



Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park

Matt Sponheimer^{a,b,*}, Julia Lee-Thorp^b, Darryl de Ruiter^c, Daryl Codron^b,
Jacqui Codron^b, Alexander T. Baugh^d, Francis Thackeray^e

^aDepartment of Anthropology, University of Colorado at Boulder, Boulder, CO 80309

^bDepartment of Archaeology, University of Cape Town, Rondebosch, WP 7701

^cDepartment of Anthropology, Texas A&M University, College Station, TX 77843

^dInstitute for Neuroscience, University of Texas at Austin, Austin, TX 78712

^eDepartment of Palaeontology, Transvaal Museum, Pretoria, GP 0001

Received 22 August 2004; accepted 27 November 2004

Abstract

Stable carbon isotope analyses have shown that South African australopiths did not have exclusively frugivorous diets, but also consumed significant quantities of C₄ foods such as grasses, sedges, or animals that ate these foods. Yet, these studies have had significant limitations. For example, hominin sample sizes were relatively small, leading some to question the veracity of the claim for australopith C₄ consumption. In addition, it has been difficult to determine which C₄ resources were actually utilized, which is at least partially due to a lack of stable isotope data on some purported australopith foods. Here we begin to address these lacunae by presenting carbon isotope data for 14 new hominin specimens, as well as for two potential C₄ foods (termites and sedges). The new data confirm that non-C₃ foods were heavily utilized by australopiths, making up about 40% and 35% of *Australopithecus* and *Paranthropus* diets respectively. Most termites in the savanna-woodland biome of the Kruger National Park, South Africa, have intermediate carbon isotope compositions indicating mixed C₃/C₄ diets. Only 28% of the sedges in Kruger were C₄, and few if any had well-developed rhizomes and tubers that make some sedges attractive foods. We conclude that although termites and sedges might have contributed to the C₄ signal in South African australopiths, other C₄ foods were also important. Lastly, we suggest that the consumption of C₄ foods is a fundamental hominin trait that, along with bipedalism, allowed australopiths to pioneer increasingly open and seasonal environments.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Hominins; Paleodiet; Carbon isotopes; Sedges; Termites; Kruger National Park

* Corresponding author. Matt Sponheimer, Department of Anthropology, University of Colorado at Boulder, Boulder, CO 80309. Tel.: +1 303 735 5774.

E-mail address: msponheimer@yahoo.com (M. Sponheimer).

Introduction

Over the past decade, stable carbon isotope analysis of tooth enamel has been used to study the diets of early hominins in South Africa (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., 2003). The premise of these studies is that you are what you eat, and that the stable carbon isotope composition of your food is ultimately reflected in your tooth enamel, even at several million years remove. Previous research, using non-isotopic techniques, had suggested that australopiths ate diets dominated by fleshy fruits or hard objects most likely originating from trees or bushes (e.g., Kay, 1985; Grine, 1986; Grine and Kay, 1988). These types of plants use the C₃ photosynthetic pathway which discriminates markedly against ¹³C, leading to very depleted ¹³C/¹²C ratios (about -27‰). In contrast, plants that utilize the C₄ photosynthetic pathway, such as tropical grasses and some sedges, discriminate less against ¹³C and are consequently less depleted (about -12‰) (Smith and Epstein, 1971). These distinct isotopic signatures are passed down into the tissues of animals that eat these plants. For instance, the tissues of zebra, which eat C₄ grass, are more enriched in ¹³C than the tissues of giraffe, which eat leaves from C₃ trees. Consequently, it was expected that early hominins, like the modern frugivorous chimpanzee, would have a C₃ isotopic signature (Schoeninger et al., 1999; Carter, 2001). Unexpectedly, however, all of the carbon isotope studies to date have shown australopiths to be rather enriched in ¹³C, suggesting that foods other than fruits were also important dietary components (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., 2003).

While these isotopic studies were significant in providing evidence that our understanding of australopith diets was too narrow, they had limitations. First, the number of individual hominins analyzed was relatively small. While this has been substantially remedied through recent publication (van der Merwe et al., 2003), the total number of published hominin carbon isotope ratios is still small compared to the number from

C₃- and C₄-consuming fauna to which they are statistically compared (Sponheimer and Lee-Thorp, 2003). This limitation in sample size, together with concerns that diagenesis may have affected some results, has led some to question whether or not australopiths really differed from their C₃ plant consuming coevals or modern chimpanzees (Schoeninger et al., 2001).

Another limitation of these studies was that, although they suggested that non-C₃ foods were consumed in significant quantities, they were not able to identify what these foods might have been. Thus, C₄ grasses, C₄ sedges, and animals that ate these foods were all offered as possible australopith foods (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., 2003; Peters and Vogel, in press). Amongst the reasons for this inability to identify the C₄ dietary source was a lack of data available on the carbon isotope compositions of potential C₄ foods other than grasses and large vertebrates. For instance, a recent investigation of bone tools at Swartkrans suggested that they have wear formed by digging in termite mounds, leading the researchers to hypothesize that consumption of C₄ grass-eating termites might explain the ¹³C-enriched isotopic signature of the australopiths (Backwell and d'Errico, 2001). Although this possibility was both intriguing and plausible given that some termite taxa (e.g., *Trinervitermes*, *Hodotermes*) consume grass, it remained speculative as there were no published data on the carbon isotope compositions of African savanna termites excepting a single species *Macrotermes michaelseni* (Boutton et al., 1983).

We encountered a similar problem with sedges. Conklin-Brittain et al. (2002) recently proposed that underground storage organs (USOs) in wetlands and river margins, such as the starchy rhizomes of some sedges, were important foods for australopiths; and since many sedges utilize C₄ photosynthesis, sedges represent a potential source of the non-C₃ signal observed in early hominins (Sponheimer and Lee-Thorp, 1999a, 2003; Lee-Thorp et al., 2003; van der Merwe et al., 2003). Unfortunately, however, although an estimated 33% of the world's sedges utilize C₄ photosynthesis (Sage et al., 1999), relatively little is known

about the isotopic compositions of sedges in modern South African environments that are most similar to those associated with australopiths (but see Stock et al., 2004). Thus, it was difficult to evaluate the likelihood that C₄ sedges were even available for consumption by South African hominins.

