

REVIEW

A brief review of the archaeological evidence for Palaeolithic and Neolithic subsistence

MP Richards^{1*}

¹*Department of Archaeological Sciences, University of Bradford, Bradford, UK*

Knowledge of our ancestor's diets is becoming increasingly important in evolutionary medicine, as researchers have argued that we have evolved to specific type of 'Palaeolithic' diet, and many modern nutritional disorders relate to the mismatch between the diet to which we have evolved, and the relatively newer agricultural-based 'Neolithic' diets. However, what is the archaeological evidence for pre-agricultural diets and how have they changed over the four million years of hominid evolution? This paper briefly introduces the three lines of evidence we have for Palaeolithic and Neolithic diets; morphological changes, archaeological material evidence, and direct measurement of diet from bone chemistry. The morphological changes, increasing gracilization of the mandible and increasing brain size have been interpreted (based on analogies with living primates) as the move from plants to higher-quality, more digestible, animal meat, although this is debated. The archaeological evidence is especially weak, as many organic materials, especially plants, do not survive well, and are therefore invisible in the archaeological record. Artefacts, such as stone tools which are likely to be used for hunting and animal bones with evidence of human processing and butchering do indicate that hunting did occur at many times in the past, but it is impossible to judge the frequency. Direct evidence from bone chemistry, such as the measurement of the stable isotopes of carbon and nitrogen, do provide direct evidence of past diet, and limited studies on five Neanderthals from three sites, as well as a number of modern Palaeolithic and Mesolithic humans indicates the importance of animal protein in diets. There is a significant change in the archaeological record associated with the introduction of agriculture worldwide, and an associated general decline in health in some areas. However, there is an rapid increase in population associated with domestication of plants, so although in some regions individual health suffers after the Neolithic revolution, as a species humans have greatly expanded their population worldwide.

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Introduction

Human nutrition researchers are increasingly exploring the role evolution has played in the development of modern human physiology and are becoming aware of various nutritionally related disorders in Western societies that are not observed in a number of modern hunter-gatherer populations (Cordain *et al*, 2000; Eaton & Konner, 1985). This has led a number of researchers to conclude that humans are maladapted to diets of domesticated and processed plant foods (Cordain, 1999) as these foods are recent in evolutionary timescales, and a number of medical doctors and

nutritionists are starting to advocate a return to a so-called Palaeolithic (pre-agricultural) diet (Eades & Eades, 2000; Atkins, 1999; Worm, 2002). What, however, is the evidence of human diet and nutrition, and human health, before the adoption of agriculture? Archaeologists often see the reconstruction of past human subsistence as vital to our understanding of past societies, and therefore have produced a large body of literature concerning past subsistence practices. Unfortunately, due to limited data and often coarse methodology, we only have a partial picture of past diets.

This paper is written primarily as an introduction for non-specialists to briefly introduce the methods archaeologists use to infer past human and hominid subsistence, as well as provide a brief overview of the existing evidence for hominid subsistence from the rise of our line in Africa, *ca* 4 million years ago, up to the first adoption of agriculture approximately 10 000 years ago.

*Correspondence: MP Richards, Department of Archaeological Sciences, University of Bradford, Bradford, West Yorkshire BD7 1DP, UK.
E-mail: m.p.richards@bradford.ac.uk

Tools for reconstructing past diets

Archaeological sites dating to before 10 000 years ago are rare, and many of the artefacts that were present when the site was formed have disappeared through time. The organic remains of food consumption are among our best evidence of past subsistence, but rarely survive. Plant remains are missing from a large part of the archaeological record, but when they are present it may be possible for specialists, archaeobotanists, to identify species present, including domesticated vs wild species (Harlan, 1992). Bone, however, often does survive, and zooarchaeologists can determine the species and number of individual animals in a faunal assemblage (O'Connor, 2000). Through careful study of bone taphonomy (Lyman, 1994) and natural bone deposition processes (ie by carnivores) it is possible to identify human-modified animal bone that is the result of purposeful butchering and hunting in the past. Animal and plant remains are indirect measures of past diets, and may relate to single events, such as a special feast, but we cannot know how representative of everyday diets they are. Direct methods of dietary reconstruction, on the other hand, focus on the study of hominid remains directly, and have the potential of telling us about daily subsistence. Earlier hominid bone remains are rare, but when found provide a wealth of information on past diets, particularly through analogy with modern primates (eg mandible size). Osteoarchaeologists look for evidence of nutritional health as manifested in the skeleton, and look for pathologies that indicate nutritional stress (Larsen, 1997). Our newest tool for reconstructing past diets lies in the chemical analyses of these hominid bones, particularly stable isotope analysis, which provides a direct measure of these past diets (Schwarcz & Schoeninger, 1991; DeNiro, 1987).

