

Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites

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Abstract

The environmental contexts of the karstic hominin sites in South Africa have been established largely by means of faunal associations; taken together these data suggest a trend from relatively closed and more mesic to open, drier environments from about 3 to 1.5 Ma. Vrba argued for a major shift within this trend ca. 2.4–2.6 Ma, an influential proposal that posited links between bovid (and hominin) radiation in Africa and the intensification of Northern Hemisphere Glaciation. Yet faunal approaches often rely on habitat and feeding preferences of modern taxa that may differ from those of their extinct predecessors. Here we explore ways of extending $^{13}\text{C}/^{12}\text{C}$ data from fossil mammals beyond denoting “presence” or “absence” of C_4 grasses using the evolution of open environments in South Africa as a case study. To do so we calculated the relative proportions of C_3 -, mixed-, and C_4 -feeding herbivores for all the hominin sites for which we have sufficient data based on $^{13}\text{C}/^{12}\text{C}$ analyses of fossil tooth enamel. The results confirm a general trend towards more open environments since 3 Ma, but they also emphasize a marked change to open grassy habitats in the latest Pliocene/early Pleistocene. Mean $^{13}\text{C}/^{12}\text{C}$ for large felids also mirrored this trend.

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Introduction

Many have argued for a causal link between climate change and human evolution (e.g., Brain, 1981; deMenocal, 1995). Yet, while trends and cycles of global climate change during the Pliocene and early Pleistocene are reasonably well-known from marine sediment records (e.g., Imbrie et al., 1992; Tiedemann et al., 1994), their effects on African continental climates and environments are poorly understood. To some degree this is due to high environmental variability across the continent, which is large, topographically varied, and which occupies a position straddling the Equator. One outcome is that the various regions are subject to different climate forcing. Therefore, we have to be careful about extrapolating shifts and long-term

trends evident in one part of the continent to another. This is not to assert that common trends did not occur—they undoubtedly did—but that we cannot assume them.

Another major impediment is the rarity of long, continuous (or even semi-continuous) continental records. There are important exceptions; for instance, continental dust or pollen in marine records (deMenocal, 1995; Dupont et al., 1998) provides regional information about continental climate and floral composition, but a good deal of the existing evidence has been pieced together from many paleontological sites. Detecting environmental conditions and trends from the South African early hominin sites presents further challenges because of the nature of the deposits. With few exceptions they are karst infills confined to the distribution of the Proterozoic Malmani dolomites (Partridge, 2000), the faunal and sedimentary contents of which represent relatively crude snapshots of conditions pertaining at the time. Notwithstanding recent advances

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using paleomagnetism and cosmogenic nuclides (Partridge et al., 2003), the working models for chronology and sequence are still based largely on lithostratigraphy (Partridge, 2000) and biostratigraphy (e.g., Vrba, 1975, 1982). Although debate about absolute ages has continued (e.g., Berger et al., 2002; Clarke and Partridge, 2002), the broad sequence of events is not disputed.

Fossil faunal abundances, and in particular those of bovids, are widely applied tools for extracting information about paleoenvironmental conditions (Vrba, 1975, 1980, 1988, 1995, 2000; Plummer and Bishop, 1994; Behrensmeyer et al., 1997; Kappelman et al., 1997; Spencer, 1997). A series of influential hypotheses about environmental change and African mammalian evolutionary responses grew out of studies of the fossil bovids in the South African hominin sites (Vrba, 1982, 1988, 1995, 2000).

In a literature review of bovid population statistics in 16 modern game reserves, Vrba (1980) observed that the percentage of alcelaphini and antilopini, together, was never >30% of the total bovid population in areas with considerable tree and bush cover (“closed” habitats) but always >60% in areas with high grass cover but few trees and bushes (“open” habitats). Since the abundance of fossil alcelaphini plus antilopini (alcelaphini + antilopini criterion, or AAC) was relatively low (28%) in the earlier site of Makapansgat (~3 Ma) and increased in the later sites of Sterkfontein, Swartkrans, and Kromdraai, it was inferred that environments had become progressively more open over time (Vrba, 1975, 1985). Based on these observations and subsequent work including East African material, Vrba (1982, 1988, 1995, 2000) argued for a major African faunal turnover at about 2.4–2.6 Ma within this trend. This finding formed a pillar of the “Turnover Pulse Hypothesis” that proposed a direct correlation between an evolutionary turnover in bovids and in hominins and global climate changes inferred from oxygen isotopes in marine cores.

