The development of chemical approaches to fossil hominin ecology in South Africa

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When Dart recognised the fossilised skull of the Taung Child as a hominin ancestor, he also observed that its "sere environment" produced few foods preferred by African apes in equatorial forests. He thus set in motion an inquiry into the dietary and environmental proclivities of fossil hominins. His observations ultimately led him to suggest a strong reliance on meat-eating, later elaborated into a hunting model. Subsequent investigations into the diets of the South African australopithecines led to the development of new approaches including dental microwear, stable light isotopes, and trace element analyses, which together led to a new focus on the prime importance of plant foods, for which there had been little direct behavioural evidence. Here we review why and how stable and radiogenic isotope approaches to hominin diet and residence patterns were developed in South Africa, the problems that had to be addressed, and the subsequent outcomes.

Significance:

We outline how a distinctive set of circumstances in South Africa combined to produce world-leading progress in palaeoanthropological and archaeological research based on fossil isotope biogeochemistry. They include a unique natural and fossil heritage, investment in scientific infrastructure and researchers well-versed in cross-disciplinary science. Together they played leading roles in addressing important questions about African fossil heritage. We point to where we believe future progress is required and we suggest that closer attention is paid to the role of plants because, as the basis of all ecosystems, they represent the most important element in the diets of most primates and hominins.

[Abstract in** Setswana**]

Introduction

Raymond Dart's recognition of the Taung skull as an early hominin in 1925[1] set in motion the discovery of further sites and hominin specimens and taxa in South Africa and later in eastern Africa. The taxa of primary interest in our review of events here are *Australopithecus africanus* from Taung, Makapansgat, and Sterkfontein, and *Paranthropus robustus* from Swartkrans, Kromdraai, and Drimolen. Dart recognised that the dentognathic morphology of the Taung fossil differed from that of extant African apes and believed that the ancient environment of the Buxton Quarry, North Western Province was arid and open compared to the favoured forests of chimpanzees and gorillas.[1] These observations led him to consider how they survived and what they ate in such an apparently unforgiving "sere" landscape. Given the apparent paucity of food favoured by forest-loving apes, Dart began to explore the possible role of animal flesh.[1,2] In the early 20th century, the existence of large-scale environmental shifts in the southern African Pleistocene was not yet recognised, although the extensive freshwater tufas and calcrete deposits associated with Taung attested to wetter periods in the past[3], nor did the associated fauna suggest particularly arid conditions[4].

Dart further developed the meat-eater interpretation based on his findings at the older site of Makapansgat, where he found further *A. africanus* specimens and especially abundant mandibles, distal humeri, and proximal radii and ulnas of varied fauna. He concluded that these remnants were weapons used to hunt and prepare prey, leading to his "osteodontokeratic culture" hypothesis for *A. africanus* behaviour.[5] This interpretation was highly influential and underpinned a belief that early hominins, and by implication humans, were naturally bloodthirsty killers – "not in innocence and not in Asia was mankind born"[6]. Dart's "osteodontokeratic culture" ideas comported well with the "Man the Hunter" framing concept, which remained influential for decades.[7]

Dart's ideas were also testable and ultimately led to the founding of several new, crucially important fields in African palaeoanthropology. The first is broadly related to the formation of bone-rich cave deposits where the South African palaeontologist C.K. Brain dissected the evidence at Makapansgat and similar karst dolomitic sites. He concluded that the bone remnants were rather the products of carnivore damage and depositional fragmentation.[8] In doing so he built a distinctive field of taphonomy related to Plio-Pleistocene cave site processes, and more broadly, to palaeoanthropological site formation processes. The next important outcome was the development from the late 1970s onwards of a suite of quantifiable approaches to examine hominin diet. These included analysis of dentognathic morphology[9], dental microstructure[10], and macroscopic damage patterns from crushing, biting, or chewing food items[11]. Scanning electron microscopy was used for the first time to characterise the microscopic traces of damage on molar surfaces resulting from food processing and consumption[12,13] – an approach well-placed to test the 'hard object' hypothesis first mooted by Jolly[14]. Fred Grine's work at the University of the Witwatersrand showed significant distinctions between *Australopithecus africanus* and *Paranthropus robustus* molar occlusal surfaces, suggesting the consumption of "hard brittle objects" (e.g. hard fruits and nuts) for *P. robustus*, but not *A. africanus*. The latter's molar microwear seemed most consistent with a diet of fleshy fruit and leaves.[12,15]

