

## Icarus, Isotopes, and Australopith Diets

MATT SPONHEIMER  
 JULIA LEE-THORP  
 DARRYL DE RUITER

Early hominin diets can be studied in many ways, such as dental allometry/morphology, dental microwear, and archaeology (e.g., Robinson, 1954; Isaac, 1971; Grine, 1981). Although these and other techniques are commonly used to reconstruct “diet,” we rarely question the degree to which they are actually capable of doing so. For instance, in the strictest sense, dental morphology cannot tell us about the totality of an organism’s diet, but it can tell us about the foods that proved challenging to that organism’s ancestors, whether they were consumed daily, seasonally, or only during short periods of extreme privation. Thus, while there certainly is an important relationship between dental morphology and diet, it is far less direct than researchers often assume. Dental microwear, in turn, does reveal something of what an individual ingested; yet, it probably tells us mostly about the mechanical properties of these foods and the exogenous grit with which they are associated. A main point of this discussion is not to suggest that these tools and others are not useful because they patently are useful and important, but rather that we often talk about reconstructing “diet” when we are in fact illuminating only facets of the complicated interactions between an organism and its environment that broadly constitute diet.

In this chapter, we will discuss a recently developed technique called *stable carbon isotope analysis* that has allowed us to illumine another facet of our ancestors’ diversity of hominins, including anatomically modern humans (Richards et al., 2001), Neanderthals (Fizet et al., 1995; Richards et al., 2000; Bocherens, Billou, and Mariotti, 2001), and australopiths (Lee-Thorp, van der Merwe, and Brain, 1994; Sponheimer and Lee-Thorp, 1999c; van der Merwe et al., 2003; Sponheimer et al., 2005). However, these advances have also served to highlight just how much remains unknown about early hominin diets in general, as well as the inherent limitations of sta-

ble isotope analysis. Like all paleodietary techniques, it does some things very well and other things not so well. We hope to spell these things out in the following pages. Due to space constraints, our particular focus will be on stable carbon isotopes and australopith diets, and just what they allow us to say without flying too high.

### The Known

#### Methodological Background

The stable carbon isotope studies of australopiths are founded on our knowledge of photosynthesis in plants, in particular the fixation of atmospheric CO<sub>2</sub> (see Ehleringer and Monson, 1993, for a review of photosynthetic pathways). In tropical savannas, trees, bushes, shrubs, and forbs use the C<sub>3</sub> photosynthetic pathway, while tropical grasses and some sedges use the C<sub>4</sub> pathway. Another pathway known as crassulacean acid metabolism (CAM) is found primarily in succulent plants such as cacti and euphorbias. However, because CAM plants make up a small part of most ecosystems, we will ignore them at present, although we will return to them a bit later. Because of both anatomical and biochemical differences, C<sub>3</sub> plants discriminate more heavily against <sup>13</sup>C during photosynthesis than do C<sub>4</sub> plants. As a result, C<sub>3</sub> plants have highly depleted <sup>13</sup>C/<sup>12</sup>C ratios, which are expressed as  $\delta$  values in parts per thousand (‰) relative to the Pee Dee Belemnite (PDB) standard (a Cretaceous cephalopod, *Belemnella americana*, which is highly enriched in <sup>13</sup>C, resulting in most terrestrial plants and animals having negative carbon isotope ratios). C<sub>4</sub> plants, on the other hand, are much less depleted in <sup>13</sup>C (Smith and Epstein, 1971; Vogel, Fuls, and Ellis, 1978). This contrast can be seen in figure 8.1, which shows the  $\delta^{13}\text{C}$  values of C<sub>3</sub> (trees and forbs) and C<sub>4</sub> plants (grasses) in Kruger National

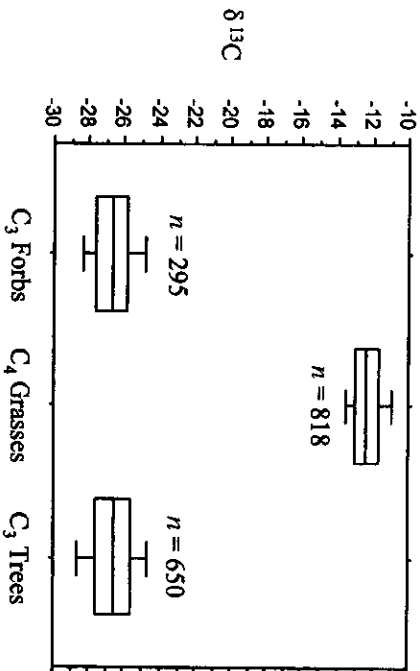


Figure 8.1  $\delta^{13}\text{C}$  of trees, forbs, and grasses in Kruger National Park, South Africa. The boxes represents the twenty-fifth to seventy-fifth percentiles (with the medians as horizontal lines) and the whiskers show the tenth to ninetieth percentiles. Note that the C<sub>3</sub> plants are highly distinct from the C<sub>4</sub> plants, with no overlap in their carbon isotope compositions.

Park, South Africa. Although there is some variability within the C<sub>3</sub> and C<sub>4</sub> groups, it tends to be fairly small within any given savanna ecosystem (Codron et al., 2005); however, δ<sup>13</sup>C of C<sub>3</sub> vegetation, in particular, can change significantly between semi-open environments (relatively enriched δ<sup>13</sup>C), and damp, closed canopy forests (relatively depleted δ<sup>13</sup>C; Vogel, 1978b; Ehleringer and Cooper, 1988; van der Merwe and Medina, 1991). Thus, plant (and animal) stable isotope values can serve as environmental indicators.

We also know that the stable carbon isotopes in plants are passed down into the tissues of animals that eat them. Thus, the tissues of animals that eat C<sub>3</sub> plants, such as giraffes, have very different δ<sup>13</sup>C than those that eat C<sub>4</sub> grasses, such as zebra (e.g., Ambrose and DeNiro, 1986; Lee-Thorp, Sealy, and van der Merwe, 1989). However, the relationship between dietary and tissue stable isotope compositions varies between tissues. For instance, muscle and hair tend to be enriched by about 1–3‰ compared with diet, while fat is depleted by a few parts per thousand compared with diet (Vogel, 1978a; Tieszen and Fagre, 1993; Sponheimer, Lee-Thorp, et al., 2003). Yet, from a paleontological perspective, we are only concerned with the hard tissues that constitute the vast majority of the fossil record. The carbon isotopes in bone and enamel mineral readily provide dietary information in modern animals, but only enamel mineral has proved reliable with fossils (e.g., Lee-Thorp and van der Merwe, 1987; Cerling, Harris, and Leakey, 1999; Sponheimer, 1999). Bone is highly organic and poorly crystalline, which leaves it very susceptible to diagenetic processes, while enamel has very little organic content and is highly crystalline, making it essentially “prefossilized” and much less susceptible to postmortem alteration (see LeGeros, 1991). For this reason, enamel is preferentially used for paleontological paleodietary studies and is the only material we will discuss. Studies of large mammals in the field and in semicontrolled settings have shown that enamel mineral is enriched by about 13‰ compared with dietary δ<sup>13</sup>C (Lee-Thorp, Sealy, and van der Merwe, 1989; Cerling and Harris, 1999; Balasse, 2002). Thus, a browser eating a typical C<sub>3</sub> diet with a δ<sup>13</sup>C value of –27‰, will have tooth enamel δ<sup>13</sup>C of about –14‰. We will discuss this relationship between dietary and enamel δ<sup>13</sup>C in the “Unknown” section below.

