Isotopic Evidence for the Diet of an Early Hominid, *Australopithecus africanus*

Matt Sponheimer and Julia A. Lee-Thorp

Current consensus holds that the 3-million-year-old hominid *Australopithecus africanus* subsisted on fruits and leaves, much as the modern chimpanzee does. Stable carbon isotope analysis of *A. africanus* from Makapansgat Limeworks, South Africa, demonstrates that this early hominid ate not only fruits and leaves but also large quantities of carbon-13–enriched foods such as grasses and sedges or animals that ate these plants, or both. The results suggest that early hominids regularly exploited relatively open environments such as woodlands or grasslands for food. They may also suggest that hominids consumed high-quality animal foods before the development of stone tools and the origin of the genus *Homo*.

Little is known about the diets of hominids that predate the genus *Homo*, because they did not leave archaeological traces such as "kitchen middens" and stone tools. Consequently, researchers have made dietary inferences based on craniodental morphology (*1*–*4*), gross dental wear (*1*, *2*, *5*), and dental microwear (*6*, *7*). Some researchers have stressed the importance of animal foods in the diets of these hominids (*1*, *8*, *9*); others have suggested that they were primarily adapted for the consumption of plant foods such as grass seeds and roots (*3*, *4*). The current consensus, however, is that these early hominids ate fleshy fruits and leaves (*6*, *7*, *10*, *11*). This agrees with evidence that they occupied relatively heavily wooded habitats, not open savannas (*12*–*16*). In contrast, there is evidence suggesting that the later hominids (~2.5 million years ago) *Homo* and *Paranthropus* inhabited more open environments (*13*, *16*) and were omnivorous (*17*–*20*). Here we provide direct isotopic evidence of the diet of an early hominid, the 3-million-year-old *Australopithecus africanus* from Makapansgat Limeworks in Northern Province, South Africa (*13*, *16*, *21*).

Previous studies have shown that the ratio of ^{13}C to ^{12}C in tooth enamel can be used to provide dietary information about extinct fauna (*19*, *22*). The foundation of this approach is our knowledge of photosynthesis in plants. Trees, bushes, shrubs, and forbs (C_3 plants) discriminate more markedly against the heavy ^{13}C isotope during fixation of CO_2 than do tropical grasses and sedges (C_4 plants). As a result, C_3 plants have δ^{13}C values of –22 per mil (‰) to –30‰, with an average of about –26.5‰ (*23*), whereas C_4 plants have δ^{13}C values of –10 to –14‰, with an average of about –12.5‰ (*24*, *25*). Animals incorporate their food's carbon into their tooth enamel with some additional fractionation (*26*). Hence, the relative proportions of C_3 and C_4 vegetation in an animal's diet can be determined by analyzing its tooth enamel with stable isotope mass spectrometry. Animals that eat C_3 vegetation (including fruits, leaves, and the roots of trees, bushes, and forbs) have δ^{13}C values between about –10 and –16‰; animals that eat C_4 tropical grasses (including blades, seeds, and roots) have δ^{13}C values between 2 and –2‰; and mixed feeders that eat both fall somewhere in between these two extremes. Carnivores have tooth enamel δ^{13}C values similar to those of their prey (*26*).

We sampled molar tooth enamel from 4 of the 14 *A. africanus* individuals (MLD 12, MLD 28, MLD 30, and MLD 41) that have been unearthed at Makapansgat. We also analyzed the enamel of associated 3-million-year-old fauna (65 individuals from 19 mammalian taxa) in order to place *A. africanus* within a broader ecological context (Table 1) (*27*). Makapansgat's C_4 consumers (grazing taxa) include the equid *Hipparion lybicum*; the suid *Notochoerus capensis*; and the bovids *Parmularius braini*, *Parmularius* sp. nov., and *Redunca darti*. The C_3 consumers (browsers and browser/frugivores) include the giraffid *Giraffa jumae*; the rhinocerotid *Diceros bicornis*; the chalicothere *Ancylotherium hennigi*; and the bovids *Tragelaphus* sp. aff. *angasi*, *T. pricei*, *Oreotragus* cf. *oreotragus*, and *Cephalophus* sp. The bovids *Makapania broomi* and *Simatherium* cf. *kohllarseni* are the only mixed feeders that we analyzed. *Aepyceros* sp., *Gazella gracilior*, and *G. vanhoepeni* were all C_3 consumers (*28*), despite the fact that their extant kin are generally mixed feeders. This demonstrates the danger of assuming that fossil taxa had the same diets as their closest extant relatives.

