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## Review

# Differential resource utilization by extant great apes and australopithecines: towards solving the C<sub>4</sub> conundrum<sup>☆</sup>

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## Abstract

Morphological and biogeochemical evidence suggest that australopithecines had diets markedly different from those of extant great apes. Stable carbon isotope analysis, for example, has shown that significant amounts of the carbon consumed by australopithecines were derived from C<sub>4</sub> photosynthesis in plants. This means that australopithecines were eating large quantities of C<sub>4</sub> plants such as tropical grasses and sedges, or were eating animals that were themselves eating C<sub>4</sub> plants. In contrast, there is no evidence that modern apes consume appreciable amounts of any of these foods, even in the most arid extents of their ranges where these foods are most prevalent. Environmental reconstructions of early australopithecine environments overlap with modern chimpanzee habitats. This, in conjunction with the stable isotope evidence, suggests that australopithecines and great apes, even in similar environments, would utilize available resources differently. Thus, the desire or capacity to use C<sub>4</sub> foods may be a basal character of our lineage. We do not know, however, which of the nutritionally disparate C<sub>4</sub> foods were utilized by hominids. Here we discuss which C<sub>4</sub> resources were most likely consumed by australopithecines, as well as the potential nutritional, physiological, and social consequences of eating these foods.

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## 1. Introduction

Ideas about early hominid diets have changed dramatically since the discovery of *Australopithecus africanus* in 1924 (Dart, 1925). Initially, the potential importance of animal foods was stressed because hominids were believed to have inhabited

arid environments that contained few foods utilized by extant great apes (Dart, 1925, 1926; Robinson, 1954). This thinking began to change by the 1980s as new environmental reconstructions demonstrated that australopithecines did not inhabit severe, arid environments (Vrba, 1985; Bonnefille, 1983; Cadman and Rayner, 1989; WoldeGabriel et al., 1994; Reed, 1997). In addition, a series of dental microwear studies revealed similarities in the microscopic pitting and scratching on the molars of *Australopithecus africanus* and extant chimpanzees (*Pan troglodytes*) (Grine, 1986; Grine and Kay, 1988). These similarities were interpreted as meaning that early hominids were not

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first and foremost omnivores, but rather herbivores that concentrated on fleshy fruits and leaves.

Nevertheless, many studies have documented craniodental adaptations in *Australopithecus* that suggest its diet differed significantly from that of chimpanzees (Robinson, 1954; Jolly, 1970; Wolpoff, 1973; Hatley and Kappelman, 1980). The thick enamel, large post-canine dentition, and thickened mandibular corpus of *A. africanus* bespeaks an increased emphasis on masticating hard objects, a morphological trend that reached its ultimate expression in the later robust australopithecines (Teaford et al., 2002). However, while the robust australopithecines may have been hard object specialists (Grine and Kay, 1988), the morphologically intermediate dentition of *A. africanus* would be ideal for a generalist with increased dietary diversity compared to extant great apes.

Studies of stable carbon isotopes in australopithecine tooth enamel also suggested that these hominids were not exclusively fleshy fruit and leaf eaters (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., in press). These studies were based upon fractionation of carbon isotopes during photosynthesis. In tropical Africa, grasses and some sedges utilize the  $C_4$  photosynthetic pathway while trees, bushes, shrubs and forbs use the  $C_3$  photosynthetic pathway. As a result of these biochemical differences, these plants have very different ratios of  $^{13}C/^{12}C$  in their tissues (Smith and Epstein, 1971; Vogel et al., 1978). These disparate  $^{13}C/^{12}C$  ratios are then passed down into the tissues of herbivores, albeit fractionated in predictable ways (Lee-Thorp et al., 1989; Cerling and Harris, 1999). Thus, animals that eat  $C_3$  vegetation such as giraffes (*Giraffa camelopardalis*) have very different  $^{13}C/^{12}C$  ratios than animals that eat  $C_4$  vegetation such as zebra (*Equus burchelli*), making carbon isotope analysis a useful technique for studying the diets of modern wildlife (e.g. DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Tieszen and Boutton, 1988; Koch et al., 1995). Almost any tissue can be used to study modern wildlife, but for fossil studies, only the mineral components of bones and teeth (bioapatite) are regularly preserved. Enamel bioapatite is the material of choice for these studies, as it contains few pore spaces, little organic material (~1%), and is highly-crystalline, rendering it essentially 'prefossilized' and less susceptible to post-burial contamination than bone or dentine bioapatite (Wang and Cerling, 1994; Michel et al.,

