

# Contributions of Biogeochemistry to Understanding Hominin Dietary Ecology

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**ABSTRACT** Dietary ecology is one key to understanding the biology, lifeways, and evolutionary pathways of many animals. Determining the diets of long-extinct hominins, however, is a considerable challenge. Although archaeological evidence forms a pillar of our understanding of diet and subsistence in the more recent past, for early hominins, the most direct evidence is to be found in the fossils themselves. Here we review the suite of emerging biochemical paleodietary tools based on stable isotope and trace element archives within fossil calcified tissues. We critically assess their contribution to advancing our understanding of australopith, early *Homo*, and Neanderthal diets within the broader context of non-biogeochemi-

cal techniques for dietary reconstruction, such as morphology and dental microwear analysis. The most significant outcomes to date are the demonstration of high trophic-level diets among Neanderthals and Late Pleistocene modern humans in Glacial Europe, and the persistent inclusion of C<sub>4</sub> grass-related foods in the diets of Plio-Pleistocene hominins in South Africa. Such studies clearly show the promise of biogeochemical techniques for testing hypotheses about the diets of early hominins. Nevertheless, we argue that more contextual data from modern ecosystem and experimental studies are needed if we are to fully realize their potential. *Yrbk Phys Anthropol* 49:131–148, 2006. © 2006 Wiley-Liss, Inc.

It is widely recognized that the pursuit and consumption of food exerts a major influence on the behavior, ecology, and biology of all animals. Most large primates spend a large proportion of their waking hours searching for, consuming, and digesting food (e.g., Altmann and Altmann, 1970; Teleki, 1981; Goodall, 1986; Whiten et al., 1991), and diet underlies ecological niche distinctions. Consequently, dietary adaptations can be considered as one of the key drivers determining the pathways of hominin evolution. The nature of hominin diets has been the subject of lively debate and not a little speculation for many years (e.g., Dart, 1926, 1957; Robinson, 1954, 1956; Jolly, 1970), although in recent years the topic has received somewhat less attention than bipedalism and brain expansion (Teaford and Ungar, 2000). The importance of dietary ecology is clear, but determining the diets of extinct hominins remains a considerable challenge. Most primates are generalists, so pinpointing their diets and dietary differences is no simple matter even among extant animals, where observational studies continue to generate new information and surprises. For instance, more detailed observations of gorillas in a variety of environments have shown that they are less devoted to folivory than previously believed, and that their diets overlap considerably with those of chimpanzees in many areas (Tutin and Fernandez, 1992). The difference lies to a significant extent in their fallback foods; in times of stress gorillas can better rely on foliage. So how best can we investigate the diets of species that have been extinct for many thousands or millions of years?

We can glean paleodietary information from many sources. However, some of the conventional sources of contextual evidence may be inappropriate, or at best provide very indirect, limited, or ambiguous information

about diet. Archeological evidence in the form of stone tools, animal bone scatters and their spatial contexts is the conventional source of information about past human diet and subsistence. There are, however, severe limitations in applications to the early fossil record, particularly where stratified archeological evidence is rare. Moreover, even where stratigraphy (or good spatial context) exists, the nature of association between the animal bones and human behavior is often controversial (e.g., Binford, 1981; Brain, 1981). There are significant interpretive problems associated with most Pliocene and Lower Pleistocene bone accumulations, where the sites are essentially palimpsests and the assemblages may have accumulated over hundreds to thousands of years. Traces that survive best are scatters of bones and stone tools which may indicate procurement strategies and butchery of vertebrate animal foods (e.g., Binford, 1981; Brain, 1981; Blumenschine, 1987; Stiner, 1994; Marean and Assefa, 1999; Speth and Tchernov, 2001). Yet, even where these traces occur, the information they provide can be ambiguous. For instance, the function of stone

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tools and the identities of their manufacturers (i.e., whether early *Homo* or australopith) is often uncertain (Brain, 1981). At present, the earliest known stone tools and cut-marked bones are from Gona and Bouri in Ethiopia, dated to ~2.5 Ma (Semaw et al., 1997; de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005), while the first potential hominins (Leakey et al., 2001; Senut et al., 2001; Brunet et al., 2002; White et al., 2006) precede these earliest archeological traces by millions of years. Thus archeological traces can tell us nothing about the diets of our lineage for most of its history.

Finally, the prominence of bones and stone tools in the record inevitably focuses attention on animal foods, whereas plant foods make up the bulk of most primate diets (Milton, 2002) and are likely to have been just as important for early hominins. Overall, technological attributes and spatial distributions of Oldowan and Acheulian stone tools may tell us more about the cognitive and fine-motor capabilities of their makers (Ambrose, 2001) and their use of the landscape (Isaac, 1981; Fèblot Augustins, 1997) than they do about their dietary ecology.

As a result, paleoanthropologists have had to develop other sources of palaeodietary information to fill these gaps. Many are focused largely on teeth—dental morphology and allometry, dental microwear, and trace element and stable isotope analysis. These techniques have advantages and limitations that are peculiar to each approach. Morphology and allometry, for instance, provide general indications about the capability of a species to process foods with certain mechanical properties, relying heavily on comparisons with living primates (Kay, 1975a, b, 1985). Dental microwear and chemical tools also rely on comparisons with modern systems for interpretation, but they are more immediate and direct indicators of palaeodiet. Microwear, in turn, is largely limited to telling us about the mechanical properties or consistency of foods eaten (Walker, 1981; Teaford, 1988a; Teaford and Ungar, 2000). The information available from chemical analyses in the form of stable light isotope and trace element patterns in bones and teeth is limited to certain broad dietary classes. Postmortem taphonomy and diagenesis remains an ever-present problem that can compromise or destroy dietary information for both microwear and chemical approaches (Teaford, 1988b; Sillen, 1989; Koch et al., 1997; Kohn et al., 1999; Lee-Thorp, 2000; Pérez-Pérez et al., 2003; Lee-Thorp and Sponheimer, 2005).

Given the distinct limitations for each approach, ideally, they should form a complementary suite. Since we cannot observe what early humans were eating, inferences about early human diets are perforce indirect. Several comprehensive reviews of dental allometry, morphology, and microwear exist in the literature (Kay, 1985; Ungar, 1998; Teaford and Ungar, 2000; Teaford et al., 2002). In this article, we provide brief overviews of these approaches to give sufficient contextual information to gauge the contributions of biogeochemical tools to hominin diets. We concentrate largely on applications to dietary ecology of the australopiths and Neanderthals, simply because this is where we have most biogeochemical data.

## DENTAL ALLOMETRY AND MORPHOLOGY

The function of teeth is to process foods, and they are abundant in the fossil record; hence the relative size and shape of teeth has been an important source of informa-

tion for many years. Robinson (1954, 1956) observed that the “robust” australopith, *Paranthropus robustus*, had absolutely smaller incisors and larger molars than did the gracile australopith, *Australopithecus africanus*, and he deduced that these differences reflected functional specializations. Specifically, Robinson argued that *Paranthropus* had an herbivorous diet that required grinding large quantities of tough plant foods, while *A. africanus* had a more omnivorous diet that required relatively more incisal preparation of meat and other foods (Robinson, 1956). This work was influential and set the stage not only for subsequent allometric and morphological studies of teeth, but also for hypothesis testing of the dietary proclivities and differences between the South African australopiths (e.g., Grine, 1981, 1986; Grine and Kay, 1988; Scott et al., 2005; Sponheimer et al., 2005a).

While continuing to consider the functional implications of relative tooth size of both anterior and posterior teeth in primates, subsequent studies have attempted to deal with a central problem. That is, since basal metabolic rate and molar occlusal surfaces are generally scaled in a similar way to body size (by ~0.75), molar size should be positively scaled to body size, because larger surfaces can process greater amounts of food (Pilbeam and Gould, 1974). Therefore, tooth size (particularly molar occlusal area) must be considered in relation to body size. However, this information is often unavailable or poorly known for the majority of fossil primates, including hominins. A related problem is that certain foods need a great deal more chewing or preparation than others. In an attempt to control this problem, Kay (1975a) compared primate taxa with similar diets. He showed that primate posterior tooth surface area varied isometrically, rather than allometrically, with body size in primate taxa with frugivorous, folivorous, and insectivorous diets, respectively. The implication is that positive allometry amongst the larger and smaller australopiths probably does denote different foods (Kay, 1975b), as Robinson had originally proposed.

Reasonable estimates for body weights of the three “gracile” australopiths—*A. anamensis*, *A. afarensis*, and *A. africanus*—have allowed an assessment of the scaling of incisors against body size (Kay, 1975b, 1985; Ungar and Grine, 1991; Teaford and Ungar, 2000). Their relative sizes are very similar, and they fall close to the regression line for a number of primates. These results suggest that the gracile australopiths tended to eat foods that required moderate amounts of incisal preparation (Teaford and Ungar, 2000).

One of the distinguishing features of the australopiths is their large and relatively flat molars (Robinson, 1956; Wolpoff, 1973; Wood and Abbott, 1983; Kay, 1985; Teaford et al., 2002). “Megadontia quotients” (relative size of molars scaled against body size) for australopiths increased over time from *A. anamensis* to *Paranthropus*, suggesting changes in the physical properties of their foods (e.g., hardness, size, and shape) to those that required a good deal of force (Demes and Creel, 1988). Another approach is to compare molar tooth areas of the M1 and M3, since this ratio is inversely correlated with percentage of leaves, flowers, and shoots in the diets of modern primates (Lucas and Peters, 2000; Teaford et al., 2002). The earlier australopiths, including *Ardipithecus*, have clearly higher M1:M3 ratios than *Paranthropus*, suggesting perhaps lower consumption of leaves, flowers, and shoots, and conversely greater degrees of frugivory (Teaford and Ungar, 2000).