Analysis of variance shows that the δ^{13}C values for *A. africanus* are significantly different from the values for grazers, browsers, and mixed feeders from Makapansgat ($P <$ 0.01) (Table 1). The only taxon from which they are not significantly different is the carnivore *Hyaena makapani*. Three of the four hominid specimens (MLD 12, MLD 28, and MLD 30) fall outside the range of C_3 (fruit, herb, or leaf) feeders at Makapansgat. MLD 30 is so enriched in ^{13}C (–5.6‰) that it falls closer to the mean of the grazers than of the browsers. The δ^{13}C values for these specimens are inconsistent with a diet of fruits and leaves (C_3 plants). One specimen (MLD 41), however, does fall within the range of C_3 eaters. These data show that (i) *A. africanus* had a highly variable diet (its range of δ^{13}C values is greater than 18 of the 19 other taxa analyzed), and (ii) the majority of the Makapansgat hominids habitually obtained dietary carbon from C_4 plants such as grasses and sedges or from animals that ate C_4 foods, or both.

Modern South African cercopithecids that range into open woodland and grassland (*Cercopithecus aethiops* and *Papio cynocephalus ursinus*) can become similarly enriched in ^{13}C, though they usually have nearly 100% C_3 diets (Table 1). Ecological studies of *Papio* have shown that grasses can be a dominant component of its diet, particularly in areas with little tree cover and during the dry season (*9*, *29*). Field studies suggest that the only modern primates that consistently consume as much or more C_4 foods than *A. africanus* are *Theropithecus gelada* (*9*, *30*), *Erythrocebus patas* (*31*), and *P. hamadryas* (*32*), all of which inhabit areas with few trees. In contrast, the majority of the Makapansgat hominids consumed somewhere between 25 and 50% C_4 foods despite a relatively high density of trees in the ancient Makapansgat Valley (*12*, *13*, *16*).

This raises the following question: Why did the Makapansgat hominids exploit C_4 resources to such an extent, despite an abundance of C_3 resources as well as evidence that they may have been well adapted for foraging in trees (*33*, *34*)? C_3 feeders are abundant at Makapansgat (*16*), so it is possible that *A. africanus* minimized competition by foraging for C_4 grasses and sedges, particularly during the dry season when a large portion of available nutrition is found in their roots (which cannot be readily accessed by most animals). An equally plausible explanation is that *A. africanus* had a preference for high-quality animal foods, which included C_4 plant-eating insects such as *Trinervitermes trinervoides* or the young of grazing mammals like *R. darti*, or both. There is limited evidence to

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M. Sponheimer, Department of Anthropology, Rutgers University, New Brunswick NJ 08901–1414, USA, and Department of Archaeology, University of Cape Town, Private Bag, Rondebosch 7701, Republic of South Africa. J. A. Lee-Thorp, Department of Archaeology, University of Cape Town, Private Bag, Rondebosch 7701, Republic of South Africa.

help us decide whether one or both of these alternatives is correct. Researchers comparing the dental microwear of *A. africanus* and modern primates did not conclude that these hominids ate grasses (*6*, *7*), but these studies included no grass-eating modern primates. A comparison of the dental microwear of *A. africanus* and modern *Papio* populations from open environments, whose diet is 25 to 50% grasses (*9*), would be ideal, but no such study has been undertaken. Recent research demonstrates, however, that the percentage of pitting versus scratching on the molars of modern *T. gelada* (~10%) (*35*) is different from the percentage previously reported for *A. africanus* (~30%) (*7*). *Theropithecus gelada* consumes grass blades, seeds, and roots nearly exclusively (*9*, *30*), making it a less than ideal analog for a hominid eating 25 to 50% grass foods. Nonetheless, the large difference in microwear features between *Theropithecus* and *A. africanus* suggests that we must seriously consider the possibility that these hominids were ^{13}C-enriched because they consumed animal foods.

Carbon isotope analysis of 1.8- to 1.0-million-year-old *Paranthropus robustus* from Swartkrans in South Africa demonstrates that it too is enriched in ^{13}C as compared to pure C$_3$ consumers (*19*). The mean δ^{13}C value for *A. africanus* (−8.2‰) is very similar to the mean for *P. robustus* (−8.5‰), although the range for the Makapansgat hominids is greater (5.7‰, as compared to 3.2‰). This is surprising because *P. robustus* lived in an area with more abundant C$_4$ grasses (*13*, *16*) and, concomitantly, animals that ate C$_4$ grasses. This similarity in δ^{13}C values, combined with the fact that the craniodental specialization of *P. robustus* may be in an incipient state in *A. africanus* (*2*, *36*), might mean that these species ate similar food items but that the further specialized *P. robustus* ate them more efficiently. Thus, *P. robustus* may have included a higher proportion of tough, fibrous foods in its diet (*6*, *7*) and may have orally processed foods (such as *Sclerocarya* nuts) that *A. africanus* could only access with hammerstones (like chimpanzees use today) (*37*). Presently there is no evidence that *A. africanus* used tools, although it is not unreasonable to assume that they could have used tools in the same manner as chimpanzees do today. Despite this, it is suggestive that the last appearance date of *Australopithecus* and the first appearance date of *Paranthropus* are close in time (~2.5 million years ago) (*13*, *16*, *38*). It is possible that *P. robustus* was better able to process foods that *A. africanus* also favored, contributing to the latter's eventual extinction.