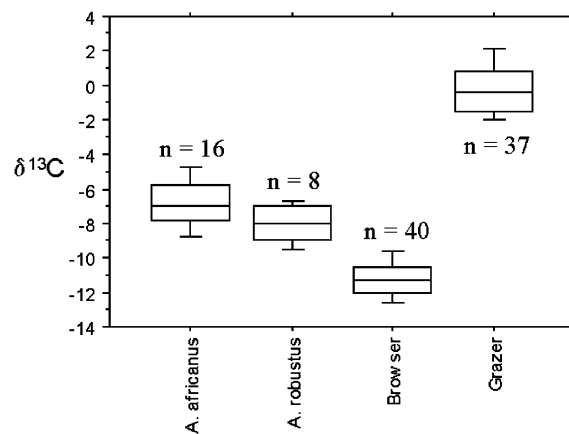


Fig. 1.  $^{13}C/^{12}C$  ratios for  $C_4$  grazers (e.g. equids),  $C_3$  browsers (e.g. giraffids), and australopithecines from Makapansgat, Sterkfontein, and Swartkrans. The box represents the 25–75th percentiles (with the median as a horizontal line) and the whiskers show the 10–90th percentiles.  $^{13}C/^{12}C$  ratios are expressed as  $\delta^{13}C$  values in parts per thousand (‰) relative to the PDB standard. Note that, although australopithecines use  $C_4$  vegetation extensively, there is a great deal of variation in their  $\delta$  values.

1995; Sponheimer and Lee-Thorp, 1999b; Hoppe et al., 2003). Numerous studies have shown that Plio-Pleistocene and even Miocene enamel bioapatite faithfully preserves paleodietary information (e.g. Lee-Thorp and van der Merwe, 1987; Bocherens et al., 1996; Cerling et al., 1997; Sponheimer et al., 1999; MacFadden et al., 1999; Zazzo et al., 2000).

Stable carbon isotope analysis provides a simple means of testing the hypothesis that australopithecines had a specialized diet of  $C_3$  fruits and leaves. If they ate these foods nearly exclusively, then their enamel bioapatite  $^{13}C/^{12}C$  ratios should not be significantly different from those of their  $C_3$  browsing coevals such as giraffe and kudu; however, analyses of South African australopithecines from Makapansgat, Sterkfontein, and Swartkrans shows this not to be the case (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., in press). Instead, both *A. africanus* and *A. robustus* have  $^{13}C/^{12}C$  ratios that are highly different from those of both  $C_3$  and  $C_4$  specialists with which they are associated (ANOVA, Scheffé;  $P < 0.0001$ ) (Fig. 1). There are, however, no differences in the stable carbon isotope compositions of the two australopithecine taxa (ANOVA, Scheffé;  $P = 0.4869$ ). On average, both *A. africanus* and *A. robustus* derived approximately

33% of their dietary carbon from C<sub>4</sub> foods, with some individuals consuming more than 50% C<sub>4</sub> resources (Fig. 1). Schoeninger et al. (2001) argued that australopithecines did not necessarily consume significant quantities of C<sub>4</sub> resources based upon our earlier, smaller data sets. This larger dataset shows this position to be untenable, given the strong statistical distinction between australopithecines and the C<sub>3</sub> consumers with which they were found. Clearly these hominids were not limited to a diet of C<sub>3</sub> fruits and leaves, but also consumed C<sub>4</sub> grasses, sedges, and/or animals that ate these foods. Chimpanzees, in contrast, do not eat appreciable amounts of C<sub>4</sub> foods, even in the most arid and open areas of their range (Schoeninger et al., 1999; Carter, 2001). This suggests that the differences in stable isotope compositions of modern chimpanzees and australopithecines are not simply due to environmental differences, but rather to how resources in the environment are exploited.