Tooth size alone is insufficient to address questions about changing amounts of fruit (or other foods) in the diets of early hominins, shape must also be considered (Wood, 1981). Changes in tooth morphology tend to reflect changes in properties of typical foods, such as their toughness (Ungar, 1998). Food is orally prepared by the shearing, crushing, and grinding actions of teeth, and these functions have different morphological correlates (Strait, 1997; Lucas and Peters, 2000). Shearing requires blades or crests, while crushing and grinding require occlusion of two relatively flat or smooth surfaces in opposition. Hence, the relative importance of these actions, which are related to the properties of typical foods, should be reflected in tooth morphology, or rather, in the capabilities of tooth forms to accomplish these actions (Strait, 1997). Hard and brittle foods, for example, require crushing between flat planar surfaces whereas tough, pliant foods require shearing by reciprocally concave, highly crested teeth. The shearing potential of molar teeth can be assessed by means of a “shearing quotient” based on observations that extant folivorous primates exhibit higher shearing quotients than brittle or soft fruit feeders, which are higher in turn than hard-object feeders (Kay, 1985). In general, australopiths had relatively flat, blunt molars and lacked prominent shearing crests (Grine, 1981; Kay, 1985; Teaford et al., 2002), suggesting that they were more capable of processing soft or brittle, rather than tough, pliant foods. Following this reasoning, it has also been suggested that the early australopiths may have lacked the capabilities for orally processing meat, while early *Homo*, which had relatively greater occlusal relief, might have had greater success processing tough, elastic foods such as meat (Lucas and Peters, 2000; Ungar, 2004). Nonetheless, variability undoubtedly exists within the australopiths, as *A. africanus* and *A. afarensis* have greater occlusal relief compared to *P. robustus*, again suggesting dietary differences between these species (Teaford et al., 2002).

In spite of this improved understanding of the functional drivers for dental morphology and allometry, the functional relationships between form and diet remain unclear (Grine et al., 2006). Moreover, ultimately these approaches imply dental capabilities rather than evidence of diet per se. Indeed, morphology is an ambiguous dietary predictor and studies have in many cases yielded conflicting results. It has been suggested, for instance, that *A. africanus* was anything from primarily herbivorous, omnivorous, to faunivorous on the basis of tooth morphology (Robinson, 1954; Jolly, 1970; Wolpoff, 1973; Szalay, 1975; Kay, 1985). The central problem is that dental morphology reflects both phylogenetic history and dietary adaptations. Dental adaptations reflect dietary drivers over geological or evolutionary timescales and they are not necessarily concordant with the actual behavior of any given individual. For instance, the relatively large incisors and bunodont molars of modern *Papio* baboons suggest a frugivorous diet (Hylander, 1975; Ungar, 1998; Fleagle, 1999), and yet many *Papio* populations consume large quantities of grass (Altmann and Altmann, 1970; Dunbar, 1983; Strum, 1987) for which they have no apparent dental capabilities. Furthermore, dietary behavior can be altered over time and space, and the facility for change is particularly evident in taxa which are dietary generalists. Pointing to these problems, Ungar (2004) proposed that dental morphology may be a better predictor of fallback dietary behavior or dietary limitations than of more typical trophic behavior.

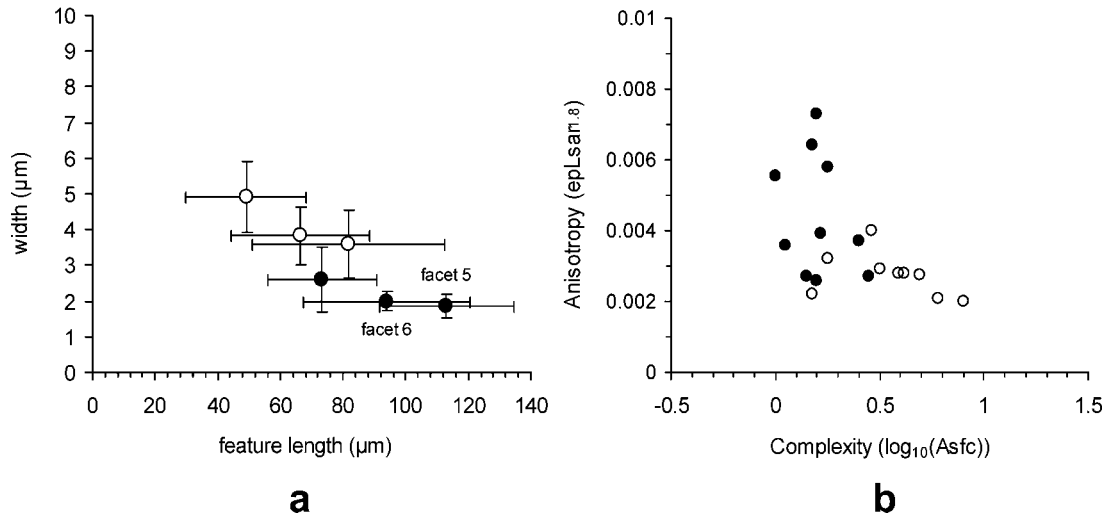
## PROCESSING DAMAGE AND MICROWEAR

Wear-related techniques can address some of these limitations. The results of gross wear pattern studies, however, have been inconclusive, resulting in opposing conclusions about the variability and distinctiveness between the South African australopiths, for instance (Robinson, 1956; Wallace, 1973, 1975; Wolpoff, 1973). Antemortem chipping occurred in both taxa (Wallace, 1973, 1975) but the dietary implications were never satisfactorily resolved. Amongst Neanderthals, rounded labial wear of incisors coupled with frequent damage in the form of chipping, microfractures, and striations is thought to be associated with use of the anterior dentition as a tool rather than with dietary wear (e.g. Klein, 1999).

Dietary microwear patterning, by contrast, has received a great deal of attention over the last two decades. Oral processing of food leaves microscopic damage on tooth enamel surfaces, which is ultimately related to the mechanical properties of foods and to the presence of exogenous grit. Thus, unlike dental allometry and morphology which reveal something about the foods that challenge an individual's ancestors, dental microwear reflects its actual experience. In fact, the immediacy is such that it reflects food processing over the previous few days to weeks at the most, as microwear is quickly obliterated (Teaford and Oyen, 1989a). In short, dental microwear can distinguish among dietary categories when they correspond to differences in physical characteristics of foods (El Zataari et al., 2005), and when the influence of taphonomic factors is excluded (Teaford, 1988b).

A particular advantage is that microwear patterns may be able to detect subtle dietary differences amongst related primate species under certain circumstances (e.g., Walker, 1976; Teaford, 1985, 1988a; Teaford et al., 2002). Most studies have concentrated on patterns of small pits and scratches resulting from chewing and crushing, and both extant and extinct primates have been extensively studied. For instance, primates that make frequent use of their front teeth tend to have high densities of microwear striations on their incisors (Ryan, 1981; Ungar and Grine, 1991). Folivores show high incidences of long narrow scratches on their molar occlusal surfaces, whereas frugivores have relatively more pits. Among frugivores, hard-object feeders have higher pit incidences than soft-fruit eaters. Hence, hard fruit- and seed-eaters, such as mangabeys (*Lophocebus albigena* and *Cebus apella*), show distinct microwear patterns compared to leaf-eaters, like mountain gorillas (*Gorilla gorilla beringei*) (Grine and Kay, 1988; Ungar, 1998). These and other relationships between microwear and feeding behaviors in living primates have been used to infer diet in fossil forms.

Observer differences and low repeatability have been major disadvantages in microwear studies (Teaford and Oyen, 1989b; Grine et al., 2002), and an area of active and ongoing development is to quantify patterns of microscopic pitting and scratching damage in as objective and repeatable a manner as possible (e.g., Ungar, 2004; Scott et al., 2005). Micrographs of small sections of tooth facets are obtained using scanning electron microscopy of high-precision molds, at high magnification (500×). A major advance was the combination of scanning confocal microscopy methods (Boyde and Fortelius, 1991) with fractal analysis to analyze tooth topography (Ungar et al., 2003). Current techniques use automated image processing of scanned micrographs using a software package (Ungar, 1995; El Zataari et al., 2005) to quantify

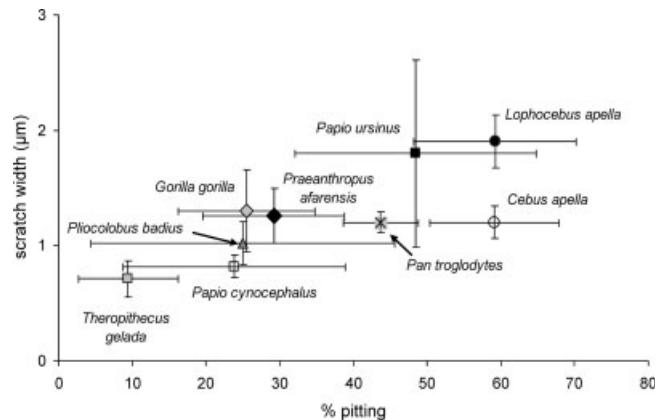


**Fig. 1.** Occlusal molar microwear differences and similarities between *A. africanus* (filled circles) and *Paranthropus* (open circles). (a) A bivariate plot of microwear feature width versus feature length (in µm) on M<sup>2</sup> protoconal facets using scanning electron microscopy shows that the former has more scratches and the latter more pit features (data from Grine, 1986: Table 9). (b) A bivariate plot of anisotropy (epLsar<sub>1.8</sub>) and complexity [log<sub>10</sub>(Asfc)], calculated from fractal analysis of occlusal molar topography, suggests that *Paranthropus* features show less anisotropy (i.e. less directionally dependent microwear) and greater complexity, but also that there is some overlap between patterns of the two taxa (redrawn from Scott et al., 2005).

the variables—percentage of pits, scratch breadth, pit breadth, and pit length. Scale-sensitive fractal analysis has been recently applied to a hominin study to better characterize the complexity and anisotropy of three-dimensional microwear damage (Scott et al., 2005).

Microwear analyses have been frequently applied to diets of fossil primates, including Miocene Dryopithecines (Ungar, 1996), and applications to early hominin diets are ongoing. An early application to the South African australopiths provided an independent test of Robinson's hypothesis for dietary distinctions between the South African robust and gracile australopiths (Robinson, 1954, 1956). Grine (1981, 1986), and Grine and Kay (1988) demonstrated that *Paranthropus* molars showed more pitting than those of *A. africanus*, while the scratches in the latter are longer, narrower and more directed (or anisotropic) (Fig. 1a). These authors deduced that while *Paranthropus* concentrated on small, hard objects, *A. africanus* ate softer foods more frequently, such as fruits and leaves. Microwear features on *A. africanus* incisors show higher densities on all surfaces compared to *Paranthropus* (Ungar and Grine, 1991), suggesting that the former processed more foods with the anterior teeth. The results are consistent with craniodental measurements which suggest that they used a great deal of force to process hard foods (e.g., Demes and Creel, 1988). Subsequent assessments of molar microwear using automated confocal 3D image microscopy and fractal image analysis have been largely consistent with the earlier studies, although they have tended to emphasize also inter-individual dietary variability and overlap between these two species (Fig. 1b) (Scott et al., 2005).