It is believed that the encephalization of early *Homo* was made possible by the consumption of energy- and nutrient-rich animal foods to "pay" for its metabolically expensive brain (*39*, *40*). Our results raise the possibility, however, that dietary quality improved (through the consumption of animal foods) before the development of *Homo* (*41*) and stone tools (*42*) about 2.5 million years ago. Moreover, trace element (Sr/Ca) (*43*) and stable carbon isotope analyses (*44*) do not seem to indicate that early *Homo* from Swartkrans consumed more animal foods than did *A. africanus*. Therefore, the primary dietary difference between *A. africanus* and *Homo* may not have been the quality of their food but their manner of procuring it. One key difference may have been that stone tools allowed *Homo* to disarticulate bones and exploit bone marrow from large carcasses (obtained through hunting or scavenging) that *A. africanus* could not (*17*, *18*, *45*).

Table 1. Mean δ^{13}C values, ranges, standard deviations, and number of individuals we sampled for each taxon from Makapansgat Member 3. Modern cercopithecids are also included for comparison. Permanent molars were sampled, except for larger species such as *Diceros bicornis*, from which mostly juvenile dentition was available (*23*).

Species	Mean (‰)	Range	SD	*n*
C$_4$ plant consumers				
Hipparion lybicum	−0.8	0.2 to −2.0	0.9	5
Notochoerus capensis	−0.8	−0.6 to −1.0	0.3	2
Parmularius braini	0.7	1.2 to −0.2	0.7	4
Parmularius sp. nov.	0.7	1.3 to −0.2	0.8	3
Redunca darti	−1.3	1.3 to −4.5	2.4	4
C$_3$ plant consumers				
Aepyceros sp.	−12.2	−11.0 to −13.0	1.1	3
Ancylotherium hennigi	−10.3	−10.1 to −10.6	0.3	3
Cephalophus sp.	−11.5	−11.4 to −11.6	0.1	2
Diceros bicomis	−11.6	−10.8 to −13.1	1.3	3
Gazella gracilior	−11.6	−10.7 to −12.4	1.2	2
Gazella vanhoepeni	−11.9	−10.9 to −12.8	0.9	4
Giraffa jumae	−11.3	−10.5 to −12.6	0.8	7
Neotragini sp.	−11.6	−11.2 to −12.4	0.5	4
Oreotragus cf. *oreotragus*	−11.6	−11.4 to −11.7	0.2	2
Tragelaphus sp. aff. *angasi*	−11.7	−9.5 to −12.7	1.5	4
Tragelaphus pricei	−11.8	−10.9 to −12.5	0.8	3
Mixed C$_3$ and C$_4$ consumers				
Makapania broomi	−3.4	−1.0 to −5.3	1.8	4
Simatherium cf. *kohllarseni*	−4.0	−3.4 to −4.4	0.5	4
Carnivores				
Hyaena makapani	−8.7	−8.1 to −9.3	0.8	2
Primates				
A. africanus	−8.2	−5.6 to −11.3	2.4	4
Modern primates				
Papio cynocephalus ursinus	−12.3	−10.3 to −14.2	1.1	17
Cercopithecus aethiops	−12.1	−7.8 to −14.3	3.7	3

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M acetic acid to remove diagenetic carbonates. The samples were freeze-dried and placed into individual reaction vessels in a Kiel II autocarbonate device. They were reacted with phosphoric acid at 70°C, and clean dry CO_2 was obtained by cryogenic distillation. $^{13}C/^{12}C$ ratios were measured on a Finnigan MAT 252 mass spectrometer with a precision of $\pm 0.1‰$.

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Ozone Isotope Enrichment: Isotopomer-Specific Rate Coefficients

K. Mauersberger,* B. Erbacher, D. Krankowsky, J. Günther, R. Nickel

Six rate coefficients of relative ozone formation contradict the role of molecular symmetry in the process that results in the enrichment of heavy ozone isotopomers. The results show that collisions between light atoms, such as ^{16}O, and heavy molecules, such as $^{34}O_2$ and $^{36}O_2$, have a rate coefficient advantage of about 25 and 50 percent, respectively, over collisions involving heavy atoms and light molecules. These results suggest that the observed isotope effect for each isotopomer may be caused by the preponderance of a single reaction channel and not through molecular symmetry selection.