The AAC is predicated on the assumption that extinct fossil antilopini and alcelaphini preferred open landscapes and were arid-adapted several million years ago, as these tribes generally are today. While this is almost certainly the case for fossil alcelaphini from 3 Ma (Kappelman et al., 1997; Reed, 1997; Sponheimer et al., 1999), there is some evidence to suggest that it might not necessarily be the case for fossil antilopini. For instance, stable carbon isotope analyses showed that *Gazella vanhoepeni* at Makapansgat and *Antidorcas recki* at the Sterkfontein Valley sites were browsers and not mixed feeders like modern antilopini (Lee-Thorp and van der Merwe, 1993; Sponheimer et al., 1999). Combined isotopic and ecomorphological reexamination of the Makapansgat Member 3 fauna suggested that up to 25% of diets inferred from their modern descendants were incorrect (Sponheimer et al., 1999). These dietary differences suggest the possibility that habitat preferences or tolerances also differed, leading to possible biases in the environmental reconstructions.

We turn now to examine the potential for extracting information about paleoenvironmental trends based on stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) in fossil tooth enamel. This approach provides a direct measure of paleodiet in savanna

ecosystems, insofar as it reflects the relative proportions of grass and browse consumed, and hence indirectly, habitat preferences. Plants following the C_4 photosynthetic pathway (mainly tropical grasses but including some shrubs and sedges) have distinct carbon isotope compositions compared to those plants following the C_3 pathway (trees, bushes, forbs). The mean $\delta^{13}\text{C}^1$ for C_3 plants today is about -26‰ , while that for C_4 plants is -12‰ (Smith and Epstein, 1971), and this distinction is reflected in the tissues of consumers (DeNiro and Epstein, 1978; Vogel, 1978) depending on the proportions consumed and with an offset, depending on the chemistry of the tissue. In the case of enamel, a biological apatite consisting primarily of calcium phosphate with ~3% of substituted carbonate, the offset is $+12\text{--}14\text{‰}$ (Passey et al., 2005). Typical $\delta^{13}\text{C}$ values for pure browser (C_3 consumers) enamel are about -12 to -14‰ , while for grazers (C_4 consumers) they are about 0 to $+2\text{‰}$. Values for predators closely resemble those of their prey (Lee-Thorp et al., 2000), and hence predator $\delta^{13}\text{C}$ can also provide an integrated perspective on dominance of either C_3 or C_4 biomass in a particular environment.

$\delta^{13}\text{C}$ analysis of fossil tooth enamel is well suited for detecting the presence or absence of C_4 grasses and the proportions of C_3 and C_4 plants in the diets of fossil animals. This level of information is very useful for some questions, for instance, the emergence of C_4 grasses as significant biomass components after the late Miocene (Cerling et al., 1997; Ségalen et al., 2007), or shifts in the proportions of C_4 and C_3 grasses in response to changes in rainfall seasonality or temperature regimes (Vogel, 1982; Lee-Thorp and Beaumont, 1995). However, presence alone of C_4 signatures in the hominin sites’ faunal assemblages is less helpful for environmental reconstruction because these grasses could have existed in environments as different as open grassland or closed woodland. Hence, there are limits for determining patterns of environmental change over time.

A further step to quantify $\delta^{13}\text{C}$ data from faunal assemblages is required if we are to derive useful information about vegetation community structure and its evolution over time. Previously we constructed a modification of Vrba’s (1980) AAC method using two different approaches based on $\delta^{13}\text{C}$ (Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003). Both were based on the principle that in open, grassy biomes grass is the major food source and there is little C_3 vegetation available for C_3 consumers, whereas the balance is reversed with increasing proportions of woody vegetation. An increasing amount of C_3 vegetation is available for browsers, and concomitantly, more browsers and fewer grazers can survive. The advantage of such approaches is that the $\delta^{13}\text{C}$ data are derived empirically without assumptions about dietary behavior. However, since the taxa included and treatment of the data differed considerably, these studies are not directly comparable and cannot be used to determine vegetation trends over time.

¹ By convention $^{13}\text{C}/^{12}\text{C}$ ratios are expressed in the δ notation in per mil relative to the VPDB international standard as follows: $\delta^{13}\text{C}(\text{‰}) = (\text{R}_{\text{sample}}/\text{R}_{\text{ref}} - 1) \times 1000$, where $\text{R} = ^{13}\text{C}/^{12}\text{C}$.