The suggestion that *A. africanus* had a diet of primarily fleshy fruits and leaves and *P. robustus* ate small, hard, seeds, and nuts could potentially be tested based on their carbon isotope compositions. There is a sharp distinction in carbon isotopes between plants following the C_3 photosynthetic pathway (trees and most shrubs with their fruits and nuts) versus C_4 grasses or sedges (and the animals that eat them). Fortunately, the South

African australopithecine sites fall squarely in regions where the grassy vegetation is dominated by C_4 grasses.[16] Thus, *it was feasible* that carbon isotope analysis might allow one to test such dietary hypotheses. For instance, *A. africanus* should have a diet dominated by C_3 vegetation (as do chimpanzees today) if it ate fleshy fruits and leaves from trees, and the same would be true for hard-object-eating *P. robustus* unless those hard items were derived from C_4 plants (e.g. rhizomes, corms, grass seeds). The apparently insurmountable obstacle was the widely held belief that the original isotopic compositions of fossils should have long since been obliterated by diagenesis. Efforts to overcome such issues required decades of work to explore the potential and overcome the scepticism. This paper is the story of those efforts which were played out principally in South Africa. We will touch on direct extensions of this work in eastern Africa, and on other tools derived from chemistry that may be poised to contribute to the dialogue about early hominin diets. However, the story here, like that of the Taung Child, is largely South African. Other recent reviews are available for those seeking an overview of early hominin diets[17], the isotopic contributions to such research[18], and the diverse geochemical tools used for palaeodietary research[19].

Background and development of stable light isotopes in South Africa

Two South African isotope hubs

By the late 1970s, the value of stable carbon isotope patterns in plants, animals, and humans had become clear following earlier discoveries of a second photosynthetic pathway (Hatch-Slack or C_4) in tropical grasses, structurally and isotopically distinct from plants using the earlier identified Calvin-Benson/C_3 pathway.[20] These differences carry implications for the calibration of radiocarbon dates when ingested by animals and humans. At the Quaternary Dating Research Unit (QUADRU), CSIR, in Pretoria, John Vogel mapped the distribution of C_3 and C_4 grassy vegetation across South Africa, demonstrating the strong influence of rainfall seasonality and growing season temperatures[16] and then that vegetation patterns are similarly reflected in animal tissues today[21] (a publication at the same time as the well-known laboratory feeding study by DeNiro and Epstein[22]) and in the past[23]. At the same time, he began to collaborate with Nikolaas van der Merwe at the University of Cape Town to explore human bone collagen $\delta^{13}C$ patterns in archaeological sites in North America[24] and South Africa[25]. The establishment of a new stable light isotope/geochemical facility in the Archaeology Department, University of Cape Town, shortly afterwards, provided a second hub to address multiple environmental and dietary questions arising in the archaeological and palaeontological records.

A series of fundamental studies to apply stable light, and later radiogenic, isotopes to explore patterns of human diet and mobility followed. These were based on sharply defined archaeological questions and an understanding of broad landscape-scaled variability – they produced the forerunners of what are today sometimes referred to as 'isoscapes'. It was shown, for instance, that while carbon isotopes reflected the proportions of marine foods in the diets of coastal hunter-gatherers[26], nitrogen isotopes did not. Rather, they reflected not only trophic, or marine vs terrestrial inputs as earlier thought[27], but also the influence of regional aridity on plants and animal physiology[28,29]. These effects remain important considerations for understanding modern or archaeological foodwebs in eastern and southern Africa.[30,31]

