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The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet

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The diets of *Australopithecus africanus* and *Paranthropus robustus* are hypothesized to have included C_4 plants, such as tropical grasses and sedges, or the tissues of animals which themselves consumed C_4 plants. Yet inferences based on the craniodental morphology of *A. africanus* and *P. robustus* indicate a seasonal diet governed by hard, brittle foods. Such mechanical characteristics are incompatible with a diet of grasses or uncooked meat, which are too tough for efficient mastication by flat, low-cusped molars. This discrepancy, termed the C_4 conundrum, has led to the speculation that C_4 plant underground storage organs (USOs) were a source of nutrition for hominin species. We test this hypothesis by examining the isotopic ecology of African mole rats, which consume USOs extensively. We measured $\delta^{18}O$ and $\delta^{13}C$ of enamel and bone apatite from fossil and modern species distributed across a range of habitats. We show that $\delta^{18}O$ values vary little and that $\delta^{13}C$ values vary along the C_3 to C_4/CAM-vegetative axis. Relatively high $\delta^{13}C$ values exist in modern *Cryptomys hottentotus natalensis* and *Cryptomys* spp. recovered from hominin-bearing deposits. These values overlap those reported for *A. africanus* and *P. robustus* and we conclude that the USO hypothesis for hominin diets retains certain plausibility.

Keywords: hominin evolution; stable isotopes; plant underground storage organs; geophytes; Bathyergidae; *Cryptomys*

1. INTRODUCTION

The evolution of human diet is informed by multiple lines of evidence, including craniodental morphology, dental microwear, comparative primate ecology and stable isotope analysis (Teaford & Ungar 2000; Teaford *et al.* 2002). The carbon isotope composition ($\delta^{13}C$) of hominin tooth enamel indicates a diet heavily influenced by plants that use C_4 photosynthesis or Crassulacean acid metabolism (CAM). As a result, the diet of *Australopithecus africanus* and *Paranthropus robustus* is hypothesized to have included C_4 plants, such as tropical grasses and sedges, or the tissues of animals which themselves consumed C_4 plants (Sponheimer *et al.* 2005*a*). Yet inferences based on the microwear and craniodental morphology of early hominins indicate a seasonal diet governed by modestly tough foods (e.g. *A. africanus*; Scott *et al.* 2005), hard, tough foods (e.g. *A. anamensis*; Macho *et al.* 2005; cf. Grine *et al.* 2006*a*), hard, brittle foods (e.g. *A. afarensis*; Ryan & Johanson 1989; Ungar 2004; cf. Grine *et al.* 2006*b*) or hard, abrasive foods (e.g. *P. bosei* and *P. robustus*; Demes & Creel 1988; Scott *et al.* 2005). Such mechanical characteristics are incompatible with a diet of C_4 grass blades or uncooked meat; both foods are too fracture resistant for efficient mastication by flat, thickly enamelled, low-cusped molars (Lucas & Peters 2000; Teaford & Ungar 2000). In an effort to reconcile this discrepancy, termed the C_4 conundrum, authors have suggested that the contribution of C_4 tissues to hominin diets could be, in part and to different extents, derived from termites, sedges and/or plant underground storage organs (USOs; Sponheimer & Lee-Thorp 2003; Sponheimer *et al.* 2005*a*,*b*).

Plant USOs are starchy geophytic structures, such as corms, bulbs, rhizomes and tubers. They are relatively common in xeric habitats (Pate & Dixon 1982; Vincent 1985; Proches *et al.* 2006), and their importance in human evolution has received considerable theoretical attention (Robinson 1954; Coursey 1973; Hatley & Kappelman 1980; Laden & Wrangham 2005). For instance, it is hypothesized that the changes in tuber consumption facilitated the initial emergence and spread of *Homo erectus* out of Africa (Hawkes *et al.* 1998; O'Connel *et al.* 1999; Wrangham *et al.* 1999). Such arguments are challenging to test because direct evidence for USO consumption is difficult to obtain, particularly for more remote time periods. USOs themselves are perishable, as are many of the tools used to collect and process them.