Here, we seek to shed further light on the evolution of open environments in the South African interior in the Pliocene and early Pleistocene. We use frequency calculations from existing $\delta^{13}\text{C}$ data for herbivores and carnivores from a number of sites representing a timespan of ca. 3 to 1.5 Ma to provide a measure of shifts in the relative importance of C_3 and C_4 biomass. Our more general aim is to explore and illustrate the potential of fossil enamel-based $\delta^{13}\text{C}$ data for examining long-term trends in vegetation cover. A large body of fossil $\delta^{13}\text{C}$ data now exists for sites in South, Central, and East Africa that could be usefully applied for this purpose.

Methods

We used existing $\delta^{13}\text{C}$ data (both published and unpublished) from the sites of Makapansgat, Sterkfontein, and Swartkrans, all of which are located within the Malmani dolomite subgroup (Fig. 1). Conventionally, each of these heavily calcified infills have been divided into a series of Members that are believed to form a sequence from older to younger on the basis of lithostratigraphy and biostratigraphy (Brain, 1993; Partridge, 2000), but the sequences of deposition (and erosion) are rather complex. The length of time represented by Members or units within the Members is not well-known—they may represent hundreds or many thousands of years, although Brain has argued consistently for relatively rapid accumulation episodes followed by longer erosional periods (Brain, 1981, 1993). Nevertheless, the series of sites can be built into a regional sequence, albeit discontinuous and of low resolution. We followed the conventional lithostratigraphic divisions, since we are concerned with broad trends over long periods, and age assignments summarised in the review by Partridge (2000) for Makapansgat Member 3, Sterkfontein Members 4 and 5, and Swartkrans Members 1 and 2.

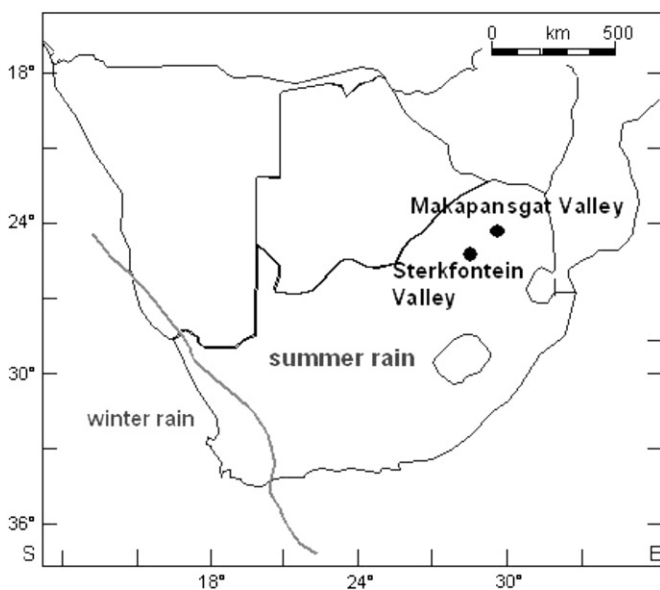


Fig. 1. Map of southern Africa showing the locations of the hominin sites in the Sterkfontein and Makapan Valleys. As indicated, most of the subcontinent falls within a summer rainfall regime so that C_4 taxa dominate the grassy flora (Vogel et al., 1978).

Isotopic measurements followed standard procedures as described in the original sources [see Appendix 1 in Supplementary material (Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2006.11.020) for data sources]. We divided data for all large herbivore specimens into three trophic categories: C_3 consumers ($\delta^{13}\text{C} < -9.0\text{‰}$), C_4 consumers ($\delta^{13}\text{C} > -3.0\text{‰}$), and mixed feeders (values between these ranges; Appendix 1 in Supplementary material). Our “ C_3 ” and “ C_4 ” consuming categories are indicative of individuals with diets dominated by C_3 and C_4 vegetation respectively, using ranges based on $\delta^{13}\text{C}$ data for modern herbivores in South Africa (Sponheimer et al., 2003). The results are represented as a series of frequency diagrams for each Member (Fig. 2). We also calculated and compared mean $\delta^{13}\text{C}$ values for all herbivores, browsers, large felids, and breccias for various units where the data allowed.