A brief summary of hominid evolution

The first hominids, including the Australopithecines and the recently named Kenyanthropines first appear in Africa approximately four million years ago, and the link between the various species remains complicated and controversial (see Lieberman, 2001, for a recent summary, and Jurmain *et al*, 2000, for a general introduction). These early hominids probably walked upright, and had robust cranial features, including massive mandibles. *Homo habilis*, believed by many to be the first species in our line, first appears in Africa approximately two million years ago. There is evidence that the first purposeful use of stone tools is linked with the appearance of this species, and this trait is therefore believed to be unique to the *Homo* line (Sussman, 1991, 1994; Isaac, 1984; Leakey, 1971), although others argue that the latest Australopithecines could also have been tool users (Semaw, 2000). As our line evolves through *Homo ergaster* to *Homo erectus*. We see the spread of hominids, for the first time, out of Africa and into Eurasia. Within the *Homo* line we see a decrease in mandible size and an increase in cranial capacity through time. These trends continue into

the more recent past and, focussing on Europe specifically, we find Neanderthals (called either *Homo sapiens neanderthalensis* or *Homo neanderthalensis*) between about 200 000 and 30 000 years ago with the largest cranial capacities of any hominid species (Mellars, 1996). Modern humans, *Homo sapiens sapiens*, first appear approximately 100 000 years ago in Africa, and we do not have evidence for modern humans in Europe until about 40 000 years ago (Gamble, 1999).

What is the evidence of subsistence changes through these four million years of hominid evolution? We have three lines of evidence that have been used to reconstruct the evolution of subsistence over this vast time period. They are the interpretation of morphology by analogy with living primates and other mammals, the material artefactual remains and, more recently, direct chemical analysis of the hominid remains themselves. These three lines of evidence will be explored below.

Morphological and dietary changes in the hominid line

Most of our interpretation of the lifestyles of the earliest hominids derives from the study of living primates such as gorillas and chimpanzees. Early hominids such as the Australopithecines and the recently discovered Kenyanthropines (Leakey *et al*, 2001) are characterized by relatively massive mandibles, and the more robust species have significant muscle attachments, such as sagittal crest on the top of the skull. These features are also found in gorillas, who have an entirely vegetarian diet and require the large mandible and strong cranial muscles for the crushing and grinding of plant foods. These features are less pronounced in subsequent species such as the more gracile *Australopithecus africanus*, and the larger-brained *Homo habilis*, ca 2.5–1.8 million years ago (Jurmain *et al*, 2000). *Homo habilis* is a relatively gracile species with cranial features more in common with chimpanzees than gorillas. Chimpanzees do consume some animals, including insects, and therefore have less need for the more expensive, in terms of energy costs, robust crania and mandibles, and this is the type of subsistence suggested for *Homo habilis*. There is another trend in time, the concomitant increase in brain size as reflected in cranial capacity. Again through analogy with modern primates like chimpanzees, this increase in brain size has been linked to increased intelligence, which, in turn, implies the increasing use of tools for the collection and processing of foods. As we move into the last million years of hominid evolution, there is only one generally accepted hominid species, *Homo erectus*, which first appears in Africa ca 1.8 million years ago. With this species we probably see the first movement of our line out of Africa which required the ability to adapt to a range of climates, which, in turn, implies a dietary breadth and flexibility that was not present in earlier species. From approximately 200 000 years onwards, and perhaps as early as 400 000, archaic *Homo sapiens* are first found. A variant of these, the Neanderthals,

are first found in Europe from approximately 130 000 and last until approximately 30 000 years ago (Smith *et al*, 1999). Neanderthals are robust, stocky hominids, which is believed to relate to an adaptation to the cold climate of Europe (Mellars, 1996). *Homo sapiens sapiens* probably appeared in Africa approximately 200 000 years ago, and then spread throughout the Old World, appearing in Europe approximately 40 000 years ago (Mellars & Stringer, 1989; Stringer & Andrews, 1988). However, this replacement model has been criticized by proponents of the regional continuity model (Thorne & Wolpoff, 1992).

