

What do Stable Isotopes tell us about Hominid Dietary and Ecological Niches in the Pliocene?

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ABSTRACT By now a reasonable set of carbon and oxygen isotope data from tooth enamel has been accumulated for South African Plio-Pleistocene hominids and associated fauna. Almost all individuals measured, independent of species and importantly, environment, show significant C₄ dietary inputs with some individuals showing very substantial C₄ inputs. This implies interactions with grassy environments for a period of well over a million years, a period that saw environments in southern Africa shift from closed woodlands to more open, grassy landscapes. Carbon isotope analysis alone is unable to permit the important distinction between direct consumption of grasses, or indirect consumption via grass-eating animals, such as small vertebrates and invertebrates. Other chemical tools provide ambiguous results. For instance, hominid strontium/calcium distributions at Swartkrans have been interpreted as supporting omnivory, but other explanations are equally plausible. Relatively low oxygen isotope values for all hominids in comparison to associated fauna show similarities with suids, monkeys and carnivores, but the causes of these similarities are as yet poorly understood. On present evidence hominid interaction with grassland foods is secure although their exact nature remains elusive. Copyright © 2003 John Wiley & Sons, Ltd.

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Introduction

The importance of the nature of diet in early hominids is twofold. Firstly, it is widely recognized that the search for, and consumption of, food exerts a major influence on behavioural and ecological differences among extant primates including humans (Ungar, 1998; Fleagle, 1999). Hence diet is often considered to be a key factor underlying differing adaptations and evolutionary trajectories amongst the hominins (Robinson, 1963). At the same time, the changing environments of the Pliocene and Pleistocene that formed

the framework of exploitable resources, are now better understood, if still imperfectly. Given the central role of diet, how can we investigate diets of species that have been extinct for millions of years? Primates are generalists, so pinpointing their diets has never been easy even among extant animals, and it remains a significant challenge for extinct hominids.

Conventional sources of archaeological information in the form of scatters of stone tools, where they exist, and animal bones, can provide limited windows into procurement of foods. On present evidence hominids have been manufacturing stone tools for the processing of animal carcasses, among other activities, for 2.5 Ma (million years) (Semaw *et al.*, 1997); prior to that time no technological clues are available. Bone tools

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have been found in the Swartkrans Member 1 (~1.7 Ma) deposits, and interpreted variously as tools for digging out underground bulbs (Brain, 1993) or termites, based on their characteristic wear patterns (Backwell & D'Errico, 2001). Contextual and interpretative problems include the presence of more than one hominid species at a site. At the South African site of Swartkrans for instance, both *Australopithecus* (or *Paranthropus*) *robustus* and early *Homo* fossils are found in the same deposits (Brain, 1993). As a result, we can never be sure which species was responsible for making and using the tools, or indeed for any of the other observed behaviours such as producing cut marks on animal bones.

Teeth are adapted for the initial processing of foods and they are abundant in the fossil record, hence inferences about early hominid diets have fallen largely to the province of dental morphology (e.g., Robinson, 1954; Tobias, 1967; Jolly, 1970; Wolpoff, 1973; Grine, 1981; Ungar, 1998). These studies have yielded conflicting results; it has been suggested that *A. africanus* was anything from a primarily herbivorous (Jolly, 1970; Wolpoff, 1973), omnivorous (Robinson, 1954), to faunivorous (Szalay, 1975) hominid. Morphology is an ambiguous predictor of primate diets even for extant taxa. For instance, the relatively large incisors and bunodont molars of *Papio* suggest a frugivorous diet (Fleagle, 1999; Ungar, 1998), yet many modern baboon populations eat high proportions of grasses (Harding, 1976; Strum, 1987). *Papio* is highly successful and widely distributed although dependent on a food source for which it is ill equipped. Dental morphology undoubtedly reflects an organism's dietary adaptations and phylogenetic history, but this is not necessarily concordant with *actual* behaviour. The problem is magnified in animals that are generalists.

Several sources of independent information have been developed to attempt to address these problems. These include occlusal enamel microwear, and a number of approaches based on the stable light isotope and trace element chemistry of fossil bones and teeth.