Most recently, Grine et al. (2006) showed that the molar microwear on the enamel of *A. afarensis* was most similar to that of gorillas and dissimilar to hard object feeders (Fig. 2), suggesting an unexpected reliance on terrestrial herbaceous vegetation rather than small hard objects, as suggested by their dental morphology and thick enamel. They also noted that *Australopithecus*



**Fig. 2.** A comparison of the two most distinguishing microwear features (scratch width and % pitting) for *Australopithecus afarensis* (or *Praeanthropus afarensis*) against similar data for a range of extant primates shows greatest similarity with *Gorilla gorilla* and not with hard object feeders (*Cebus apella* and *Lophocebus albigena*) as might have been predicted from morphology and enamel thickness (data from Grine et al., 2006: Table 7).

microwear patterns did not change with shifting environments over a period of some 400 Ka. An earlier qualitative microwear study on the anterior teeth of *A. afarensis* (Puech et al., 1983) had also suggested that a mosaic of gorilla-like fine wear striae and baboon-like pits and microflakes implied use of incisors to strip gritty plant parts, such as seeds, roots, and rhizomes (Ryan and Johansen, 1989). Other than this, little microwear data is available for the earlier australopiths, and none for *A. anamensis* and *Ardipithecus ramidus*, although a report on the microwear of the former species is forthcoming (P. Ungar, personal communication).

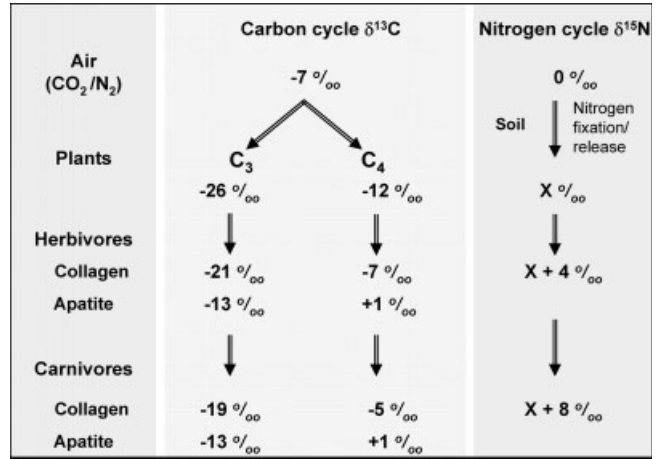
There has also been little emphasis on dental microwear in later hominins. This is partly a result of the unknown influence of cultural factors in processing of

foods, as well as the lack of appropriate comparisons. Primate comparisons are a central pillar of microwear (and morphological) applications to hominin diets, but they are less relevant to more recent populations, and comparative studies are relatively rare. One exception is the study of Pérez-Pérez et al. (2003) which suggested that the microwear feature density, length, and orientation on Middle Pleistocene hominin molar buccal surfaces were consistent with more abrasive diets than those of Late Pleistocene individuals. They suggested that microwear density appeared to increase during cold intervals and argued that this resulted from hominins eating more abrasive plant foods, such as roots and bulbs. A corollary is that Neanderthals ate more nonabrasive foods during warmer periods, and the authors argue that the most likely item was animal meat. This is a somewhat counter-intuitive outcome when one considers that animal foods were likely to be the most accessible items under glacial conditions. A forthcoming study on molar microwear of Neanderthals should resolve this argument (S. El-Zataari, personal communication).

**CHEMICAL DIETARY TOOLS**

The underlying rationale of these techniques is that the chemical composition of a mammal's tissues, including bones and teeth, reflects that of its diet, following the old adage, "you are what you eat". Thus, they can provide direct chemical means for investigating paleodiets. This is the case as long as several crucial conditions are met. One is that various food sources can be distinguished by means of isotopic or chemical composition differences, which is not always the case. The pathways of these natural abundance tracers into tissues must also be predictable and understood. Finally, the original chemical composition, or at least something close to it, must survive. Thus, the over-arching constraints for applying these tracers are related to our understanding of the pathways of essential elements and isotopes in ecosystems, and to preservation issues. Studies of isotope and trace elemental behavior in modern ecosystems are large-scale, ongoing, undertakings (e.g., Burton et al., 1999; Codron et al., 2005; Sponheimer et al., 2005b). Efforts to address problems of preservation have included a shift to tooth enamel as sample material where it is feasible and the development of reliable protocols for identifying purity and assessing whether the dietary signals are real or not.

Chemistry was first used to address questions related to diet in the more recent archeological past to detect use of maize (e.g., Vogel and van der Merwe, 1977; van der Merwe and Vogel, 1978), pastoralism (Ambrose, 1986), marine food use (Tauber, 1981), and trophic levels and dietary change (Schoeninger, 1979; Sillen, 1981). Subsequently, a good deal of effort has been devoted to pushing these tools further back in time. Over the last decade or so, several studies have emerged that have provided new insights into dietary behavior of early and later hominins. The earlier pioneering stable isotope work concentrated exclusively on bone collagen, with the first applications to early hominin diets, based on tooth enamel, appearing later (Lee-Thorp, 1989; Lee-Thorp et al., 1994). Stable isotopic studies of the diets of Late Pleistocene hominins—Neanderthals and modern humans—have so far relied on the conventional bone collagen-based methods. Similarly, trace element studies



**Fig. 3.** Schematic representation showing the patterning of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes in typical foodwebs. Global mean  $\delta^{13}\text{C}$  values are given for trophic steps in the carbon cycle (middle panel), while mean differences are given for steps in the nitrogen cycle (right panel). This is because soil  $\delta^{15}\text{N}$  values depend on the balance of nitrogen fixation and denitrification, which is affected by a host of environmental factors. Two tissues (collagen and apatite) are shown for herbivores and carnivores.

focused for some time on bone, and only recently have applications explored tooth enamel as sample material.

The discussion below briefly outlines the principles of stable light isotope and trace element pathways in ecosystems and follows first the work on Neanderthals using bone collagen, and next the isotope and trace element work on earlier hominins based on analyses of enamel and bone mineral. The emphasis on European Neanderthals and South African australopiths is a reflection of the limited degree to which stable isotopes and trace elements have been used to investigate the diets of Plio–Pleistocene hominins.

**Stable light isotopes in ecosystems**

A simplified, diagrammatic illustration of the stable isotope pathways described in the following paragraphs is shown in Figure 3.

During photosynthesis plants take in  $\text{CO}_2$  and convert it to sugars. This process discriminates strongly against  $^{13}\text{C}$  but to different degrees depending on the pathway (Smith and Epstein, 1971) and on environmental conditions to a smaller extent. Plants following the  $\text{C}_3$  pathway (all trees, shrubs and herbs, and temperate or shade-adapted grasses) are strongly depleted in  $^{13}\text{C}$  relative to atmospheric  $\text{CO}_2$ , and consequently have distinctly lower  $\delta^{13}\text{C}$  values compared to  $\text{C}_4$  plants (mainly tropical grasses). Environmental influences acting on  $\text{C}_3$  plants include the “canopy effect” in dense forests (leading to further depletion in  $^{13}\text{C}$ ) (Vogel, 1978; van der Merwe and Medina, 1989) and aridity/temperature effects (leading to

<sup>1</sup>By convention, stable isotope ratios are expressed as  $\delta$  values relative to an international standard in parts per thousand (per mil), as follows in an example for carbon isotopes:  $\delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$  where  $R = ^{13}\text{C}/^{12}\text{C}$  and the international standard is Vienna Pee Dee Belemnite (VPDB).

Standards for nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) and oxygen ( $^{18}\text{O}/^{16}\text{O}$ ) isotopes are atmospheric nitrogen (AIR), and VPDB or Standard Mean Ocean Water (SMOW), respectively.

enrichment in  $^{13}\text{C}$  under more arid and/or warm conditions and vice versa) (for a review see Tieszen, 1991). A third photosynthetic pathway, the Crassulacean Acid Metabolism (CAM) pathway, effectively utilizes both pathways with resulting  $\delta^{13}\text{C}$  values that vary extensively depending on whether they are "obligate" CAM or not and upon environmental conditions (Winter and Smith, 1996). CAM plants are primarily succulents like euphorbias that are rare outside of desert environments, and are moreover rarely used by animals (but see Codron et al., 2006 for use by baboons). They are not considered as important components of the environments inhabited by Plio-Pleistocene hominins (Reed, 1997; Peters and Vogel, 2005).

Nitrogen enters the terrestrial foodweb via  $\text{N}_2$ -fixing bacteria in soils or plants to form nitrates or ammonium ions which are utilized by plants. The net effect of biological nitrogen fixing and subsequent denitrification during decay of organic matter is slight enrichment in  $^{15}\text{N}$  in plants and soils compared to atmospheric  $\text{N}_2$  but the balance is affected by environmental conditions such as aridity (Heaton, 1987; Sealy et al., 1987; Handley and Raven, 1992; Amundson et al., 2003), although other effects such as leaching (high precipitation) and anoxia can also contribute.

Isotopic variability in plants is reflected in the bones and teeth of animals that consume them. Here understanding of the bio- and physico-chemical routes from food to tissue fixation is required, since diet-tissue fractionation varies according to the tissue and its chemistry. Isotope ratios of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) can be studied in collagen, which is the main organic component of bone and dentine. The mineral phase of bone and enamel, crystalline calcium phosphate structures known as biological apatites, yield  $^{13}\text{C}/^{12}\text{C}$  and  $^{18}\text{O}/^{16}\text{O}$  ratios from carbonate ions or  $^{18}\text{O}/^{16}\text{O}$  alone from phosphate ions. Both the structural and the isotope chemistry between diet and the organic or inorganic (mineral) compartments of skeletal tissues differ. Further, the timespan of dietary behavior reflected differs depending on whether bone or tooth tissues are analyzed; bone isotope values tend to reflect long-term averages (at least 10 years or more) whereas tooth isotope values reflect dietary behavior at the time of deposition since both enamel and dentine are incremental tissues. Where skeletal tissues are preserved at all, enamel in particular survives remarkably well for millions of years, apparently with only subtle alteration. Collagen has a much shorter "shelf-life" since it denatures and dissolves away far more quickly than the mineral, where the latter is preserved. On the other hand, where it does survive, it is relatively straightforward to obtain demonstrably intact collagen for analysis. A number of safeguards are routinely employed to demonstrate the quality of the collagen (Ambrose, 1990). Hence, the sample tissue chosen is important because this choice (often imposed by circumstances) directly affects the isotope tools and the type of information available, the age limits for the study, and the measures that must be taken to guard against diagenesis.