There are two main morphological trends through time in the evolution of the hominid line, increasing gracilization of the mandible and other cranial features, as well as an increase in cranial capacity. Many researchers interpret this mandible gracilization as being due to an increasing consumption of meat, which is less fibrous than plant foods and therefore easier to masticate. As discussed above, this inference is derived from comparisons between fossils of extinct hominids and crania of living primates whose diets are known. Researchers have also argued that there is a link between meat consumption and the second temporal trend, increasing brain size through time (Aeillo & Wheeler, 1995; Leonard & Robertson, 1994). The main inference is that larger brains mean greater intelligence; however, these larger brains are expensive in terms of energy needs, but were necessary for hominids as they allowed us to out-compete our competitors through increasingly complex culture and manipulation of the environment. The higher energy needs these larger brains required could be met by the consumption of meat, which is a more energy-efficient food than plants. The main recent proponents of this theory in the anthropological literature are Leslie Aeillo and Peter Wheeler, who published a paper in 1995 in *Current Anthropology* entitled 'The expensive tissue hypothesis' (Aeillo & Wheeler, 1995). They argue that our brains are much larger than we might predict, using ratios of expected organ masses to brain size for other mammals, and this increased brain size is due to increased needed intelligence, and the energy expense this incurs can best be met by the consumption of high-energy animal meat rather than plant foods. Their assumptions also infer an associated reduction in the size of the gut of our hominid ancestors, through time, to compensate for this increased brain size. Eating less plant food and more meat means our digestive systems do not have to work as hard, which allows this decreased gut size. The increased brain size, and therefore intelligence, allows us to manipulate our foods in ways that no other animals can, so intelligent hominids can use tools to cut up meat, as well as cook and further process foods, which also makes them easier to digest in our smaller guts.

Another fruitful line of evidence for early hominid diets is from analogy with modern humans, rather than other living primates. In a recent paper Cordain *et al*, (2001) also argue that the observed increased brain size through time in the

Homo line requires the consumption of animal products. They point out that there are two essential fatty acids, docsaehaenoic and arachidonic, that are essential to brain development in modern humans, and the best sources of these two fatty acids are bone marrow, and particularly ruminant brains. Therefore, the consumption of these animal products would have facilitated expansion in brain size and increased cranial capacity over the long term. Similar arguments regarding omega-3 fatty acids are presented by Chamberlain (1996, 1998).

The above arguments, that the morphological changes in hominid crania can be explained by the increased consumption of animal foods through time, is strongly contested by researchers such as Nestle (1999) and Milton (1993, 2000). They argue, by analogy, that the majority of living primates are largely vegetarian, and that we, as primates, are best adapted to a mainly vegetarian diet. Milton (1993) writes that mandible size decreased due to the increased consumption of energy-rich plant foods such as fruits, and not necessarily meat. The complex skills required to harvest these energy-rich plants would also result in a selection for more intelligent hominids, with resulting increased brain size through time. This alternative hypothesis highlights the inadequacy of the use of analogy with living primates as a means to understand hominid subsistence, as the same lines of evidence can be used to support two opposing views. Clearly, additional lines of evidence are needed to resolve these two alternative explanations.

Material culture and dietary changes through time

If we look at the more traditional archaeological evidence for hominid subsistence, it may be surprising just how little evidence remains. Organic material, other than fossilized bone, are extremely unlikely to survive in the distant past, and therefore we do not have any plant or animal remains from the majority of the four million years of hominid evolution. One artefact type that does survive is stone tools. As discussed above, the first tools that can be demonstrably shown to have been purposefully created by hominids are the simple Oldowan industry choppers and scrapers that appear in Africa *ca* 2.5–1.8 million years ago (Jurmain *et al*, 2000) and are widely believed to be associated with the first species in the *Homo* line. Analysis of the faunal remains and associated artefactual remains at so called 'home bases' from this time period in East Africa has led a number of researchers to conclude that meat-eating through hunting or scavenging did occur at this early period of prehistory, and this was associated with the *Homo* line (see Rose & Marshall, 1996 for a recent comprehensive review). With the appearance of *Homo erectus* we find an associated more complex stone tool industry, the Acheulian, characterized primarily by the ovate bifaces of various sizes that have been found throughout the Old World. The uses of the tools in these two traditions is still not known definitively. Experimental archaeology, where