Today, a diet of USOs is characteristic of human hunter gatherers in arid environments, particularly as a fallback food (Vincent 1985; Campbell 1986). Many of the USOs edible to humans are also consumed by African mole rats (Bathyergidae; Laden & Wrangham 2005), a radiation of rodents that have specialized in this food base for 40 Myr (Faulkes *et al.* 2004). Importantly, a survey of faunal assemblages at hominin-bearing localities reveals a statistical co-occurrence with mole rats (Laden & Wrangham 2005). This result suggests co-occupation of environments suitable for USO-bearing plants and raises the possibility that hominins and mole rats competed for similar food items. An analysis of stable carbon and oxygen isotopes is well suited to test this hypothesis.

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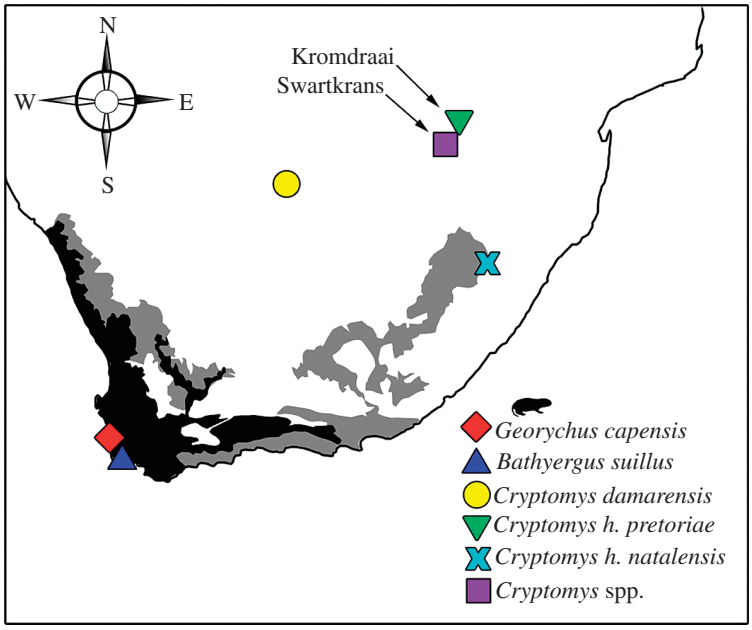

Figure 1. Southern African localities where bathyergid skulls were collected; *Bathyergus suillus* (33°58′26.4″ S; 18°37′0.6″ E; $n=11$), *Cryptomys damarensis* (27°27′42.2″ S; 23°25′50.7″ E; $n=10$), *Cryptomys hottentotus natalensis* (29°32′02.6″ S; 29°36′29.4″ E; $n=7$), *Cryptomys hottentotus pretoriae* (25°45′2.1″ S; 28°11′9.1″ E; $n=7$) and *Georychus capensis* (33°22′41.0″ S; 18°22′41.8″ E; $n=7$). Specimens of *Cryptomys* spp. ($n=23$) were recovered from Kromdraai B and Swartkrans Member 1. The black (0–25%), grey (25–75%) and white (75–100%) polygons show the proportion of C_4 species among grasses in South Africa (redrawn from Vogel *et al.* 1978).