The aim of this paper is to begin to address these limitations in two ways. Firstly, we provide new carbon isotope data from 14 australopith specimens that greatly increase the previously published sample size. Secondly, we proffer novel carbon isotope data from a study of modern termites and sedges in Kruger National Park, South Africa. As Kruger contains a variety of environments that may be similar to those inhabited by australopiths (Reed, 1997; Sponheimer et al., 1999, 2001), we believe that these data represent a reasonable first step towards understanding the isotopic compositions of their potential foods.

Methods

Hominin sampling

We sampled a total of 14 hominin permanent molars housed at the Transvaal Museum in Pretoria, South Africa for this study: these included six ~2.5 Ma *Australopithecus africanus*

teeth from Member 4 at Sterkfontein and nine ~1.8 Ma *Paranthropus robustus* teeth (8 from Member 1 at Swartkrans and 1 from Member 3 of Kromdraai B) (Table 1). The three cave sites from which the teeth originated are within 3 km of each other in the dolomites of the Sterkfontein Valley (Brain, 1981). Specimens without heavy staining or mineral inclusions were sampled and pretreated based upon protocols outlined in Sponheimer (1999). All hominin teeth had been previously fractured and enamel samples (~2 mg) were acquired from between the enamel-dentine junction and the outer surface using a rotary drill with a diamond-tipped burr. Within this constraint, we sampled as extensive an area as possible in order to obtain enamel formed over a significant period of time. Importantly, with this method our sampling did not alter the external morphology of the teeth. The enamel powder was pretreated with 1.5% NaClO for ten minutes to remove organic contaminants, and then rinsed to neutrality. It was then subjected to 0.5 ml of 0.1 M CH₃COOH for another ten minutes to remove diagenetic carbonates, and again rinsed to neutrality. Samples were lyophilized and placed in individual reaction vessels and analyzed for ¹³C/¹²C using a Kiel II autocarbonate device coupled to a Finnigan MAT 252 mass spectrometer. Carbon isotope ratios (¹³C/¹²C) are expressed as δ¹³C values in parts per thousand (‰) relative to the PDB standard. The standard deviation of working

Table 1

Specimen numbers, tooth identifications, provenience information, and δ¹³C for hominin specimens analyzed in this study.

Specimen	Tooth	Taxon	Provenience	δ ¹³ C
STS 31	RM ³	<i>Australopithecus africanus</i>	Sterkfontein M4	-6.8
STS 32	RM ³	<i>Australopithecus africanus</i>	Sterkfontein M4	-7.8
STS 45	RM ²	<i>Australopithecus africanus</i>	Sterkfontein M4	-4.0
STS 72	RM ³	<i>Australopithecus africanus</i>	Sterkfontein M4	-9.7
STS 2218	M ²	<i>Australopithecus africanus</i>	Sterkfontein M4	-5.9
TM 1600	LM ₂	<i>Paranthropus robustus</i>	Kromdraai M3	-7.9
SK 19	RM ₃	<i>Paranthropus robustus</i>	Swartkrans M1	-6.3
SK 41	LM ³	<i>Paranthropus robustus</i>	Swartkrans M1	-6.7
SK 57	LM ³	<i>Paranthropus robustus</i>	Swartkrans M1	-6.5
SK 14000	LM ³	<i>Paranthropus robustus</i>	Swartkrans M1	-5.9
SK 14132	RM ³	<i>Paranthropus robustus</i>	Swartkrans M1	-6.9
SKW 6	LM ³	<i>Paranthropus robustus</i>	Swartkrans M1	-7.0
SKW 3068	LM ²	<i>Paranthropus robustus</i>	Swartkrans M1	-8.1
SKW 4768	LM ²	<i>Paranthropus robustus</i>	Swartkrans M1	-7.4

standards analyzed concurrently with the hominins was 0.1‰.

Kruger National Park sampling

The Kruger National Park sampling was carried out seasonally (dry and rainy seasons) between June 2002 and September 2004. In order to gain an idea of the potential isotopic variety available to early hominins, we sampled termites from the northernmost and southernmost regions of the park, from closed riverine to open grassland environments, and from a variety of substrates (e.g., mounds, feces, logs). All termites were placed in ethanol inside microcentrifuge vessels and then dried when we returned to the University of Cape Town laboratory. Sedges were collected from four 10-meter circular transects at riverine sites, two in northern, and two in southern Kruger Park. All available sedge taxa were sampled from each site, but the number of samples acquired of each taxon roughly reflected its local abundance. The sedges were dried at 60 °C in the Kruger Park, and upon arrival in Cape Town were ground using a Wiley-Mill with a 1 mm screen. Termite and sedge samples were then weighed, placed in tin capsules, and analyzed for $^{13}\text{C}/^{12}\text{C}$ using a Carlo-Erba elemental analyzer coupled to a Finnigan MAT 252 mass spectrometer. The standard deviation of working standards run in conjunction with the Kruger National Park samples was 0.1‰.

Results

Hominins

New Hominins—The carbon isotope results for the australopiths analyzed in this study are presented in Table 1 and Fig. 1. *Australopithecus* ($\bar{x} = -6.8\text{‰}$, s.d. = 2.1, $n = 5$) and *Paranthropus* ($\bar{x} = -7.0\text{‰}$, s.d. = 0.7, $n = 9$) are not significantly different ($P = 0.87$ t-test; $P = 0.79$ Mann-Whitney U), as was the case in previous studies (Sponheimer and Lee-Thorp, 1999a, 2003). Not surprisingly, the new *Australopithecus* data are statistically indistinguishable from previous analyses ($P = 0.74$ t-test; $P = 0.85$ Mann-Whitney U).

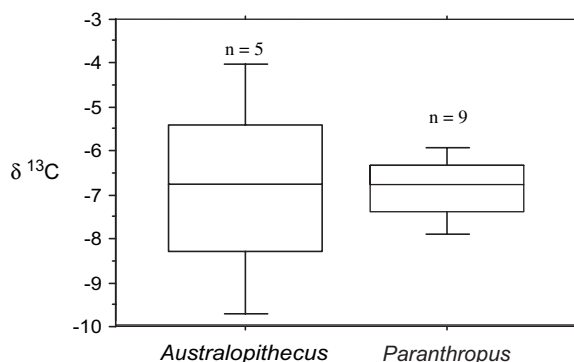


Fig. 1. $\delta^{13}\text{C}$ for *Australopithecus africanus* and *Paranthropus robustus* specimens analyzed for this study. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles.