Moreover, great variation was observed in the <sup>13</sup>C/<sup>12</sup>C ratios of australopithecines. Indeed, *A. africanus* is more variable than any other taxon occurring at the South African australopithecine sites (Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., in press). Some of this variation may result from dietary differences within a population, but the variability more likely reflects changes in diet over time due to environmental perturbations. Regardless, the variation demonstrates that *A. africanus* was capable of utilizing a wide variety of resources, and is somewhat reminiscent of the dietary flexibility exhibited by modern baboons (*Papio* spp.) (Altmann and Altman, 1970; Dunbar, 1983; Hamilton, 1987; Fleagle, 1999). Chimpanzees, in contrast, tend to exploit similar resources throughout their range, intimating that modern baboons are better ecological analogs for australopithecines.

While the variation is in itself significant, determining exactly which C<sub>4</sub> resources were utilized is important because they all have different physiological, social and behavioral implications. For instance, if australopithecines had a grass based diet similar to the modern gelada baboon (*Theropithecus gelada*), this would almost certainly indicate that their diets were less nutrient dense than those of modern apes, possibly placing important limitations on burgeoning hominid brains and sociality (Aiello and Wheeler, 1995; Milton, 1999). The converse, that australopithecines ate diets rich

in animal foods, would indicate a leap in dietary quality over modern apes which could have been a crucial step in hominid encephalization and concomitantly the development of stone tool industries (Semaw et al., 1997) and increased social complexity (Milton, 1999). Similarly, it has been suggested that consuming the underground storage organs of C<sub>4</sub> sedges would represent an increase in dietary quality compared to that of extant great apes because they would decrease dietary fiber (Conklin-Brittain et al., 2002).

To date there has been very little attention focused on which of these various foods might have contributed to the C<sub>4</sub> dietary signature of australopithecines. Here, we address this gap by discussing these possibilities in light of recently gathered stable isotope data on plants and animals in South Africa.

## 2. The case for grasses

Some researchers noted that the robust cranio-dental anatomical complex of the australopithecines might have been an adaptation for eating grass seeds and roots as do modern gelada baboons, and to a lesser extent, savanna baboons (*Papio* spp.) (Jolly, 1970; Wolpoff, 1973; Dunbar, 1983). A dental microwear study of modern geladas showed, however, that its molar microwear is dominated by scratches with virtually no evidence of pitting (Teaford, 1992), which is quite unlike the frequently pitted molars of early hominids (Grine, 1986; Grine and Kay, 1988). This result was not unexpected, however, as it would seem unlikely that relatively large-brained hominids could be sustained on diets of such limited dietary quality (high in fiber, low in protein and long chain polyunsaturated fatty acids) without supplementation of higher-quality foods. Furthermore, the stable isotope results do not indicate a pure C<sub>4</sub> diet, but rather one in which C<sub>4</sub> foods are very important, but not exclusive. Therefore, one would not expect australopithecines to have similar microwear patterns to geladas. One might expect, however, that australopithecines and savanna baboon populations that consume large quantities of grass seasonally would show similarities in dental microwear (Altmann and Altman, 1970; Harding, 1976; Dunbar, 1983; Strum, 1987). One study of *Papio* molar microwear noted a more *Australopithecus*-like frequency of pitting than was found in *Theropithecus* (Daegling and Grine,

1999). This result must be considered preliminary, however, as we would expect there to be considerable variability in the dental microwear of *Papio* populations given their catholic diets (Altmann and Altman, 1970; Harding, 1976; Dunbar, 1983; Strum, 1987). Further comparative studies of the dental microwear of *Papio* and early hominids should help clarify the degree to which grasses may have contributed to australopithecine diets.