**Australopith Diets**

Several studies of australopith diet using stable carbon isotopes (Lee-Thorp, van der Merwe, and Brain, 1994; Sponheimer and Lee-Thorp, 1999c; van der Merwe et al., 2003; Sponheimer et al., 2005) have been conducted. These studies were explicitly designed to test hypotheses about australopith diets that had been derived using other techniques; for instance, *Australopithecus* was a consumer of fleshy fruits and leaves (Grine, 1986; Grine and Kay, 1988). Thirty-seven australopith specimens from Swartkrans, Kromdraai, Sterkfontein, and Makapansgat have now been analyzed, the data for which are summarized in figure 8.2. Analysis of variance and post hoc tests of the combined datasets demonstrate that the fossil C<sub>3</sub> consumers (e.g., giraffes) and fossil C<sub>4</sub> consumers (e.g., zebra) have very different δ<sup>13</sup>C (Scheffé, *P* < 0.0001), just as is the case today. This shows that diagenesis does not obscure the dietary carbon isotope signal. The data also show that both *Australopithecus africanus* and *Paranthropus robustus* are highly distinct from the C<sub>3</sub> browsers and

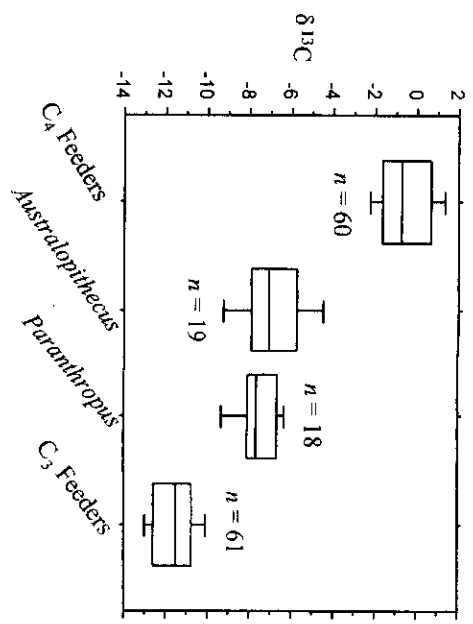


Figure 8.2 δ<sup>13</sup>C for *Australopithecus africanus* and *Paranthropus robustus* specimens, as well as C<sub>3</sub> plant consumers (browsing/fungivorous bovids and giraffids) and C<sub>4</sub>-plant consumers (grazing bovids and equids). The boxes represent the twenty-fifth to seventy-fifth percentiles (with the medians as horizontal lines) and the whiskers show the tenth to ninetieth percentiles. Given the size of this data set, there can be no doubt that australopith δ<sup>13</sup>C is highly distinct from that of associated browser/fungivores.

C<sub>4</sub> grazers with which they are associated (Scheffé, *P* < 0.0001), although they are not different from each other. This indicates that both australopiths consumed foods enriched in <sup>13</sup>C, such as C<sub>4</sub> grasses, C<sub>4</sub> sedges, or animals that ate these foods, which is quite surprising because prior studies suggested that *Australopithecus* ate fleshy fruits and leaves and that *Paranthropus* consumed small, harder foods such as nuts (e.g., Grine, 1986; Grine and Kay, 1988). The isotope results are certainly consistent with the consumption of these foods, but they also suggest that australopith diets were rather more complex and probably included significant quantities of foods that few considered to be serious possibilities (but see Jolly, 1970; Dunbar, 1983). Still, it is important to acknowledge that the australopith δ<sup>13</sup>C is highly variable, far more so than most modern and fossil taxa in South Africa (e.g., Lee-Thorp, van der Merwe, and Brain, 1994; Sponheimer, Robinson, et al., 2003; van der Merwe et al., 2003). Two or three of the thirty-seven australopiths analyzed had nearly pure C<sub>3</sub> diets, while several were extremely enriched in <sup>13</sup>C, with δ<sup>13</sup>C values within the range of the grass-eating baboon *Theropithecus oswaldi* (Lee-Thorp, van der Merwe, and Brain, 1989; Sponheimer et al., 2005).

We also know that modern chimpanzees (*Pan troglodytes*) do not typically eat detectable quantities of C<sub>4</sub> foods. This is hardly surprising for chimps in heavily forested environments where few if any C<sub>4</sub> resources are available, but it also holds true for those in semiarid woodland environments where C<sub>4</sub> foods are extremely abundant (Schoeninger, Moore, and Septl, 1999; Carter, 2001). This is not to say that we will never find a chimpanzee with a significant percentage of C<sub>4</sub> foods in its diet, but only that while this is the norm for australopiths, it would be the exception for

chimpanzees. Moreover, because many australopithecids probably inhabited environments similar to those of today's woodland chimpanzees (McGrew, Baldwin, and Tutin, 1981; Reed, 1997), this strongly suggests that different dietary adaptations, rather than environmental differences, are responsible for the disparity in their consumption of  $^{13}\text{C}$ -enriched foods. In other words, it appears likely that, even in identical woodland savanna habitats, chimpanzees would continue to consume their favored forest foods to the degree that was possible, while australopithecids would extensively supplement these with  $\text{C}_4$  resources. Although this is a reasonable hypothesis, given the available data, it represents a step away from what we know into the rather murkier territory of the unknown.

Nevertheless, australopithecids are not the only primates for which we have direct evidence of significant  $\text{C}_4$  consumption. A recent study of baboon (*Papio ursinus*) feces showed that populations in marginal environments may eat up to 50%  $^{13}\text{C}$ -enriched foods such as grasses and CAM plants, while those in more hospitable woodland environments eat only about 10%  $\text{C}_4$  vegetation (Codron, 2003). Furthermore, some of the *Papio* and *Parapapio* specimens from Swaktrams and Sterkfontein show significant  $\text{C}_4$  consumption. *Theropithecus*, of course, has been shown to be heavily dependent on  $\text{C}_4$  vegetation (Lee-Thorp, van der Merwe, and Brain, 1989), as are some specimens of the colobine monkey *Cercopithecoides williamsi* (Luyt, 2001; Codron, 2003). Thus, despite the great difference between australopithecids and contemporary ungulates, they do not stand alone from a primatological perspective—only apart from extant apes. This is a crucial point, as it is commonly postulated that a wide suite of behavioral and dietary adaptations were shared by chimpanzees and australopithecids (e.g., Wrangham, 1987; Stanford, 1999). While this "chimpanzee paradigm" is likely true to some extent, given the remarkable genetic similarity between *Pan* and extant hominins (e.g., Goodman et al., 1998), the carbon isotope data suggest that other primates, such as the papionins, which often consume significant quantities of  $\text{C}_4$  foods and, like australopithecids, are highly isotopically heterogeneous (Codron, 2003), might make better dietary analogs. This is not to say that papionin diets are, or were, like those of australopithecids but only that both taxa exhibit a dietary flexibility and willingness to use  $\text{C}_4$  resources not paralleled in chimpanzees. After all, australopithecid craniodental and locomotor adaptations as well as physical environments and biotic communities were, in aggregate, highly distinct from those of all living taxa (e.g., Grine, 1981; Stern and Susman, 1983; Reed, 1997). Thus, australopithecid diets may have been quite dissimilar in character from those of all living primates, although there is reason to believe there was considerable dietary overlap with extant hominoids (e.g., Grine, 1986; Grine and Kay, 1988; Ungar, 2004).