They do, however, slightly extend the previously published range of $\delta^{13}\text{C}$ for confidently identified *Australopithecus* samples, as one specimen was extremely enriched in ^{13}C (-4.0‰). Nonetheless, the mean and great range (5.7‰) for *Australopithecus* is exactly what was anticipated from previous work (see Discussion for more on this variability). The situation for *Paranthropus* is somewhat different. The new *Paranthropus* $\delta^{13}\text{C}$ values are slightly (1.3‰), but significantly enriched compared to previous analyses ($P = 0.01$ t-test; $P = 0.01$ Mann-Whitney U). Furthermore, they extend the previously known range for this taxon, with one specimen being quite enriched in ^{13}C (-5.9‰). Despite these differences, however, the general character of the *Paranthropus* data is in accord with previous results in that their mean is indistinguishable from *Australopithecus* yet they are less variable (Fig. 1).

All Hominins—Given the greatly expanded hominin dataset, we now briefly address the question: are hominins really different from known C_3 consumers? The answer is an unequivocal “yes” (Fig. 2). To address this question, we merged hominin and non-hominin data from Swartkrans, Sterkfontein, and Makapansgat for statistical analysis. Such conflation would not be warranted in all contexts, as vegetation $\delta^{13}\text{C}$ can differ in small but meaningful ways over time and space. The $\delta^{13}\text{C}$ of C_3 vegetation, in particular, can change significantly between sere, open environments and

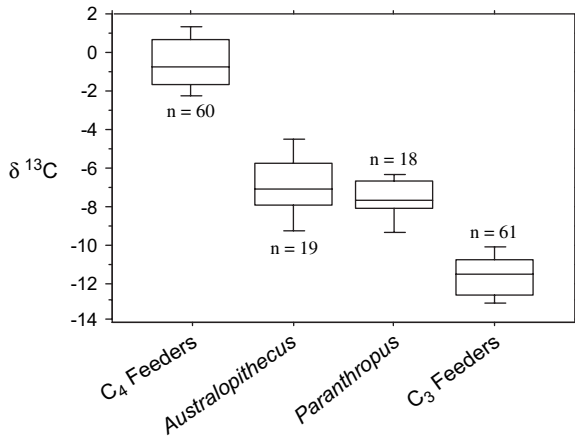


Fig. 2. $\delta^{13}\text{C}$ for new and previously analyzed *Australopithecus africanus* and *Paranthropus robustus* specimens, as well as C_3 plant consumers (browsing/frugivorous bovids and giraffids) and C_4 plant consumers (grazing bovids and equids). The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles. Given the size of this dataset, there can be no doubt that australopith $\delta^{13}\text{C}$ is highly distinct from that of associated browser/frugivores.

damp, closed canopy forests (Ehleringer and Cooper, 1988; van der Merwe, 1989; Cerling et al., 2003; Codron, 2003). However, the $\delta^{13}\text{C}$ of C_3 consumers at these sites does not vary significantly (ANOVA, $P = 0.09$), nor does linear regression reveal any trend in their $\delta^{13}\text{C}$ over time ($P = 0.38$, $R^2 = .01$). Thus, merging data from these sites is justified.

Both *Australopithecus* ($x = -7.1\text{‰}$, s.d. = 1.8, $n = 19$) and *Paranthropus* ($x = -7.6\text{‰}$, s.d. = 1.1, $n = 18$) are strongly different from the C_3 consuming bovids, giraffids, and chalicotherids ($x = -11.5\text{‰}$, s.d. = 1.3, $n = 61$) (ANOVA, Scheffé; $P < 0.0001$) with which they are associated (Tables 1 & 2). Both hominin taxa are also highly distinct from associated C_4 -grazing bovids, equids and suids ($x = -0.6\text{‰}$, s.d. = 1.8, $n = 60$) (ANOVA, Scheffé; $P < 0.0001$), but cannot be distinguished from each other (ANOVA, Scheffé; $P = 0.62$). This new larger dataset confirms our previous work showing that early hominins were distinct from both C_3 and C_4 consuming fauna. This disparity cannot be ascribed to diagenesis, as there is no evidence that browser or grazer $\delta^{13}\text{C}$ has

been irrevocably altered, and diagenesis should affect hominins and non-hominins alike. It appears, however, that we previously *underestimated* the importance of non- C_3 foods to australopiths (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a). We previously estimated that about 25% of australopith diets came from non- C_3 sources. We arrived at this estimate by comparing the mean australopith $\delta^{13}\text{C}$ values to the mean values for associated C_3 -browsers and C_4 -grazers which were taken as indicators of “pure” C_3 and C_4 diets (endmembers) respectively. This comparative method is the most appropriate for estimating C_4 intake in fossil fauna as it requires no assumptions about the carbon isotope composition of ancient vegetation (Lee-Thorp, 1989). For example, it makes no difference in the percent C_4 estimate if the $\delta^{13}\text{C}$ of C_3 vegetation was -29‰ or -25‰ , as these differences would be reflected in the $\delta^{13}\text{C}$ of the C_3 -consuming fauna to which the hominins are being compared. Thus, our percent C_4 estimates are likely to be robust. Nevertheless, it should be understood that these are rough estimates (rounded to the nearest 5%) that have been included primarily to allow discussion of hominin $\delta^{13}\text{C}$ without constant reference to biogeochemical terminology.

With this caveat in mind, the data suggest that *Australopithecus* and *Paranthropus* ate about 40% and 35% C_4 -derived foods respectively. Such a significant C_4 contribution, *whatever its origin*, is very distinct from what has been observed for modern chimpanzees (*Pan troglodytes*). Schoeninger et al. (1999) found no evidence of C_4 foods in chimpanzee diets even in open environments with abundant C_4 -grass cover. Similarly, Carter’s (2001) analysis of mammals in Kibale National Park showed the $\delta^{13}\text{C}$ of chimpanzees and C_3 -eating duiker antelope (*Cephalophus* spp.) to be indistinguishable. Thus, unlike our closest living relatives, both hominin taxa appear to have extensively utilized non- C_3 derived foods.