### 3. The case for sedges

Sedges have also received attention as a potential C<sub>4</sub> food for australopithecines. Conklin-Brittain et al. (2002) argued that a trend towards dessication in the Pliocene eroded forests and ultimately forced australopithecines into new, more open habitats. Although the degree, manner, and timing of this deterioration is a matter of some debate, the fact that it occurred is not (Vrba, 1985; DeMenocal, 1995; Feibel, 1997). Conklin-Brittain et al. (2002) reasoned that this loss of forest habitat forced australopithecines into environments that were most similar to their ancestral forest habitats, namely wetlands, swamps and river margins. Sedges are readily available in these environments and have been argued to be among the possible sources of the C<sub>4</sub> signal in australopithecines (Sponheimer and Lee-Thorp, 1999a; Conklin-Brittain et al., 2002). Some sedges have underground storage organs that have protein levels equal to those of most chimpanzee foods (9% crude protein), but much lower fiber levels (16% fiber) than foods consumed by chimpanzees (33%) (Conklin-Brittain et al., 2002). Equally important, these underground parts are abundant yet inaccessible to most other mammals, making sedges a high-quality resource for which there is very little competition. Thus, the regular inclusion of sedges in australopithecine diets would represent an increase in dietary quality over extant great apes.

But how likely is it that the observed C<sub>4</sub> signal in early hominids was derived from C<sub>4</sub> sedges? Approximately 33% of the world's sedges use the C<sub>4</sub> photosynthetic pathway, many of which are found in tropical African environments (Sage et al., 1999). It is wrong to assume, however, that all or even most sedges available to australopithecines would have utilized the C<sub>4</sub> pathway. A recent survey of sedges in South Africa showed that only approximately 40% of available sedges use C<sub>4</sub> photosynthesis (Stock, personal communication).

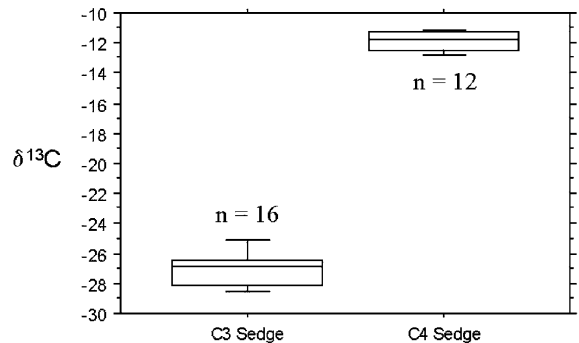


Fig. 2. Boxplot showing  $\delta^{13}\text{C}$  values for C<sub>3</sub> and C<sub>4</sub> sedges collected in June, 2002 from Kruger National Park, South Africa. The box represents the 25–75th percentiles (with the median as a horizontal line) and the whiskers show the 10–90th percentiles. Sedges from Kruger utilize both C<sub>3</sub> and C<sub>4</sub> photosynthesis, although the C<sub>3</sub> sedges are more common (57%).

Moreover, we recently gathered sedges from a variety of localities in Kruger National Park, South Africa. Only 43% of the sedges we encountered utilized C<sub>4</sub> photosynthesis (Fig. 2). Consequently, it would appear that, in South Africa at least, australopithecines would have had to have been extreme sedge specialists to explain the 33% C<sub>4</sub> signature observed in most individuals. More specifically, if we accept that approximately 40% of the sedges that hominids encountered used the C<sub>4</sub> pathway, over 90% of their diet would have had to have been sedges to account for a 33% C<sub>4</sub> signature.

These data suggest that even if sedges did comprise an important resource for early hominids, they were likely supplemented with other C<sub>4</sub> foods. Alternatively, if other C<sub>4</sub> foods were not consumed, australopithecines would have had to have been true sedge specialists to account for the strong C<sub>4</sub> signatures observed in most specimens.