### Stable isotopes in bone collagen

The difference ( $\Delta$ ) between diet and collagen  $\delta^{13}\text{C}$  is about +5‰, but controlled feeding studies have shown that the relationship is largely between dietary protein and collagen because dietary amino acids are preferentially utilized for collagen tissue construction, while carbon from dietary carbohydrate and lipids makes a lesser

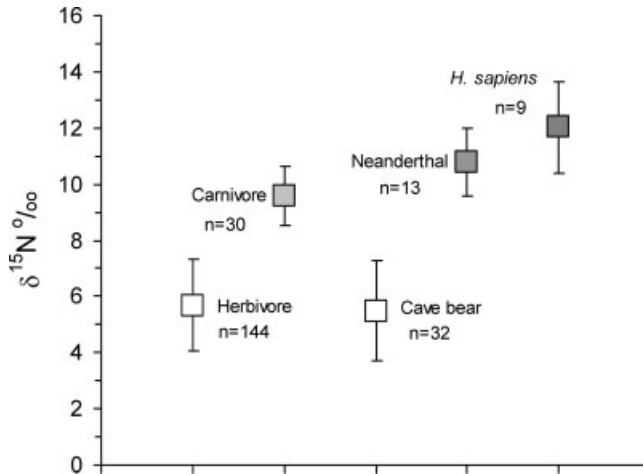
contribution (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). A stepwise trophic shift of +3–5‰ in  $\delta^{15}\text{N}$  from plants to herbivores, and from herbivores to carnivores has been widely documented in marine and terrestrial foodwebs (Minigawa and Wada, 1984; Schoeninger and DeNiro, 1984; Sealy et al., 1987). A significant outcome of the routing of dietary protein to tissue proteins is that  $\delta^{13}\text{C}$  in bone collagen (and  $\delta^{15}\text{N}$  by default) is "biased" towards the high protein component of an individual's diet. Consequently, animal foods will be overrepresented in bone collagen at the expense of low-protein (vegetable) foods, and this bias must be considered when interpreting collagen stable isotope data.

Progress in extracting good quality collagen from older material has demonstrated that under the right conditions, bone collagen can survive for up to 200,000 years (Ambrose, 1998; Jones et al., 2001). This has made it possible to analyze the bone collagen of Late Pleistocene hominins in certain cases. At these time depths, strict quality controls that demonstrate collagen preservation are essential because degradation is known to alter collagen stable isotope ratios significantly (Ambrose, 1990).

**Neanderthal diets.** Bocherens et al. (1991) performed the first stable isotope analysis of a single Neanderthal individual and associated fauna from 40,000-year-old bones at the site of Marillac in France. Although the quality control methods relied on amino acid profiles that might not be considered adequate today, subsequent analyses from this site (Fizet et al., 1995) have shown the original observations to be robust. The study paved the way for subsequent analyses of Neanderthals from Marillac (Fizet et al., 1995), Scladina Cave, Awirs Cave, and Betche-al-Roche Cave in Belgium (Bocherens et al., 1997, 2001), and Vindija Cave in Croatia (Richards et al., 2000).

All native European plants are  $\text{C}_3$ , and consequently have similar  $\delta^{13}\text{C}$  values with the exception of plants in densely wooded environments that are more depleted in  $^{13}\text{C}$  due to the canopy effect (Vogel, 1978; van der Merwe and Medina, 1989). Thus,  $\delta^{13}\text{C}$  composition of bone collagen reveals little about the diets of Neanderthals, except that they likely utilized few food resources from closed, densely forested environments (Bocherens et al., 1999; Richards et al., 2000). The  $\delta^{15}\text{N}$  composition of Neanderthal bone collagen is more revealing. Although nitrogen isotope distributions in foodwebs are often complicated due to heterogeneity in plant  $\delta^{15}\text{N}$  and the disparate physiological adaptations and requirements of different animals (Ambrose, 1991; Sponheimer et al., 2003), the general pattern of stepwise shifts in  $\delta^{15}\text{N}$  of about +3–4‰ is robust (Fig. 3). Thus,  $\delta^{15}\text{N}$  analysis of Neanderthal bone collagen can address the question of trophic level and hence of meat consumption. This is particularly relevant as the degree of carnivory and manner of carcass acquisition (hunting or scavenging) amongst Neanderthals has been the subject of debate (e.g., Binford, 1981; Stiner, 1994; Marean and Assefa, 1999; Speth and Tchernov, 2001).

All published isotopic studies have shown that Neanderthals have much higher  $\delta^{15}\text{N}$  than that of contemporaneous (or near-contemporary) herbivores such as horse (*Equus caballus*), reindeer (*Rangifer tarandus*), and bison (*Bison priscus*) and similar to that of carnivorous wolves (*Canis lupus*), hyenas (*Crocuta spelaea*), and lions (*Panthera spelaea*) (Bocherens et al., 1991, 1997, 2001, 2005; Fizet et al., 1; Richards et al., 2000). Overall,



**Fig. 4.** Neanderthal bone collagen  $\delta^{15}\text{N}$  data from the sites of Marillac, Sladina, Vindija, Engis, and Spy shown in relation to herbivores and carnivores from the same sites (combined), and compared against data for mid-Upper Paleolithic humans (labeled *H. sapiens* for brevity). Mean values are shown as boxes along with standard deviations and the number of individuals in each case. Neanderthal data are summarized from Bocherens et al. (1991, 1999, 2001), Fizet et al. (1995), and Richards et al., (2000), while the Upper Paleolithic human data is from Richards et al. (2001) and Pettitt et al. (2003).

Neanderthal  $\delta^{15}\text{N}$  is not only significantly higher than herbivore  $\delta^{15}\text{N}$ , but also slightly higher than carnivores (Fig. 4) (Sponheimer and Lee-Thorp, 2006b). Even given the bias towards animal foods in bone collagen, these data suggest that Neanderthals were significantly carnivorous, and that little of their dietary protein came from plant foods (Richards et al., 2000, 2001; Bocherens et al., 2005). These authors have argued that enrichment in  $^{15}\text{N}$  compared to (other) carnivores could be taken as an indication of dependence on herbivores with relatively high  $\delta^{15}\text{N}$ , such as mammoths (*Mammuthus primigenius*), or even the consumption of omnivorous bears (*Ursus* spp.) (Richards et al., 2000; Bocherens et al., 2001). Bocherens et al. (2005) used a mixing/resource partitioning model developed in modern ecosystem studies (Phillips, 2001; Phillips and Gregg, 2003) to calculate on the basis of statistical probability that a major component of Neanderthal diet was mammoth. However, a number of problems underlie the use of this statistical model, not the least of which is that values for *all* resources must be known.

It has not yet been possible to compare directly the stable isotope composition of Neanderthals and Upper Paleolithic *Homo sapiens* (UPHs) from similar periods and places. However Richards et al. (2001) were able to compare data from nine near-contemporaries from the mid-Upper Paleolithic (~28–20 Ka) at Brno-Francouzská and Dolni Vestonice (Czech Republic), Kostenki, Mal'ta, and Sungir (Russia), and Paviland (Great Britain) with data from the five Neanderthals that had been published at the time. They observed that the modern humans were even more elevated in  $\delta^{15}\text{N}$ , suggesting, if one follows the same arguments applied to Neanderthals, that these modern humans were also highly dependent on animal foods. In this case, however, they suggested contributions from freshwater aquatic resources such as fish and waterfowl, which can be more enriched in  $^{15}\text{N}$  than terrestrial resources (Dufour et al., 1999)

and that this implied diversification of the resource base (Richards et al., 2001). This suggestion was unexpected, as there is little archeological evidence for exploitation of such foods at this time. With the subsequent addition of several new Neanderthal and mid-Upper Paleolithic human analyses (Bocherens et al., 2001; Pettitt et al., 2003); however, there is no longer any statistically significant difference in the  $\delta^{15}\text{N}$  of Upper Paleolithic humans and Neanderthals (Sponheimer and Lee-Thorp, 2006b) (Fig. 4).

Interpretation of these data is not straightforward and there remain a number of unanswered questions. For instance, why are both hominins so enriched in  $^{15}\text{N}$  compared to associated carnivores? The consumption of herbivores with unusually high  $\delta^{15}\text{N}$  such as mammoths, or aquatic resources, offers one possible, but nevertheless rather unsatisfactory explanation. There may be an alternative physiological explanation for their extremely high  $\delta^{15}\text{N}$  values. Controlled feeding studies have shown that when herbivores are fed diets with protein contents much greater than their nutritional requirements, their diet-tissue spacing ( $\Delta$ , denoting the isotopic difference between dietary and tissue values) exceeds the average of +3–4‰ (Sponheimer et al., 2003). Hence, if the consumption of animal-rich high-protein diets in the prevailing glacial environment led to Neanderthals' exceeding their protein requirements, their  $\Delta$  might well exceed +3–4‰ and increase their  $\delta^{15}\text{N}$  compared to other taxa. The anomalously high  $\delta^{15}\text{N}$  of mammoths and low  $\delta^{15}\text{N}$  of cave bears (Bocherens et al., 1997; Ambrose, 1998) also hints at the importance of unknown physiological adaptations in determining an organism's nitrogen isotope composition. These studies of glacial-age Neanderthals and modern humans in Europe illustrate the complexity in interpreting  $\delta^{15}\text{N}$  data in a paleo-ecosystem for which we have incomplete information and no modern analogue.

It is worth noting that even if the Neanderthals did have an unusually increased diet-tissue spacing due to a high-protein intake, it might erase their distinctiveness from other carnivores but would certainly not make them look herbivorous. The  $\delta^{15}\text{N}$  data leave little doubt that Neanderthals and mid-upper Pleistocene modern humans consumed large quantities of animal foods.