Ratios of stable carbon isotopes ($^{13}C/^{12}C$) distinguish plants that use different photosynthetic pathways. Plants that have carbon-concentrating, or double carboxylation, mechanisms have advantages in warm, highly xeric and/or seasonal environments (Keeley & Rundel 2003). Some plants segregate carboxylation steps in time (CAM plants), while others segregate them in space with specific tissues (C_4 plants; Keeley & Rundel 2003). These mechanisms lead to different isotope compositions relative to plants that use a single carboxylation pathway (C_3 plants; Ehleringer & Rundel 1989). Ratios of $^{13}C/^{12}C$ are maintained in the tissues of animals that consume these plants or the animals that eat these primary consumers (Koch 1998). Accordingly, an isotopic analysis of consumer tissues can reveal the types of primary production supporting a food web. Consumption of C_3 plants is indicated by relatively low $^{13}C/^{12}C$ ratios, whereas that of C_4 plants is indicated by relatively high $^{13}C/^{12}C$ ratios. CAM plants tend to have intermediate values, but in many environments they are indistinguishable from C_4 plants (Keeley & Rundel 2003).

Additionally, ratios of oxygen isotopes ($^{18}O/^{16}O$) are diagnostic of certain dietary characteristics and environmental conditions (Koch 1998). For instance, oxygen in the bioapatite of bones and teeth is derived from body water; oxygen in the body water of terrestrial animals is supplied chiefly by oxygen in food or drinking water. Consequently, the factors that alter the oxygen isotope composition of ingested water can influence the $^{18}O/^{16}O$ ratios of bioapatite. For instance, the oxygen isotope composition of meteoric water (water that is derived from the atmosphere) is positively correlated with annual and seasonal temperatures; the isotopic values of surface water are increased by preferential loss of ^{16}O during evaporation. The water in plant roots and stems is similar to the source water, whereas that in leaves may be substantially enriched in ^{18}O due to evapotranspiration. As a result, the changes in $^{18}O/^{16}O$ ratios in consumers may indicate changes in diet, although temporal or spatial variation of these ratios due to climate shifts often eclipses suspected dietary signals.

In tandem, the analysis of stable carbon and oxygen isotopes can reveal important aspects of an organism's feeding ecology (Koch *et al.* 1994), and comparative studies of modern and fossil taxa may yield insight into the diet of extinct animals. Here, we report on the isotopic ecology of modern and Plio–Pleistocene mole rats in order to inform hypotheses on the diet of hominin species. A referential model based on mole rats is advantageous for three reasons. First, it can falsify or strengthen the hypothesis that ^{13}C-enriched isotope values are associated with a diet of USOs. Second, it can determine whether ^{13}C-enriched plants with USOs were temporally and spatially available to *A. africanus* and *P. robustus*. Third, a comparison of modern mole-rat dietary proclivities and stable isotope ratios may signify which types of USO, if any, were plausible food items for hominins.

2. MATERIAL AND METHODS

(a) *Sample provenience and preparation*

We analysed bone apatite from the mandibular ramus of five South African mole-rat taxa, two of which are different subspecies (figure 1). The species were chosen for their geographical and dietary breadth; each relies on USOs to a different extent (table 1). We also analysed enamel and bone apatite from the incisors and dentary, respectively, of *Cryptomys* spp. recovered from Kromdraai B and Swartkrans Member 1 (*ca* 1.9–1.7 Myr ago; Vrba 1985). The specimens, collectively catalogued as JY001–JY003, are housed in the Transvaal Museum, Pretoria, South Africa ($n=23$). We used a precision dental drill to collect approximately 5 mg apatite.