Results and discussion

Frequencies for browsers, mixed feeders, and herbivores for all sites are shown in Fig. 2, while the individual $\delta^{13}\text{C}$ values on which the calculations are based are provided in Supplementary material. The results show a decline in the proportions of browsers through the sequence, and a concomitant rise in the proportions of grazers, largely consistent with Vrba’s results (Vrba, 1980, 1985). The $\delta^{13}\text{C}$ -based frequency data differ slightly in that they show high proportions of C_3 herbivores in Makapansgat M3 (Member 3), suggesting a densely wooded environment, whereas the bovid abundance

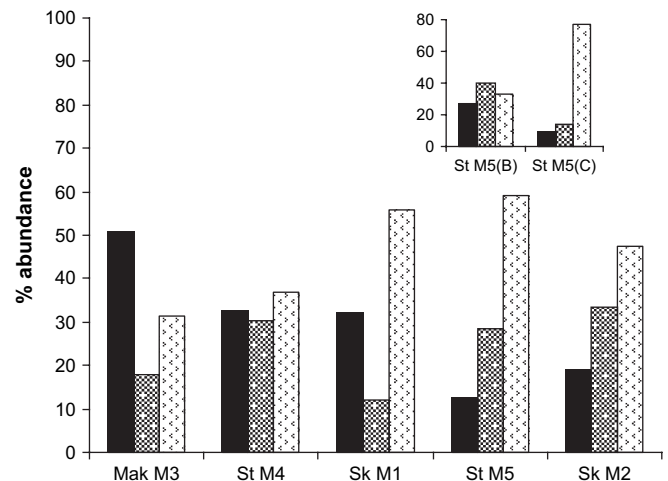


Fig. 2. Frequency diagram showing the relative abundances of large herbivores consuming C_3 , C_4 , and mixed diets in three sites, based on $\delta^{13}\text{C}$ data ranges as given in the text. C_3 -, mixed, and C_4 -feeding herbivores are shown as dark solid, grey stippled, and light stippled bars respectively. The sites and members are designated as follows: Makapansgat Member 3 (Mak M3), Sterkfontein Member 4 and 5 (St M4 and St M5), and Swartkrans Member 1 and 2 (Sk M1 and Sk M2). Chronology is discussed in the text. The data is presented in approximate chronological order, but it must be borne in mind that some Members overlap in age. Inset: separation of a subset of the Sterkfontein Member 5 faunal data into Unit B (older, with Oldowan stone tools) and Unit C (younger, appearance of Acheulean tools) shows that grazers formed a far higher proportion of herbivores in the youngest unit. Sources for the $\delta^{13}\text{C}$ data and numbers are given in Appendix 1 in Supplementary material.

data suggested that the site barely fell into the woodland/closed category. The $\delta^{13}\text{C}$ frequency data are consistent with Reed's (1997) analysis that pointed to denser woodland than the AAC, based on significant numbers of arboreal fauna. The proportions of C_3 herbivores in Sterkfontein M4 and Swartkrans M1 may have also been previously slightly underestimated. Mixed feeders show no obvious trend, but their proportions in some Members (Fig. 2; Appendix 1 in Supplementary material) are relatively high compared to most South African faunas today.

Notwithstanding these small differences, and consistent with the AAC results, C_4 grazers are clearly more abundant in the younger deposits (Sterkfontein M5, and Swartkrans M1, M2). The patterns of browser, mixed feeder, and grazer frequencies are almost identical for Sterkfontein M5 and Swartkrans M2, whereas Swartkrans M1 shows a higher proportion of browsers. We were able to obtain slightly higher resolution for changes within Sterkfontein M5, since some specimens could be assigned to Unit B or C, respectively. Unit B contains fauna and Oldowan stone tools similar to Olduvai Bed I and lower Bed II suggesting an age of ca. 1.7 Ma, or older while tools in Unit C are early Acheulean suggesting that it postdates the appearance of hand-axe technology after ~ 1.6 Ma (Kuman and Clarke, 2000; Partridge, 2000). The results suggest a major change in the youngest Unit (Fig. 2, inset). The distinction between the Units and similarity of the composite Sterkfontein M5 data to Swartkrans M2 [ca. 1.5 Ma (Brain, 1993)] may imply that an unequivocally open, grassy environment dominated by grazers existed from about 1.6 Ma. Alternatively, the difference between Swartkrans M1 on the one hand, and Swartkrans M2 and Sterkfontein M5 on the other, may reflect smaller scale fluctuations within the long-term pattern, as suggested by cyclical shifts in the Buffalo Cave $\delta^{13}\text{C}$ speleothem data (Hopley, 2004).