modern replicas are made and used in a variety of ways, has shown that these tools, such as the handaxe, are remarkably diverse, and could be used to effectively butcher animals as well as cut up plant foods. Microwear analysis (Keeley, 1980), where the pits and scrapes on tools are recorded with a microscope, has been used in a number of locations to infer the use of some of these early stone tools. These studies generally give mixed signals, indicating that most tools were used for a variety of purposes, or that the method is flawed, and can be confounded by the addition of new microwear after deposition. Later stone tool traditions, such as the Mousterian, associated with Neanderthals, and the Upper Palaeolithic Gravettian, associated with modern humans, are more sophisticated (see Gamble, 1999, for primary references). Their uses have been determined again experimentally, but also through analogy with stone tools used by modern, indigenous peoples. Although some of these more recent stone tools probably have multiple uses, the majority of them are clearly for hunting and butchering of game. This is supported by the very rare finds of hunting weapons embedded in the hunted animals, such as the wooden spear found embedded in a red deer skeleton from Lehringen, Germany (Jacob-Friesen, 1956), as well as a Middle Palaeolithic Levallois point in an *Equus* cervical vertebra from Umm el Tiel in Syria (Boëda *et al*, 1999).

In these later periods we do start to find more organic materials in the archaeological record, and in particular faunal remains that show clearer signs of being hunted and butchered. For example, the remarkably well-preserved site of Boxgrove in Southern England, *ca* 500 000 years old, has a large number of Acheulian hand axes and associated faunal remains (eg rhinoceros and horse) that have cut marks on them, which are signs of being purposefully butchered by hominids (Roberts, 1986; Pitts & Roberts, 1997). There are also other sites with remarkable preservation from the time period 500 000–300 000, such as Miesenheim and Bilzingsleben, Germany, and at Hoxne and Swanscombe, England (Gamble, 1999). We have much more faunal evidence, from the Middle Palaeolithic (Stiner, 1994), and a recent review of Neanderthal faunal assemblages showed the emphasis on the hunting and processing of larger herbivores (Patou-Mathias, 2000).

What is missing from the archaeological record, even up to more recent time periods such as the Upper Palaeolithic, is plant remains. They only rarely survive, and as they may not have required sophisticated stone tools to collect and process, we may not recognize the stone tools that may have been used to collect and process them.

To summarize, the archaeological record, consisting of stone tools and animal bones, is most likely biased and unrepresentative of the daily subsistence practices of hominids. Our inferences, from what we do have, is of a strongly meat-based subsistence, starting with the appearance of our line, *Homo*, in Africa, as evidenced by the remains of butchered animals and increasingly sophisticated stone tools.

Direct stable isotope evidence of early hominid subsistence and dietary evolution

There is, however, an opportunity to directly measure past hominid diets through the chemical analysis of surviving tissue, primarily bone collagen and tooth enamel, using stable isotopes of the elements carbon and nitrogen. These methods are destructive and require the hominid specimens to be well preserved, so have been rarely applied (see Schoeninger, 1995, for a recent review).

The ratio of stable carbon ($^{13}\text{C}/^{12}\text{C}$, the $\delta^{13}\text{C}$ value) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, the $\delta^{15}\text{N}$ value) in bone collagen reflect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dietary protein (Ambrose, 1993, 2000; Ambrose & Norr, 1993). Measurement of these values allows us to determine the sources of the average dietary protein over the long-term (*ca* 10 years) and can distinguish between marine and terrestrial protein, C_3 and C_4 photosynthetic pathway plants and the animals that consume them ($\delta^{13}\text{C}$) and the trophic level of dietary protein ($\delta^{15}\text{N}$). Tooth enamel hydroxyapatite $\delta^{13}\text{C}$ values, on the other hand, reflect blood bicarbonate $\delta^{13}\text{C}$ values, and are therefore a reflection of total diet, with contributions from lipids and carbohydrates as well as protein (Ambrose & Norr, 1993; Lee-Thorp *et al*, 1989).