Studies based on extant and fossil primates have shown that distinctive microwear patterns on tooth enamel distinguish consumers of hard fruits from consumers of soft fruits, and frugivorous primates from folivores (Grine & Kay, 1988;

Teaford, 1992; Ungar, 1998). Application to the South African australopithecines suggested that *A. africanus* ate fleshy fruits and leaves, while the megadont *A. robustus* ate harder, more fibrous foods (Grine, 1981; Grine & Kay, 1988). These reconstructions seemed reasonable given palaeoenvironmental reconstructions that favour woodland or forest for *A. africanus* sites while more open country with patches of gallery forest seems to have characterized *A. robustus* habitats (Vrba, 1985; Cadman & Rayner, 1989; Rayner *et al.*, 1993; Reed, 1997). The drawbacks of microwear analysis include restriction mainly to the consistency of foods, the 'last supper' effect and invisibility of certain foods such as animal flesh and insects.

Chemical tracers

Stable carbon isotopes

The pathways and fractionation undergone by the two stable carbon isotopes of ^{13}C and ^{12}C comprise the best understood isotopic system, and their application to hominid fossils has provided information about both diets and prevailing environments not available from other sources. The foundation for this tool in African savannas lies in the differential degree of discrimination against ^{13}C by plants following the C_3 and C_4 photosynthetic pathways. Trees, bushes, shrubs, and forbs follow the C_3 pathway, which discriminates more markedly against ^{13}C compared to the C_4 pathway utilized by savannah grasses and some sedges. Hence $^{13}\text{C}/^{12}\text{C}$ is lower in C_3 plants, with an average $\delta^{13}\text{C}$ value of about -26.5‰ ,¹ while C_4 plants have values averaging -12.5‰ (Smith & Epstein, 1971; Vogel *et al.*, 1978). Herbivores incorporate the plant carbon they consume into their tissues, which then reflect proportions of C_4 grasses and C_3 browse eaten (Vogel, 1978, Lee-Thorp *et al.*, 1989; Cerling & Harris, 1999). Grazing animals like zebras (*Equus burchelli*) and wildebeests (*Connochaetes*) are enriched in ^{13}C compared to animals that eat C_3 foods such as the leaves or fruits of trees and

¹ $^{13}\text{C}/^{12}\text{C}$ ratios are expressed as delta (δ) values in parts per mil (‰), relative to the PDB standard.

bushes, such as giraffes (*Giraffa camelopardalis*) and chimpanzees (*Pan*).

At present isotopic studies of very old fossil animals are limited to the mineral phases (or biological apatites) of bone and tooth enamel. Following a number of early, controversial, attempts to retrieve $\delta^{13}\text{C}$ values from bone (Sullivan & Krueger, 1981; Schoeninger & DeNiro, 1982), preservation of biogenic carbon isotopic signatures in carbonate substituted in the enamel structure of ancient fauna (millions of years old) was satisfactorily demonstrated (Lee-Thorp & van der Merwe, 1987). It was shown that, after pretreatment in dilute acetic acid to remove contaminating carbonates, fossil grazers (e.g., equids and alcelaphines) had C_4 -dominated signatures, while fossil browsers had C_3 -dominated signatures like their modern counterparts. It was observed that bone was more susceptible to isotopic alteration (diagenesis) during fossilization than enamel, which thereafter became the sample material of choice. Stable carbon isotope analysis of enamel mineral has since been used widely to address anthropological and palaeontological questions (e.g., Bocherens *et al.*, 1996; Cerling *et al.*, 1997), including that of the diets of South African australopithecines (Lee-Thorp *et al.*, 1994, 2000; Sponheimer & Lee-Thorp, 1999a; van der Merwe *et al.*, in press).

The first carbon isotope results were obtained from specimens of *A. robustus* from the site of Swartkrans. A mean $\delta^{13}\text{C}$ value of -8.5‰ (Figure 1) showed that these individuals ($n = 6$) had obtained their carbon primarily from C_3 sources, but a significant contribution came from C_4 sources (Lee-Thorp *et al.*, 1994). Carbon isotopes alone cannot indicate whether these sources were grasses or animals that ate grasses. It was inferred, however, that animal foods likely contributed much of the C_4 input, given that microwear studies (Grine, 1981) had shown no evidence for grass phytolith scratches on *A. robustus* enamel molar surfaces. No significant differences in *A. robustus* $\delta^{13}\text{C}$ between Members 1 (~ 1.7 Ma) (Brain, 1993) and 2 (of uncertain age but probably near 1.4 Ma) were observed. Subsequent analysis of rarer *Homo ergaster* (or *H. erectus*) fossils from Member 1 in the same site showed very similar values (Lee-Thorp *et al.*, 2000).