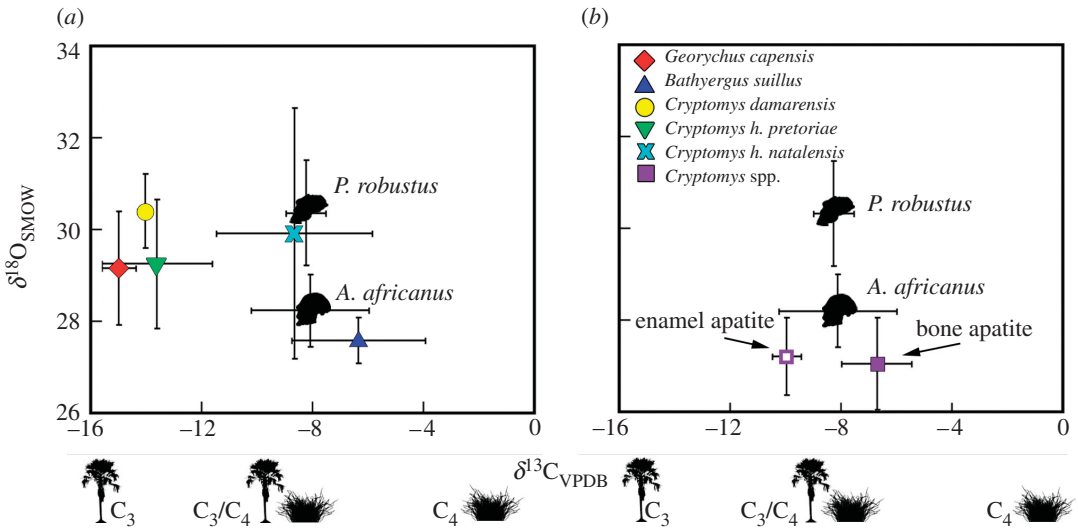

Figure 2. (*a*) Modern mole rats versus Plio–Pleistocene hominins: the $\delta^{13}C$ and $\delta^{18}O$ values of modern mole-rat tooth enamel (data available in table 1 in the electronic supplementary material) plotted with values reported for *A. africanus* and *P. robustus* (Sponheimer *et al.* 2005*a*). (*b*) The $\delta^{13}C$ and $\delta^{18}O$ values of Plio–Pleistocene *Cryptomys* spp. bone and tooth enamel plotted with the values reported for *A. africanus* and *P. robustus*.

The samples were ground with an agate mortar and pestle, washed in 2–3% NaOCl and soaked in 1 M acetic acid with calcium acetate buffer (pH 5.2) to remove diagenetic carbonates. Each sample was washed, dried and weighed to approximately 1.5 mg.

(b) *Analytical procedure*

We analysed samples using a Micromass Optima dual inlet mass spectrometer located in the Departments of Earth and Planetary Sciences and Ocean Sciences, University of California, Santa Cruz. Isotope ratios for C and O are presented as δ values, where $\delta = 1000((R_{sample}/R_{standard})-1)$ and R = either $^{13}C/^{12}C$ or $^{18}O/^{16}O$. Reference standards are Vienna PeeDee belemnite for carbon and standard mean oceanic water for oxygen. Units are expressed as parts per thousand (‰).

To compare the modern isotopic data with those from Plio–Pleistocene specimens, carbon isotope values were corrected for the global decrease in the ^{13}C content of atmospheric CO_2 due largely to fossil fuel burning over the last 150 years (the Suess effect; Idermühle *et al.* 1999). Based on ice core records (Francey *et al.* 1999), we applied a −1.2‰ correction to all Plio–Pleistocene samples (Leuenberger *et al.* 1992; table 1 in the electronic supplementary material).

(c) *Statistical analyses*

Statistical tests were performed with JMP v. 5.0.1 for Macintosh. When possible, analysis of variance was used to assess differences in carbon and oxygen isotope composition between species. Because some data violated the assumptions of parametric statistical analysis, non-parametric Wilcoxon Z (two-sample) and Kruskal–Wallis χ^2 (multiple comparison) tests were used when necessary; further comparisons of significance were investigated with the Tukey HSD *post hoc* test. Orthogonal regression was used to assess correlations between the $\delta^{18}O$ values of mole rats against modelled $\delta^{18}O$ values of regional meteoric precipitation using the 'OIPC: online isotopes in precipitation calculator' of Bowen (2006) and mean annual precipitation (figures 1 and 2 in the electronic supplementary material).

