 grasses, browsers (C_3 plant-eaters) have average collagen values of $-21.5\,^0/_{00}$, while pure grazers average $-7.5\,^0/_{00}$. Mixed feeders fall somewhere in between. For the mineral phase of bone, the enrichment is more extreme (Sullivan and Krueger 1981; Krueger and Sullivan 1984; Lee-Thorp 1989; Lee-Thorp and van der Merwe 1987), at about $+12\,^0/_{00}$, which results in browser apatite of about $-14.5\,^0/_{00}$ and grazer apatite of about $-0.5\,^0/_{00}$. The collagen of carnivores is enriched by a further $2\,^0/_{00}$ or so, but their apatite has about the same value as that of their herbivore prey. Lions in C_4 grassland, for example, have collagen values of about $-5.5\,^0/_{00}$,

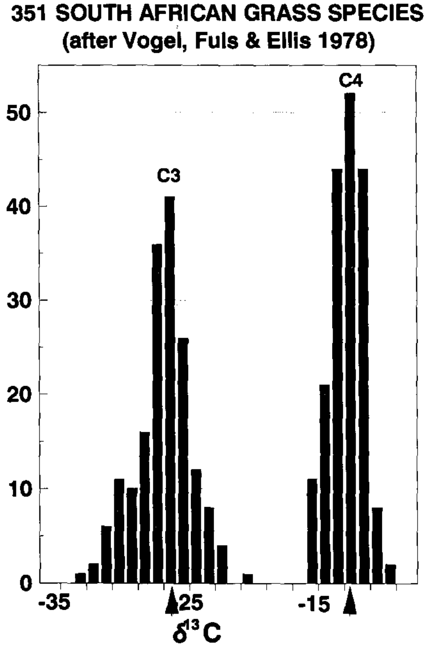

Figure 1. $\delta^{13}C$ values of 351 South African grasses illustrate the clear separation between C_3 and C_4 plants. (After Vogel *et al.* 1978).

while their apatite values average about $-0.5\,^0/_{00}$, like those of the grazing animals they feed on.

The carbon cycle in the oceans is more complicated than that on land (Sealy 1986). The source carbon includes atmospheric carbon dioxide, dissolved bicarbonates, and large deposits of marine carbonates that are continuously dissolved. The first trophic level is represented by various planktonic forms, which exhibit carbon isotope values that vary with water temperature. The second trophic level includes grazing and filter-feeding molluscs and zooplankton; on them are based a complicated foodweb with many trophic levels and a wide range of carbon isotope ratios. Human consumers of seafood may exploit this foodweb at many levels or only a few, depending on preference and technology, with concordant effects on their isotopic ratios. Two marine systems I have studied in detail are those of the Benguela current (western Cape coast, South Africa) described later and the Humboldt current of Ecuador (van der Merwe *et al.* in prep.). Both systems are cold temperate, with cold upwelling from the deep, and are very similar in carbon isotope composition. Foods available to humans vary from mollusc meat near $-18\,^0/_{00}$ to predatory ocean fish and seals with meat near $-12\,^0/_{00}$. In a diet consisting primarily of seafood, energy is provided mostly

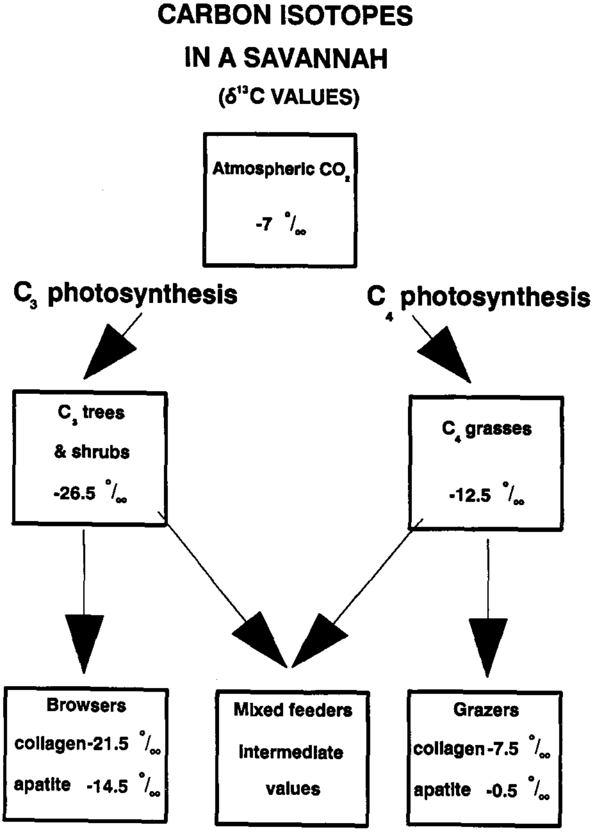

Figure 2. Flow diagram of δ^{13}C values in a savannah foodweb, where the trees and shrubs are C_3 and the grasses are C_4 plants.