Sedges and termites in Kruger National Park

Termites—There are two particularly conspicuous results from the carbon isotope analyses of the Kruger National Park’s termites ($x = -20.1\text{‰}$,

Table 2

Specimen numbers, taxon, provenience, $\delta^{13}\text{C}$, and publication date for all other australopith specimens. In the provenience column, site abbreviations (SK = Swartkrans, MAK = Makapansgat, ST = Sterkfontein) are followed by the appropriate Member number. The 1994 publication is Lee-Thorp et al., 1994; the 1999 publication is Sponheimer and Lee-Thorp, 1999a; the 2000 publication is Lee-Thorp et al., 2000; and the 2003 publication is van der Merwe et al., 2003.

Specimen	Tooth	Taxon	Provenience	$\delta^{13}\text{C}$	Published
SK1512	P	<i>Paranthropus robustus</i>	SK1	-8.8	1994
SK879	M	<i>Paranthropus robustus</i>	SK1	-8.5	1994
SKX5015	LM ₃	<i>Paranthropus robustus</i>	SK1	-9.6	1994
SK878	RP ₃	<i>Paranthropus robustus</i>	SK1	-6.8	1994
SK879	M	<i>Paranthropus robustus</i>	SK1	-8.1	1994
SKX1312	LM ¹	<i>Paranthropus robustus</i>	SK2	-8.1	1994
SKX333	RM ₁	<i>Paranthropus robustus</i>	SK2	-10.0	1994
SKX35025	RM	<i>Paranthropus robustus</i>	SK3	-7.9	1994
SK876	M	<i>Paranthropus robustus</i>	SK1	-6.7	2000
MLD 30	RM ¹	<i>Australopithecus africanus</i>	MAK3	-5.6	1999
MLD 41	M	<i>Australopithecus africanus</i>	MAK3	-11.3	1999
MLD12	RM ³	<i>Australopithecus africanus</i>	MAK3	-7.7	1999
MLD28	RM ³	<i>Australopithecus africanus</i>	MAK3	-8.1	1999
STW 73	RM ²	<i>Australopithecus africanus</i>	ST4	-8.8	2003
STW 276	LM ₁	<i>Australopithecus africanus</i>	ST4	-8.0	2003
STW 252	RM ¹	<i>Australopithecus africanus</i>	ST4	-7.4	2003
STW 211	M	<i>Australopithecus africanus</i>	ST4	-7.3	2003
STW 304	M	<i>Australopithecus africanus</i>	ST4	-7.4	2003
STW 14	LM ₁	<i>Australopithecus africanus</i>	ST4	-6.7	2003
STW 315	Ldm ₂	<i>Australopithecus africanus</i>	ST4	-5.7	2003
STW 309b (409)	LM ₁	<i>Australopithecus africanus</i>	ST4	-6.1	2003
STW 229	P	<i>Australopithecus africanus</i>	ST4	-5.8	2003
STW 303	RM ²	<i>Australopithecus africanus</i>	ST4	-4.3	2003

s.d. = 3.6, n = 40; Fig. 3). First, they are highly variable, ranging from nearly pure C₃ to pure C₄ consumers, which is quite similar to the range of variation that has been observed in Australian savanna termites (Tayasu et al., 1998). Second, despite this variability, most have a mixed C₃/C₄ signal regardless of substrate (mounds or logs). Hence, they are highly distinct from both C₃ trees (x = -26.4‰, s.d. = 1.8, n = 550) and C₄ grasses (x = -12.2‰, s.d. = 1.1, n = 777) collected during the course of the two-year Kruger study (ANOVA, Scheffé; P < 0.0001). As expected, termites from open environments with abundant C₄ grasses (x = -15.3‰, s.d. = 2.7, n = 10) are enriched in ¹³C compared to those in more closed environments (x = -21.7‰, s.d. = 2.1, n = 30) (P < 0.001 t-test; P < 0.001 Mann-Whitney U), indicating that they consumed greater quantities of C₄ vegetation. Unexpectedly, however, termites in closed riverine environments also ate significant amounts of C₄ vegetation, despite the local

dominance of C₃ woody vegetation. Indeed, assuming a diet-termite spacing of about +1‰ (following Boutton et al., 1983), the closed environment termites consumed about 25% C₄ vegetation, while termites in open environments ate around 70% C₄ vegetation, resulting in an average of 35% for the entire park. Thus, C₄ plant consumption appears to be important for the vast majority of termites in the park, or at least for those that are most readily accessible (in mounds and logs) by modern hominin gatherers. In contrast, termites in the tropical forests of Cameroon (and presumably elsewhere) have nearly pure C₃ diets (Tayasu et al., 1997).

Sedges— The Kruger sedges fall neatly into two distinct groups, those using the C₃ (x = -27.2‰, s.d. = 1.4, x = 54) and those using the C₄ (x = -11.7‰, s.d. = 1.1, n = 21) photosynthetic pathway (P < 0.001 t-test; P < 0.001 Mann-Whitney U)(Fig. 4). Surprisingly, however, despite the common assumption that most African sedges in

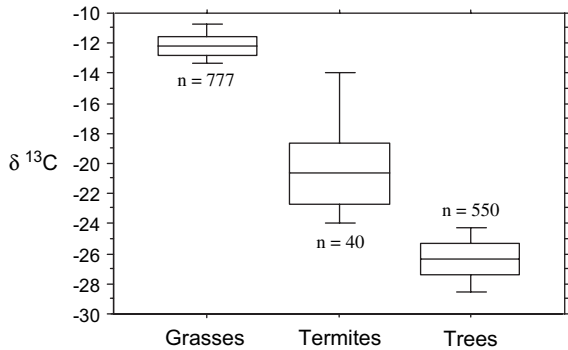


Fig. 3. $\delta^{13}\text{C}$ for termites, trees, and grasses in Kruger National Park. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles. Note that while termites have highly variable carbon isotope compositions, the vast majority of specimens have mixed C_3/C_4 signatures.

summer rainfall zones utilize C_4 photosynthesis, 72% of the specimens we analyzed were C_3 plants (which reflects the local abundance). This unexpected result has been affirmed by a recent herbarium survey of South African sedges which found that 65% use C_3 photosynthesis (Stock et al., 2004). These authors found that the distribution of C_4 sedges differs markedly from that of C_4 grasses, and is likely controlled by different climatic factors. In contrast, a study of Kenyan sedges found that 65% use C_4 photosynthesis (Hesla et al., 1982). Thus, it appears that C_4