### Stable isotopes in enamel apatite

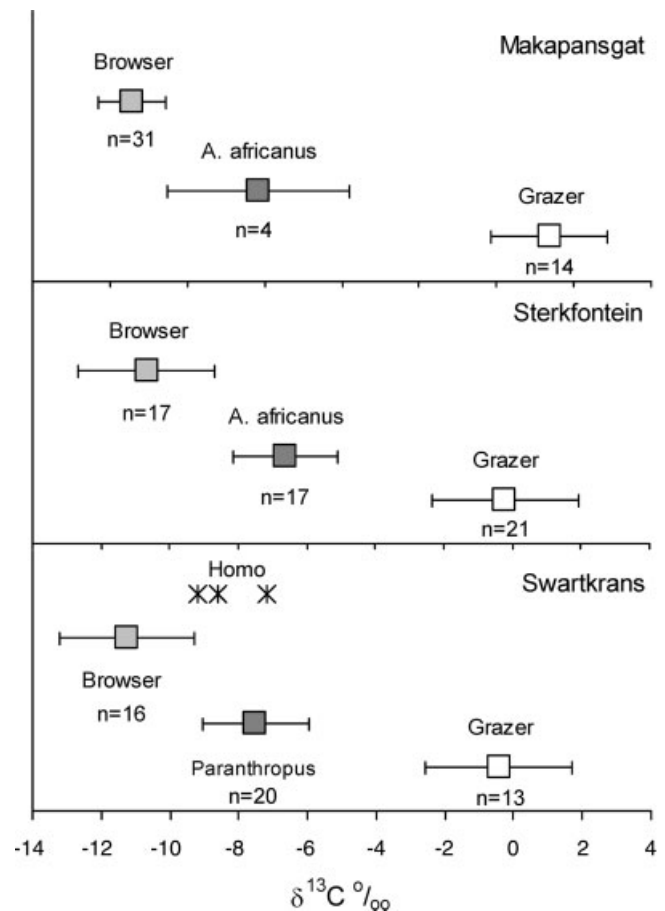
Bone collagen is rarely preserved beyond the Late Pleistocene (Jones et al., 2001), so this avenue is not an option for analysis of older hominin material. However, the carbon isotopes in the mineral component can also be used as dietary proxies (Sullivan and Krueger, 1981; Lee-Thorp and van der Merwe, 1987). Although bone mineral clearly persists beyond bone collagen, it is inevitably altered postmortem, often (but not always) resulting in the loss of the biogenic dietary signal (Lee-Thorp, 2000; Lee-Thorp and Sponheimer, 2003). This is due to bone's high organic content, porosity, and small crystal size (LeGeros, 1991; Elliot, 1994), which make it susceptible to dissolution/precipitation phenomena that facilitate the incorporation of exogenous carbonate ions. Thus paleodietary studies based on bioapatite were forestalled until it could be shown that dental enamel from ancient fauna with well-understood diets reliably retained biogenic isotope compositions. This was accomplished by demonstrating that known fossil grazers had  $\delta^{13}\text{C}$  values indicative of  $\text{C}_4$ -grass diets, while known fossil browsers

had  $\delta^{13}\text{C}$  values indicative of browsing diets (Lee-Thorp and van der Merwe, 1987). Numerous empirical and theoretical studies have substantiated this finding (e.g., Cerling et al., 1997; Sponheimer and Lee-Thorp, 1999b; Zazzo et al., 2000), which is hardly surprising given that enamel is denser, has a very low organic content and is more crystalline (LeGeros, 1991; Elliott, 1994) which renders it effectively more inert and “pre-fossilized.”

Therefore, only tooth enamel has been used for stable isotope analysis of hominin and non-hominin specimens that are millions of years old. Although at first relatively large samples (~200 mg) were needed, rendering this a destructive method of analysis, subsequent advances in mass spectrometry have reduced the required sample to a few milligrams (Lee-Thorp et al., 1997; Sponheimer, 1999). As a result, it has become possible to remove small samples with minimal, barely observable damage, and consequently larger numbers of analyses became possible. It is worth noting that different pretreatment protocols designed to eliminate contamination (Koch et al., 1997; Lee-Thorp et al., 1997; Sponheimer, 1999) can lead to small but significant differences in a sample's stable isotope composition (especially for oxygen), and therefore one must compare stable isotope values for teeth analyzed following different protocols with caution.

Apatite carbonate forms from blood bicarbonate, and isotopic fractionation is tightly controlled by physicochemical processes during apatite formation. The relationship between dietary, breath  $\text{CO}_2$  (which is equilibrated with blood bicarbonate), and enamel apatite  $\delta^{13}\text{C}$  has been well-studied (Passey et al., 2005). Overall, the diet to enamel shift averages about 13‰ for most large mammals (Fig. 3) (Lee-Thorp et al., 1989; Passey et al., 2005). Nevertheless, some variability has been documented, for instance measurements on small rodents on controlled diets indicate a diet-apatite spacing of just less than 10‰ (Ambrose and Norr, 1993; Tieszen and Fagre, 1993), while studies of some large ruminants indicate values of up to +14‰ (Cerling and Harris, 1999). This variation likely reflects mass balance differences related to metabolism and/or dietary physiology. Unlike collagen, apatite reflects the  $\delta^{13}\text{C}$  of the bulk diet, and not just the protein component (Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Thus, apatite and bone collagen  $\delta^{13}\text{C}$  provide different perspectives on an individual's diet, and indeed analysis of both components would provide the most complete picture. Most important, for our purposes, is that enamel apatite provides a good average dietary signal that equally reflects the consumption of vegetable and animal foods.

**Australopith and early Homo diets.** Isotopic dietary studies of early hominins are founded primarily upon the distinct  $\delta^{13}\text{C}$  composition of  $\text{C}_3$  and  $\text{C}_4$  plants, which in African savanna environments reflect carbon sources from trees, bushes, shrubs, and forbs for the former, and tropical grasses and some sedges for the latter. In the early 1990s, it was widely believed that *A. africanus* had a diet that consisted primarily of fleshy fruits and leaves, much like the modern chimpanzee, while *P. robustus* consumed more small, hard foods such as nuts (Grine, 1981; Grine and Kay, 1988; Ungar and Grine, 1991). As these are all  $\text{C}_3$  foods, it could then be predicted that *A. africanus* and *P. robustus* should have  $\delta^{13}\text{C}$  values indistinguishable from those of  $\text{C}_3$  browsers and frugivores.



**Fig. 5.** Enamel  $\delta^{13}\text{C}$  data for *Australopithecus africanus*, *Paranthropus robustus*, and *Homo* specimens from the sites of Makapansgat, Sterkfontein, and Swartkrans compared with  $\text{C}_3$  plant consumers (browsers) and  $\text{C}_4$  plant consumers (grazers); all data are shown as means (boxes), standard deviations, and numbers ( $n$ ) of individuals except for the three Swartkrans *Homo* values which are shown as stars. Data are from Lee-Thorp et al. (1994, 2000) for Swartkrans, Sponheimer, and Lee-Thorp (1999a) for Makapansgat, van der Merwe et al. (2003) for Sterkfontein, and Sponheimer et al. (2005a) for the remaining Sterkfontein data.

This turned out not to be the case. A total of 40 certain hominin specimens from the sites Makapansgat, Sterkfontein, Kromdraai, and Swartkrans have now been analyzed. The data demonstrate unequivocally that the  $\delta^{13}\text{C}$  of both australopiths is very distinct from that of  $\text{C}_3$ -consuming coevals ( $P < 0.0001$ ), but that *A. africanus* and *P. robustus* cannot be distinguished from each other (Sponheimer and Lee-Thorp, 1999a; Lee-Thorp et al., 1994, 2000; van der Merwe et al., 2003; Sponheimer et al., 2005b) (Fig. 5). The distinction between the hominins and other fauna cannot be ascribed to diagenesis, as there is no evidence that browser or grazer  $\delta^{13}\text{C}$  has been altered, and diagenesis should affect all fauna alike. If we take the mean  $\delta^{13}\text{C}$  of  $\text{C}_4$  and  $\text{C}_3$  consuming herbivores as indicative of pure  $\text{C}_4$  and  $\text{C}_3$  diets respectively, it would indicate that both *Australopithecus* and *Paranthropus* obtained about 30% or more of their carbon from  $\text{C}_4$  sources. Thus, both taxa were eating considerable quantities of  $\text{C}_4$  resources, and these resources must have consisted of grasses, sedges, or animals that ate these plants.

This result was unexpected, since extant apes consume minimal C<sub>4</sub> resources if at all (McGrew et al., 1981, 1982; Goodall, 1986). Even in more open environments where C<sub>4</sub> foods are readily available,  $\delta^{13}\text{C}$  analyses of chimpanzees do not indicate any C<sub>4</sub> consumption (Schoeninger et al., 1999; Carter, 2001; Sponheimer et al., 2006). Thus, the  $\delta^{13}\text{C}$  data suggests a fundamental niche difference between the australopiths and extant apes. Furthermore, this association with C<sub>4</sub> resources persists through diachronic environmental trends from relatively closed habitats in the Pliocene at the sites of Makapansgat (~3 Ma) and Sterkfontein Member 4 (~2.5 Ma) through to the later, open environments of Swartkrans Member 1 (~1.5–1.8 Ma) (Fig. 5). The hominin  $\delta^{13}\text{C}$  data are also more variable than virtually all modern and fossil taxa that have been analyzed in South Africa (Lee-Thorp et al., 1994, 2000; Sponheimer and Lee-Thorp, 1999a, 2001, 2003; Codron, 2003; van der Merwe et al., 2003). This suggests that australopiths were opportunistic primates with wide habitat tolerances, an observation which is consistent with Wood and Strait's (2004) suggestion that these early hominins were eurytopic (dietary generalists) rather than ecological specialists.

How do these data compare with early *Homo*? Based on the prediction that if *Homo* consumed more animal foods (as is widely held), their  $\delta^{13}\text{C}$  should be more positive compared to *P. robustus* from the same Swartkrans Member 1 deposits, data from three early *Homo* specimens were compared with the australopith data (Lee-Thorp et al., 2000). Again this turned out not to be the case; *Homo*  $\delta^{13}\text{C}$  was very similar to that of the australopiths (Fig. 5), and the results must be interpreted in the same way. Roughly 25% of their dietary carbon came from C<sub>4</sub> sources that included C<sub>4</sub> plants, C<sub>4</sub> animal products, or some combination of these. However, only three *Homo* specimens from one site have been analyzed and published so far, and thus comparisons with the more numerous australopith data must be viewed with caution. Unpublished  $\delta^{13}\text{C}$  data from East Africa show a strong difference between *Paranthropus* and *Homo*; in this case the former is strongly enriched in <sup>13</sup>C, while values for the latter resemble those for the Swartkrans individuals (van der Merwe, personal communication).

This leaves us with the question about what exactly these C<sub>4</sub> resources were? The answer to this question is significant, because the outcome has a variety of physiological, social, and behavioral implications. For instance, if australopiths had a grass-based (graminivorous) diet similar to the modern gelada baboon (*Theropithecus gelada*), it would suggest that their diets were less nutrient rich than those of modern apes, placing limitations on brain expansion and sociality (Aiello and Wheeler, 1995; Milton, 1999). The converse that australopiths ate diets rich in animal foods would indicate a leap in dietary quality over modern apes (Milton, 1999). At the time Lee-Thorp et al. (1994, 2000) argued that savanna grasses are unlikely staple food sources for hominins and that consumption of C<sub>4</sub>-consuming insects and vertebrates was a more plausible explanation. This argument was based partly on the lack of dental and digestive "equipment" to deal with grasses per se, and partly on the limited seasonal availability and difficulties of harvesting grass seeds, which are denser, if tiny, food packages.