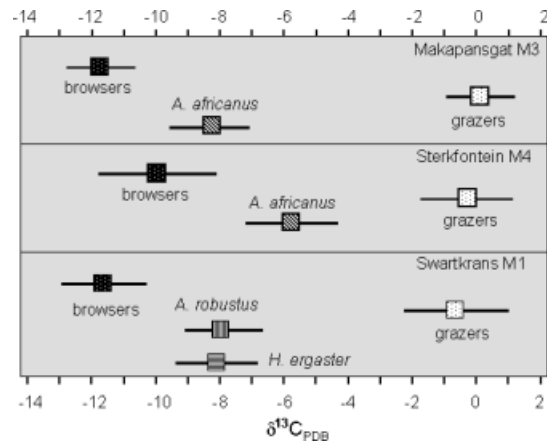


Figure 1. From top to bottom, the distributions of $\delta^{13}\text{C}$ in enamel of browsers, grazers and hominids at Makapansgat Member 3 (≥ 3 Ma), Sterkfontein Member 4 (~ 2.4 – 2.6 Ma), and Swartkrans Member 1 (~ 1.7 Ma). Data shown as means and standard distributions are from Sponheimer & Lee-Thorp (1999a), van der Merwe *et al.* (in press) and Lee-Thorp *et al.* (2000). Although the species differ for each site, in each case typical browsers are herbivores demonstrating entirely C_3 diets and grazers conversely showing C_4 grass diets, based on their $\delta^{13}\text{C}$ values, habits of extant forms and/or dental morphology.

Unexpectedly, analysis of *A. africanus* from Makapansgat Limeworks Member 3 (≥ 3 Ma) also yielded similar results, again showing that, on average, $\sim 25\%$ of their dietary carbon came from C_4 foods. The range of values is greater, however. One individual ate approximately 50% C_4 foods, while another consumed very little (Sponheimer & Lee-Thorp, 1999a). The results were unexpected on two counts. Firstly, *A. africanus* was held to have been a fruit and leaf-eater, based on microwear observations and analogies with diets of forest-loving primates like chimpanzees (Grine, 1981; Grine & Kay, 1988). These foods are C_3 , and they would have imparted a corresponding C_3 carbon isotope signature to *A. africanus*, similar to that of browsers. As can be seen in Figure 1, however, this is not the case. Secondly, the ca. 25% C_4 contribution occurs in spite of a far more closed, wooded habitat at Makapansgat (Vrba, 1985; Rayner *et al.*, 1993; Reed, 1997; Sponheimer *et al.*, 1999).

The pattern is also maintained for the Member 4 hominids from Sterkfontein (~ 2.4 – 2.6 Ma) (van der Merwe *et al.*, in press). Again the $\delta^{13}\text{C}$ results are more variable than those of *A. robustus* and *Homo* in Swartkrans, but the overall pattern is

similar. Furthermore, faunal and stable carbon isotope data suggest that the environment in Sterkfontein Member 4 times was also more closed compared to the period after about 1.8 Ma, if not as closed as the environment at 3 Ma (Reed, 1997; Luyt, 2001).

Thus, none of the South African hominids analysed so far ate a diet like that of the modern chimpanzee (*Pan*) or gorilla (*Gorilla gorilla*), both of which eat nearly 100% C₃ foods. This is not to say that the Australopithecines and *Homo* did not eat considerable quantities of fruits and leaves—they very likely did. The carbon isotope data make it clear, however, that they also incorporated significant quantities of other tropical grasses and sedges, animals that ate C₄ plants (including insects and vertebrates), or both. We must seek information from other sources of data to distinguish between these possibilities. Two possible avenues based on the oxygen isotope and trace element chemistry are explored below.