Beyond bone collagen – bone and enamel biominerals

Early in the 1980s, collagen, the main protein in bone, was the tissue of choice in both carbon (and later nitrogen) isotopes and radiocarbon research because it was relatively well characterised and understood and could be readily and quantifiably purified.[32] The mineral phases of both bone and tooth enamel (calcium phosphate bioapatites) include carbon in the form of substituted carbonate (CO_3^{2-}) from blood bicarbonate as the product of catabolic and respiratory processes.[33,34] Enamel is more stable due to higher crystallinity and long-range order in the form of prisms. But it has a far lower organic content and, as bone collagen had become important in both radiocarbon and palaeodietary research, early efforts to determine whether reliable isotopic information could be extracted from bone concentrated on attempts to remove, chemically, diagenetic components from bone. Two influential publications suggested that archaeological bone bioapatite could[35], or could not[36], be purified to deliver reliable carbon isotope data when compared with bone collagen from the same samples. The first used a protocol developed for radiocarbon dating, applying a dilute acetic acid wash to bone powders, which yielded consistent relationships in $\delta^{13}C$ values between animal bone collagen and bioapatite.[35] This conclusion was disputed based on a study of human and faunal bones, using a different (concentrated) acid wash protocol, which showed significant excursions for the human bones.[36] Both the distinct pretreatment protocols and the inclusion of humans turned out to be important.[37]

A different approach was needed to test whether carbon isotopes in bioapatite could be extended further back in time, which did not rely on collagen $\delta^{13}C$ as the benchmark. The solution was to construct a time-series of bioapatite carbonate $\delta^{13}C$ from fauna with well-understood diets, with a focus on browsers with predictably C_3 diets (trees, shrubs, and herbs) and therefore relatively negative $\delta^{13}C$ values (ca. $-12‰$).[38] The expectation was that diagenesis should shift browser values towards the more positive matrix ($\delta^{13}C$ near $0‰$). Purification protocols were tested for their effects on bioapatite chemistry.[39] The 3 Ma $\delta^{13}C$ time series showed that the sharp distinction between grazers and browsers held even in the oldest samples[38], and, notably amongst the older Plio-Pleistocene samples, enamel was more reliable than bone apatite[39,40]. Enamel has since become the standard tissue of choice in fossil biogeochemical studies.

Pretreatment protocols have nevertheless continued to be a controversial topic, partly because the mechanisms – via internal crystal rearrangement and/or ionic exchange – remained unclear. Experiments monitored by infrared spectroscopy and Isotope Ratio Mass Spectrometry (IRMS) showed that the changes in enamel during fossilisation were primarily rearrangements of carbonate ions rather than external replacement.[41] This suggests that not all forms of diagenesis impact isotopic composition, which remains surprisingly robust in enamel. Some pretreatment protocols can, however, cause shifts in isotopic composition, for instance, even standard Chlorox treatments to eliminate organic components lead to measurable addition of modern carbon to bone apatite carbonate.[42] It seems that a light touch is preferable.

Applications in the fossil record

Stable light isotopes

These findings paved the way for application in the fossil record. Two baboon taxa from Swartkrans, *Theropithecus oswaldi* and *Papio robinsoni*, believed to be C_4 grass and C_3 feeders, respectively, following their dentognathic morphology and the habits of their modern congeners[14], were shown to be sharply distinguishable based on their stable carbon isotope compositions. This finding opened the door for permission to address the diets of hominins in Swartkrans, and later, other sites. Although dental microwear had suggested *P. robustus* ate small hard objects (e.g. seeds or nuts from C_3 plants)[12,15], carbon isotope ratios showed a modest but significant incorporation of C_4-derived carbon. The data suggested that 20–30% of carbon was derived from C_4 plants directly or indirectly via ingestion of animals dependent on those resources. The hominin carbon isotope data were distinct from the baboons present at the site (*P. robinsoni* and the large-bodied *Dinopithecus ingens*).[43] The same pattern was repeated at other sites where *Paranthropus* occurred (Kromdraai, Drimolen).[44] Analysis of older *A. africanus* at Makapansgat Member 3 gave somewhat similar, although more variable results.[45] A similar pattern emerged for Sterkfontein M4.[46] We now know that variability amongst *A. africanus* individuals is higher than almost all other hominins for which we have data.[47] It is greater than that of all cercopithecids from the South African hominin sites combined.[48,49] This variability speaks to occupation of a broad ecological niche.