Other data that might also reflect subtler environmental changes are not expressed in the frequency diagram. For instance, mean $\delta^{13}\text{C}$ values for browsers at Makapansgat ($-11.5 \pm 0.9\text{‰}$, $n = 37$) are depleted in ^{13}C compared to later browsers (where adequate samples are available), although only the comparison with Sterkfontein Member 5 ($-9.9 \pm 1.1\text{‰}$, $n = 14$) is significant (Fisher's PLSD; $p < 0.01$). The lower values for Makapansgat may indicate moister conditions or denser tree cover compared to Sterkfontein M5, since C_3 plants discriminate more strongly against ^{13}C under cooler and/or more shaded conditions. Mean grazer values remain near -0.5‰ with the exception of Swartkrans M2 ($-1.40 \pm 1.33\text{‰}$); these values are all slightly lower than those reported for fossil grazers in East Africa (Cerling et al., 1997) and for modern bovids in East (Cerling et al., 2003) and South Africa (Sponheimer et al., 2003). The differences are slight but might point to a small remnant component of C_3 grass flora (for instance in shady areas, or on the cooler south-facing slopes of hills), or alternatively, to some grazing taxa that were less specialized than their modern counterparts.

We calculated mean $\delta^{13}\text{C}$ values for large felids for Members where sufficient data was available (Table 1). The means indicate trends essentially similar to the herbivore data (Fig. 3). Mean $\delta^{13}\text{C}$ for Swartkrans M1 felids are identical

Table 1

The table of $\delta^{13}\text{C}$ values for large felids from Sterkfontein M4 and 5, and Swartkrans M1 and 2, giving the museum reference number, species assignments, and enamel $\delta^{13}\text{C}$ values. The sources for the data, again published and unpublished, are given in the final column

Specimen #	Species	$\delta^{13}\text{C}$	Source
Sterkfontein Member 4			
S94-2	<i>Panthera leo</i>	-7.0	Luyt, 2001
S94-9	<i>Dinofelis barlowi</i>	-8.2	"
STS132	<i>Dinofelis barlowi</i>	-4.6	"
SF420	<i>Homotherium latidens</i>	-7.7	"
SF434	<i>Homotherium latidens</i>	-8.3	"
STS397	<i>Homotherium latidens</i>	-7.6	"
STS388	<i>Homotherium latidens</i>	-8.7	"
Sterkfontein Member 5			
SF 4151	<i>Panthera leo</i>	-7.8	Luyt, 2001
S94-149	<i>Panthera leo</i>	-8.0	"
SF 2858	<i>Panthera leo</i>	-10.3	"
SF94-23	<i>Panthera leo</i>	-2.6	"
SF94-7228	<i>Panthera leo</i>	-3.7	"
BP/3/19777	<i>Panthera leo</i>	-4.1	"
Swartkrans Member 1			
SK 342	<i>Panthera leo</i>	-8.3	Lee-Thorp et al., 2000
SK 348	<i>Panthera leo</i>	-7.8	"
SK 352	<i>Panthera pardus</i>	-9.8	"
SK 5960	<i>Panthera pardus</i>	-8.0	"
SK 1953	<i>Panthera pardus</i>	-2.2	"
SK 347	<i>Panthera pardus</i>	-8.9	"
SK 353	<i>Panthera pardus</i>	-8.7	"
SK 356	<i>Panthera pardus</i>	-9.4	"
SK 345	<i>Panthera pardus</i>	-6.1	"
SK 337	<i>Megantereon</i>	-8.6	"
SK 335	<i>Dinofelis</i>	-3.7	"
Swartkrans Member 2			
SK 303	<i>Panthera pardus</i>	-4.3	Lee-Thorp et al., 1997
SK 346	<i>Panthera pardus</i>	-5.3	Lee-Thorp et al., 2000
SK 1806	<i>Panthera pardus</i>	-7.7	"
SK 1869	<i>Panthera leo</i>	-2.5	"
SK 1188	<i>Panthera leo</i>	-0.5	"
SK 359	<i>Panthera leo</i>	-3.3	"
SK 360	<i>Panthera leo</i>	-2.5	"