Stable oxygen isotopes

Oxygen isotope (¹⁸O/¹⁶O) data are obtained naturally during the course of ¹³C/¹²C measurements of carbon dioxide (CO₂) released from the carbonate substituted in biological apatites. These data were ignored for some time because of the greater likelihood of diagenesis (carbonate oxygen may exchange readily with water). Most research on δ¹⁸O in calcified tissues has been directed at oxygen extracted from the stable phosphate ions in the apatite structure, where the main goal is to derive continental palaeotemperature indicators (Longinelli, 1984). Studies have shown that biogenic δ¹⁸O can also be retained in ancient enamel carbonate (Bocherens *et al.*, 1996; Iacumin *et al.*, 1996; Cerling *et al.*, 1997; Sponheimer & Lee-Thorp, 1999b), an observation that has enhanced the potential for ecological applications. One of the first observations is that the intra- and inter-specific δ¹⁸O variations, which had long perplexed the palaeotemperature researchers, has emerged as coherent patterning *within each ecosystem* (Kohn, 1996; Kohn *et al.*, 1996; Bocherens *et al.*, 1996; Sponheimer & Lee-Thorp, 2001).

Our understanding of the systematics of δ¹⁸O in animals is due largely to the work of phosphate researchers (e.g., Longinelli, 1984; Luz *et al.*, 1984), who established the framework of δ¹⁸O mass balance for animals from field observations and experiments. δ¹⁸O from carbonate and phosphate ions in mineral have a large offset (almost 10‰) but are highly correlated (Bryant *et al.*, 1996; Iacumin *et al.*, 1996); in both cases δ¹⁸O_{apatite} is a function of δ¹⁸O of total oxygen entering and exiting the body. The main variable inputs are water (including water in food), and oxygen bound in food. Liquid water δ¹⁸O is highly variable; isotopic variation of meteoric or surface water (i.e., water available for drinking) occurs with latitude, altitude, temperature and amount of precipitation (Dansgaard, 1964). Root and stem water in plants resembles groundwater but leaf water is enriched in H₂¹⁸O due to preferential evapo-transpiration of H₂¹⁶O, an effect that is strongest in arid conditions (Yakir, 1992). δ¹⁸O of oxygen bound in organic plant matter, such as cellulose, is tightly linked to leaf water composition with strong positive fractionation (Epstein *et al.*, 1977; Sternberg, 1989). Outputs include liquid water (as urine and sweat) which is similar to body water, whereas water vapour lost through skin, nose, and mouth in panting animals favours H₂¹⁶O. Thus thermophysiological adaptations can have significant effects on δ¹⁸O_{bodywater} and hence δ¹⁸O_{enamel} (Kohn, 1996; Kohn *et al.*, 1996). Although it has been argued that metabolic rate and body size affect δ¹⁸O mass balance (Bryant & Froelich, 1995), this effect has only been demonstrated for rats (Luz *et al.*, 1984) and it has not been observed in δ¹⁸O measurements of suites of fauna in modern ecosystems (Kohn *et al.*, 1996; Sponheimer & Lee-Thorp, 2001).

In Figure 2, δ¹⁸O is shown plotted against δ¹³C from enamel for representative samples of the Makapansgat fossil fauna, and the Morea Estate modern fauna. Patterning is observed in the fossil fauna that echoes that of the modern assemblage, that is, where comparisons are possible. Herbivores that obtain relatively more water from leaf water (mostly browsers or mixed feeders) have higher δ¹⁸O than those, which must drink regularly. Another explanation for the high values for impala (*Aepyceros melampus*)—observed in a