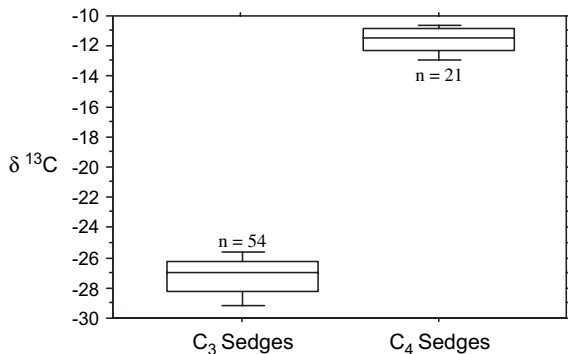


Fig. 4. $\delta^{13}\text{C}$ for C_3 and C_4 sedges in Kruger National Park. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles. Note that a wide majority of the sedges (72%) utilize C_3 photosynthesis.

sedges are much less common in South African woodlands than they are in previously studied East African environments.

Discussion

The new hominin $\delta^{13}\text{C}$ data demonstrate two things. First, with a total of 37 australopiths now analyzed, there can be no question that their carbon isotope compositions are highly distinct from those of their C_3 -consuming contemporaries. This is in stark contrast to modern chimpanzees and gorillas, both of which have essentially pure C_3 signatures (Schoeninger et al., 1999; Carter, 2001; Sponheimer, unpublished data). This is not to say that we will never find a chimpanzee that deviates from this pattern. What is clear, however, is that a chimpanzee with a non- C_3 signature would be an exception, whereas non- C_3 signatures represent the norm for australopiths. Thus, australopiths and chimpanzees clearly ate different resources, perhaps because of fundamentally disparate dietary adaptations or habitat differences. The latter possibility seems less likely, as even in woodland savanna with nearly continuous C_4 -grass cover, chimpanzee hair retains no evidence of C_4 consumption (Schoeninger et al., 1999). Moreover, as this environment is similar to the woodland/bushland environments believed to have been inhabited by the South African australopiths (Reed, 1997), it seems most parsimonious to conclude that australopiths and chimpanzees, when in similar environments, would have utilized the available resources in different ways. Simply put, chimpanzees largely ignore the available C_4 resources that constituted a major component of australopith diets. This is, of course, not terribly surprising given the marked differences in the craniodental morphology of australopiths and *Pan* (e.g., Grine, 1981; Kay, 1985; Ungar, 2004).

Second, these data demonstrate enormous variability in the $\delta^{13}\text{C}$ of South African hominins, especially within the taxon *Australopithecus africanus*. This high degree of variability is very unusual among both modern and fossil faunas in South Africa (Lee-Thorp et al., 1994, 2000; Sponheimer et al., 1999, 2001, 2003; Codron,

2003; van der Merwe et al., 2003), and might be ascribed to environmental heterogeneity. There is considerable evidence that South African australopith habitats became more open between ~ 3.0 Ma and 1.8 Ma (Vrba, 1980, 1985; Reed, 1997; Luyt and Lee-Thorp, 2003), and in fact the $\delta^{18}\text{O}$ data for the hominins in this study are consistent with increasing aridity in the Sterkfontein valley as 1.8 Ma *Paranthropus* ($x = -0.6\text{‰}$, s.d. = 1.1, $n = 9$) is significantly enriched in $\delta^{18}\text{O}$ compared to 2.5 Ma *Australopithecus* ($x = -2.6\text{‰}$, s.d. = 0.8, $n = 5$; Fig. 5) ($P < 0.01$ t-test; $P < 0.01$ Mann-Whitney U). Factors other than the $\delta^{18}\text{O}$ of meteoric water are important determinants of mammalian $\delta^{18}\text{O}$, however, so we cannot rule out the possibility that this difference is the product of ecological rather than climatic differences (Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999b; Sponheimer and Lee-Thorp, 2001). Regardless, given the abundant evidence of environmental change through time, one might expect that it would explain some of the observed variability in hominin carbon isotope ratios. Yet, linear regression demonstrates that there is no relationship between hominin $\delta^{13}\text{C}$ and time ($P = 0.63$, $R^2 = 0.01$; Fig. 6), and there are no

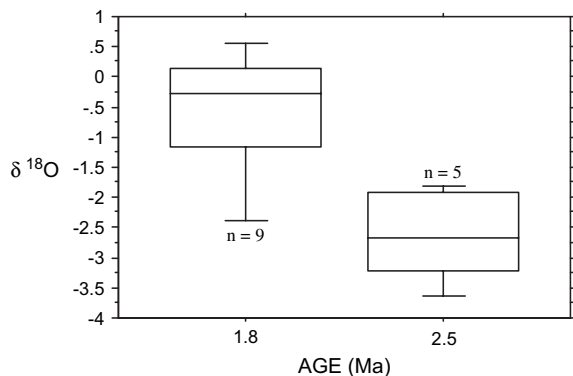


Fig. 5. $\delta^{18}\text{O}$ of the new hominin specimens analyzed for this paper through time. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles. The relatively depleted $\delta^{18}\text{O}$ of *Australopithecus* at 2.5 Ma compared to *Paranthropus* at 1.8 Ma may indicate either increasing aridity in the Sterkfontein Valley over time, or an ecological distinction between the taxa.

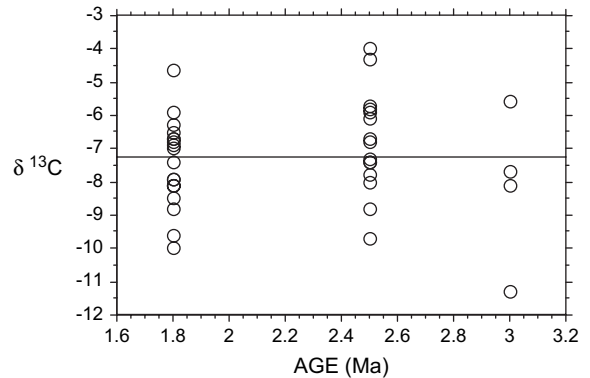


Fig. 6. $\delta^{13}\text{C}$ of South African hominins through time. No temporal trend is evident, despite abundant evidence that South African hominin environments changed during this time.

significant differences in hominin $\delta^{13}\text{C}$ between 3.0 Ma Makapansgat Member 3, 2.5 Ma Sterkfontein Member 4, or 1.8 Ma Swartkrans Member 1 (ANOVA, $P = 0.14$).