to those of Sterkfontein M4 and are relatively depleted in ^{13}C (both -7.4‰) suggesting that their prey consisted mostly of C_3 herbivores. The mean felid values for Sterkfontein M5 ($-6.1 \pm 3.05\text{‰}$) are slightly but not significantly enriched in ^{13}C by comparison, while Swartkrans M2 ($-3.7 \pm 2.32\text{‰}$) represents a statistically significant shift to C_4 prey (Fisher's PLSD; $p < 0.01$). The relatively low mean for Swartkrans M1 emphasises the distinction implied by the higher numbers of C_3 -feeding herbivores observed in the frequency data compared to Sterkfontein M5 and Swartkrans M2. No data for large felids are available for Makapansgat.

We note that $\delta^{13}\text{C}$ values for attached breccia or calcite inclusions in fossil samples show a rather similar trend towards more positive values (Fig. 4). Makapansgat M3 (-4.9‰) is significantly depleted in ^{13}C compared to later accumulations (Sterkfontein M4 at -3.4‰ and Sterkfontein M5 at -0.7‰ ; Fisher's PLSD; $p < 0.001$), while Sterkfontein M4 is significantly depleted compared to M5 (Fisher's PLSD; $p < 0.001$). The trend could be considered to be suggestive of increasing

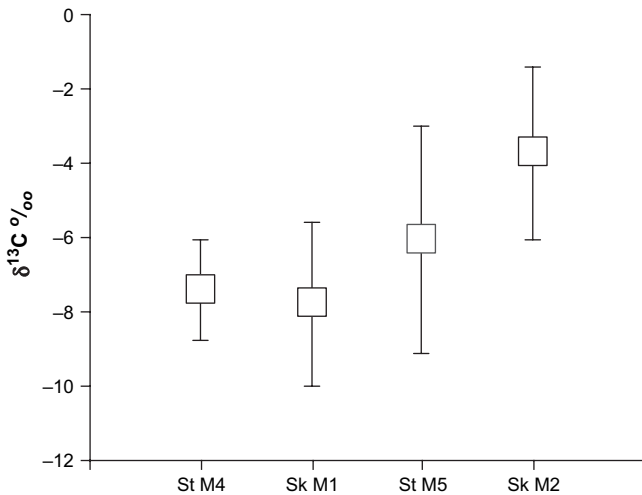


Fig. 3. Means shown as open boxes and standard deviations for $\delta^{13}\text{C}$ data from enamel of large felids from Sterkfontein and Swartkrans. Site and member designations are as for Fig. 2. Individual $\delta^{13}\text{C}$ data points, species assignments, numbers, and the sources are given in Table 1.

contributions of C_4 plant biomass over time due to the influence of plant-respired CO_2 on secondary carbonates in karst systems (Schwarcz, 1986). We cannot use these values, however, to indicate absolute contributions of C_3 and C_4 plant biomass, since processes other than plant CO_2 also influence the isotopic composition of secondary carbonates (e.g., parent dolomite, see Hopley et al., 2007) and unlike speleothems, the provenience of these samples in the karst system is unknown. The significant difference in $\delta^{13}\text{C}$ for breccia from Sterkfontein M4 and M5, however, may be helpful in distinguishing between these sediments in cases where bones and teeth have carbonate inclusions but uncertain context.

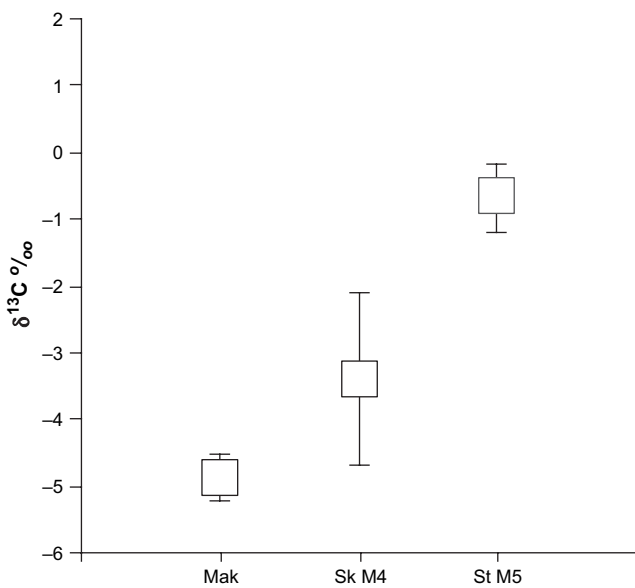


Fig. 4. Means and standard deviations for $\delta^{13}\text{C}$ of secondary carbonates found as attachments or inclusions in faunal samples from Makapansgat (Sponheimer, 1999) and Sterkfontein (Luyt, 2001) show clear differences. Site designations are as for Fig. 2. No data are available from Swartkrans.