The earliest hominids that have been studied are Australopithecines from South Africa (Sponheimer & Lee-Thorp, 1999; Lee-Thorp *et al*, 1994). By comparing *Australopithecus afarensis* tooth enamel $\delta^{13}\text{C}$ values to $\delta^{13}\text{C}$ values of tooth enamel from a range of contemporary species, Sponheimer & Lee-Thorp (1999) concluded that the Australopithecines had, on average, $\delta^{13}\text{C}$ values most like hyaenas, with a mix of C_3 and C_4 plants, although the four samples they measured had a wide range of $\delta^{13}\text{C}$ values. It is unclear why they argue that the presence of a C_4 signal necessarily means that the hominids were carnivorous. If the majority of C_4 plants were grasses, and therefore inedible to hominids (which is not known), the C_4 signal must have come from consuming animals (or insects) that consumed C_4 plants. However, they do indicate the probable presence of tubers of C_4 plants that could have been consumed by the *Australopithecus afarensis*. More significantly, studies of bone and tooth bioapatite $\delta^{13}\text{C}$ values are plagued by problems with diagenesis where new carbon can be incorporated into enamel and bone, and existing carbon can leave the tissue (Koch *et al*, 1997; Schoeninger & DeNiro, 1982). Samples are given a mild pre-treatment to try to remove contaminants, but there is currently no way of knowing if the carbon measured in bioapatite is the original carbon or was deposited post-depositionally, and recent experimental evidence has shown that these pre-treatments actually remove the carbonates of interest where no organic material remains in bone (Nielsen-Marsh & Hedges, 2000). Therefore, the results of this study, and others using this same method (Lee-Thorp *et al*, 1994, 2000; Sponheimer *et al*, 1999) are likely to be unreliable and inaccurate.

The use of bone collagen stable isotope analysis avoids many of the problems outlined above. Collagen has been found to be well preserved in bones up to 100 000 years old

(Bocherens *et al*, 1999; Ambrose, 1998) and, through checks of the quality of the collagen such as the C:N ratio and amino acid analysis, it is possible to discard poorly preserved and contaminated collagen (DeNiro, 1985). The earliest hominids that this method can be applied to are the Neanderthals, and there have been three studies carried out so far. The first application of collagen isotope analysis to early hominids was by Bocherens, at the site of Marillac Cave in France, to two Neanderthals that were approximately 40 000–45 000y old (Bocherens *et al*, 1991; Fizet *et al*, 1995). The next study was also by the same group, of a Neanderthal from Scladina Cave in Belgium, dating to approximately 130 000–80 000y old (Bocherens *et al*, 1999). The third study was by Richards *et al* (2000b), of the two youngest dated Neanderthals in Europe, *ca* 28 000 years old, from Vindija cave in Croatia. In all of these studies the collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of associated herbivores and carnivores were measured to build up a picture of the ecosystem isotope values. In all three studies the Neanderthal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were compared with contemporary species of known diets and in all cases the Neanderthals, based on the $\delta^{13}\text{N}$ values, were most similar to top-level carnivores. This means that, for these five individuals from three different areas of Europe and ranging in age from approximately 100 000 to 28 000 years old, there is a remarkably similar adaptation. These five Neanderthals were all top-level carnivores who derived the vast majority of their protein from animal sources, likely to be large herbivores.