3. RESULTS

We analysed four species and two subspecies of modern mole rats (figure 1). The $\delta^{13}C$ values varied significantly along the C_3 to C_4/CAM-vegetative axis (Kruskal–Wallis $\chi^2_5 = 36.86$; $p < 0.0001$; figure 2*a*). Three species (*Cryptomys damarensis*, *Cryptomys hottentotus pretoriae* and *Georychus capensis*) had isotopic values indicative of a C_3-based diet. Two species (*Bathyergus suillus* and *Cryptomys hottentotus natalensis*) showed considerable variation and had less negative $\delta^{13}C$ values (Tukey HSD $Q = 2.87$; $p < 0.05$). The $\delta^{18}O$ values for all modern mole rats (except *B. suillus*) were similar, ranging from 27 to 31‰ (Kruskal–Wallis $\chi^2_5 = 4.80$; $p = 0.19$; figure 2*a*). *Bathyergus suillus* had $\delta^{18}O$ values significantly less positive than other species (Tukey HSD $Q = 2.87$; $p < 0.05$).

The $\delta^{13}C$ values of enamel ($n = 3$) and bone apatite ($n = 23$) from Plio–Pleistocene *Cryptomys* spp. differed (Wilcoxon $Z = -2.65$; $p = 0.008$; figure 2*b*), indicating post-mortem alteration of the bone apatite, which is a well-known effect at these sites (Lee-Thorp & van der Merwe 1987; Lee-Thorp & Sponheimer 2003). The $\delta^{18}O$ values of Plio–Pleistocene *Cryptomys* spp. bone apatite and enamel apatite were similar statistically (Wilcoxon $Z = 0.00$; $p = 1.00$), suggesting little or no post-mortem alteration of oxygen ratios in bone apatite. The isotopic composition of the enamel apatite indicates a diet influenced by either CAM or C_4 plants, similar to that of modern *C. h. natalensis*. Oxygen isotope δ values of Plio–Pleistocene *Cryptomys* spp. were lower than those for all modern populations ($F_{1,64} = 31.32$; $p < 0.0001$), except *B. suillus* (Wilcoxon $Z = 1.62$; $p = 0.11$).

Despite spatial and temporal differences, the $\delta^{13}C$ and $\delta^{18}O$ values of modern *C. h. natalensis* did not differ from those reported for *A. africanus* and *P. robustus* ($\delta^{13}C$ values: Wilcoxon $Z = -0.34$; $p = 0.73$; $\delta^{18}O$ values: Wilcoxon $Z = -0.30$; $p = 0.77$; figure 2*a*). Although a robust statistical analysis of Plio–Pleistocene *Cryptomys* spp. enamel apatite is precluded on the basis of limited samples ($n = 3$), a non-parametric test revealed overlapping $\delta^{13}C$ and $\delta^{18}O$ values with those of *A. africanus* ($\delta^{13}C$: Wilcoxon

Table 1. Dietary characteristics of mole-rat species in the present study. (Plant genera that fix carbon via the C_4 pathway are indicated in bold text; plant genera capable of fixing carbon via the CAM photosynthetic pathway are indicated with an asterisk. Cormous, bulbous and tuberous classifications follow Manning *et al.* (2002) or the personal observations of N. C. Bennett.)