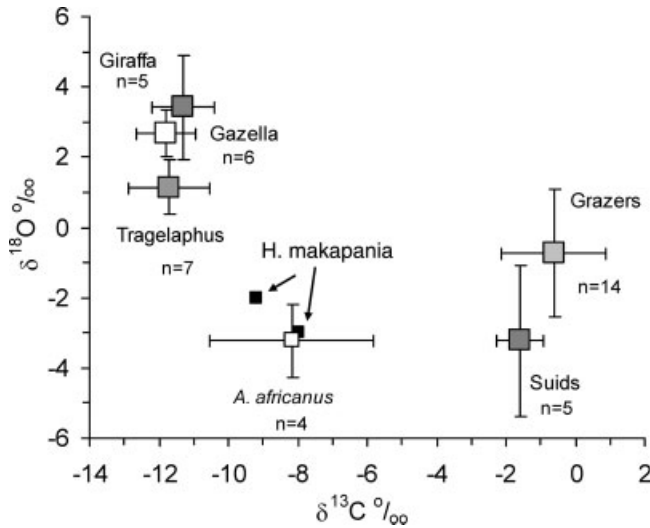
This list of possibilities has been reconsidered (e.g., Peters and Vogel, 2005; Sponheimer and Lee-Thorp, 2006b). Recently edible sedges have received attention as potential C<sub>4</sub> foods for hominins (Conklin-Brittain et al.,

2002), argued to have been part of a strategy focused on wetlands. Sedges are common in these habitats and in some cases can represent reasonably high quality foods, for which there was likely little competition (Conklin-Brittain et al., 2002). However, the distribution of C<sub>4</sub> sedges has different climate or environmental controls compared to C<sub>4</sub> grasses (Stock et al., 2004), and it cannot be assumed that most sedges utilize the C<sub>4</sub> pathway even in African savannas. Only 35% of sedges in South Africa overall are C<sub>4</sub> (Stock et al., 2004), and a study of sedges in riverine habitats similar to those inhabited by australopiths found <30% abundance (Sponheimer et al., 2005a), with very few being edible. Unless the distribution of sedges was markedly different during the Pliocene, and/or the australopiths sought out large quantities of C<sub>4</sub> sedges, sedge consumption could not produce the observed 35–40% C<sub>4</sub> contribution to hominin diets. Thus, a sedge specialization is unlikely in South Africa, although that does not rule out some contribution. In contrast, some habitats in East Africa where C<sub>4</sub> sedges, such as the Olduvai Gorge wetlands, are far more common (Hesla et al., 1982; DeoCampo et al., 2002) likely provided richer edible C<sub>4</sub> sedge opportunities. The very positive  $\delta^{13}\text{C}$  values obtained for *P. boisei* would be consistent with heavy utilization of C<sub>4</sub> sedges.

The other possibility considered in Lee-Thorp et al. (2000)—that of animal foods—has also been more closely examined. It was envisioned at the outset as a broad category comprising insects, lizards, rodents, hyraxes, eggs, and small antelopes (as suggested originally by Dart (1926) for the Taung hominin), rather than necessarily flesh from large vertebrate mammals. It was assumed that a majority of such animal foods would be enriched in <sup>13</sup>C, as the bulk of the biomass in savanna environment derives from C<sub>4</sub> sources. A recent analysis of predators from all size classes in the Kruger National Park, South Africa, has shown this to indeed be the case (Codron, Sponheimer, Lee-Thorp, unpubl. data). These foods can be acquired by gathering. Baboons are known to eat grass-eating grasshoppers (Acrididae) (Hamilton, 1987), and grass-eating termites represent another plausible source, particularly since bone tool wear studies have suggested that they were used for excavating termite mounds (Backwell and d'Errico, 2001). Savanna termites are widely distributed and range from C<sub>3</sub> to pure C<sub>4</sub> consumers, but most consume significant proportions of C<sub>4</sub> plants, and termites in the Kruger National Park ate 35% C<sub>4</sub> vegetation on average (Sponheimer et al., 2005a). Again, it's unlikely that termite consumption alone was the source of the strong C<sub>4</sub> signal in australopiths because it would require a diet of nearly 100% termites, or at least, a very large amount of grass-specialist termites. Thus, termite consumption plausibly contributed to the  $\delta^{13}\text{C}$  values of australopiths, but other C<sub>4</sub> resources were almost certainly consumed as well.

Clearly, carbon isotope ratios alone cannot address the question of the source of C<sub>4</sub> carbon in australopith diets, or indeed that of the slightly larger C<sub>3</sub> component. One other possible source of information may come from  $\delta^{18}\text{O}$  in enamel apatite. Oxygen isotopes are not usually considered as dietary but rather as climate indicators, since the primary input in ecosystems is from environmental drinking water, which is subject to a range of strong climate influences (e.g., vapour source, storm paths, temperature, and altitude) (Dansgaard, 1964).

Recent studies have shown that  $\delta^{18}\text{O}$  from apatite carbonate or phosphate can also be influenced by dietary

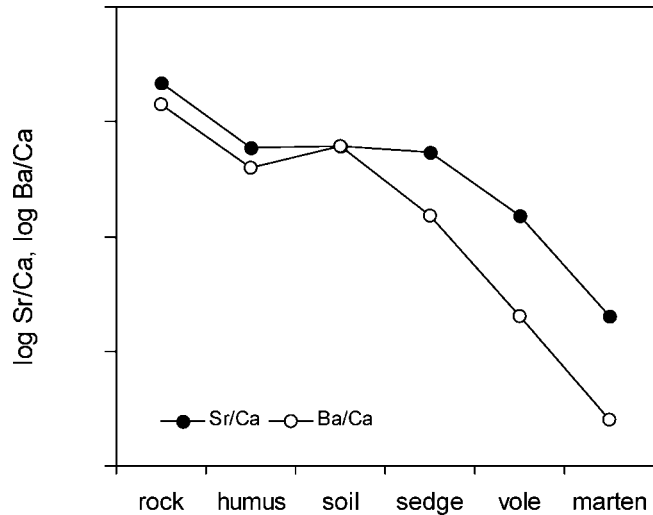


**Fig. 6.** Bivariate plot of  $\delta^{13}\text{C}$  versus  $\delta^{18}\text{O}$  for *A. africanus* and selected fauna from Makapansgat Member 3, shown as means (boxes) and standard deviations. The hominins ( $n = 4$ ), although variable in  $\delta^{13}\text{C}$ , cluster with *Hyena makapania* in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ .

ecology (Bocherens et al., 1996; Kohn, 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999b). In herbivores this occurs largely because of the input of oxygen from plant water and carbohydrates in leaves that are enriched in  $^{18}\text{O}$  as a result of evapo-transpiration isotope effects. Consequently, animals such as giraffes that rely less on free drinking water and feed in the upper canopy (Cerling et al., 1997) have higher  $\delta^{18}\text{O}$  values than obligate drinkers in the same environment. Distribution of  $\delta^{18}\text{O}$  in bioapatites, unexpectedly, also reflects trophic behavior. In southern Africa, the faunivores, *Otocyon megalotis*, *Crocota crocuta*, and *Orycteropus afer*, are significantly depleted in  $^{18}\text{O}$  compared to herbivores in two modern ecosystems (Lee-Thorp and Sponheimer, 2005). Low values for faunivores are likely linked to their high lipid, high protein diets (Sponheimer and Lee-Thorp, 1999b). Suids and many primates also have relatively lower  $\delta^{18}\text{O}$  (Sponheimer and Lee-Thorp, 1999b; Carter, 2001).

Australopith  $\delta^{18}\text{O}$  data from Makapansgat and Swartkrans overlap with those of carnivores in the same strata (Lee-Thorp, 2002; Lee-Thorp et al., 2003) (Fig. 6). Although at first sight, this could be seen as reinforcement of the animal-food hypothesis, it is not that simple. The causes of the relatively low  $\delta^{18}\text{O}$  values for many primates and suids are obscure: they may be linked to frugivory, the use of underground storage organs, or water dependence, but given our present limited understanding of  $\delta^{18}\text{O}$  patterning in foodwebs, this is merely speculative. Clearly there is overlap in the inputs from different sources and, fuller interpretation of these data awaits more detailed ecosystem studies.

Despite these uncertainties, we should not lose sight of a significant finding from these isotope data, namely that australopiths increased their dietary breadth compared to extant apes by consuming novel  $\text{C}_4$  resources, whatever these resources were. Thus, a fundamental difference between australopiths and extant apes might be that when confronted with increasingly open areas, apes continued to use the foods that are most abundant in for-



**Fig. 7.** The results of the classic trace element discrimination study of a terrestrial grazing ecosystem in North America. Sr/Ca and Ba/Ca ratios are plotted on a logarithmic scale (y-axis), and "soil" is used as shorthand for "soil moisture". This study was designed to calculate biopurification factors for calcium with respect to strontium and barium uptake. The plant: vole:pine marten curves nicely illustrate systematic reduction in Sr/Ca and Ba/Ca in this foodweb, with stronger discrimination against Ba. This study was subsequently taken as representing trophic relations everywhere. Data are redrawn from Elias et al. (1982).

est environments (McGrew et al., 1982), whereas australopiths began to exploit the novel  $\text{C}_4$  resources.

### Trace elements

The distribution of trace elements in foodwebs forms the basis for another important chemical means for tracing diets in the past. Mammals discriminate against the alkaline earth metals, strontium (Sr) and barium (Ba), with respect to calcium (Ca) in the digestive tract and kidneys in a process known as biopurification of Ca (Spencer et al., 1973; Elias et al., 1982). As a result, herbivore tissues have lower Sr/Ca<sup>2</sup> and Ba/Ca ratios than the plants that they eat, and carnivores in turn have lower Ba/Ca and Sr/Ca than the herbivores they consume (Elias et al., 1982; Sealy and Sillen, 1988; Burton et al., 1999). Since Sr and Ba are found in bones and teeth, where they substitute for calcium in the calcium phosphate apatite structure, they can in principle be used to investigate trophic behavior of fossil fauna (Fig. 7). Other trace elements have been applied from time to time, for instance zinc (Zn), but applications are severely limited since so little is known about their distribution in foodwebs and fixation in bone.