There have only been two studies of Palaeolithic modern humans, *Homo sapiens sapiens*. A study of the isotope values of humans from the late Upper Palaeolithic (*ca* 13 000 years old) site of Gough's and Sun Hole Cave in Southern England (Richards *et al*, 2000a) indicated, again by the $\delta^{15}\text{N}$ values, that the main source of dietary protein was animal-based, and most likely herbivore flesh. The second study (Richards *et al*, 2001) was a survey of isotope values of humans from Gravettian and later (approximately 30 000–20 000 years old) Eurasian sites. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values here indicated high animal protein diets, but the type of animal protein was more varied than the Neanderthals, incorporating aquatic foods in their diets. As this study was a survey, and associated faunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not measured, it is not possible to further pinpoint the sources of dietary protein at all of these sites. Interestingly, this adaptation to aquatic resources becomes more extreme in much later (*ca* 10 000–5000 BP, depending on area) Mesolithic periods in parts of Europe. For example, isotope studies of Mesolithic humans from the Danube Gorges in Southeastern Europe indicate that the majority of protein was from freshwater fish, which is supported by the archaeological evidence of fishing equipment and large numbers of fish bones (Bonsall *et al*, 1997). Also, on the Atlantic coast of Europe in the Late Mesolithic a range of isotope studies have also found a significant use of marine foods, and in some regions such as Britain and Denmark, marine fish were the main protein source (Richards & Mellars, 1998; Tauber, 1981).

Dietary changes at the 'Neolithic revolution'

Approximately 10 000 years ago, associated with climate variation at the start of the Holocene, modern humans in the Near East began to cultivate plants, and later on to domesticate animals (Bar-Yosef & Belfer-Cohen, 1992). This 'Neolithic revolution' led to an increase in population, sedentism and eventually to urbanization. This adoption of agriculture also occurred independently in other parts of the world, such as in Asia, where rice was the main domesticated plant (Imamura, 1996; Bellwood, 1996; Crawford, 1992), and in the New World, with the domestication of maize (Flannery, 1973; Blake *et al*, 1992). We see the gradual spread of agriculture throughout the Old and New Worlds in the Holocene, and the generally (but not universally) associated traits are an increase in population, and in many cases a general decline in health and stature and the appearance of new nutritional disorders (Cohen & Armelagos 1984).

As an example of the changes in society and health associated with the adoption of agriculture we can look to the Near East. We have evidence for human control, or domestication, of wild plants and animals in the Near East at the start of the Holocene, about 10 000 BC (Miller, 1996; Hillman, 1996; Bar-Yosef & Belfer-Cohen, 1992). The indications are that this is a gradual process in this region as people respond to climate fluctuations. One theory is that the uncertainty in the availability of foods that the climate changes brought about may have led people to start to plant crops and raise their own animals so that they could be assured of a food resource, as they could no longer rely on wild foods that they would hunt and collect in this period of instability. Eventually they became dependent on the new domesticates, as their population sizes significantly increased beyond the carrying capacity of the local environment. A specific example of these changes is the site of Abu-Hureyra, Syria. In the latest Palaeolithic period people relied on gathering plant foods and hunting gazelle (Molleson, 1994). In the climate fluctuations of the Early Holocene they could no longer rely on collecting wild plants so they start to plant their own; also, the gazelle slowly disappeared because of the climate change and probably from overhunting, so plant foods become a necessity as there are fewer animals to hunt. Domesticated animals such as sheep and goat began to replace hunted animals in the diets, but plant foods in the form of porridges and breads became the dietary staple. The indirect evidence for this dietary change is in the archaeological record, with decreasing amounts of gazelle found through time, and then the appearance of domesticated sheep and goats, and also the appearance of tools associated with grinding plant foods. The direct evidence for the changes in diet is from the skeletal evidence. Molleson (1994) has argued that there are changes in the bones of women that are task-related and associated with cereal grinding. Also, there is a significant change in the dentition between the Palaeolithic and the Neolithic (Molleson *et al*, 1993). In the Palaeolithic people have fairly healthy teeth

with almost no caries, but in the Neolithic there is an increased use of plant foods which contain carbohydrates, so there is an increased caries rates. Neolithic teeth are also more worn down and pitted owing to hard inclusions from poorly ground-up flour.