	dietary characterization				
species	general descriptive characteristics	cormous genera	bulbous genera	tuberous genera	source
Bathyergus suillus	>60% aerial vegetation (***Cynodon dactylon***[a]); roots, small geophytes	*Babiana, Cyanella, Moraea* (=*Homeria*)	*Lachenalia, Ornithogalum, Oxalis**	*Othonna**, *Wachendorfia*	Davies & Jarvis (1986); Bennett & Jarvis (1995); Smith & Winter (1996); Sage *et al.* (1999); N. C. Bennett (personal observation, 2005)
Cryptomys damarensis	geophytes, large and dispersed		*Dipcadi, Ledebouria, Ornithogalum*	*Acanthosicyos, Eriospermum, Talinum**	Jarvis & Bennett (1990); Bennett & Jarvis (1995); Jarvis *et al.* (1998)
Cryptomys hottentotus[b]	geophytes and grass rhizomes	*Cyanella, Moraea* (=*Hexaglottis*) (=*Homeria*), *Micranthus, Romulea*	***Alloteropsis***[c], *Ornithogalum, Oxalis**	*Herrea, Trachyandra, Wachendorfia*	Genelly (1965); Lovegrove & Jarvis (1986); Smith & Winter (1996); Sage *et al.* (1999); N. C. Bennett (personal observation, 2005)
Georychus capensis	<15% aerial vegetation; small geophytes	*Geissorhiza, Micranthus, Moraea* (=*Hexaglottis*) (=*Homeria*), *Ornithogalum, Romulea*	*Albuca, Lachenalia, Ornithogalum, Oxalis**	*Herrea, Trachyandra*	Du Toit *et al.* (1985); Lovegrove & Jarvis (1986); Smith & Winter (1996); Spinks *et al.* (1999); N. C. Bennett (personal observation, 2005)

[a] Grass blades and rhizomes.
[b] *Cryptomys hottentotus* is interpreted to include the subspecies *Cryptomys h. natalensis* and *Cryptomys h. pretoriae*. Another subspecies, *Cryptomys h. hottentotus*, is known to consume *Romulea* corms (Bennett & Jarvis 1995), while some colonies consume *Ornithogalum* bulbs (more than 90% of diet) or *Lachenalia* bulbs (more than 60% of diet) selectively (Spinks *et al.* 1999).
[c] A population studied by Genelly (1965) consumed the bulbs and seeds of *Alloteropsis* (Poaceae) nearly exclusively.

$Z=-0.91$; $p=0.36$; $\delta^{18}O$: Wilcoxon $Z=-1.82$; $p=0.07$; figure 2*b*).

4. DISCUSSION

> The man who has nothing to boast of but his illustrious ancestry is like the potato—the best part under ground.
> Thomas Overbury—*Characters* (1613)

Three conclusions are evident from this study. First, the $\delta^{13}C$ values of modern mole rats evince a high degree of variance along the C_3 to C_4/CAM-vegetative axis. Second, relatively high $\delta^{13}C$ values exist in *Cryptomys* spp. specimens recovered from hominin-bearing deposits. Third, the hypothesis that the diet of *A. africanus* and *P. robustus* included USOs to some extent retains certain plausibility on the basis of comparative isotopic ecology.

(a) *The isotopic ecology of mole rats*

The $\delta^{18}O$ values of mole rats showed little systematic variation. We assessed whether this variation can be explained by modelled $\delta^{18}O$ variation in meteoric water across Africa (Bowen 2006) or by mean annual rainfall. We found a negative correlation between the $\delta^{18}O$ values of mole rats and meteoric water ($r=-0.47$; figure 1 in the electronic supplementary material), which suggests that mole rats may obtain their water from plants. A negative correlation between mole-rat values and regional mean annual rainfall ($r=-0.43$; figure 2 in the electronic supplementary material) is consistent with this suggestion, as environmental moisture influences $\delta^{18}O$ variability in plants. The $\delta^{18}O$ values of mole rats therefore appear to be influenced most strongly by environmental moisture levels, as mediated by the evaporative effects on plant waters, rather than the $\delta^{18}O$ values of meteoric water itself. A similar effect of moisture level on the $\delta^{18}O$ values of herbivores has been detected previously (Ayliffe & Chivas 1990; Levin *et al.* 2006).