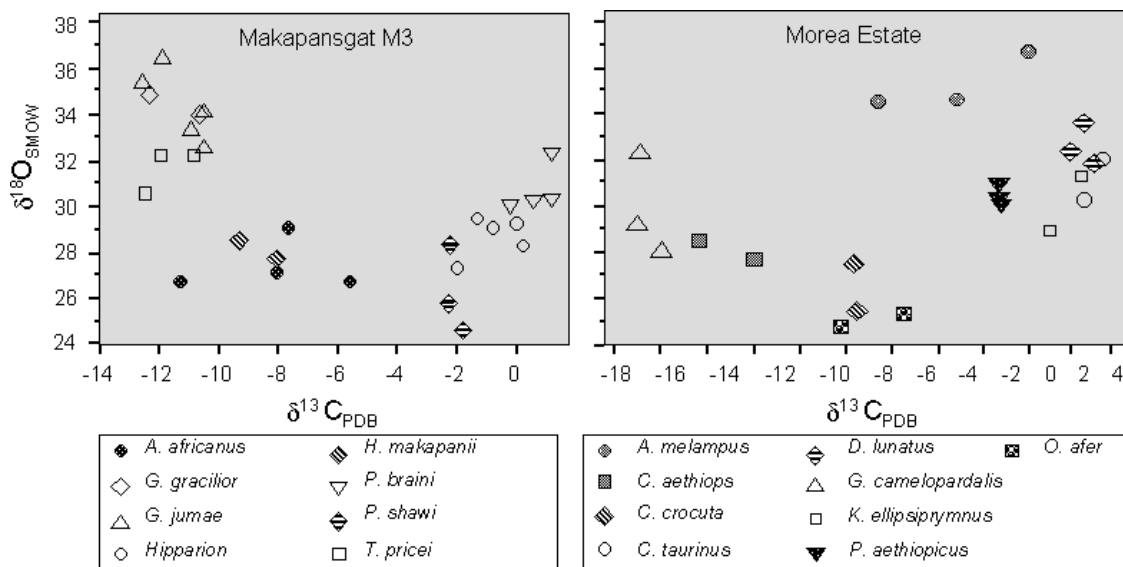


Figure 2. $\delta^{13}\text{C}$ plotted against $\delta^{18}\text{O}$ from enamel for a representative sample of animals from Makapansgat Member 3 (left), and the Morea Estate modern fauna (right). The Morea Estate fauna were collected within a few years (data from Sponheimer & Lee-Thorp, 2001), while the accumulation rate of the Member 3 fauna is uncertain.

variety of ecosystems, concerns their ability to withstand high body temperatures (Sponheimer & Lee-Thorp, 2001). Faunivores, represented by *Hyaena makapania* in the fossil, and spotted hyaena (*Crocuta crocuta*) and armadillo (*Oryzomys afer*) in the modern assemblage, have relatively lower $\delta^{18}\text{O}$ than most of the other fauna. A similar observation was noted previously for leopards (*Panthera pardus*) in Swartkrans (Sponheimer & Lee-Thorp, 1999b).

Apart from a single blue monkey specimen in Morea (not shown here) the primates (modern and fossil) are also relatively low, including all four *A. africanus* specimens. A difficulty in interpreting these patterns is that there are several plausible explanations for these observations. For instance, the faunivores may have lower $\delta^{18}\text{O}$ values in comparison to browsing and grazing herbivores because they regularly drink meteoric water, or because they incorporate oxygen from metabolic sources low in $\delta^{18}\text{O}$ such as lipids and proteins, or both. For the primates shown here low values may be related to faunivory, copious drinking of free water, and/or water from underground storage organs. These data do help to exclude some possibilities, however. Low $\delta^{18}\text{O}$ values for all of the hominids analysed in Makapansgat and Swartkrans distinguish them

from higher values for leaf-eating herbivorous ungulates (Figure 2), and in particular, from one of the few extinct primates to show high $\delta^{18}\text{O}$. This is the giant baboon, *Papio (Dinopithecus) ingens*, which may have been predominantly a leaf-eater (Lee-Thorp, 2002).

Trace elements (Sr/Ca)

Questions about folivory, carnivory and consumption of underground storage organs may also be addressed from the perspective of trace element, principally strontium/calcium (Sr/Ca), analyses. Calcium is a principle element in bone and tooth mineral, but chemically similar strontium substitutes to some extent for calcium in biological apatites. Mammals discriminate against strontium compared to calcium in the gut and preferentially excrete strontium—this is known as 'biopurification of calcium' (Elias *et al.*, 1982). The result is that very much lower proportions of strontium relative to calcium occur in calcified tissues compared to Sr/Ca in food, and Sr/Ca is reduced stepwise at higher trophic levels (Elias *et al.*, 1982). As a result most studies employing this tool have concentrated on trophic level effects in diet (e.g., Price & Kavanaugh, 1982;

Sillen, 1992), which are often simply translated as the amount of meat eaten.

It has become apparent, however, that considerable variability exists among plants and between plant parts (Runia, 1987; Sealy & Sillen, 1988; Burton *et al.*, 1999), and it is well-known that soils themselves differ in concentrations of available calcium and strontium related to local geology and geomorphology. Compared to leaves, roots and stems have elevated Sr/Ca, similar to levels of available strontium and calcium in soils, a phenomenon likely due to transport phenomena of calcium and strontium in plants (Runia, 1987). Hence leaf-eating herbivores should have lower Sr/Ca in bone compared to herbivores that eat more stem material, and animals that eat underground parts would have significantly higher Sr/Ca (Sillen *et al.*, 1995). This complicates inferences about trophic levels, because a carnivore has reduced Sr/Ca compared only to its *particular* prey species, and overlaps with herbivores are entirely possible. Few identified predator-prey pairs have been studied for Sr/Ca, and indeed it is not at all certain that, in its strict sense, this is an appropriate concept in complex modern or fossil foodwebs. A further complication is the high level of variability for each species, something of the order of 30% in a modern foodweb (Sillen, 1988, 1992; Burton *et al.*, 1999).