A high-resolution laser-ablation-based carbon isotope study of molar crown tooth fragments of *P. robustus* and *A. africanus* individuals showed that high inter-individual variability was accompanied by high intra-individual variability in both hominins, speaking again to a broad isotopic dietary niche for individuals and groups.[50,51] It must be acknowledged, however, that the true extent of intra-individual variability is muted by the effects of enamel maturation and inevitable sampling across growth lines even with high-resolution laser sampling. So we must accept some smoothing.[50,51]

These carbon isotope data reflect the mix of C_3 or C_4 plants at the base of the food chain and where multiple carnivores, omnivores, and herbivores are present, they provide a means to interrogate predation patterns amongst the remains. The carbon isotope ratio data suggest that the australopithecines and baboons were most likely targeted by leopards, hyenas, and *Megantereon*, lending support to Brain's 'predated by leopards' hypothesis.[52]

There were broader outcomes that touched on variability in $\delta^{13}C$ of both modern and fossil fauna.[48,53] These data have contributed significantly to a better understanding of niche space, breadth, and overlap amongst modern and extinct animals. At the continental sub-Saharan African scale, large-scale diachronic C_3-C_4 vegetation shifts visible from the pedogenic carbonate $\delta^{13}C$ record of eastern Africa were mirrored in faunal tooth enamel and ratite eggshell $\delta^{13}C$ records, suggesting that the timing of C_4 grass expansion in the Late Miocene began earlier in low-latitude eastern Africa compared to South Africa.[54] Subsequently, analyses of multiple late Miocene herbivore lineages from northern Kenya showed that a switch to C_4 grasses varied between and amongst families. Equids became the earliest dedicated C_4 grazers after 10 Ma, while suids and bovids were slower and more varied in response through time.[55] Patterns related to Plio-Pleistocene hominins are discussed below.

Exploration of the potential and implications of the oxygen isotope ($\delta^{18}O$) composition of enamel in addition to $\delta^{13}C$ occurred in both eastern and South Africa, based on data from both modern ecosystems and the fossil record. Interest in $\delta^{18}O$ was initially directed at inferences related to precipitation[56], but it became apparent from studies of modern and fossil assemblages that dietary and water source related information could be extracted.[57–59] For example, it was observed that water-independent animals had higher $\delta^{18}O$ values than those that drank frequently or lived in water (from which a palaeoaridity index was derived)[60], carnivores had lower $\delta^{18}O$ values than most herbivores[59], and $\delta^{18}O$ values increased as animals fed higher in the canopy[61]. Most isotopic studies now routinely report both isotope compositions and large databases exist for both South and eastern Africa.

Strontium and hominin behaviour

In the University of Cape Town's (UCT's) Archaeometry Laboratory, parallel developments were pursued in the realm of trace elements, mostly Sr/Ca ratios, and later strontium isotopes in collaboration with Geological Sciences. The Sr/Ca approach had long been considered a means to address trophic level, given the known discrimination against strontium in the mammalian gut, resulting in a trophic cascade in simple systems.[62] Initial work focused on developing protocols to extract unaltered or at least minimally altered bone apatite.[63,64] As a result of UCT's proximity to good African mammal collections, strong differences were soon noted in the Sr/Ca ratios of herbivores depending on the nature of the plants they ate. For instance, grazer Sr/Ca ratios were higher than those of browsers, which, in turn, overlapped strongly with carnivores.[65] Although initially surprising, the outcome follows the principles of Sr transport in plants.[66] It suggested that Sr/Ca ratios in fauna were dominated less by trophic level (as assumed for decades) than previously thought and led to the exploration of trace element patterns in tooth enamel rather than bone apatite.[67,68] These patterns showed that grazers, browsers, and carnivores from Kruger National Park and South African australopithecine sites could be distinguished using elemental ratios (Sr/Ca, Ba, Ca, Sr/Ba). Further, application to *A. africanus* and *P. robustus* showed distinctions between the two species, with the former having high Sr concentration and low Ba concentrations that are most consistent with the consumption of underground storage organs.[67] Overall, the trace element data for both australopithecines are consistent with herbivory, although some animal food consumption cannot be excluded. A subsequent study of early *Homo* from Swartkrans suggested it consumed more animal foods than the australopithecines[68], but interpretation of these data remains equivocal[69]. One important outcome of these studies is that we can deduce that plants and their distributions are important determinants of fossil trace element ratios.