by fats, which are depleted by 5 ‰ or more relative to the meat protein in the same animal (Lee-Thorp *et al.* 1989; Figure 3). The result is that the δ^{13}C values of collagen and apatite in human consumers with high seafood diets are very close together, instead of being spaced by about 8 ‰ as in herbivores. Close spacing of collagen and apatite δ^{13}C values is a general indication of diets high in meats and fats. Omnivores, with carbohydrates and fats in their diets to provide energy, have spacing somewhere between that of herbivores and carnivores.

The carbon isotope values described here have been arrived at through field studies. Experiments with mice and chickens show enrichments of only 1 or 2 ‰ between laboratory food and consumer collagen (DeNiro and Epstein 1978; Bender *et al.* 1981). In field studies, plant food δ^{13}C values are those of whole foliage, which include a range of food components and

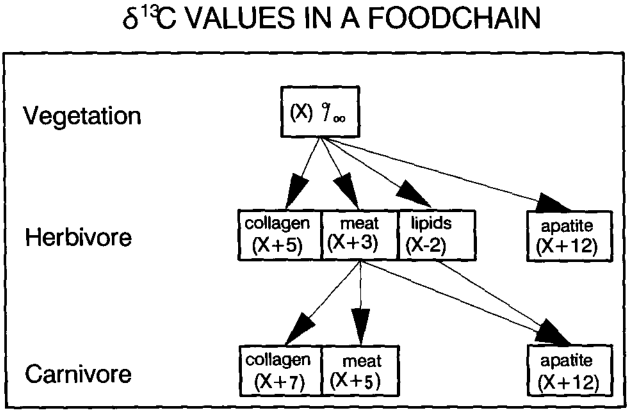

Figure 3. Flow diagram of $\delta^{13}C$ values on three trophic levels, showing the different storage tissues in animals. (After Lee-Thorp 1989).

cellulose. These differences do not imply that models based on field studies are wrong, but they do underscore the need for more refined models based on laboratory studies which use controlled combinations of different food components. Feeding studies with laboratory rats, designed to answer some of these questions, are currently being conducted by Lambert (Northwestern University), Buikstra (Chicago) and Ambrose (Illinois). A specialised feeding study with pigs (Hare *et al.* 1991) has shown how different amino acids in food translate into consumer tissue. We may expect to learn a great deal about human and animal metabolism from these and similar studies.

3. Prehistoric diets and carbon isotopes

This section includes descriptions of case studies which illustrate the use of carbon isotope ratios to decode prehistoric diets.

3.1 Maize in the American woodlands

The carbon isotope record of human skeletons from the North American Woodlands, particularly the Lower Illinois Valley, provided one of the earliest and most dramatic demonstrations of this dietary tracing technique (van der Merwe and Vogel 1978). In the 1970's and earlier, the consensus of archaeological interpretations held that maize agriculture had been introduced to this region by about AD 400 or earlier. With hindsight, this interpretation can be seen to have been based on little or no direct evidence for the presence of maize, but it provided a plausible subsistence base for the villages that were present and for the large constructions produced by