## The Unknown

### Methodological Background

There is still much that we do not know about stable isotope distributions in many modern ecosystems, and this is especially the case for modern primates, on which there have only been a handful of published stable isotope studies (Schoeninger, Iwaniec, and Glander, 1997; Schoeninger, Iwaniec, and Nash, 1998; Schoeninger, Moore, and Sept, 1999; Cerling, Hart, and Hart, 2004). In addition, we cannot

meaningfully distinguish between diets as different as frugivory, folivory, and carnivory in forest ecosystems, because all are ultimately based on  $\text{C}_3$  plants. Some data, however, suggest we might be able to distinguish between these diets, at least in some cases. Fruits, for instance, tend to be slightly enriched in  $^{13}\text{C}$  (~1.5‰) compared with leaves, which might allow us to distinguish between frugivory and folivory (Chodron et al., 2005). Indeed, Carter (2001) found that frugivorous  $\text{C}_3$  consumers (2004) found no difference in the  $\delta^{13}\text{C}$  of folivores and frugivores. Both of these studies were quite small, however, and more data are clearly needed. Similarly, animals that feed high in the canopy would be expected to be enriched compared with those that feed nearer to the ground, as upper canopy foods are relatively enriched in  $^{13}\text{C}$ , but there are far too few data to confirm this (see Schoeninger, Iwaniec, and Glander, 1997; Schoeninger, Iwaniec, and Nash, 1998).

We also need to know more about the relationship between dietary and enamel  $\delta^{13}\text{C}$ . As mentioned earlier, large mammal enamel apatite is enriched in  $^{13}\text{C}$  by about 13‰ compared to diet. Controlled-feeding studies of rodents, however, show their bone mineral to be enriched by only 10‰ (Ambrose and Norr, 1993; Teszen and Fagre, 1993). Strangely, we can only speculate as to why this is the case. It may be because the rodent studies used bone mineral rather than enamel or because of some difference in rodent digestive physiology, but the truth is that we simply do not know. Although this is not a problem for the hominin isotope studies (as hominins are most decidedly not rodents), it does underscore that there is much yet to be learned. Moreover, there is even minor disagreement about the proper diet-enamel fractionation for larger mammals. Lee-Thorp, Sealy, and van der Merwe (1989) conducted a field study that suggested that enamel was enriched by about 12‰ or possibly a bit more. And while a recent controlled-feeding experiment with pigs also argued for an enrichment of 12.5‰ (Young, 2002), two semicontrolled studies suggested an enrichment between 13.4‰ and 14.1‰ (Cerling and Harris, 1999; Balasse, 2002). Although the difference between 12‰ and 14‰ is fairly small, it is potentially important, especially if it turns out there are systematic differences between taxa with disparate digestive physiologies. One possibility, for instance, is that ruminants that produce and expel great amounts of highly  $^{13}\text{C}$ -depleted methane would end up with blood bicarbonate and enamel slightly more enriched in  $^{13}\text{C}$  than animals that produce less methane, such as primates (Cerling and Harris, 1999; Hedges and van Klinken, 2000). If this is the case, then it might mean that most modern primates and early hominins have a diet-enamel fractionation of about 12‰, but that the ruminants have a fractionation of 14‰. This would mean that we cannot directly compare the  $\delta^{13}\text{C}$  of ruminants and hominins, but would rather have to adjust the values of the hominins by about 2‰ to make them comparable. This would then mean that we have underestimated the amount of  $^{13}\text{C}$ -enriched foods that early hominins consumed, and that 50% would be closer to correct than the 35% to 40% we currently accept (Sponheimer et al., 2005). Indeed, there is some reason to believe that this is the case, as a recent field study suggested that fractionation in primates is slightly more than 1‰ less than that for ungulates (Cerling, Hart, and Hart, 2004). Clearly, more research in this area is required. However, there is little doubt that much of the unknown in this area can be revealed with appropriate field and experimental studies.

Since we are on the topic of the unknown, it might be worth addressing a few tangential, yet methodologically related, issues: what might we derive from oxygen and nitrogen isotopes in australopitids? We routinely produce oxygen isotope ( $\delta^{18}\text{O}$ ) data during analysis for carbon isotopes, as the isotope abundances are derived from  $\text{CO}_2$  gas. And while students of human evolution are no doubt familiar with the use of oxygen isotopes for paleoclimatic reconstruction (especially in foraminifera, e.g., Prentice and Denton, 1988), few realize that mammalian oxygen isotope compositions may also tell us something about an animal's diet and thermophysiological adaptations. For example, mammals that get most of their water through food (like many browsing bovids) tend to be enriched in  $^{18}\text{O}$  because evapotranspiration leaves leaf water relatively enriched in  $^{18}\text{O}$  compared with meteoric water, which is the primary water source for regular drinkers (Kohn, Schoeninger, and Valley, 1996; Sponheimer and Lee-Thorp, 1999b). In contrast, animals that eat roots and meat tend to be depleted in  $^{18}\text{O}$  (Sponheimer and Lee-Thorp, 1999b; Sponheimer and Lee-Thorp, 2001). Furthermore, there is some theoretical and empirical basis for believing that folivore  $\delta^{18}\text{O}$  is higher than that of frugivores, once again due to the evaporative enrichment that occurs in leaves (Carter, 2001; Sponheimer and Lee-Thorp, 2001; Cerling, Hart, and Hart, 2004). Alas, comprehensive intertaxonomic studies of mammalian oxygen isotope compositions within modern ecosystems have not been carried out (but see Kohn et al., 1996; Sponheimer and Lee-Thorp, 2001; Smith, Sharp, and Brown, 2002 for limited attempts); most data have been collected so as to eschew this ecologically induced variability because it makes paleoclimatic reconstruction difficult, if not impossible. Thus, even though we have oxygen isotope data for australopitids and other fossil taxa, we are not yet in a position to interpret them meaningfully. It is worth noting that *Australopithecus* from Sterkfontein is significantly depleted in  $^{18}\text{O}$  compared with *Paranthropus* from Swartkrans (Sponheimer et al., 2005; fig. 8.3). This might indicate that the prevailing

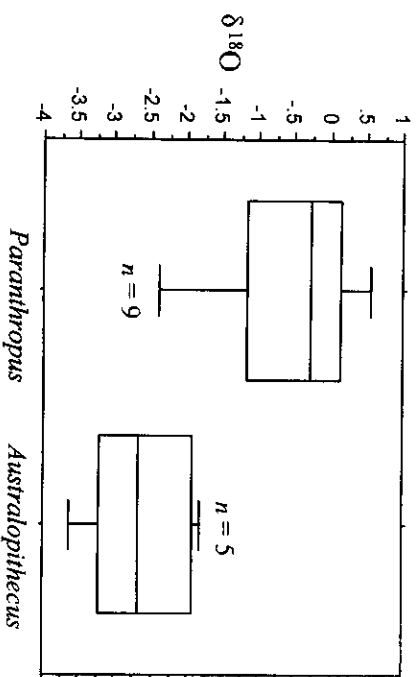


Figure 8.3  $\delta^{18}\text{O}$  of 2.5 Ma *Australopithecus africanus* and 1.8 Ma *Paranthropus robustus*. The boxes represent the twenty-fifth to seventy-fifth percentiles (with the medians as horizontal lines) and the whiskers show the tenth to ninetieth percentiles. The relatively depleted  $\delta^{18}\text{O}$  of *Australopithecus* at 2.5 Ma compared to *Paranthropus* at 1.8 Ma may indicate either increasing aridity in the Sterkfontein Valley over time ecological differences in these taxa.

environmental conditions for *Paranthropus* were more arid than those for *Australopithecus* or it might also reveal a fundamental ecological or thermophysiological difference. At present, we cannot meaningfully distinguish between these possibilities.