### 4. The case for animal foods

Animal foods can mean many different things including large and small vertebrates, invertebrates, and even bird's eggs. These foods can also be acquired in a variety of ways including active hunting of large game, passive scavenging, and gathering of insects and eggs. Although chimpanzees are known to hunt a variety of small vertebrates such as red colubus monkeys (*Ptilocolobus badius*) and blue duiker (*Cephalophus monticola*), these are pure C<sub>3</sub> consumers (Teleki, 1981; Good-

all, 1986; Mitani et al., 2002). Therefore, intake of these foods could not contribute to the  $C_4$  component of australopithecine diets. More likely sources of the reported  $C_4$  signal include small grass-eating taxa such as hyraxes (*Procavia* spp.) and cane rats (*Thryonomys swinderianus*). The young of larger species would also be tempting targets. For instance, the young of antelope like reedbuck (*Redunca arundinum*) lie hidden and largely helpless for the first several months of life, making them easy prey for enterprising hominids. Arthropods are also potential  $C_4$  foods. Baboons are known to eat grass-eating grasshoppers (Acrididae) almost exclusively during temporary gluts (Hamilton, 1987). Grass eating termites represent another intriguing possibility, particularly given recent studies suggesting that bone tools from Swartkrans were used to extract termites from mounds (Backwell and D'Errico, 2001). Some termites are known to consume  $C_4$  grasses (e.g. *Hodotermes*, *Trinervitermes*), but no studies have quantified the percentage of grass eating done by African mound building termites in general. As a result, it has been difficult to address the possibility that termite consumption led to the observed  $C_4$  signal of australopithecines.

To address this gap, we collected termites from 12 separate mounds in Kruger National Park, South Africa. In an effort to determine the limits of variation likely to be encountered, we sampled from mounds in the northernmost and southernmost areas of the park, as well as in open and closed riverine environments. Although many termite species in Australia have pure  $C_3$  diets (Tayasu et al., 1998), none of the termites we collected in Kruger were pure  $C_3$  eaters, not even those that had mounds in closed riverine environments (Fig. 3). And while a few available termites had nearly 100%  $C_4$  signatures (*Hodotermes*, *Trinervitermes*), the vast majority had approximately 50%  $C_4$  signals irrespective of the environment. These results suggest that hominid consuming termites from mounds in South Africa would undoubtedly have some  $C_4$  input, even if only in more closed riverine environments. On the other hand, the fact that so few termites have a pure  $C_4$  signal makes it unlikely that termite consumption alone was the source of the strong  $C_4$  signal of australopithecines, unless termite foraging was a specialized, habitual behavior. For instance, because termites are approximately 50%  $C_4$  on average, a hominid's diet would have to include about 66% termites to

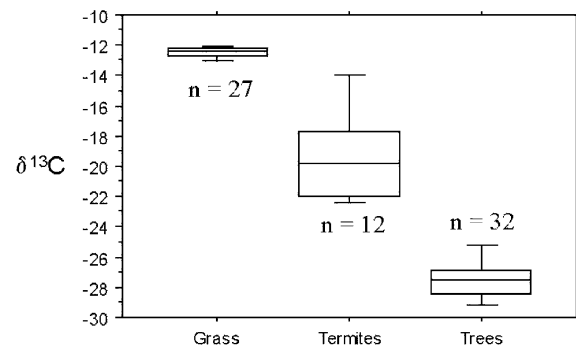


Fig. 3. Boxplot showing  $\delta^{13}C$  values of termites from 12 termite mounds in Kruger National Park, South Africa. The box represents the 25–75th percentiles (with the median as a horizontal line) and the whiskers show the 10–90th percentiles. Note that the termites generally have intermediate  $\delta^{13}C$  values between those of  $C_3$  and  $C_4$  vegetation. This same pattern held true in both closed and open environments.

produce the 33%  $C_4$  signature observed in australopithecines. This might be offset to some extent by the greater digestibility of animal foods compared to most plant foods, but nonetheless, this degree of specialization on termites seems unlikely.

It has been suggested that hominid dental anatomy was not well-suited for the processing of animal foods (Teaford et al., 2002), but this observation only pertains to a limited class of animal foods. A great many animal foods require little if any oral processing. Termites, grasshoppers, ants, grubs, eggs and a variety of other insect delicacies may be consumed whole, and even small vertebrates can be swallowed whole or in a few pieces (Smithers, 1983). Brains, marrow and other soft tissues can also be consumed without oral processing. In addition, no experiments have been conducted to investigate the actual oral and/or pre-oral processing necessary to consume the muscle tissue of small vertebrates. Thus, it seems unwise to unduly limit the potential foods for australopithecines until such studies have been undertaken. Furthermore, consumption of animal foods is common among mammals without seemingly appropriate dentition. One obvious example is the aardwolf (*Proteles cristatus*) which consumes hundreds of thousands of termites per night with largely non-functional, obsolescent dentition (Smithers, 1983). In some cases this apparent disjunction between dental morphology and trophic behavior might result from the dentition being adapted for other, more mechanically challenging