The conventional sample tissue for trace element distribution studies in fossils is bone mineral, because most teeth (with the exceptions in humans of the later erupting teeth C and M3) develop relatively early in life when discrimination against strontium may not have developed fully (Sillen, 1986). The focus on bone, which is far more susceptible to 'resetting' of biogenic signatures compared to enamel, has necessitated a good deal of effort to try to circumvent the problems posed by diagenesis. The 'solubility profile' technique targets, and extracts, strontium and calcium from only those solubilized compartments with the correct stoichiometric characteristics of biological mineral (Sillen, 1986; Sillen & LeGeros, 1991).

The study of Sr/Ca distribution in the Swartkrans Member 1 represents the most comprehensive trace element characterization of a fossil foodweb (Figure 3). Distribution of Sr/Ca shows some patterns similar to those observed

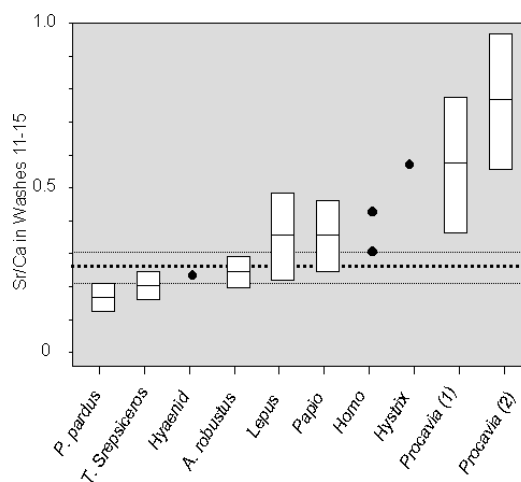


Figure 3. Distribution of Sr/Ca in solubility profile washes 11–16 from faunal bones in the Swartkrans Member 1 foodweb, shown as means and standard deviations where $n > 2$. Data from Sillen (1992). The 'solubility profile' method, in which solutions of calcium and strontium are successively extracted by buffered acetic acid digestion from finely ground, is described in Sillen (1986, 1988, 1992) and Sillen & LeGeros (1991).

in modern African foodwebs (Sillen, 1988, 1992; Sillen *et al.*, 1995) but the range of variation is greatly reduced. Highest Sr/Ca occurs in hyrax (*Procavia*) and porcupine (*Hystrix*) as observed in a modern southwestern Cape foodweb (Sealy & Sillen, 1988). The two carnivores measured, leopard (*Panthera pardus*) and hyena (*Hyaena* sp.) show reduced Sr/Ca compared to most of the other animals including the primates, but not the browsing kudu, *Tragelaphus cf strepsiceros*. Sr/Ca for *A. robustus* is relatively low, a pattern that was held to be inconsistent with that of a root, rhizome or seed-eating herbivore, and consistent with omnivory (Sillen, 1992). There are, however, other possible explanations, including leaf- or fruit-eating, or specialization for a wet microhabitat where Sr/Ca is typically low. Slightly higher Sr/Ca in two *Homo* individuals were used to postulate consumption of more underground storage organs (Sillen *et al.*, 1995), but the differences are small, especially in the latter case.

A preliminary study of the Morea faunal assemblage was based entirely on late-forming tooth enamel Sr/Ca, and included a wider range of savannah animals (absent in the southwestern Cape study) (Figure 4). Powdered tooth enamel was dissolved in HNO_3 before measurement of trace elements in a Perkin Elmer ICP-MS.