Now, let us briefly turn to nitrogen isotopes. Nitrogen isotope compositions therefore be used as trophic level indicators (e.g., Mungawa and Wada, 1984; Schoeninger and DeNiro, 1984; Amthor and DeNiro, 1986). Indeed, nitrogen isotope analysis of Neanderthals has been used to good effect, showing that they are enriched in  $^{15}\text{N}$ , which is most consistent with a high degree of carnivory (Fizet et al., 1995; Richards et al., 2000; Bocherens, Billon, and Mariotti, 2001). We have been unable to analyze nitrogen isotopes in australopitids, however, because they reside in organic material (e.g., collagen) that is rarely preserved for tens of thousands, much less millions of years. There is, nevertheless, tantalizing evidence that autochthonous organic material (osteocalcin and enamelin) can survive relatively intact for many millions of years (Glimcher, 1990; Collins et al., 2000). Thus, it is possible that recent advances in mass spectrometry that allow analysis of extremely small samples and individual compounds may make it possible to obtain biological nitrogen isotope data from australopitids in the next few years—but then again, maybe not.

#### Australopith Diets

We now return to stable isotopes and australopith diets. We possess overwhelming evidence that australopitids consumed foods that are enriched in  $^{13}\text{C}$  such as  $\text{C}_4$  grasses,  $\text{C}_4$  sedges, or animals that ate these plants, but the stable isotope studies have created a new unknown, namely, which of these foods were actually utilized? Answering this question is important, as the use of these different resources might have a variety of physiological, social, and behavioral implications. For instance, if australopitids had a grass-based diet similar to the modern gelada baboon (*Theropithecus gelada*), this would almost certainly indicate that their diets were less nutrient-dense than those of modern apes, possibly placing important limitations on burgeoning hominin brains and sociality (Aiello and Wheeler, 1995; Milton, 1999). The converse, that australopitids ate diets rich in animal foods, would indicate a leap in dietary quality over modern apes, which could have been a crucial step toward hominin encephalization, the development of stone tool industries, and increased social complexity (Milton, 1999). Similarly, it has been suggested that consuming underground storage organs of plants like  $\text{C}_4$  sedges could represent an increase in dietary quality over that of extant great apes because, when they are edible, they are lower in dietary fiber than ape fallback foods (Conklin-Brittain, Wrangham, and Smith, 2002).

Yet, we are still uncertain as to which  $^{13}\text{C}$ -enriched foods were consumed by australopitids. Part of the difficulty is that we do not know enough about the potential variety and availability of  $^{13}\text{C}$ -enriched foods, although we have been working to rectify this gap (see Sponheimer et al., 2005). Recent work has shown, for instance, that in some savanna woodland environments, sedges are a less likely  $\text{C}_4$  resource than was previously supposed. While it is certainly true that the underground parts of some sedges (e.g., *Cyperus papyrus*, *Cyperus esculentus*) would make an attractive

food for tool-wielding hominins, at least seasonally, it was found that there are few edible  $C_4$  sedges in South African woodland environments (Peters and Vogel, 2005; Sponheimer et al., 2005), although they are abundant in perennial wetlands like the Okavango Delta (Elbery et al., 1995). Indeed, only 28% of the sedges in Kruger National Park use  $C_4$  photosynthesis (Sponheimer et al., 2005). Thus, while sedges could certainly have contributed, it is unlikely that their consumption alone could account for the observed  $^{13}C$ -enrichment of australopiths. However, other early hominin habitats, such as the wetlands of the Eastern Lacustrine Plain at Olduvai Gorge (Hay, 1976; Decampo et al., 2002), might have been better sources of edible  $C_4$  sedges. The extremely enriched  $\delta^{13}C$  of *Paranthropus boisei* might indicate that  $C_4$  sedges were locally abundant and heavily used (van der Merwe, Cushing, and Blumenshine, 1999). Puech and colleagues (1986) have also suggested that the dental microwear of early East African hominins is consistent with the consumption of such foods.

Animals are another potential  $^{13}C$ -enriched food. Of course, animal foods can be many different things, including large and small vertebrates, invertebrates, birds' eggs, and even honey. These foods can also be acquired in a variety of ways, including active hunting of large game, passive scavenging, and gathering of insects and eggs. Although chimpanzees are known to hunt a variety of small vertebrates such as red colobus monkeys (*Procolobus badius*) and blue duiker (*Cephalophus monticola*), these are pure  $C_3$  consumers (Teleki, 1981; Goodall, 1986). Therefore, intake of such foods could not contribute to the  $C_4$  component of australopith diets. More likely sources of the reported  $C_4$  signal include small grass-eating taxa, such as hyraxes (*Procavia* spp.), cane rats (*Thryonomys swinderianus*), young antelope (Bovidae), and arthropods. Baboons are known to eat grass-eating grasshoppers (Acrididae) almost exclusively during temporary gluts (Hamilton, 1987). Grass-eating termites represent another intriguing possibility, particularly given recent studies suggesting that bone tools from Swartkrans were used to extract termites from mounds (Backwell and D'Errico, 2001). Stable isotope studies of termites in African savanna environments have shown that they could have contributed to the australopiths'  $^{13}C$  enrichment (Boutton, Arshad, and Tieszen, 1983; Sponheimer et al., 2005). While termites range from nearly pure  $C_3$  to pure  $C_4$  consumers, the vast majority of savanna termites, even in densely wooded riverine microhabitats, consume significant proportions of  $C_4$  foods. In fact, termites throughout Kruger National Park eat 35%  $C_4$  vegetation on average (Sponheimer et al., 2005). Thus, termite consumption by australopiths in woodland savanna and even in riverine forest would be expected to impart some  $C_4$  carbon to consumers. Nevertheless, the fact that so few termites have a pure  $C_4$  signal makes it unlikely that termite consumption alone was the source of the strong  $C_4$  signal of australopiths because it would require a diet of nearly 100% termites. Alternatively, if the hominins selectively preyed on grass-specialist harvester termites (*Trinervitermes*, *Hodotermes*) with virtually pure  $C_4$  diets, a diet of about 35% to 40% termites would be sufficient to produce the observed hominin carbon isotope ratios. This scenario, however, is highly unlikely because these  $C_4$  termites are much less common than those with mixed  $C_3/C_4$  diets in woodlands today; and while harvester termites are more abundant in open grasslands and during acute droughts (Brack

and Kruger, 2003), there is no reason to believe that australopiths frequented such open environments or that drought conditions were so preponderant. Moreover, while *Trinervitermes* builds highly visible aboveground nests (mounds), *Hodotermes* does not, making it much less conspicuous on the landscape (Carruthers, 1997; Stuart and Stuart, 2000). Thus, it is possible and even likely that termites contributed in some way to the unusual  $\delta^{13}C$  values of australopiths, but other  $C_4$  resources were almost certainly consumed in considerable quantities.