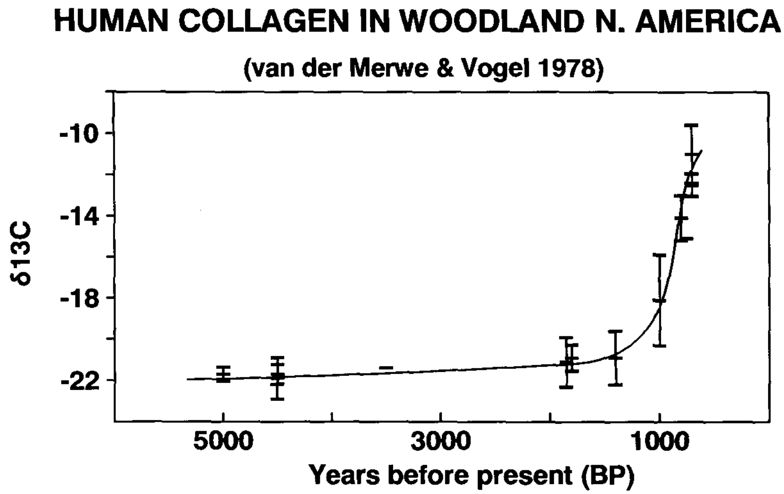

Figure 4. Changes in the $\delta^{13}C$ values of human skeletal collagen herald the adoption of maize agriculture in the North American Woodlands after 800 AD.

Hopewell peoples. A study of the dietary pathologies evident in the human skeletons led Jane Buikstra to conclude that the health problems associated with high maize diets did not appear until after AD 800, thus contradicting a generation's worth of archaeological beliefs (reviewed in Buikstra and Milner 1991).

The woodlands provide an ideal situation for determining the importance of a C_4 plant like maize with carbon isotopes, since this biome has essentially no indigenous C_4 plants. Skeletal $\delta^{13}C$ values for this region (Figure 4) proved to average about $-21.5\,^0/_{00}$ throughout the Archaic, Early Woodland and Middle Woodland periods, a value identical to that of C_3 herbivores. After AD 800, the carbon isotope ratios changed rapidly to reach $-10\,^0/_{00}$ after AD 1000. The latter value indicates that 75 per cent of the carbon in bone collagen was derived from C_4 plants, as can still be observed among maize-dependent peoples who live in C_3 biomes in other parts of the world. This period of rapid carbon isotope change in the Illinois valley was accompanied by large population increases and a change in settlement patterns, as people moved from villages in the valley bottoms to the uplands and concentrated in larger settlements. These results amply confirmed Buikstra's observations on the dietary status of human skeletons.

In retrospect, two items are noteworthy regarding the diets of Woodland peoples. In the 1980's, archaeologists documented a pre-maize period of horticulture based on indigenous C_3 plants for eastern North America (Smith 1989). This serves to resolve the apparent contradiction between archaeological observations about the complexity of Early and Middle Woodland cultures and the demonstrated absence of maize agriculture. Secondly, a careful study of the carbon isotope values for these periods show that maize may have been present in small quantities, below a level that can be conclusively documented with isotopic measurements. This would mean that the acceptance of maize as a staple was resisted for nearly half a millennium after it was first encountered. This resistance to changes in dietary staples (and their concomitant changes in lifestyle) has been observed ethnographically in many parts of the world; it should be expected as the norm rather than the exception in prehistoric studies of diet.

3.2 Maize in Amazonia

Maize is not an important crop among contemporary forest peoples of Amazonia, who depend on a traditional system of cassava swidden cultivation for calories and forest animals and river fish for protein. In the 1970's, most archaeologists assumed that this tropical forest system had provided the subsistence base for all food-producing peoples in Amazonia before European contact. The dense concentrations of people and incipient kingdoms observed by early European explorers in the floodplains of the lower Orinoco and Amazon were interpreted as intensified examples on fertile soil of the same subsistence base. Anna Roosevelt (1980) and others argued that intensive cassava cultivation could not have supported such large populations, since the modest availability of forest animals and fish during the rainy season limited the protein supply. They argued that another protein source such as maize and beans would have been necessary, and that these crops could have been grown in the floodplains during the short dry season, whereas cassava could not survive the seasonal waterlogging of the soil.

Roosevelt's excavations at Parmana on the lower Orinoco showed that significant cultural changes had taken place in this region between about 800 BC and AD 400. The number of villages and amount of refuse increased significantly, indicating population increases. The artefacts associated with food production changed from flint chips (set in resin on boards to grate cassava) and large ceramic griddles (for drying cassava pulp) to grindstones (for the processing of cereal grains). These changes, she argued, showed that maize agriculture had been adopted in the floodplains by AD 400, and had set the population on a path which resulted in the large concentrations of people seen in early historic times.