foods in an animal's diet. For example, capuchin monkeys (*Cebus apella*) have large, bunodont dentition with thick enamel adapted for consuming fruits and hard nuts. Nonetheless, up to 50% of capuchin diets can come from animal foods, although the average is closer to 25% (Fleagle, 1999; Rosenberger and Kinzey, 1976; Rosenberger, 1992).

## 5. Conclusion

Several lines of evidence suggest that australopithecine diets differed from those of extant great apes. However, the nature of this difference remains unknown. The thicker enamel, larger post-canine dentition, and greater mandibular corpus robusticity point to the consumption of hard objects, which might have increased dietary breadth (Teaford et al., 2002). Stable carbon isotope data also argue for increased dietary breadth, with C<sub>4</sub> foods being added to ancestral ape diets (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999a; van der Merwe et al., in press). Although C<sub>4</sub> grasses, sedges, and animal foods could have contributed importantly to australopithecine diets, the data presented here suggest it is more likely that two or more of these resources were utilized. Regardless, the fundamental difference between australopithecines and extant apes might be that when confronted with increasingly open areas, apes continue to exploit the foods that are most abundant in forest environments (McGrew et al., 1981), whereas australopithecines utilized novel C<sub>4</sub> resources afforded by the new landscapes in addition to forest foods.

There would have been a number of advantages to such a dietary strategy. It would have allowed australopithecines to survive and even thrive in a much greater variety of habitats than do modern great apes, potentially allowing expansion of their range. Similarly, the increased dietary breadth could have buffered australopithecines against climatic change and habitat loss. Another implication of increased dietary flexibility might be decreased foraging time and mobility, allowing for increased social interaction and possibly greater social complexity. This dietary flexibility could also have increased dietary quality over that of extant apes by adding low fiber underground storage organs and protein- and lipid-rich animal foods to australopithecine menus. This might have been an important step leading to greater encephalization and

development of the genus *Homo* (Aiello and Wheeler, 1995; Milton, 1999; Conklin-Brittain et al., 2002).

If increased dietary breadth was a fundamental australopithecine adaptation, what are we to make of the later robust australopithecines (*A. robustus* and *A. boisei*) in which the dental adaptations reached their 'highest' form? They are believed to have been specialist hard object feeders that were eventually replaced by our *Homo* forebears who, for the first time, had regular access to higher quality animal foods (Aiello and Wheeler, 1995; Milton, 1999). An alternative explanation, however, is that the robust australopithecines were the quintessence of the trend towards dietary diversity because they could access the foods of their progenitors as well as harder foods. One might then argue that they were supplanted by *Homo* not because they ate different kinds of foods, but because *Homo* was more efficient at procuring these resources due to increased use of extra-oral processing (e.g. stone tools) and greater planning depth. It is believed, for instance, that early *Homo* increased access to bone marrow from scavenged or hunted carcasses of medium to large mammals by using stone tools (Blumenshine, 1987), whereas robust australopithecines might, but might not have fully developed this technology (e.g. Semaw et al., 1997). Furthermore, where australopithecines may have eaten antelope lambs only when they stumbled upon them, *Homo* may have had superior planning depth and followed female antelope back to their young, capturing them only when the mother left once more.

While we still have much to learn about the diets of our early hominid ancestors, the topic has gained considerable attention over the past few years. Importantly, foods such as underground storage organs, which have received relatively little attention in the past, are being reconsidered as potential early hominid foods (Hatley and Kappelman, 1980; O'Connell et al., 1999; Conklin-Brittain et al., 2002). These new ideas, coupled with further technical advances in dental microwear (Ungar, 1998), stable light isotope, and elemental analyses (Sillen et al., 1995) of fossil teeth should greatly improve our understanding of early hominid diets.

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