As far as the consumption of mammals goes, we know that many with  $C_4$  signatures were available for consumption by australopiths (Lee-Thorp, van der Merwe, and Brain, 1994; Sponheimer and Lee-Thorp, 1999c). However, most evidence also suggests that  $C_3$  mammals were very common, especially at Makapansgat and Sterkfontein (Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003). Thus, as with our discussion of sedges and termites, unless the hominins were eating very large quantities of these animals, or concentrating on  $C_4$  mammals alone, mammals are not a likely source of the  $^{13}C$  enrichment on their own. In short, what we now know about isotopic compositions of  $^{13}C$ -enriched foods suggests that none, save  $C_4$  grasses themselves, appear to be capable of producing a high degree of  $^{13}C$  enrichment on their own. Indeed, from an isotopic perspective, it seems far more likely that several  $C_4$  foods were consumed in tandem, but this conclusion is based on a lack of evidence for the consumption of one  $^{13}C$ -enriched food, rather than direct isotopic evidence for the consumption of a variety of resources.

We also do not know about possible seasonal differences in  $C_4$  consumption. Our traditional sampling protocols provide us with stable isotope abundances for enamel that is formed over many months and, in some cases, years (see Sponheimer et al., 2005). Consequently, the stable isotope data are generally telling us something about an individual's "average" diet. It would be a mistake, therefore, to assume that  $^{13}C$ -enriched resources were important foods for australopiths year round. Primate diets are known to change from season to season, sometimes profoundly so (e.g., Altmann and Altmann, 1970; Dunbar, 1983; Wrangham, Conklin-Brittain, and Hunt, 1998). As such, it might well be that  $C_4$  resources were largely fallback foods that made up the bulk of australopith diets during the dry season when preferred resources were no longer available or when their nutritional quality was no longer acceptable. Then again, australopiths might have consumed  $^{13}C$ -enriched resources all year, perhaps  $C_4$  grass and sedge underground storage organs (USOs) during the dry season and grass seeds during the rains. We simply do not know, which is quite unfortunate, as it is potentially a very important point for understanding the relationship between environmental/climatic change and hominin evolution. We could, in theory, sample for stable isotopes along the growth axes of teeth and, in doing so, trace the diets of individuals over time (e.g., Balasse et al., 2002; Passey and Cerling, 2002); but such sampling is far more destructive than our traditional bulk analyses and as such has not been attempted on rare hominin specimens. Nonetheless, preliminary work using a laser ablation technique to measure stable carbon isotopes along the growth axes of teeth has been promising and may allow us to obtain temporal data while producing minimal damage (Sponheimer, de Ruiter, and Lee-Thorp, 2004). Thus, this particular "unknown" is fast becoming "knowable," and should soon become "known."

On a side note, this high-resolution analysis should allow us to address other previously unassailable questions, such as "When were australopiths weaned?" as carbon and oxygen isotope values are known to change during the weaning process (Wright and Schwarcz, 1998; Witt and Ayliffe, 2001). Thus, incremental sampling along an australopith  $M_1$  is likely to provide evidence of the isotopic shift that accompanies weaning and contribute to our nascent understanding of australopith life history. Moreover, it has been suggested that the metabolic disturbance associated with weaning increased susceptibility to predation among hominins, which in turn could significantly bias fossil assemblages (White, 1978). Consequently, age of weaning data might also have significant taphonomic implications.

To make one last foray into the unknown, we would like to quickly discuss what stable carbon isotopes do not tell us at present about australopith paleoenvironments. As discussed earlier, we know that the  $\delta^{13}\text{C}$  of  $\text{C}_3$  vegetation is sensitive to a variety of environmental parameters, which makes enamel  $\delta^{13}\text{C}$  a potential source of paleoenvironmental information. However, making the jump from the  $\delta^{13}\text{C}$  of fossils to that of paleovegetation is much more complicated than many researchers, even within the stable isotope community, appreciate. There are several reasons for this, the first of which is the old *bête noire* of stable isotope paleodietary studies—diagenesis. It has been shown repeatedly that diagenesis does not obscure the primary dietary signal in enamel apatite (e.g., Lee-Thorp and van der Merwe, 1987; Lee-Thorp, van der Merwe, and Brain, 1994; Cerling, Harris, and Leakey, 1999). This does not mean, however, that enamel is altogether unaffected by diagenesis (e.g., Michel, Hildebrand, and Morin, 1995; Kohn, Schoeninger, and Barker, 1999; Sponheimer and Lee-Thorp, 1999a; Schoeninger et al., 2003). In fact, there is good reason to believe carbon isotope values are altered, albeit only slightly. This is best evidenced by the isotopic separation between  $\text{C}_4$  grazers and  $\text{C}_3$  browsers. In modern savanna ecosystems, they tend to be different by about 13‰, but this difference shrinks to ~11‰ at South African fossil sites (M. Sponheimer, unpublished data), which probably reflects some small degree of diagenesis. At South African australopith sites, grazer and browser carbon isotope values are probably pulled slightly together because the matrix in which they are interred has intermediary  $\delta^{13}\text{C}$  values. This change affects *all* fauna, and although it is slight, it is nonetheless real. While it does not affect our ability to compare taxa to each other in any significant way (as all boats are lifted by the same isotopic tide), it does make reconstructing paleovegetation  $\delta^{13}\text{C}$  more difficult.

A second problem is the aforementioned uncertainty with regard to the relationship between dietary and enamel  $\delta^{13}\text{C}$ . Take a hypothetical fossil browser like a kudu with a  $\delta^{13}\text{C}$  value of -12‰. If we assume that enamel is enriched by +12‰ over diet (Lee-Thorp, Sealy, and van der Merwe, 1989), it would translate to a paleovegetation value of about -24‰. If we subtract a further 1.5‰ to adjust for the fossil fuel effect (combustion of  $^{13}\text{C}$ -depleted fossil fuels has lowered the  $\delta^{13}\text{C}$  of atmospheric  $\text{CO}_2$  in the past century; see Friedli et al., 1986), we then have a value of -25.5‰, which is typical of dry areas with less than 500 mm of rainfall a year. What if, however, the kudu became enriched by +1.5‰ because of diagenesis, and what if the proper diet to enamel relationship is 14‰? After correcting for the fossil fuel effect, this would translate to a paleovegetation value of -29‰ and would be more indicative of a well-watered closed woodland or forest—quite a different picture in-

deed! A final difficulty is that stable isotope studies are subject to the same taphonomic biases that bedevil all faunal environmental reconstructions and which can lead to assemblages not accurately reflecting the living community at any one moment in time (e.g., Brain, 1981; Lyman, 1994). Nonetheless, our point here is not to say that any attempt to reconstruct paleoenvironments from enamel  $\delta^{13}\text{C}$  is bankrupt from the start, but only that we must be cognizant of these limitations.