Indeed, what is most striking about these data is the lack of change in hominin $\delta^{13}\text{C}$ in the face of pronounced environmental change. Somewhat paradoxically, however, within any given time period (Member) hominin $\delta^{13}\text{C}$ is highly variable. This might be attributed to changing environments during the accumulation of these faunas, yet this would run counter to the fact that the mean hominin values do not change over a period of at least a million years during which local environments become more open. On the other hand, the variability might simply be an indication of the australopiths being extremely opportunistic primates with wide habitat tolerances that always inhabited a similarly wide-range of microhabitats regardless of broad-scale environmental flux. This would be consistent with Wood and Strait's (2004) recent suggestion that early hominins, including the robust australopiths, were eurytopic rather than ecological specialists.

In the case of *A. africanus*, the variability is so great that one might be excused for asking if there are not two ecologically distinct taxa presently commingled within its hypodigm. In fact, if one includes the numbers for three teeth (STW 236, STW 213i, STW 207) that are possibly, but not definitively, attributed to *A. africanus* (van der

Merwe et al., 2003), then this taxon would range from nearly pure C₃ to nearly pure C₄ diets. Stated otherwise, the range of $\delta^{13}\text{C}$ within *A. africanus* (−1.8‰ to −11.3‰) would be nearly as great as the entire range for ecologically disparate *Papio* and *Theropithecus* combined (+0.4‰ to −12.6‰) (Lee-Thorp et al., 1989). Stable isotopes in and of themselves cannot address the question of *A. africanus* unity, but numerous researchers have suggested that *A. africanus* might demonstrate more morphological variability than would be expected for a single taxon (Kimbel and White, 1988; Clarke, 1994; Lockwood, 1997; Moggi-Cecchi et al., 1998). Hence the possibility of two taxa, one highly dependent on C₄ foods and the other much less so, cannot be dismissed. Further work addressing this hypothesis is warranted. Nonetheless, we continue to work under the assumption that the specimens currently assigned to *A. africanus* represent a single species.

We now return to the question: what were the C₄ foods exploited by the australopiths? Grasses, sedges, and animal foods have all been considered as possible C₄-derived food sources (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a, 2003; van der Merwe et al., 2003; Peters and Vogel, in press). Our data bear directly on two of these possibilities: sedges and termites. Termites are a favored food of chimpanzees (e.g., Goodall, 1986; McGrew, 1992), and from our study of termites in Kruger National Park, it is clear that they could have contributed to the australopiths' ¹³C-enrichment (see Backwell and d'Errico, 2001). Even in densely wooded riverine environments, almost all of the termites we sampled consumed significant proportions of C₄ foods, and termites throughout Kruger Park ate 35% C₄ vegetation on average. Thus, termite consumption by australopiths in woodland savanna and even in riverine forest would be expected to impart some C₄ carbon to consumers. It seems very unlikely, however, that termites alone could account for the large non-C₃ signal in these hominins, because a diet of nearly 100% termites would be necessary to explain the 35%–40% C₄ component of australopith diets. Alternatively, if the hominins selectively preyed upon harvester termites (*Trinervitermes*, *Hodotermes*) with virtually pure

C₄ diets, a diet of about 35%–40% termites would be sufficient to produce the observed hominin carbon isotope ratios. This scenario, however, is highly unlikely. Our opportunistic foraging in woodland environments showed these termites to be much less common than those with mixed C₃/C₄ diets (and see Braack and Kryger, 2003). And while these harvester termites are more abundant in open grasslands and during acute droughts (Braack and Kryger, 2003), there is no reason to believe that such open environments were frequented by australopiths or that drought conditions were so preponderant. Moreover, while *Trinervitermes* builds highly visible above ground 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 $\delta^{13}\text{C}$ values of australopiths, but other C₄ resources were almost certainly consumed in considerable quantities.

We now return to the case for sedges. Sedges are another potentially attractive C₄ source for a number of reasons. For one, sedges like *Cyperus esculentus* and *C. papyrus* have long served as foods for modern humans (Tackholm and Drar, 1973; Defelice, 2002). Western lowland gorillas (*Gorilla gorilla gorilla*) have also been observed consuming the pith of aquatic plants (including sedges), although in small quantities (Doran and McNeillage, 1998). Additionally, the underground portions of sedges (as well as other plants) would be relatively inaccessible to most mammals, yet readily accessible to hominins with crude digging implements (Hatley and Kappelman, 1980). And, perhaps most importantly, the USOs of certain sedges would represent a relatively low-fiber resource (compared to *Pan* fallback foods; Conklin-Brittain et al., 2002) that would still be available during the dry season when preferred dietary resources were scarce.

Yet, while attractive, there are several potential problems with this scenario. Firstly, while sedges are relatively abundant around watercourses in Kruger National Park and South Africa in general, those that we encountered in Kruger's riverine woodlands (e.g., *C. textilis*) rarely if ever

had well-developed rhizomes or tubers. Thus, while extensive stands of sedges with well-developed USOs are common in extensive wetlands like the Okavango Delta (Ellery et al., 1995), they are not abundant in South African riverine woodlands today. Similarly, the South African australopiths are generally associated with woodland/bushland environments (albeit with some evidence of edaphic grasslands) (Reed, 1997), making it unlikely that large quantities of edible sedges with well-developed USOs were readily available for australopith consumption (Peters and Vogel, in press). Most significantly, only 28% of the sedges we encountered utilized the C_4 photosynthetic pathway. So unless hominins were deliberately seeking out C_4 sedges, or the distribution of C_3 and C_4 sedges was markedly different in the Pliocene, australopiths would have had to have had a diet of 100% sedges to come close to producing the observed 35%–40% C_4 signature. We think this degree of sedge specialization to be unlikely, especially given the high predation risk around South African watercourses today. On the whole, while it is certainly possible that sedges contributed to the C_4 signal of South African australopiths, we find it highly improbable that sedge consumption alone was responsible. It is worth noting, however, that early hominin habitats such as the wetlands of the Eastern Lacustrine Plain at Olduvai Gorge (Hay, 1976; Deocampo et al., 2002) might have been better sources of C_4 sedges. Puech et al. (1986) have also suggested that the dental microwear of early East African hominins is consistent with the consumption of such foods.