The gallery forests of the lower Orinoco valley have no C_4 plants, although the savannahs further from the river do. The forests and swidden fields also have pineapples, which have CAM photosynthesis (crassulacean acid metabolism) and can mimic the carbon isotope values of C_4 plants under certain circumstances. For Roosevelt's argument about a change in protein

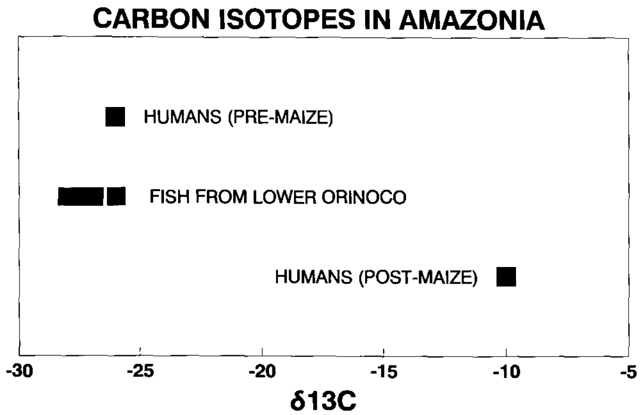

Figure 5. $\delta^{13}C$ values for skeletal collagen of humans and fish in the lower Orinoco show a shift in protein source from fish to maize between 800 BC and AD 400.

source to be sustained, the most telling support from carbon isotope measurements would be a change in human collagen values from pure C_3 to readings with a significant C_4 component. The results proved to be $-26\,^0/_{00}$ for skeletons of about 800 BC and $-10\,^0/_{00}$ for those of about AD 400 (Figure 5). These measurements amply proved her case and showed that the later group was fully dependent on maize as a staple crop.

A quick comparison of the Illinois and Orinoco examples spotlights the unusual value of $-26\,^0/_{00}$ for pre-maize humans in the latter case. In order to explain this value convincingly, it proved necessary to study in detail the carbon isotope ratios in Amazonian foodwebs. For this study (van der Merwe and Medina 1989, 1991) we collected river fish, forest animals, forest and swidden plants, and forest air along the upper Rio Negro in the Amazon basin. The results show (Figure 6) that the entire foodweb of this region has more negative $\delta^{13}C$ values than those encountered in open habitats (e.g., Figure 2). This is especially the case for fish, with collagen values as negative as $-29\,^0/_{00}$ in both the Rio Negro (Figure 6) and the Orinoco (Figure 5); the forest animals have collagen values between -22 and $-25\,^0/_{00}$. The pre-maize humans of the Orinoco appear to have acquired most of their protein from fish.

The depletion of ^{13}C in Amazonian foodwebs is the result of carbon recycling in the dense forests, where abundant leaves from the canopy $(-30\,^0/_{00})$ mix with those of less abundant undergrowth $(-36\,^0/_{00})$ to produce a thick layer of leaf litter $(-31\,^0/_{00})$ on the ground. The rotting leaf litter and the mat of air roots under it release large amounts of carbon dioxide to produce an air mixture under the canopy which is depleted in ^{13}C; this air is recycled by photosynthesis in the forest. Since the forest foodweb is ultimately

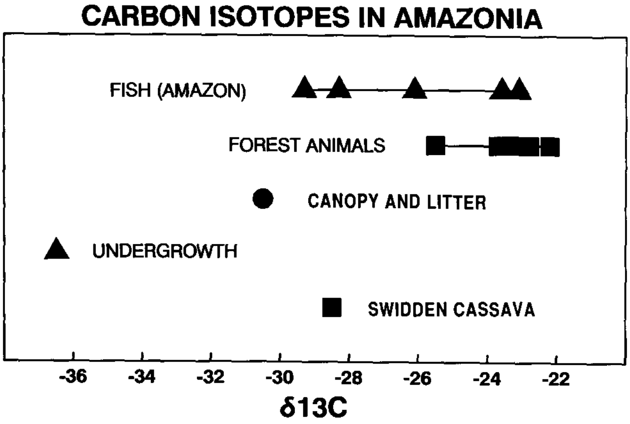

Figure 6. Extremely negative $\delta^{13}C$ values in Amazonian foodwebs are the result of recycled carbon from rotting leaf litter in the forests, as illustrated by this case from the upper Rio Negro.

based on forest plants, the depletion is transmitted through it. This argument does not account entirely for the very negative values in river fish, which are, on average, also more negative in the lower Orinoco than in the upper Rio Negro. This may be due to the contribution of water plants to the river foodweb. Such plants photosynthesise carbon dioxide from air dissolved in the surface waters. This air is derived from forest leaf litter, and the river dissolves more as it flows: in the lower reaches, the water is supersaturated with air isotopically more negative than the forest air (Martinelli *et al.* 1991).