### The Unknownable

The boundaries between the known, the unknown, and the unknownable are often fuzzy or ephemeral. At least part of this problem is semantic: We tend to couple the words "known" and "true", yet, one can "know" something that in hindsight is untrue. People knew for eons that the sun traveled around the earth, scientists knew for decades the humans had forty-eight chromosomes (as do chimpanzees), but alas, knowing was not quite what it was cracked up to be. Indeed, people can know a great many things, including mutually incompatible notions. This does not mean, of course, that all such notions are equally true (and this is assuming that *The X-Files* is the ultimate epistemological arbiter and therefore "the truth is out there") but rather that while as scientists we are always seeking some form of external truth that is "out there," what we know at any given moment stands in an uncertain relationship with this external truth. Thus, in practice, it might well be argued that we know very little about the diets of early hominins (ironically, perhaps, both more and less than we knew fifty years ago). What we do have is a great many reasonable hypotheses for which there are greater or lesser degrees of empirical and theoretical support. There can be little doubt that some fifty years hence, many will look back at what we know today and shake their heads with wry amusement. We are probably on the right track about many things, but like all of our predecessors, we are undoubtedly incorrect in many ways—even in some areas that we feel fairly secure—perhaps our "chimpancentric" notions of early hominin ecology included?

However, this difficulty with the known and the unknown aside, it might be that the distinction between the unknown and the unknownable is even more fluid and tenuous. Imagine taking a fiery brand out of a campfire on a dark night and then twirling it with superhuman speed before you. Those looking at this spectacle from a few hundred meters away will see nothing but a ring of fire. Sure enough, the ring of fire itself would be illusory, as the entire ring would never exist at any given moment. Yet, from their perspective, the ring is all that they would, and ever could, see. The truth that they are looking on a twirling brand rather than a ring of fire would be forever unknowable to them—so long, that is, that they looked on the phenomenon with human eyes. With high-speed photography, telephoto lenses, and slow-motion playback, however, they could discern the truth. The basic point here is that the unknowable is not some land that is separated from the unknown by a massive epistemological discontinuity, but that the unknowable is often defined by the "eyes" with which you observe the phenomenon at hand. And with changes in technology and in our thinking (paradigm shifts), the "eyes" available to scientists are in constant flux. One hundred years ago, who would have imagined that we would be able to analyze carbon locked in a hominin's tooth that was derived from a fig consumed on a breezy

afternoon or that we could look on a tooth's microscopic pits and scratches to reveal the contents of an ancestor's last supper? These things would have been unthinkable a century ago, but science has given us the eyes of mass spectrometry and electron microscopy, and we surely see all the better into the distant past for them. No doubt, technology will continue to advance, and will make it possible to address many questions about the diets of early hominins that would now be relegated to the realm of science fiction.

Thus, we are hesitant to talk about the unknowable, except perhaps in the sense of what is unknowable given current technology. If we are further restrictive, however, and use "unknowable" in the sense of what we cannot know from stable isotopes alone, then the realm of the unknowable is considerable indeed. For one, it would be impossible to ever know which  $C_4$  resources australopithecids used because of insurmountable equifinality problems. In other words, there are many diets that can conceivably produce the same carbon isotope signature. Therefore, there is no one-to-one relationship between any stable isotope signature and a given diet (e.g., crabs, bovids, fruits). This point must not be overlooked, although it frequently is in practice, lest our paleodietary interpretations fly (metaphorically) beyond our data. It would be impossible, for instance, for stable carbon isotopes of tooth enamel carbonate to ever distinguish between a purely vegetarian hominin that ate 50%  $C_3$  fruits and 50%  $C_4$  grass and a highly predacious hominin that ate nothing but  $C_3$  and  $C_4$ -derived mammal flesh in roughly equal proportions. Stable isotopes will never be up to the task of reconstructing early hominin "menus" (e.g., 60% figs; 20% bovid burgers; 10% grass roots; 5% honey; 5% Coco Puffs), which is rather unfortunate, because "Eat Like an Australopithec" has the ring of an international best-seller.

Fortunately, however, stable isotope studies do not operate in a vacuum. We can always use insights gleaned from nutritional analysis, dental microwear, elemental analysis, and other areas to aid in interpreting stable isotope data. Moreover, advances in these other areas may allow us to better interpret carbon isotope data in the future. For instance, perhaps microwear will be able to conclusively rule out the consumption of  $C_4$  grass seeds and roots. If this were to happen, it would likely mean that both  $C_4$  sedges and animal foods were important resources, especially for those hominin specimens that are most enriched in  $^{13}C$ , as it would be very difficult to attain *Theropithecus*-like  $\delta^{13}C$  through the consumption of sedges or animal foods alone.

In the end, stable carbon isotope analysis has provided us with significant insights into the diets of early hominins. Ten years ago, very few paleoanthropologists would have countenanced the idea that australopithecids consumed significant quantities of grasses, sedges, or animal foods, but stable isotope studies have forced us to confront these possibilities. However, as important as these studies have been in forcing us to broaden the potential australopithecid dietary, we still need to improve our knowledge of stable isotope distributions in modern ecosystems and better our understanding of the relationship between dietary and enamel stable isotope compositions if we are to get the most out of stable carbon isotope studies. But this caveat aside, stable isotopes still have a great deal to tell us about early hominin diets. To date, the South African australopithecids are the only early hominins that have been analyzed for stable carbon isotopes to a significant extent, which leaves entire continents and vast periods of

time ripe for investigation with this technique. There can be little doubt that stable carbon isotope analysis, especially when performed as part of a larger, integrated paleodietary investigation, will reveal much about the diets of these hominins.

#### References

- Aiello, L.C., and Wheeler, P., 1995. The expensive tissue hypothesis. *Curr. Anthropol.* 36, 199-221.
- Altmann, S.A., and Altmann, J., 1970. *Baboon Ecology*. University of Chicago Press, Chicago.
- Ambrose, S.H., and DeNiro, M.J., 1986. The isotopic ecology of East African Mammals. *Oecologia* 69, 395-406.
- Ambrose, S.H., and Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert J.B., and Grube, G. (Eds.), *Pleistocene Human Bone: Archaeology at the Molecular Level*. Springer, Berlin, pp. 1-37.
- Backwell, L.R., and d'Errico, F., 2001. Evidence of termite foraging by Swartkrans early hominids. *Proc. Natl. Acad. Sci.* 98, 1358-1363.
- Balase, M., 2002. Reconstruction dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling. *Int. J. Osteoarchaeol.* 12, 155-165.
- Balase, M., Ambrose, S.H., Smith, A.B., and Price, T.D., 2002. The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. *J. Archaeol. Sci.* 29, 917-932.
- Bocherens, H., Bignon, D., and Mariotti, A., 2001. New isotopic evidence for dietary habits of Neanderthals from Belgium. *J. Hum. Evol.* 40, 497-505.
- Bouton, T.W., Arshad, M.A., and Teszen, L.L., 1983. Stable isotope analysis of termite food habits in East African grasslands. *Oecologia* 59, 1-6.
- Braack, L., and Kyger, P., 2003. Insects and savanna heterogeneity. In: du Toit, J.T., Rogers, K.H., and Biggs, H.C. (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington DC, pp. 263-275.
- Brain, C.K., 1981. *The Hunters or the Hunted?* University of Chicago Press, Chicago.
- Caruthers, V., 1997. *The Wildlife of Southern Africa*. Southern Book Publishers, Halfway House.
- Carter, M.L., 2001. Sensitivity of stable isotopes ( $^{13}C$ ,  $^{15}N$ , and  $^{18}O$ ) in bone to dietary specialization and niche separation among sympatric primates in Kibale National Park, Uganda. PhD diss., University of Chicago.
- Cerling, T.E., and Harris, J.M., 1999. Carbon isotope fractionation between diet and biogenic in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347-363.
- Cerling, T.E., Hart, J.A., and Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138, 5-12.
- Cerling, T.E., Harris, J.M., and Leakey, M.G., 1999. Browsing and grazing in elephants: The isotope record of modern and fossil proboscideans. *Oecologia* 120, 364-374.
- Codron, D.M., 2003. Dietary Ecology of Chacma Baboons (*Papio ursinus*) and Pleistocene Cercopithecoidea in Savanna Environments of South Africa. MSc thesis, University of Cape Town.
- Codron, J., Codron, D., Sponheimer, M., Lee-Thorp, J., Bond, W.J., de Ruiter, D., and Grant, R., 2005. Taxonomic, anatomical, and spatio-temporal variations in stable carbon and nitrogen isotopic composition of plants from an African savanna. *J. Archaeol. Sci.* 32, 1757-1772.
- Collins, M.J., Gernaey, A.M., Nielsen-Marsh, C.M., Vermeer, C., and Westbroek, P., 2000. Osteocalcin in fossil bones: Evidence of very slow rates of decomposition from laboratory studies. *Geology*, 28, 1139-1142.
- Conklin-Brittain, N.L., Wrangham, R.W., and Smith, C.C., 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., and