Conclusion

We had two primary goals in this paper: first, to present new data that should erase any doubts that hominin carbon isotope ratios are fundamentally different from those of associated C_3 and C_4 plant consumers; and second, to proffer data showing that while two of the proposed foods for South African australopiths (termites and sedges) could have contributed to their C_4 signal, they were unlikely to be solely responsible. We still must consider the possibility that grasses (seeds or roots)

and animal foods made important contributions to early hominin diets. Grass roots, grasshoppers, bird's eggs, lizards, rodents and young antelope might have been important resources, particularly during the dry season when little other food was readily available. Succulent plants like euphorbias (Euphorbiaceae) and aloes (Aloaceae) (which are rare in most woodlands but have $\delta^{13}C$ values that are sometimes indistinguishable from those of C_4 grasses) are also possibilities; for although they are often poisonous to humans (and presumably chimpanzees) they are occasionally utilized by baboons and humans (Codron, 2003; Peters and Vogel, in press). Determining the nature of the C_4 resources consumed by australopiths is important, as it could have profound physiological, social, and behavioral implications. For instance, if australopiths were consuming large quantities of C_4 grass like modern geladas (*Theropithecus gelada*), this would indicate that their diets were less nutritionally dense than those of extant chimpanzees, and possibly place important limitations on burgeoning hominin brains and sociality. Alternatively, if they were consuming large quantities of animal foods, it might signify a leap in dietary quality beyond that of extant apes, ultimately relaxing nutritional constraints on encephalization and social complexity (Aiello and Wheeler, 1995; Milton, 1999). Further work on dental microwear and morphology, Sr/Ca analysis, and the potential availability and nutritional properties of foods, may make it possible to identify these C_4 resources with greater confidence.

Despite the uncertainty as to the exact resources that australopiths consumed, it is clear that many australopiths heavily utilized C_4 foods that are typically overlooked by African apes. Moreover, it is probable that, in conjunction with adaptations like bipedalism, utilization of these resources allowed hominins to not only cope with dwindling forests, but pioneer new, more open environments in their increasingly arid and seasonal world. We believe it likely that diets containing significant quantities of C_4 -derived foods are fundamental hominin traits which will be found in all species with clear adaptations for bipedalism. This hypothesis can be tested by analysis of earlier East African hominin specimens.

Acknowledgments

We would like to thank Bob Brain, Heidi Fourie, Teresa Kearney, and Stephany Potze of the Transvaal Museum and Phillip Tobias, Ron Clarke, Bruce Rubidge, and Lee Berger of the University of Witwatersrand for their help and access to specimens. Ethan Codron, Yasmin Rahman, and Karim Sponheimer all provided invaluable support during sample analysis and preparation of this manuscript. We thank Sandi Copeland, Kaye Reed, and three anonymous reviewers who provided valuable comments on the manuscript. We also thank Charles Peters for access to an unpublished manuscript and Nikolaas van der Merwe for the many discussions we have had with him on this topic over the years. This work was funded by the National Science Foundation (USA), National Research Foundation (RSA), Leakey Foundation (USA), Wenner-Gren Foundation (USA), and the University of Cape Town.

References

- Aiello, L.C., Wheeler, P., 1995. The expensive tissue hypothesis. *Curr. Anthropol.* 36, 199–221.
- Backwell, L.R., d'Errico, F., 2001. Evidence of termite foraging by Swartkrans early hominids. *Proc. Natl. Acad. Sci. U.S.A.* 98, 1358–1363.
- Boutton, T.W., Arshad, M.A., Tieszen, L.L., 1983. Stable isotope analysis of termite food habits in East African grasslands. *Oecologia* 59, 1–6.
- Braack, L., Kryger, P., 2003. Insects and savanna heterogeneity. In: du Toit, J.T., Rogers, K.H., Biggs, H.C. (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington, pp. 263–275.
- Brain, C.K., 1981. *The Hunters or the Hunted?* University of Chicago Press, Chicago.
- Carruthers, 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. Ph.D. Dissertation, University of Chicago.
- Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African Bovidae based on stable isotope analysis. *J. Mammal.* 84, 456–470.
- Clarke, R., 1994. Advances in understanding the craniofacial anatomy of South African early hominids. In: Corruccini, R., Ciochon, R. (Eds.), *Integrative Paths to the Past*. Prentice Hall, Englewood Cliffs, pp. 205–222.
- Codron, D.M., 2003. Dietary ecology of Chacma Baboons (*Papio ursinus* (Kerr, 1792)) and Pleistocene Cercopithecoidea in Savanna Environments of South Africa. M.Sc. Thesis, University of Cape Town.
- Conklin-Brittain, N.L., Wrangham, R.W., Smith, C.C., 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P.S., Teaford, M.F. (Eds.), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport, pp. 61–76.
- Defelice, M.S., 2002. Yellow nutsedge *Cyperus esculentus* L.—snack food of the Gods. *Weed Technol.* 16, 901–907.
- Deocampo, D.M., Blumenshine, R.J., Ashley, G.M., 2002. Wetland diagenesis and traces of early hominids, Olduvai Gorge, Tanzania. *Quat. Res.* 57, 271–281.
- Doran, D.M., McNeillage, A., 1998. Gorilla ecology and behavior. *Evol. Anthropol.* 6, 120–131.
- Ehleringer, J.R., Cooper, T.A., 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76, 562–566.
- Ellery, W.N., Ellery, K., Rogers, K.H., 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.
- Goodall, J., 1986. *The Chimpanzees of Gombe*. Cambridge University Press, Cambridge.
- Grine, F.E., 1981. Trophic differences between gracile and robust australopithecines. *S. Afr. J. Sci.* 77, 203–230.
- Grine, F.E., Kay, R.F., 1988. Early hominid diets from quantitative image analysis of dental microwear. *Nature* 333, 765–768.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. *J. Hum. Evol.* 15, 783–822.
- Hatley, T., Kappelman, J., 1980. Bears, pigs, and Pliocene hominids: case for exploitation of belowground food resources. *Hum. Ecol.* 8, 371–387.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge*. Univ. of California Press, Berkeley.
- Hesla, A.B.I., Tieszen, L.L., Imbaba, S.K., 1982. A systematic survey of C_3 and C_4 photosynthesis in the Cyperaceae of Kenya, East Africa. *Photosynthetica* 16, 196–205.
- Kay, R.F., 1985. Dental evidence for the diet of *Australopithecus*. *Annu. Rev. Anthropol.* 14, 315–341.
- Kimbel, W.H., White, T.D., 1988. Variation, sexual dimorphism, and taxonomy of *Australopithecus*. In: Grine, F.E. (Ed.), *Evolutionary History of the "robust" Australopithecines*. Aldine de Gruyter, New York, pp. 175–192.
- Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochim. Cosmochim. Acta* 60, 3889–3896.
- Lee-Thorp, J.A., 1989. Stable carbon isotopes in deep time: the diets of fossil fauna and hominids, Ph.D. thesis, University of Cape Town.
- Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.* 18, 183–190.
- Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *J. Hum. Evol.* 27, 361–372.