3.3 Terrestrial and marine foods in South Africa

Reconstructions of the subsistence strategies of Holocene hunter-gatherers of the southwest Cape Province in South Africa has been the subject of a running debate and interactive research between archaeologists and isotope specialists at the University of Cape Town for several years. This is probably the most intensively studied area anywhere as far as the seasonality of archaeological food remains and their isotopic expression in human collagen is concerned. The debate has served to refine archaeological models for human subsistence in the area, and has raised many questions about human metabolism and the building of collagen from different food groups.

The southwest Cape Province is an arid coastal plain (annual rainfall below 400 mm) defined by a mountain range some 100 km inland from the shore. This is a winter rainfall area, with the result that the plant cover is essentially of the C_3 type (Figure 7). During the winter food is abundant at the coast: drowned seal pups wash ashore from island rookeries and shellfish are less likely to be contaminated by the toxic red tides that occur mostly in

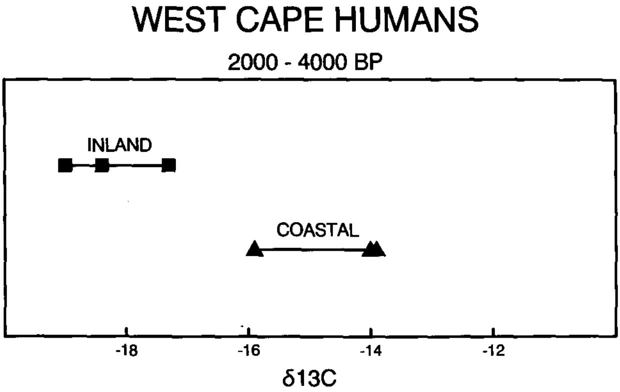

Figure 7. The $\delta^{13}C$ values for human skeletal collagen of hunter-gatherers of the southwestern Cape Province in South Africa between 4000 and 2000 years ago show differences between coastal and inland peoples. (After Sealy 1989).

summer months. During the summer, food is more abundant in the interior, consisting especially of the carbohydrate-rich corms of flowering geophytes and a variety of small antelope, tortoises, and hyrax (rock rabbits). Archaeological remains from cave sites at the coast and in the mountains reflect such seasonal abundances. These data have led John Parkington and co-workers to develop a model of seasonal movement between the coast and the interior for Holocene hunter-gatherer subsistence (Parkington 1976, 1977, 1984).

Isotopic data for human skeletons from the coast and the interior contradict such a model. The debate has settled on the period between 4000 and 2000 years ago, during which the archaeological data for seasonal movement are most persuasive. The carbon isotope ratios for coastal skeletons of this period range between -14 and $-16\,^0/_{00}$, while inland skeletons range between -17 and $-19\,^0/_{00}$ (Sealy and van der Merwe 1985; 1986; Figure 7). Marine foods (fish, shellfish and seal meat) range in $\delta^{13}C$ values between about -12 and $-18\,^0/_{00}$, with an average of $-15.5\,^0/_{00}$, while terrestrial foods (meat and plants) average about $-25\,^0/_{00}$ (Figure 8). We interpret these results to mean that the skeletons of the coast and the interior were from groups of people who did not have the same subsistence strategies—the inland people acquired some of their food at the coast, but the coastal people acquired more. It would appear that the region accommodated more than one lifestyle.

Parkington has questioned the interpretation of the carbon isotope data at various times as the debate has unfolded, particularly as regards the relative contributions of marine protein and plant carbohydrates to collagen carbon (e.g., Parkington 1991). Many of these questions have been incor-

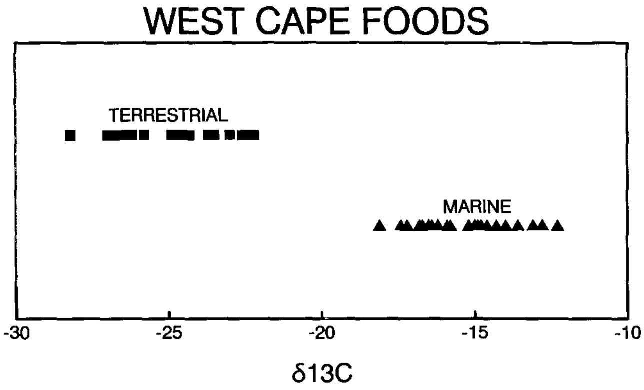

Figure 8. Marine foods (shellfish, fish, seals, birds) and terrestrial foods (plants and animals) of the southwestern Cape Province in South Africa have distinctly different $\delta^{13}C$ values. (After Sealy 1989).