- Teaford, M.F. (Eds.), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport, pp. 61–76.
- Deocampo D.M., Blumenschine R.J., and Ashley G.M., 2002. Wetland diagenesis and traces of early hominids, Olduvai Gorge, Tanzania. *Quatern. Res.* 57, 271–281.
- Dunbar, R.L.M., 1983. Theropithecines and hominids: Contrasting solutions to the same ecological problem. *J. Hum. Evol.* 12, 647–658.
- Ehleringer, J.R., and Cooper, T.A., 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76, 562–566.
- Ehleringer, J.R., and Monson, R.K. (1993). Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24, 411–439.
- Elley W.N., Elley K., Rogers K.H., and McCarthy T.S., 1995. The role of *Cyperus papyrus* L. in channel blockage and abandonment in the northeastern Okavango Delta, Botswana. *Afr. J. Ecol.* 33, 2549.
- Fizet, M., Martotti, A., Bocherens, H., Lange-Badré, B., Vandermeersch, B., Borel, J.P., and Bellon, G., 1995. Effect of diet, physiology and climate on carbon and nitrogen isotopes of collagen in a late Pleistocene anthropic paleoecosystem (France, Charente, Marillac). *J. Archaeol. Sci.* 22, 67–79.
- Friedli, H., Lottschner, H., Oeschger, H., Siegenhauer, U., and Stauffer, B., 1986. Ice core record of the  $^{13}\text{C}/^{12}\text{C}$  ratio of atmospheric  $\text{CO}_2$  in the past two centuries. *Nature* 324, 237–238.
- Glimcher, M.J., Cohen-Solal, L., Kossiva, D., and de Ricqlès, A., 1990. Biochemical analyses of fossil enamel and dentin. *Paleobiology* 16, 219–232.
- Goodall, J., 1986. *The Chimpanzees of Gombe*. Cambridge University Press, Cambridge.
- Goodman, M., Porter, C.A., Czelusniak, J., Page, S.L., Schneider, H., Shoshani, J., Gunnell, G., and Groves, C.P., 1998. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol. Phylogener. Evol.* 9, 585–598.
- Grüne, F.E., 1981. Trophic differences between gracile and robust australopithecines. *S. Afr. J. Sci.* 77, 203–230.
- Grüne, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. *J. Hum. Evol.* 15, 783–822.
- Grüne, F.E., and Kay, R.F., 1988. Early hominid diets from quantitative image analysis of dental microwear. *Nature* 333, 765–768.
- Hamilton, W.J., 1987. Omnivorous primate diets and human overconsumption of meat. In: Harris, M., Ross, E.B. (Eds.), *Food and Evolution: Toward a Theory of Human Food Habits*. Temple University Press, Philadelphia, pp. 117–132.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge*. University of California Press, Berkeley.
- Hedges, R.E.M., and van Klinken, G.J., 2000. "Consider a Spherical Cow"—on Modeling and Diet. In: Ambrose, S., and Katzenberg, M.A. (Eds.), *Biogeochemical Approaches to Paleodietary Analysis*. Kluwer Academic/Plenum, New York, pp. 211–242.
- Isaac, G.L., 1971. The diet of early man: Aspects of archaeological evidence from lower and middle Pleistocene sites in Africa. *World Archaeol.* 2, 278–298.
- Jolly, C.J., 1970. The seed-eaters: A new model of hominid differentiation based on a baboon analogy. *Man* 5, 5–26.
- Kohn, M., Schoeninger, M.J., and Barker, W.W., 1999. Altered states: Effects of diagenesis on fossil tooth chemistry. *Geochim. Cosmochim. Acta* 63, 2737–2747.
- Kohn, M.J., Schoeninger, M.J., and Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. *Geochim. et Cosmochim. Acta* 60, 3889–3896.
- Lee-Thorp, J.A., Sealy, J.C., and van der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *J. Archaeol. Sci.* 16, 585–599.
- Lee-Thorp, J.A., and van der Merwe, N.J., 1987. Carbon isotope analysis of fossil bone apatite. *S. Afr. J. Sci.* 83, 712–715.
- Lee-Thorp, J.A., van der Merwe, N.J., and Brain, C.K., 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.* 18, 183–190.
- ICARUS, ISOTOPES, AND AUSTRALOPITHEC DIETS 147
- Lee-Thorp, J.A., van der Merwe, N.J., and Brain, C.K., 1994. Diet of *Australopithecus* robustus at Swartkrans from stable carbon isotope analysis. *J. Hum. Evol.* 27, 361–372.
- LeGeros, R.Z., 1991. *Calcium Phosphates in Oral Biology and Medicine*. Karger, Paris.
- Luyt, C.J., 2001. Revisiting palaeoenvironments from the hominid-bearing Plio-Pleistocene sites: New isotopic evidence from Sterkfontein. MSc. thesis, University of Cape Town.
- Luyt, J., and Lee-Thorp, J.A., 2003. Carbon isotope ratios of Sterkfontein fossils indicate a marked shift to open environments ca. 1.7 Ma. *S. Afr. J. Sci.* 99, 271–273.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.
- McGrew, W.C., Baldwin, P.J., and Tutin, C.E., 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *J. Hum. Evol.* 10, 227–244.
- Michel, V., Hildebrand, P., and Morin, G., 1995. Chemical and structural changes in Cervus elephas tooth enamels during fossilization (Lazaret Cave): A combined IR and XRD Rietveld analysis. *Appl. Geochem.* 10, 145–159.
- Milton, K., 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol.* 8, 11–21.
- Mnagawa, M., and Wada, E., 1984. Step-wise enrichment of  $^{15}\text{N}$  along food chains: further evidence and the relationship between  $\delta^{15}\text{N}$  and animal age. *Geochim. Cosmochim. Acta* 48, 1135–1140.
- Passley, B.H., and Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series. *Geochim. Cosmochim. Acta* 66, 3225–3234.
- Peters, C.R., and Vogel, J.C., 2005. Africa's wild  $\text{C}_4$  plant foods and possible early hominid diets. *J. Hum. Evol.* 48, 219–226.
- Penrice, M.L., and Denton, G.H., 1988. The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution. In: Grüne, F.E. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 383–403.
- Puech P.F., Cianfrani F., and Albertini H., 1986. Dental microwear features as an indicator for plant food in early hominids: A preliminary study of enamel. *Hum. Evol.* 1, 507–515.
- Reed, K., 1997. Early hominid evolution and ecological change through the African Pliocene. *J. Hum. Evol.* 32, 289–322.
- Richards, M.P., Pettit, P.B., Suter, M.C., and Trinkaus, E., 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Palaeolithic. *Proc. Natl. Acad. Sci.* 98, 6528–6532.
- Richards, M.P., Pettit, P.B., Trinkaus, E., Smith, F.H., Pannovic, M., and Karavanic, I., 2000. Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proc. Natl. Acad. Sci.* 97, 7663–7666.
- Robinson, J.T., 1954. Prehominid dentition and hominid evolution. *Evolution* 8, 324–334.
- Schoeninger, M.J., and DeNiro, M.J., 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim. Cosmochim. Acta* 48, 625–639.
- Schoeninger, M.J., Hallin, K., Reeser, H., Valley, J.W., and Fournelle, J., 2003. Isotopic alteration of mammalian tooth enamel. *Int. J. Osteoarchaeol.* 13, 11–19.
- Schoeninger, M.J., Iwaniec, U.T., and Glander, K.E., 1997. Stable isotope ratios indicate diet and habitat use in New World monkeys. *Am. J. Phys. Anthropol.* 103, 69–83.
- Schoeninger, M.J., Iwaniec, U.T., and Nash, L.T., 1998. Ecological attributes recorded in stable isotope ratios of arboreal primate hair. *Oecologia* 113, 222–230.
- Schoeninger, M.J., Moore, J., and Sept, J.M., 1999. Subsistence strategies of two savanna chimpanzee populations: the stable isotope evidence. *Am. J. Primatol.* 49, 297–314.
- Smith, B.N., and Epstein, S., 1971. Two categories of  $^{13}\text{C}/^{12}\text{C}$  ratios for higher plants. *Plant Physiol.* 47, 380–384.
- Smith, K.F., Sharp, Z.D., and Brown, J.H., 2002. Isotopic composition of carbon and oxygen in desert fauna: investigations into the effects of diet, physiology, and seasonality. *J. Arid Environ.* 52, 419–430.
- Sponheimer, M., 1999. Isotopic ecology of the Makapansgat Limeworks fauna. PhD diss., Rutgers University.