The above discussion of the changes associated with the Neolithic have focused on the Near East specifically, but similar changes occurred in society in other regions (Cohen & Armelegos, 1984). Focusing on morphology, there are changes in stature and caries rates with the introduction of agriculture in Europe, although these changes often were not manifested until the Bronze Age (Angel, 1984; Lubell *et al*, 1994; Fox, 1996; Thomas, 1996; Zvelebil & Lillie, 2000; Price, 2000). There are increases in caries rates associated with the domestication of rice in South Asia (Lukacs, 1996; Kennedy, 1984), and an overall decrease in health and stature associated with the spread of maize agriculture into North America (Goodman *et al*, 1984; Rose *et al*, 1984; Cook, 1984; Larsen, 1984), Central America (Ubelaker, 1984; Norr, 1984), and South America (Allison, 1984). There is often good archaeological evidence of subsistence associated with the adoption of agriculture, which is in sharp contrast to the sparse pre-agricultural evidence for diet as discussed above for the Palaeolithic. For example, as agriculture was introduced relatively recently, it is common to find the remains of domesticated plants that have survived, especially at sites in dry environments, providing direct evidence of their domestication. We have stone tools that are inferred to be for plant processing, such as sickles and grinding stones, as well as pottery for the first time. Also, we have the faunal remains of domesticated animals. In many areas we also have direct stable isotope evidence of these diets. In a seminal stable isotope paper Van der Merwe & Vogel (1978) tracked changes in $\delta^{13}\text{C}$ values associated with the adoption of maize (as a C_4 plant) into diets in North America. The importance of maize in Central America (DeNiro & Epstein, 1981; White & Schwarcz, 1989), North America (Riley *et al*, 1994; Larsen *et al*, 1992) and South America (van der Merwe *et al*, 1981; Burger & van der Merwe, 1990) has been confirmed by stable isotope studies. There are also studies indicating the importance of C_3 plants in post-Neolithic diets in coastal Europe, associated with a move away from marine foods (Tauber, 1981; Richards & Hedges, 1999; Lubell *et al*, 1994), as well as preliminary studies indicating the importance of millet in China (Cai & Qui, 1984) and rice in Japan (Chisholm & Koike, 1996).

Conclusions

To conclude, it is difficult to accurately determine the nature of past hominid diets, or define the 'Palaeolithic' diet, due to the limitations of the archaeological record, a problem which is amplified in the Palaeolithic period where survival of organic materials is very rare.

We can infer, based on changes in cranial morphology, such as increased gracilisation of the mandible and increase in brain size through time, that there is evidence

for an increase in meat consumption in the *Homo* line through time. However, as this conclusion is based on analogies with living primates it is ambiguous, and the same data has been interpreted as being evidence of increasing use of energy-rich plant foods through time. Other lines of evidence are needed to address this debate, but perhaps the best interpretation of the morphological data is that hominids, and especially modern humans, have been very successful as highly adaptable omnivores, that probably had a significant input of animal products into their diets.

The artefactual evidence for diet is poor, especially from earlier periods. In Palaeolithic Africa and Europe stone tools have been inferred to have been used for hunting and butchering animals. Almost no plant remains survive, and animal bones have marks on them to indicate that they were butchered and hunted. However, there is a danger of placing too much emphasis on this evidence, as Marion Nestle writes 'Since bones are better preserved than vegetable matter, they give the impression that hunted animals must have been primary food sources' (Nestle, 1999, p 215).

As a contrast, bone chemistry, especially stable isotope evidence, provides direct evidence of diets, and indicates, for the few limited studies, that Neanderthals were top-level carnivores. Two studies of Upper Palaeolithic modern humans in Europe have also indicated the significant importance of animal products in the diets, and similar evidence of the consumption of animal meat is also found in the later Mesolithic periods in Europe.

There is a significant change in the archaeological record associated with the introduction of plant domestication (ie the Neolithic period in Europe and the Near East), such as the appearance of pottery, stone tools for plant processing, and the remains of the domesticated plants themselves (Gebauer & Price, 1992). There is, in many areas, an associated general decrease in body stature, dentition size, and an increase in caries rates. The smaller dentition is not due to more meat, but instead to the consumption of easier to chew processed foods like bread and porridges, and the carbohydrate contents of those foods result in the increased caries rates. There is also a range of diseases associated with the consumption of these processed foods and related to the sedentism and urbanization that often follow from the increased reliance on domesticated plants (Cohen & Armelegos, 1984).

However, associated with the general decrease in health associated with the adoption of agriculture, as evidenced in skeletal remains, is a significant and dramatic population increase, which is the trade-off that our ancestors made. To increase population size food production must increase beyond the carrying capacity of the environment, and domestication and control of plants and animals allow this. However, associated with this is overcrowding and the observed general decline in individual health, and we are still living with the effects of this Neolithic revolution today.

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