porated in the isotopic research agenda. In her doctoral thesis, Sealy (1989) expanded the chemical evidence relating to dietary tracing in the southwest Cape by using nitrogen isotope, strontium isotope, and strontium/calcium ratios. Nitrogen isotope ratios of marine and terrestrial animals in this region proved to overlap substantially, due to aridity, while strontium/calcium ratios were shown to distinguish meat eaters from plant eaters only if one knows exactly which animals a particular carnivore preys on. For omnivores like humans the system is much too complex to determine the amount of meat in the diet by means of strontium/calcium ratios. Strontium isotope ratios, however—which differ substantially between the ocean and coastal marine sediments on the one hand and the rocks of the interior on the other —contribute isotopic signatures to human bone apatite which confirm the dichotomy between coastal and inland skeletons.

By now, the starting point of this debate has receded into the distance, even as it has served to drive archaeological and isotopic interpretations toward greater refinement. It continues to do so.

4. Further isotope studies

Isotopic studies of prehistoric diets are expanding into many parts of the world, as far as both practitioners and applications are concerned. Projects at the top of my own list include archaeological studies in Belize and Ecuador. The Belize case is a collaboration with Norman Hammond (Boston University), excavator of the site of Cuello. The preliminary isotope data from this site indicate that the pre-classic Maya had a substantial maize component in their diet, but were not as dependent on it as, for example, people of the post-classic period. They appear to have fattened some of their dogs on maize for eating, while leaving others to scavenge—these may have been different breeds of dogs. Contrary to some earlier speculation on our part, however, they did not feed maize to the deer in the vicinity to make them easier to kill. In Ecuador, Scott Raymond (University of Calgary), Julia Lee-Thorp (Cape Town) and I are trying to resolve the controversy over whether the people of the Valdivia culture of about 4000 BC - one of the earliest Formative culture in the Americas - depended primarily on maize or marine foods for subsistence. In this case the answer appears to be "neither", and we may have to start considering tubers more seriously.

These are examples of straightforward applications of our current knowledge of isotopes in bone, but what of future developments? My own curiosity pulls me in four directions: metabolic pathways, source tracing, isotope signatures in apatite, and past environments:

i) In order to make isotopic dietary tracing truly quantitative we need laboratory feeding experiments with isotopically labelled foods and isotopic measurements at the level of amino acids. Crucially, we need a chromatograph/mass spectrometer that can do rapid isotopic analysis of specific amino acids.

ii) We have demonstrated that a combination of isotope ratios (carbon, nitrogen, strontium) can serve to pinpoint the habitat in which an elephant tusk originated (van der Merwe *et al.* 1990) and are now doing the same for rhino horn. These techniques can be expanded to other biological materials, and have some obvious applications in archaeology.

iii) Apatite carries a dietary carbon isotope signal (Sullivan and Kreuger 1981) which can be isolated from fossil tooth enamel when collagen has disappeared. Sufficient work has now been done (Kreuger 1991; Lee-Thorp and van der Merwe 1987, 1991) to show that the biogenic signal can be isolated from diagenetic carbonates, following early objections (Schoeninger and DeNiro 1982). This technique has been used to determine the diets of C_3- and C_4-eating baboon species 1.8 million years old (Lee-Thorp 1989; Lee-Thorp *et al.* 1989). We are now using it to compare the diets of early hominid species, for which the C_4 dietary component apparently came from grazing animals and thus acts as an indirect measure of meat in their diets.

iv) Carbon isotopes in tooth enamel of mammal-like reptiles of 200 million years ago show that the mass extinctions of the Late Permian were coincident with substantial changes in the carbon isotope composition (and therefore carbon content) of the atmosphere (Thackeray *et al.* 1990). This technique provides one way of studying past climates and primary productivity of our planet.

There seems to be plenty to do.

Acknowledgements

I thank the many collaborators who worked on the problems described in this article. John Lanham and David Killick produced the drawings.

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