A further outcome of this work was the development of strontium isotopes to explore ranging or residence patterns. The highly variable but patterned geology of the Cradle was shown to be reflected in significant strontium isotope differentiation across landscapes.[70] Sillen et al.[70] suggested that hominins could be "tracked" across the isotopically patterned landscape by comparing their $^{87}Sr/^{86}Sr$ values to that of rodents and other fauna whose movement patterns could be reasonably conjectured. Firmly establishing predictable strontium isotopic patterning across the highly varied geology of the Cradle zone was a crucial step in this endeavour that is now considered essential in all such studies.[70,71] Laser ablation analysis of australopith tooth enamel showed that small-toothed (inferred to be female) individuals were more likely to be non-local than the large-toothed (assumed to be male) individuals, suggesting dispersal patterns similar to those of chimpanzees and bonobos.[71] Subsequent work supported this interpretation.[72] New developments in enamel-based palaeoproteomic sexing may allow the finding of female dispersal to be tested with more rigour[73], promising that we may be in a position to distinguish between male and female residence and mobility behaviours.

Beyond South Africa

Many of these new approaches were expanded to hominins and fauna in eastern and central African sites, which span from at least 5 Ma across multiple basins. However, obtaining access to the fossils took years, and only became possible after a small study of Tanzanian specimens of *Paranthropus boisei* and early *Homo*.[74] Van der Merwe and colleagues showed that *Homo* and *P. boisei* had highly distinct $\delta^{13}C$ values. This finding was not unexpected given the large differences in masticatory morphology of these taxa, but the strong C_4 signal in *P. boisei* was unlike that of any living or fossil hominoid encountered previously. The study was hampered by its small sample size: three *Homo* and two *P. boisei* specimens, and, despite the exciting results, such meagre evidence did not convince palaeoanthropologists to abandon decades of thinking about masticatory functional morphology and hominin diet. It was enough, however, on which to base a successful proposal to sample hominins from the National Museums of Kenya by one of us (M.S.), Thure Cerling, and Fred Grine. The result was a flood of new hominin isotopic data.

There is now a large body of data documenting shifting dietary ecologies of fauna and hominin taxa. These data from southern and eastern Africa, as well as from one site in the Sahara, point to increasing engagement with C_4 plants that began at least 3.7 Ma years ago[75], which, while somewhat later than other African herbivore lineages[55], increased in variable degrees until an apogee represented by *P. boisei* in eastern Africa[74,76].

The standout result is that *P. boisei* consumed astonishingly large amounts of C_4 carbon, perhaps 80%, before becoming extinct at about 1.3 Ma.[74,76,77] Their dedicated C_4 diets, with very low isotopic niche breadths, stand in strong contrast to those of early *Homo* in eastern Africa, which were highly variable but mostly C_3 until 1.65 Ma when they encroached on *P. boisei* carbon isotope 'space'.[74,78,79] When the carbon isotope data are combined with evidence from dental microwear[80] and tooth chipping[81] that suggest a folivorous diet, the most likely C_4 resource consumed by *P. boisei* is grass or sedges. This comports well with comparative mammalian studies, as all large-bodied herbivores with *P. boisei*-like carbon isotope composition eat grasses, especially their above-ground parts. The underground storage organs (USOs) of grasses and sedges are also potential candidate foods for *P. boisei*, and there is no reason to expect they were not eaten to at least some extent. The chief argument for USO consumption among *P. boisei* is that its teeth are flat, which is typically what we find in primates that eat hard foods like nuts, and not tough foods like leaves.[9] The main argument against a diet of underground storage organs comes from dental microwear, as primates that eat such foods have heavily pitted and chipped teeth[47,81] because of adherent grit particles. *Theropithecus*, the only grass-eating specialist among the catarrhine primates, also lacks heavily-pitted molars despite the consumption of USOs, but it eats larger quantities of above-ground foods.[82] For the USO interpretation to hold, evidence showing that primates can have diets dominated by USOs without pitting and chipping caused by adherent grit is required (see [83]).