A problem in molecular and atmospheric physics has puzzled scientists for almost two decades: the unusually high enrichment in most of the heavy isotopomers of ozone (*1*). This isotope effect has been observed in tropospheric (*2*) and stratospheric (*3*) ozone and has been studied in detail in numerous laboratory experiments (*4*). Despite the progress that has been made during the past 10 years, a convincing physical explanation of the process that results in enrichment is still missing. Ozone is perhaps the most important trace gas in the atmosphere, and its isotope effect is not only an unresolved problem in molecular physics but is also of importance for atmospheric chemistry (*5*).

Laboratory production of ozone in atmospheric oxygen (*6*) permits the determination of isotopomers $^{48}O_3$, $^{49}O_3$, and $^{50}O_3$, where ^{17}O is substituted in the second molecule and ^{18}O is substituted in the third molecule of these isotopomers. After the discovery of an almost equal enrichment (*7*) in the two heavy ozone molecules, which cannot be understood as a conventional isotope effect, a symmetry-selective process in the formation reaction was suggested (*8*). For ozone species $^{49}O_3$ and $^{50}O_3$, about one-third of all molecules are symmetric (for example, $^{16}O^{18}O^{16}O$), and two-thirds are asymmetric (for example, $^{16}O^{16}O^{18}O$); it was proposed (*8*) that the asymmetric reaction intermediate in the O + O_2 collision has a longer lifetime than the symmetric reaction intermediate, which results in an efficient quenching to ground state ozone [a proposal that was not confirmed by experiments (*4*)].

An apparent role of symmetry was found again when the distribution of all ozone isotopomers was measured (Fig. 1). A slight depletion of heavy symmetric molecules $^{17}O^{17}O^{17}O$ and $^{18}O^{18}O^{18}O$ was observed, whereas the highest enhancement (~18%) was measured in the isotopic combination $^{16}O^{17}O^{18}O$, which is an isotopomer with a mass of 51 atomic mass units (amu) and is composed exclusively of asymmetric molecules. All other isotope fractionations are about one-third less. Because of this, Anderson *et al.* (*9*) proposed a mechanism in which, during the ozone formation process, symmetry-selective relaxation from low-lying electronic metastable states to the ground state occurs. Metastable states have indeed been found (*10*), but a connection to the isotope effect has not been made to date.

Gellene (*11*) recently modeled the isotope fractionation shown in Fig. 1 based on nuclear symmetry. In his approach, symmetry restrictions arise for homonuclear diatomics (for example, $^{16}O^{16}O$ and $^{18}O^{18}O$) involved in the O + O_2 collision because a fraction of their rotational states (*f* parity) correlate with those of the corresponding ozone molecule. In contrast, in the case of heteronuclear oxygen molecules (for example, $^{16}O^{18}O$), all of their rotational states (*e* and *f* parity) correlate with those of the resulting ozone molecule. Gellene's theory can reproduce the general features of the enrichment pattern quite well. A number of other attempts have been made (*12*) to find an explanation for the isotope anomaly; none were able to account for the experimental results (*4*).

The role of molecular symmetry was questioned by Anderson *et al.* (*13*), who presented rate coefficients of four selected ozone formation channels. Whereas three channels

$$^{16}O + {}^{16}O^{16}O + M \rightarrow {}^{16}O^{16}O^{16}O + M \tag{1}$$

$$^{18}O + {}^{16}O^{16}O + M \rightarrow {}^{18}O^{16}O^{16}O + M \tag{2}$$

$$^{18}O + {}^{18}O^{18}O + M \rightarrow {}^{18}O^{18}O^{18}O + M \tag{3}$$

had similar rates of formation, which were consistent with a value of $\sim 6 \times 10^{-34}$ cm^6 s^{-1}, the fourth reaction channel

$$^{16}O + {}^{18}O^{18}O + M \rightarrow {}^{16}O^{18}O^{18}O + M \tag{4}$$

resulted in a rate coefficient that was 50% higher than the other three; M represents a third-body molecule. The difference in the rate coefficients of reactions 2 and 4 was unexpected. As seen in Fig. 1, molecules with masses of 50 and 52 amu that were substituted with ^{18}O show similar isotope enrichments of ~13.0 and 14.4%, respectively (*14*). Reactions 2 and 4 produce mainly asymmetric molecules (with the colliding atom becoming the end member of the ozone molecule) (*15*). Thus, the difference in the rate coefficients of reactions 2 and 4 does not support an important role of symmetry in the isotope enrichment process. A similar conclusion was reached by Sehested *et al.* (*16*), who performed rate coefficient studies for the ^{16}O-^{18}O system on dual-channel processes, using CO_2 and Ar as third-body molecules, but

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Max-Planck-Institut für Kernphysik, Division of Atmospheric Physics, P.O. Box 103 980, D-69029 Heidelberg, Germany.

*To whom correspondence should be addressed.