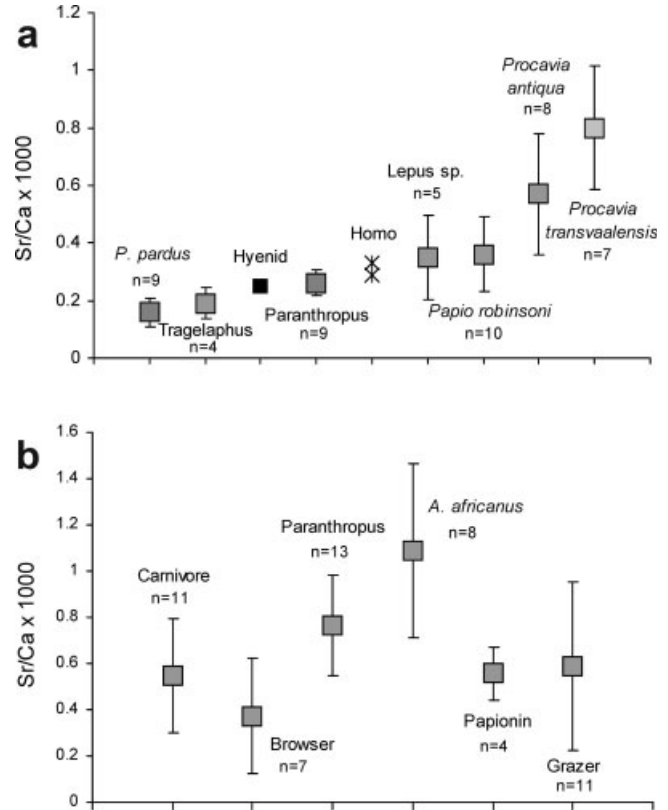
There are two major constraints in application of Sr and Ba to paleodietary reconstruction. One is diagenesis. Although early researchers were largely unaware of the extent of the problem (e.g., Toots and Voorhies, 1965;

<sup>2</sup>Since Ca is a major element in skeletal tissues, with very high concentrations, the Sr and Ba composition is usually expressed as a ratio compared to Ca, ie. as Sr/Ca and Ba/Ca or as log Sr/Ca and log Ba/Ca.

Wyckhoff and Doberenz, 1968; Brown, 1974; Schoeninger, 1979), it was subsequently widely recognized (e.g., Sillen, 1981, 1989). Traditionally, archeological and paleontological trace element studies have been carried out on bone. This is because infants lack the adult capacity to discriminate against strontium and barium (Lough et al., 1963; Sillen and Kavanagh, 1981), and many teeth are formed in early development. A major drawback of bone, however, is its susceptibility to post-mortem chemical alteration (Sillen, 1989; Tuross et al., 1989) that can quickly obliterate the biological Sr/Ca signal.

To address the problem, Sillen (1981, 1992) developed a “solubility profiling” technique based on the premise that diagenetic apatite has differing solubility to biogenic fossil apatite. In this technique, highly soluble and poorly soluble diagenetic apatites are, in effect, stripped away from the biogenic material and the solutes, not the solid materials, are measured (Sillen, 1981, 1992). While ingenious, this method is technically challenging and laborious, greatly limiting wider application, but more importantly, several studies have shown that even when it is applied, diagenetic strontium often cannot be eradicated from bone and dentine (Budd et al., 2000; Hoppe et al., 2003; Lee-Thorp and Sponheimer, 2003; Trickett et al., 2003). This has led to recent attempts to investigate paleoecology using elemental ratios in modern enamel (Sponheimer et al., 2005a; Sponheimer and Lee-Thorp, 2006a), which as a denser, far more crystalline and ordered apatitic tissue (LeGeros, 1991; Elliott, 1994), is much more resistant to postmortem elemental alteration than bone (Budd et al., 2000; Hoppe et al., 2003; Lee-Thorp and Sponheimer, 2003; Sponheimer and Lee-Thorp, 2006a). The problem of poor biopurification in infants can be easily avoided by analyzing late developing teeth.

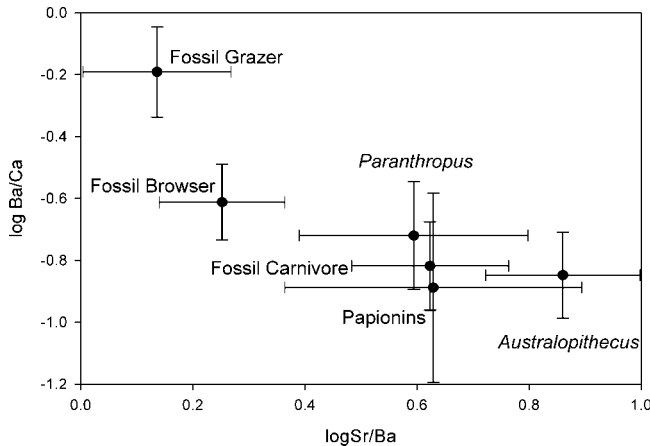
Perhaps a more immediate constraint in current trace element studies is the requirement for understanding their very complex pathways in foodwebs, which can result in significant variation between habitats and within a trophic level. The importance of local geology in controlling absolute availability of alkaline earth elements has been known from the early stages of development of the trace element method (Toots and Voorhies, 1965), if sometimes ignored. However, inherent variability within trophic levels in ecosystems and indeed within sympatric species has been largely unappreciated. For many years trace element paleodietary studies were based almost entirely on an “archetypal” grazing terrestrial foodweb study in North America (Elias et al., 1982) (Fig. 7), and only gradually has the necessity to study many modern foodwebs, and in more detail, been appreciated. For instance, sympatric browsing and grazing herbivores can be readily distinguished by their Sr/Ca and Ba/Ca ratios as can be carnivores and insectivores (Sillen, 1988; Sponheimer et al., 2005a; Sponheimer and Lee-Thorp, 2006a), yet the mechanisms that lead to such differences are at present poorly understood. The key lies in plant variability as plants, and plant parts (ie. underground, stem, fruit, leaves) differ considerably in their strontium distributions due to capillary action in their vascular systems (Runia, 1987). However, strontium and barium distributions in plants are still poorly studied. Probably for this reason, coefficients of variation (CV) for Sr/Ca for a single mammalian species in a single location are typically 30–40% (Sillen, 1988; Price et al., 1992; Sponheimer et al., 2005a). Hence, the natu-



**Fig. 8.** Trace element data for the South African hominins from two studies. (a) shows Sr/Ca data for *Paranthropus*, *Homo*, and a suite of fauna from Swartkrans based on bone analysis, shown as means (Sr/Ca × 1,000) and standard deviations (data from Sillen, 1992). (b) shows enamel data for *A. africanus* and *Paranthropus* and associated fauna from Makapansgat, Sterkfontein, and Swartkrans shown as means and standard deviations (data from Sponheimer et al., 2005b; Sponheimer and Lee-Thorp, 2006a). The data from the three sites were combined because of the similarity in geology and Sr/Ca ratios for modern fauna from the Sterkfontein and Makapans Valleys.

ral variation in mammalian elemental compositions is such that large numbers of samples are required to adequately characterize dietary ecology. These problems are compounded by non-linear relationships between dietary and tissue Sr/Ca (Burton and Wright, 1995).

**Early hominin diets.** The first significant attempt to investigate the diets of Plio–Pleistocene hominins was made by Sillen (1992). He found that the bones of *Paranthropus* at Swartkrans had similar Sr/Ca to carnivores and lower Sr/Ca than primarily herbivorous taxa like *Papio* and *Procavia* (Fig. 8a.) This, in conjunction with observations from dental microwear (Grine and Kay, 1988) and stable isotopes (Lee-Thorp, 1989) led him to conclude that *Paranthropus* was unlikely to be “purely herbivorous”. Subsequently, two bone specimens of early *Homo* from Swartkrans were observed to have slightly higher Sr/Ca than *P. robustus* (Sillen et al., 1995), a result that was quite unexpected given the generally accepted belief that early *Homo* was the first hominin to include significant amounts of animal food in its diet (e.g., Aiello and Wheeler, 1995). Therefore Sillen et al. (1995) argued that early *Homo* consumed significant quantities of strontium-rich underground storage organs,



**Fig. 9.** Bivariate logarithmic plot of Ba/Ca versus Sr/Ba ( $\times 1,000$ ) for combined fauna and hominins from Makapansgat, Sterkfontein, and Swartkrans distinguishes *Australopithecus* from *Paranthropus*, although they overlapped in Sr/Ca (Fig. 8). These data suggest that *Australopithecus* may have consumed foods with an unusual combination of high [Sr] and low [Ba] (data from Sponheimer and Lee-Thorp, 2006a).

an argument that has since received support from other quarters (O'Connell et al., 1999; Conklin-Brittain et al., 2002). As intimated, however, the results from just two specimens can have no statistical significance given the inherent variability of the tool.

Concerned about diagenesis, we investigated Sr/Ca and Ba/Ca ratios in enamel from late forming teeth of modern and fossil fauna, including hominins from Makapansgat, Sterkfontein, and Swartkrans (Sponheimer et al., 2005a). Since these sites share a similar geology, the data from all three could be combined. The results show that *A. africanus* had significantly higher Sr/Ca than *Paranthropus* and both taxa have higher Sr/Ca than contemporaneous browsing herbivores and papionins (Fig. 8b). Thus, there is no reason to believe that *Paranthropus* consumed greater amounts of animal foods than contemporaneous baboons as suggested by (Sillen, 1992). In addition, even if the Sr/Ca of one or both of these australopithecus species was low, it would still provide only limited support for omnivory, given our nascent understanding of Sr/Ca throughout African foodwebs. For instance, diets rich in leaves (as observed in browsers) also lead to low Sr/Ca, and while a diet rich in leaves is unlikely for the australopithecus given their extremely low shearing crests (Kay, 1985; Ungar, 2004) and low  $\delta^{18}\text{O}$  values (see above), we cannot rule out the consumption of other low Sr/Ca foods. At present we know very little about the Sr/Ca of different kinds of African fruits, although we would expect many fruits to have low Sr/Ca as has been shown to be the case with tomatoes (Haghiiri, 1964). Consequently, our limited knowledge of Sr/Ca in plant foods and amongst African savanna mammals, makes detailed dietary interpretation of this Sr/Ca data difficult.

We have also applied multiple element analysis of tooth enamel to investigate the diet of *A. africanus* (Sponheimer and Lee-Thorp, 2006a). In combination, Ba/Ca and Sr/Ba ratios suggest that this taxon was significantly distinct compared to contemporaneous grazers, browsers, and carnivores, which were in turn different from each other (Fig. 9). The *Australopithecus* fossils are characterized by high Sr/Ba that is quite distinct from

all other fossil specimens that have been analyzed, suggesting the possibility that they consumed very different foods than all of these groups, with unusually high Sr and relatively low Ba concentrations (Fig. 9). One food that could meet this requirement is grass seeds, another is underground storage organs (roots, rhizomes, and bulbs). The evidence for this is indirect, and based partly on observations that three specimens of African mole rat (*Cryptomys hottentotus*), a species which is known to consume only underground roots and bulbs, had the highest Sr/Ba of any animal we have studied. The possibilities of both grass seed and underground storage organ consumption, both of which have been suggested as possible early hominin foods requires further consideration.