- Sponheimer, M., de Ruiter, D., and Lee-Thorp, J., 2004. Seasonality and Australopithecine Diets: New High-Resolution Carbon Isotope Data. *Am. J. Phys. Anthropol.* Suppl. no. 38, 12, 186.
- Sponheimer, M., and Lee-Thorp, J., 2003. Using bovid carbon isotope data to provide paleoenvironmental information. *S. Afr. J. Sci.* 99, 273-275.
- Sponheimer, M., and Lee-Thorp, J.A., 1999a. The alteration of enamel carbonate environments during fossilisation. *J. Archaeol. Sci.* 26, 143-150.
- Sponheimer, M., and Lee-Thorp, J.A., 1999b. The ecological significance of oxygen isotopes in enamel carbonate. *J. Archaeol. Sci.* 26, 723-728.
- Sponheimer, M., and Lee-Thorp, J.A., 1999c. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283, 368-370.
- Sponheimer, M., and Lee-Thorp, J.A., 2001. The oxygen isotope composition of mammalian enamel carbonate: A case study from Morea Estate, Mpumalanga Province, South Africa. *Oecologia* 126, 153-157.
- Sponheimer, M., Lee-Thorp, J., de Ruiter, D., Codron, D., Bauch, A.T., and Thackeray, F., 2005. Hominins, sedges, and termites: New carbon isotope data from the Sterkfontein valley and Kruger National Park. *J. Hum. Evol.* 48, 301-312.
- Sponheimer, M., Lee-Thorp, J., de Ruiter, D., Smith, J., van der Merwe, N., Reed, K., Ayliffe, L., Heidelberg, C., and Marcus, W., 2003. Diets of southern African Bovidae: stable isotope evidence. *J. Mammal.* 84, 471-479.
- Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E., Cerling, T., Dearing, D., and Ehleringer, J., 2003. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Can. J. Zool.* 81, 871-876.
- Stanford, C., 1999. *The Hunting Apes*. Princeton University Press, Princeton.
- Stem, J.T., and Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279-317.
- Stuart, C., and Stuart, T., 2000. *A Field Guide to the Tracks and Signs of Southern and East African Wildlife*. Stalk Publishers, Cape Town.
- Tejeki, G., 1981. The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania. In: Harding, R.S.O., and Tejeki, G. (Eds.), *Omnivorous Primates*. Columbia University Press, New York, pp. 303-343.
- Tieszen, L.L., and Fagre, T., 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO<sub>2</sub>, bone collagen, bioapatite, and soft tissues. In: Lambert, J.B., Grappe, G. (Eds.), *Prehistoric Human Bone: Archaeology at the Molecular Level*. Springer, Berlin, pp. 121-155.
- Ungar, P., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J. Hum. Evol.* 46, 605-622.
- van der Merwe, N.J., Cushing, A.E., and Blumenschine, R.J., 1999. Stable isotope ratios of fauna and the environment of paleolake Olduvai. *J. Hum. Evol.* 34, A24-A25.
- van der Merwe, N.J., and Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *J. Archaeol. Sci.* 18, 249-259.
- van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A., and Luyt, J., 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *J. Hum. Evol.* 44, 581-597.
- Vogel, J.C., 1978a. Isotopic assessment of the dietary habits of ungulates. *S. Afr. J. Sci.* 74, 298-301.
- Vogel, J.C., 1978b. Recycling of carbon in a forest environment. *Oecol. Plantar.* 13, 89-94.
- Vogel, J.C., Fuls, A., and Ellis, R.P., 1978. The geographical distribution of kranz grasses in South Africa. *S. Afr. J. Sci.* 74, 209-215.
- White, T.D., 1978. Early hominid enamel hypoplasia. *Am. J. Phys. Anthropol.* 49, 79-84.
- Witt, G.B., and Ayliffe, L.K., 2001. Carbon isotope variability in the bone collagen of red kangaroos (*Macropus rufus*) is age dependent. *J. Archaeol. Sci.* 28, 247-252.
- Wright, L.E., and Schwarz, H.P., 1998. Stable carbon and oxygen isotopes in human tooth enamel: Identifying breastfeeding and weaning in prehistory. *Am. J. Phys. Anthropol.* 106, 1-18.

- Wrangham, R.W., 1987. The significance of African apes for reconstructing human social evolution. In Kinzey, W.G. (Ed.), *Primate Models of Hominid Evolution*. SUNY Press, Albany, pp. 51-71.
- Wrangham, R.W., Conklin-Britain, N.L., and Hunt, K.D., 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* 19, 949-970.
- Young, S., 2002. Metabolic mechanisms and isotopic investigation of ancient diets with an application to human remains from Cuello, Brazil. PhD diss., Harvard University.