Our analysis of $\delta^{13}C$ values in mole-rat tissues permits increased dietary resolution among populations. As many as three species of mole rat live in the same habitat (Lovegrove & Jarvis 1986), hence niche partitioning is expected. A reliance on USOs does vary between species (table 1), and some species, such as *B. suillus*, consume aboveground resources. The relatively ^{13}C-enriched values of *B. suillus* are consistent with a previous report based on bone collagen (Sealy & van der Merwe 1986) and with observations of foraging behaviour. The diet of *B. suillus* is nearly 60% *Cynodon dactylon*, a C_4 grass, or more variably composed of stems and leaves (Reichman & Jarvis 1989; Bennett & Jarvis 1995). The $\delta^{13}C$ values of *C. damarensis* and *C. h. pretoriae* are also consistent with previous reports of dietary specialization; they consume the corms and bulbs of C_3 plants (table 1) despite living in an environment where most grass species are C_4 (figure 1). In contrast, *C. h. natalensis*—which also relies on bulbs, corms and grass rhizomes in a C_4-dominated system—has elevated $\delta^{13}C$ values. Specimens of *B. suillus* and *G. capensis* co-occur along the southwestern Cape, but they have very different $\delta^{13}C$ values, indicating divergent feeding strategies. This analysis reveals that the mere presence of mole rats in a C_4 ecosystem cannot predict the availability of C_4 USOs (cf. Laden & Wrangham 2005). Additionally, mole rats that live in the same habitat can display distinctly different isotopic signatures.

The genus *Cryptomys* has been a member of the southern African ecosystem for *ca* 17 Myr ago (Faulkes *et al.* 2004). Based on the retention of specialized morphological characteristics known to correspond with a diet of USOs, such food items were likely available for a comparable period. In fact, consumption of C_4 resources has been documented in non-USO specialist rodents from Late Pliocene South African deposits (Hopley *et al.* 2006). Our analysis of *Cryptomys* from Kromdraai B and Swartkrans Member 1 demonstrates that it consumed C_4 or CAM foods 1.9–1.7 Myr ago. This result suggests that the USOs of C_4 or CAM plants—bulbs and corms in particular—were available to hominins recovered from the same localities, and thus could have contributed to the elevated $\delta^{13}C$ values of *A. africanus* and *P. robustus*.

(b) *USOs and the C_4 conundrum*

Uncertainty exists as to whether C_4 USOs existed in quantities sufficient to result in the elevated $\delta^{13}C$ values of *A. africanus* and *P. robustus*. This uncertainty stems from differing opinions on the habitats available to foraging hominins. Peters & Vogel (2005) observed that edible C_4 plants are typically restricted to marshes, wetlands and disturbed ground, and that environmental models available for early South African hominin sites do not indicate such habitats. Yet habitat models based on mammalian faunal assemblages suggest a moist grassland characterized by trees, streams and rivers (Reed 1997; Avery 2001), and recent theoretical considerations have suggested that wet river margins and associated habitats were critical to hominin origins (Conklin-Brittain *et al.* 2002; Wrangham 2005). Such environments tend to be rich in USOs (Copeland 2004); furthermore, CAM plants (which may have $\delta^{13}C$ values similar to C_4 plants) occur across the African habitats regardless of surface moisture. CAM plants range from forests and edaphic grasslands to semiarid savannahs and desert environments, and frequently have USOs (Manning *et al.* 2002). Importantly, chimpanzees living in relatively dry habitats consume little or no C_4 plant food (Schoeninger *et al.* 1999; Sponheimer *et al.* 2006*a*), which limits to some extent the value of modelling hominin diets on the foraging behaviour of chimpanzees in savannah-like environments.

Other chemical analyses of food webs in Africa bear on the USO question. Sr/Ca ratios may indicate consumption of USOs because underground plant tissues are thought to have unique Sr/Ca patterns (Sillen *et al.* 1995; Sponheimer *et al.* 2005*b*). An analysis of Sr/Ba ratios revealed relatively high values in *Cryptomys hottentotus* when compared with other fauna in South Africa (Sponheimer & Lee-Thorp 2006). Although promising, more research and larger sample sizes are needed to better understand how Sr/Ca and Sr/Ba ratios fractionate within modern ecosystems, particularly among the USO-bearing plant groups and the animals known to consume them. Isotopic subsampling of the dental perikymata of *P. robustus* has revealed highly variable $\delta^{13}C$ values, which has been interpreted as evidence for seasonal foraging on very different foods (Sponheimer *et al.* 2006*b*). Alternatively, because much of this variation is within the range exhibited by USO specialists, this result may instead

indicate foraging on different proportions of seasonally abundant USO-bearing plants.