Another potential explanation for the high Sr/Ca of *Australopithecus*, and to a lesser extent *Paranthropus*, is insectivory. Our modern pilot data show that a modern insectivore (*Orycteropus afer*) has much higher Sr/Ca than carnivores, again emphasizing that not all faunivores are equivalent in Sr/Ca. Yet, these pilot data also show that insectivores have high Ba/Ca, unlike the hominins, making it less likely that the elevated hominin Sr/Ca results from insectivory. At present we have analyzed far too few insectivores to seriously address this possibility.

In summary, although there is clearly ecological patterning to be found in the trace element ratios of early hominins and associated fauna, interpretation of these data remains problematic. The difficulty stems from the lack of work on trace element distributions in modern African ecosystems. No detailed studies have been published that demonstrate the elemental distributions in African plants and animals, although some promising work has been carried out in North America (Burton et al., 1999). The reason is two-fold. In the early days of trace element studies, there was insufficient appreciation for the variation that existed in plants and animals, and therefore it was assumed that trace element ratios simply reflected trophic level. Later, as researchers became disabused of this overly simplistic notion, concerns about diagenesis greatly reduced the time and effort put into trace element studies. Thus, soon after trace element analysis was first applied to early hominins in 1992, it lapsed into virtual disuse except for a few specialized applications. Now that it has been demonstrated that trace element compositions retain much of their fidelity in enamel; studies investigating elemental distribution in modern foodwebs are urgently required.

**Neanderthal diets.** Just one trace element application to the diet of Neanderthals has been carried out based on Sr/Ca and Ba/Ca ratios of a variety of faunal bones and a single Neanderthal specimen from Saint Césaire (Balter et al., 2002). Recently, Balter and Simon (2006) compared the Sr/Ca, Ba/Ca,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the Saint Césaire individual to other fauna using partitioning models (Phillips, 2001; Phillips and Gregg, 2003) similar to that used by Bocherens et al. (2005). They concluded that this individual ate virtually no plant food and that its diet was dominated by bovids (71%) with smaller amounts of horses, rhinos, and mammoths consumed. Although this is an interesting approach, the results must be treated with caution. First, only a single Neanderthal individual was analyzed, and given the inherent natural variability of trace elements in ecosystems, very little can be gleaned about the diets of Neanderthals in general. Secondly, the study used bone rather than

enamel and thus problems due to diagenesis cannot be discounted. We also know little about geological variability in the terrain that might have been used by this individual, and geological differences could render the entire faunal comparison and reconstruction invalid. It must be said that application of resource partitioning models in paleo-ecosystems is a risky undertaking. This is because we cannot know the isotopic and more particularly the trace element compositions of all potential dietary items, and this is a requirement of the model which is statistically based. This is a very significant and inherent limitation given that both plants (and plant parts) and mammals vary widely in these compositions. Application of trace elements to Neanderthal diets will need a great deal more basic data to provide a framework that may eventually inform the broader debate.

### COMBINING DIETARY TOOLS

In the preceding sections we provided an overview of what each of the various dietary tools can and cannot tell us about hominin diets and gave some pointers to their relative strengths and weaknesses. For instance, although the nature of the information obtained from morphology/allometry and microwear sources primarily concerns the properties of foods, there are strong differences in the nature of the observations obtained. Dental morphology and allometry essentially provides the broader phylogenetic/historical framework for the properties of foods a species is capable of eating, while microwear provides more direct information about the effects of foods actually ingested by an individual. Information at the level of the individual is important since it enables intragroup comparisons to be made. Amongst the biochemical tools, isotope analysis provides quantitative information at the individual level, facilitating intragroup and intergroup statistical comparisons. This is not the case for trace element methods, however, because very high natural variability restricts available information to general group-specific levels, and moreover, the foodweb pathways are still very poorly understood.

How can we best summarize and combine all this evidence? Or, what are the solid outcomes, where do these approaches reinforce each other and where are they in disagreement? In the case of Neanderthals the biochemical data can be compared mostly with archeological evidence and the single microwear study published so far. The  $\delta^{15}\text{N}$  data suggest high trophic level diets for European Neanderthals in the last Glacial. Hence they have been portrayed as effective top level predators with diets consisting primarily of meat (Richards et al., 2000; Bocherens et al., 2005). The  $\delta^{15}\text{N}$  evidence is consistent with widespread archeological evidence that suggests that Neanderthals were efficient hunters, since large quantities of animal flesh are extremely unlikely to have been obtained by scavenging. As Richards et al. (2000) and Bocherens et al. (2005) have argued, this pattern places Neanderthals and their capabilities in a different light, contradicting suggestions by some (e.g., Binford, 1981) that they lacked the planning resources required for efficient hunting of large game as observed in the Upper Paleolithic. In this case, the isotope evidence has in effect provided a more radical solution than the archeology in suggesting extreme meat-rich diets. Some practitioners have further exploited the biochemical data, using multi source mixing models to argue for heavy reliance of the Saint-Cèsaire I individual on woolly rhi-

noceros and mammoth based on its  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Bocherens et al., 2005), while Balter and Simon (2006) added trace element data in a similar exercise to argue rather for 60% reliance on bovids. However, while the conclusions may be seductive, use of such resource partitioning models requires detailed knowledge of the isotopic and/or trace element composition of the entire paleo-ecosystem that we simply do not have. This is a particular concern for trace element composition given inherently high variability and susceptibility of bone to diagenesis. Leaving the trace element data aside, the rather more robust  $\delta^{15}\text{N}$  data showing consistently high trophic diets for Neanderthals would appear to be contradicted by the buccal microwear study showing striation patterns and high variability more consistent with processing of tough, abrasive plant foods and enhancement of abrasion damage in colder periods (Perez-Perez et al., 2003). However, we also need to consider the inherent limitations of each of these approaches; for  $\delta^{15}\text{N}$  the constraint lies in the bias towards high protein foods while other explanations may exist for buccal surface microwear data.

The range of paleodietary methods applied to the South African hominins provides a good case study for comparisons, and allows elimination of at least some possibilities. Some firm results have emerged. For one, the  $\delta^{13}\text{C}$  data clearly show that overall both australopith taxa and early *Homo* consumed significant proportions of  $\text{C}_4$  or  $\text{C}_4$ -derived foods. These results can only be accounted for by consumption of  $\text{C}_4$  grass,  $\text{C}_4$  sedges, or animals which ate these plants, but we cannot tell what these possibilities are from these data alone. The low  $\delta^{18}\text{O}$  is consistent with consumptions of rhizomes or other roots, as well as animal foods. The microwear data discounts gelada-like graminivory, since the australopiths' pitted molars (Grine, 1986; Grine and Kay, 1988) are unlike those of modern geladas whose molar microwear is dominated by scratches (Teaford, 1993). On the other hand, two recent molar microwear studies of savanna *Papio* baboon populations noted a higher frequency of pitting than was found in *Theropithecus* (Daegling and Grine, 1999). These baboons consume moderate amounts of savanna grasses on a seasonal basis. The trace element data from australopith tooth enamel showed that *Australopithecus*, and to a lesser extent *Paranthropus*, had higher Sr/Ca ratios than contemporaneous carnivores, browsers, and papionins. The unusual combination of high Sr/Ca and low Ba/Ca in *Australopithecus* has only been found in modern fauna that heavily utilize the underground portions of grasses, such as warthogs (*Phacochoerus africanus*) and African mole rats (*Cryptomys hottentotus*) (Sponheimer et al., 2005b). These elemental data are still preliminary, and certainly cannot be used to state firmly that early hominins consumed grass rhizomes. Nevertheless, they are entirely consistent with the possibility and suggest avenues for future research.

Comparing the results from the various techniques may also give us the opportunity to question some of the assumptions on which we base interpretations of the results. For instance, it has been suggested that hominid dental anatomy was not well suited for the processing of animal foods (Lucas and Peters, 2000; Teaford et al., 2002; Ungar, 2004), while the chemical evidence points towards some consumption of animal foods. It has perhaps not been appreciated that these anatomical observations pertain only to a limited class of animal foods (ie. flesh or meat-eating), while a great many animal foods require little if any oral processing. Termites,

grasshoppers, ants, grubs, eggs, and a variety of other insects may be eaten whole. Soft tissues can also be consumed without oral processing if they can be reduced to a suitable size through extra-oral means. Moreover, in some cases apparent disjunctions between dental morphology and actual trophic behavior can result from the dentition being adapted for other, more mechanically challenging foods in an animal's diet. For example, capuchin monkeys (*Cebus apella*) have large, bunodont dentition with thick enamel adapted for consuming fruits and hard nuts. Nonetheless, close to 25% of capuchin diets can come from animal foods (Rosenberger and Kinzey, 1976; Fleagle, 1999). Similarly, Grine et al. (2006) showed that *A. afarensis* microwear closely resembled that of gorillas while their dental and enamel morphology suggested other affinities. These observations are consistent with Ungar's (2004) argument that among hominoids, differences in dental morphology primarily reflect their multifarious fallback foods, rather than their preferred foods during times of plenty.

As for the australopiths, stable isotopes suggest that they broadened the ancestral ape resource base to include  $C_4$  foods which, coupled with bipedalism, allowed them to pioneer increasingly open and seasonal environments. Yet, there are equifinality problems that are common in stable isotope and trace element studies. That is, many different diets can lead to the same stable isotope (or trace element) composition (Peters and Vogel, 2005). Although some progress has been made using further indicators, including  $\delta^{18}O$  and trace elements, there is little reason to believe that this problem can be circumvented entirely by relying on chemical means. In the end, stable isotopes are one tool among many, all of which provide a slightly different window into the diets of our ancestors. Stable isotopes will prove most informative when pursued as part of a larger, integrated paleodietary investigation.

All of these tools also require a great deal of active development to improve our understanding of how they work in ecosystems today. For instance, we still have much to learn about of the stable isotope compositions of modern plants and mammals, and how physiology affects diet-tissue spacing. We must also continue to test comfortable assumptions. As a good example, earlier notions of a simple stepwise trophic system from trace elements that distinguishes, herbivores, omnivores, and carnivores has been gradually refined after a series of modern ecosystem studies in different environments (Sillen, 1988; Burton et al., 1999; Sponheimer and Lee-Thorp, Kruger National Park Project, unpubl. data). Rather than a simple trophic level indicator, Sr/Ca and Ba/Ca ratios may ultimately provide just as much information about plant foods. Hopefully, such actualistic and experimental work will serve to further refine the entire suite of paleodietary tools.

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