Returning to the $\delta^{13}\text{C}$ faunal data, notwithstanding the more subtle distinctions, the frequency data do suggest that open, grassy environments became dominant components of the landscape after 1.7 Ma. The Buffalo Cave speleothem also shows a shift towards more C_4 input at about this time (Hopley, 2004). Open environments were also evident in East Africa from 1.7 Ma (Cerling et al., 1988; Plummer and Bishop, 1994; Kappelman et al., 1997; Reed, 1997). Together these data suggest a shift towards open landscapes dominated by C_4 grasses in both South and East Africa. This marked change has perhaps been neglected because of the focus on the earlier (2.4–2.6 Ma) faunal shifts and the search for climate drivers in that earlier period.

The success of C_4 -dominated ecosystems in both the low and low/mid-latitudes in Africa suggests that conditions were highly favorable for C_4 grasses and concomitantly less favorable for tree growth. C_4 grasses thrive under conditions where there is high solar radiation and minimum temperatures above $\sim 22^\circ\text{C}$ in the growing (rainy) season (Vogel et al., 1978; Ehleringer et al., 1997). Hence, they can tolerate dry and/or cold conditions in the nongrowing season. Near the Equator seasonal temperature differences are minimal, but in the low/mid-latitudes of the South African hominin sites (the Sterkfontein Valley is about 26°S), this seasonal pattern occurs with large amplitude seasonal differences in moisture and temperature between the summer/rainy and winter/dry seasons. Thus, in southern Africa at least, C_4 grassland dominance from the latest Pliocene-early Pliocene (after ca. 1.7 Ma) might be linked to development of these modern conditions. This scenario is consistent with the suggestion for intensification of the Walker atmospheric system at about this time (Ravelo et al., 2004).

How might these environmental trends have influenced the course(s) of hominin evolution? The links may not have been directly via the most common resources available for sustenance in particular habitats. By now we have a good idea of the proportions of C_3 - and C_4 -derived foods in the diets of at least two South African hominin taxa: *Australopithecus africanus* and *Paranthropus robustus*, which suggest that C_4 -derived foods formed consistently significant contributions to their diets with an overall estimate of 30–35% (Sponheimer et al., 2005). We have rather few data for *Homo* (Lee-Thorp et al., 2000), but it is clear that both australopithecids and early *Homo* were engaging actively in C_4 foodwebs, whether the environments they inhabited were relatively closed and wooded (as at Makapansgat M3 and Sterkfontein M4) or more open and grassy (as in Swartkrans M2 and Sterkfontein M5). There is no evidence that the isotopic composition of their diets varied over time (Sponheimer et al., 2005), despite a great deal of evidence (shown here and elsewhere) that environments changed considerably. This is surprising given that these hominins are highly isotopically heterogeneous within any discrete time slice, and thus seem quite capable of surviving on a variety of different foods. This behavior stands in marked contrast to chimpanzees that seem not to incorporate measurable amounts of C_4 resources even in relatively open savanna environments (Schoeninger et al., 1999; Sponheimer et al., 2006).

Hence, most early hominins may have been capable of flourishing in a broader array of environments than extant great apes, and the grassy or woody nature of their environments does not seem to have influenced their dietary ecology to a great extent. However, the isotopic dietary data we have so far strongly suggests that these hominins were well-able to exploit C₄ foods from a relatively early period. In other words, these australopithecids may have been “pre-adapted” to successfully exploit emerging more open C₄ grass savannas. Thus, they may be considered as archetypal, terrestrial, savanna-adapted primates more closely analogous (in respect of dietary behavior and foraging opportunism at least) to baboons than to the great apes. When C₄ grasses became a dominant component of African landscapes in the latest Pliocene and early Pleistocene, both *Paranthropus* and *Homo* were well-placed to exploit these environments.

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Appendix 1. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2006.11.020

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