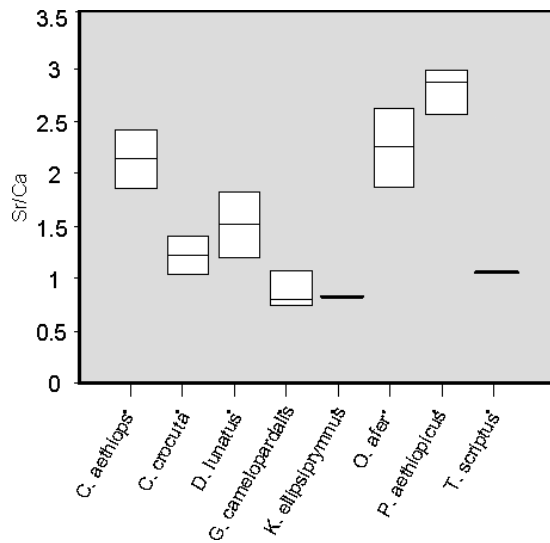


Figure 4. Distribution of Sr/Ca from enamel of fauna from Morea Estate, shown as means (solid lines) and standard deviations (boxes). Preparation and trace element analysis methods differed from the study shown in Figure 3, see text.

These pilot data show that use of tooth enamel as sample material does not obscure patterned trace element distribution. In this data set, animals showing lowest Sr/Ca are not carnivores but leaf-eaters—giraffe (*Giraffa camelopardalis*), bushbuck (*Tragelaphus scriptus*) and waterbuck (*Kobus ellipsiprymnus*). While the latter is a grazer never far from water, the former are both reliable browsers (Estes, 1991). Highest Sr/Ca occurs in warthog (*Phacochoerus aethiopicus*), armadillo (*Orycteropus afer*) and vervet monkey (*Cercopithecus aethiops*). Higher Sr/Ca for the warthog, which reputedly feeds partly on underground plant organs, is in agreement with higher values of those food parts. But this explanation cannot hold for the armadillo (an insectivore) and vervet monkey (a fruit and leaf-eater); therefore higher Sr/Ca can be ascribed to several mechanisms.

Although indicating greater complexity especially for trophic level interpretations, these preliminary data present intriguing possibilities for helping to distinguish insectivory from carnivory and perhaps exploitation of underground foods.

Summary and conclusions

Carbon isotope data offer the clearest indications about the diets of hominids in the Pliocene and

Pleistocene. $\delta^{13}\text{C}$ data for the South African hominids, at all periods, show that they participated to a significant extent in the savannah grassland ecosystem. On average about 25% of carbon was obtained from C_4 sources. This proportion remained consistent through widespread environmental changes, which saw the landscape change from a closed wooded environment with patches of grass, to more open habitats dominated by grasslands after ~ 1.8 Ma. These data suggest that, regardless of the habitat and their specific diets, hominids were willing to eat C_4 resources that are generally ignored by the other great African apes, chimpanzees and gorillas.

Chimpanzees are not known to eat grasses, or animals that eat grasses, even when they are locally abundant (McGrew *et al.*, 1981). They tend to move through grassy patches to reach concentrated C_3 resources such as figs. When they do eat animal foods, they eat mammalian and insect species that consume C_3 vegetation such as red colobus monkey and blue duiker (Teleki, 1981; Goodall, 1986). The same is true of *Gorilla gorilla* and *Pongo pygmaeus* (Tutin & Fernandez, 1992; Fleagle, 1999). Thus, it appears that hominids broadened the ancestral hominoid diet (if chimpanzees, gorillas, or orangutans are good analogues for the ancestral hominoid) to include new C_4 foods, whether they were plants or animals. We propose that chimpanzees are perhaps poor analogues for ancient human behaviour and diet in this particular respect. It may be that Chacma or Hamadryas baboons represent a better model, as they are known to consume C_4 foods. Alternatively, if these hominids regularly obtained underground roots of C_4 sedges around watercourses, there may be no reasonable extant primate analogue.

Our results suggest that the South African australopithecines broadened their resource base to include foods not exploited by extant great apes. This was likely a seminal step in the development of the hominid lineage necessitated by the drying trend during the Pliocene, when forests were gradually and later rapidly being replaced by woodlands and grasslands (e.g., Coppens, 1975; Brain, 1981; Vrba, 1985; Feibel, 1997). In the process, closed habitats of the kinds preferred by chimpanzees shrunk and their ranges contracted, while species capable of utilizing C_3

and C₄ resources were less pressed. Survival under such conditions would certainly be facilitated by a broader range of dietary resources, which could serve as a buffer against the periodic loss and recrudescence of preferred foods. Thus, even if these hominids spent the preponderance of their time amidst the trees, one fundamental, new, hominid adaptation may have been the ability to utilize woodland, grassland resources or possibly reverie resources.

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