(c) *Converging lines of evidence for USO usage*

The behaviour of living primates suggests that hominins probably selected foods on the basis of specific mechanical and nutritional properties. Mechanically, the craniodental morphology and the microwear of early hominin species indicate a diet characterized frequently or occasionally by relatively hard, gritty foods (Teaford *et al.* 2002). Some USOs would appear to fit these criteria, yet relevant studies are few. When chacma baboons (*Papio ursinus*) consume USOs during the dry season, their molar microwear bears a resemblance to the extensive pitting observed on specimens of *P. robustus* (Daegling & Grine 1999). This study suggests that USOs are abrasive; however, an analysis of the mechanical characteristics of putative hominin foods, particularly corms and bulbs, may yield further insights. For instance, the tubers of *Kirkia wilmsii* are two to nine times more puncture resistant than the bulbs of *Cyperus usitatus* (Peters & Maguire 1981). In this regard, Stahl (1984, p. 156) may have been prescient: 'it would seem important to distinguish types of storage organs in discussing their potential as food sources for early hominids'.

Compellingly, USOs also vary in their nutritional properties. Bulbs and corms are a relatively rich source of starch carbohydrates when compared with tubers (Orthen 2001; Schoeninger *et al.* 2001), and Conklin-Brittain *et al.* (2002) suggested that a dietary shift to USOs among australopith-grade hominins led to a reduction in fibre intake and an overall improvement in nutritional quality. In fact, the fibre content of wild USOs in the diet of modern *Cryptomys* is much lower than that of fruit and pith in the diet of chimpanzees (Bennett & Jarvis 1995). Typically, a fibrous diet favours a digestive system capable of caeco-colic fermentation (Alexander 1993), which is characteristic of hominoid primates (Lambert 1998). A mole-rat species with a similar isotopic composition to hominins, *Bathyergus suillus*, is a caeco-colic fermenting herbivore, rather than a caecal fermenter, as is the case in most rodent species (Kotze *et al.* 2006). Such an anatomical resemblance suggests that the digestive kinetics of the hominoid gut would not preclude an adaptive shift towards the consumption of USOs.

In conclusion, our isotopic analysis of modern and Plio–Pleistocene mole rats reveals the inclusion of ^{13}C-enriched foods in their diets. Since mole rats are USO specialists, this enriched isotopic signature is certain to be derived to a large extent from the USO-bearing plants. Accordingly, the consumption of USOs by early hominins cannot be refuted on the basis of δ^{13}C values, although it is apparent that other food objects could have contributed to the ^{13}C-enriched values of hominin teeth, such as termites and the flesh of grazing animals (Backwell & d'Errico 2001; Peters & Vogel 2005; Sponheimer *et al.* 2005*b*), or, perhaps, the flesh of mole rats themselves (Henshilwood 1997). Finally, although we have focused on C_4 USOs, it is important to emphasize that CAM plants may also have contributed to the ^{13}C-enriched values of *A. africanus* and *P. robustus*. Many South African CAM plants are geophytic; indeed, 20% of the Cape flora is characterized as such (Proches *et al.* 2006). In some areas, geophytic plants represent 40% of the total flora (Snijman & Perry 1987; Manning *et al.* 2002). Perhaps not surprisingly, accumulations of cormous tunics are widespread in the Early Holocene archaeological record of the western Cape (Deacon 1976), indicating the importance of USOs, or corms and bulbs specifically, as an important food resource. Future directions will include a study of δ^{13}C values among geophytic species and an analysis of USO mechanical characteristics.

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