- Lee-Thorp, J.A., Thackeray, J.F., van der Merwe, N., 2000. The hunters and the hunted revisited. *J. Hum. Evol.* 39, 565–576.
- Lee-Thorp, J.A., Sponheimer, M., van der Merwe, N.J., 2003. What do stable isotopes tell us about hominin diets. *Int. J. Osteoarchaeol.* 13, 104–113.
- Lockwood, C.A., 1997. Variation in the face of *Australopithecus africanus* and other African hominoids. Ph.D. dissertation, University of the Witwatersrand, Johannesburg.
- Luyt, J., 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.
- McGrew, W.C., 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge.
- Milton, K., 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol.* 8, 11–21.
- Moggi-Cecchi, J., Tobias, P.V., Beynon, A.D., 1998. The mixed dentition and associated skull fragments of a juvenile fossil hominid from Sterkfontein, South Africa. *Am. J. Phys. Anthropol.* 106, 425–466.
- Peters, C.R. and Vogel, J.C. Africa's wild C₄ plant foods and possible early hominid diets. *J. Hum. Evol.*, in press doi:10.1016/j.jhevol.2004.11.003.
- Puech, P.F., Cianfarani, F., 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 Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Sage, R.F., Wedin, D.A., Li, M., 1999. The biogeography of C₄ photosynthesis. In: Sage, R.F., Monson, R.K. (Eds.), *C₄ Plant Biology*. Academic Press, New York, pp. 313–373.
- Schoeninger, M.J., Bunn, H.T., Murray, S., Pickering, T., Moore, J., 2001. Meat-eating by the fourth African ape. In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-eating and Human Evolution*. Oxford University Press, Oxford, pp. 179–195.
- Schoeninger, M.J., Moore, J., Sept, J.M., 1999. Subsistence strategies of two savanna chimpanzee populations: the stable isotope evidence. *Am. J. Primatol.* 49, 297–314.
- Smith, B.N., Epstein, S., 1971. Two categories of ¹³C/¹²C ratios for higher plants. *Plant Physiol.* 47, 380–384.
- Sponheimer, M., Lee-Thorp, J.A., 1999a. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283, 368–370.
- Sponheimer, M., Lee-Thorp, J.A., 1999b. The ecological significance of oxygen isotopes in enamel carbonate. *J. Archaeol. Sci.* 26, 723–728.
- Sponheimer, M., Lee-Thorp, J.A., Reed, K., 2001. Isotopic ecology of the Makapansgat Limeworks Perissodactyla. *S. Afr. J. Sci.* 97, 327–329.
- Sponheimer, M., 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.A., 2003. Differential resource utilization by extant Great Apes and Australopithecines: towards solving the C₄ conundrum. *Comp. Biochem. Physiol.* 136, 27–34.
- Sponheimer, M., Lee-Thorp, J., DeRuiter, D., Smith, J., van der Merwe, N., Reed, K., Ayliffe, L., Heidelberger, C., Marcus, W., 2003. Diets of southern African Bovidae: stable isotope evidence. *J. Mammal.* 84, 471–479.
- Sponheimer, M., 1999. *Isotopic Ecology of the Makapansgat Limeworks Fauna*. Ph.D. Dissertation, Rutgers University.
- Sponheimer, M., Reed, K., Lee-Thorp, J.A., 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. *J. Hum. Evol.* 34, 277–285.
- Stock, W.D., Chuba, D.K., Verboom, G.A., 2004. Distribution of South African C-3 and C-4 species of Cyperaceae in relation to climate and phylogeny. *Austral. Ecol.* 29, 313–319.
- Stuart, C., Stuart, T., 2000. *A Field Guide to the Tracks and Signs of Southern and East African Wildlife*. Stuk Publishers, Cape Town.
- Tackholm, V., Drar, M., 1973. *Flora of Egypt*. vol. II. Otto Koeltz Antiquariat, Koenigstein.
- Tayasu, I., Abe, T., Eggleton, P., Bignell, D.E., 1997. Nitrogen and carbon isotope ratios in termites: an indicator of trophic habit along the gradient from wood-feeding to soil-feeding. *Ecol. Entomol.* 22, 343–351.
- Tayasu, I., Inoue, T., Miller, L.R., Sugimoto, A., Takeichi, S., Abe, T., 1998. Confirmation of soil-feeding termites (Isoptera; Termitidae; Termitinae) in Australia using stable isotope ratios. *Func. Ecol.* 12, 536–542.
- Ungar, P., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J. Hum. Evol.* 46, 605–622.
- van der Merwe, N.J., 1989. Natural variation in the ¹³C concentration and its effect on environmental reconstruction using ¹³C/¹²C ratios in animal bones. In: Price, T.D. (Ed.), *The Chemistry of Prehistoric Human Bone*. Cambridge University Press, Cambridge, pp. 105–125.
- van der Merwe, N.J., Thackeray, J.F., Lee-Thorp, J.A., Luyt, J., 2003. The carbon isotope ecology and diet of *Australopithecus africanus* at Sterkfontein, South Africa. *J. Hum. Evol.* 44, 581–597.
- Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making*. University of Chicago Press, Chicago, pp. 247–272.
- Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York, pp. 63–71.
- Wood, B., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *J. Hum. Evol.* 46, 119–162.