There is also increasing interest in using strontium isotopes to track landscape use among eastern African hominins.[84,85] Recent work has established that there can be Sr isotope differences between gallery forest and savanna grasslands in Uganda[85] (similar to [70] in South Africa), and there is preliminary work establishing Sr isotope isoscapes in Tanzania and Kenya[84]. However, a previous attempt to use Sr isotopes at Olduvai Gorge with non-hominin fossil fauna found that Sr concentrations in fossil enamel were often two to three times higher than Sr concentrations in modern enamel in the area[86], which was consistent with previous work showing enamel can be highly altered at eastern African sites[87]. In contrast, fossil rodent enamel from Sterkfontein and Swartkrans has the same concentration of Sr as modern rodents in the caves today.[88] Thus, diagenesis may yet prove a formidable obstacle to employing Sr isotopes as markers of landscape use in eastern African hominin sites.

Moving forward

So where do we go next? One pressing need is better integration of evidence from the very many palaeodietary data sources (e.g. morphology, carbon and oxygen isotopes, dental microwear, dental chipping). Further, now that we know that ^{13}C-enriched foods were important resources for many hominins, we should re-evaluate these resources in terms of their distribution, abundance, nutritional qualities, and mechanical properties to advance our understanding of hominin diets.[89,90]

Other systems based on metal isotopes (magnesium, zinc, calcium for instance[91–93]) are in active stages of development and could prove useful for addressing questions about hominin diets. In most cases, these are used principally as tools to investigate the trophic levels of fossil taxa, and while there is no doubt that they can separate herbivores and carnivores in aggregate, their mileage varies when it comes to capturing the trophic behaviour of specific taxa (see below). One overarching reason is that the distributions of these isotopes in modern ecosystems, and particularly the reasons for their relative abundances therein, are not well understood from the ground up. We have learnt from strontium trace element studies how complex, and yet how important, this patterned variation at the base of the foodweb can be for palaeodietary interpretation.[65,66] We know that plants can vary in their $\delta^{44/40}$Ca by species, plant part, leaf age (for woody plants), nutrient transport, and soil composition, but how these patterns map onto African ecosystems is largely unknown.[19] Amongst fauna, differences between herbivores and carnivores can disappear when, for instance, the latter consume flesh but not bones[94] or when the former eat bones, regularly grow antlers, and/or other physiological factors impact $\delta^{44/40}$Ca.[95]

This makes application to hominin fossils hard to justify at present. Calcium isotopes have been applied to early hominins in two cases. The first was principally concerned with the weaning behaviour of *A. africanus, P. robustus*, and suggested longer and more intense breastfeeding in *Homo*.[96] Notably, although not a focus of the study, the results did not support the contention that *Homo* consumed more animal foods.[68] The second study was focused on Turkana Basin hominins, and found that *P. boisei's* $\delta^{44/42}$Ca values were higher than those of other hominins and contemporaneous mammals.[91] As carnivores *tend* to have low $\delta^{44/42}$Ca values, this *may* suggest some form of herbivory for *P. boisei*. However, given arguments derived from dental microwear, tooth chipping, and carbon isotope research that *P. boisei* consumed fibrous plants, it is intriguing that *P. boisei* occupies the same calcium isotope space as the bamboo-feeding giant panda (*Ailuropoda*) and *Gigantopithecus*.[97] Beyond this, the results for the Turkana Basin hominins are largely uninterpretable.

One promising new avenue is the extraction of nitrogen isotopes from the infinitesimal organic fraction of enamel. In principle, such data could be used to establish trophic level[98], although variation in plant δ^{15}N values and animal physiology/diet quality can bedevil such efforts, as evidenced by rock hyraxes and springbok in the Western Cape[26], and elsewhere, mammoths[92], with carnivore-like δ^{15}N values. Efforts are also underway to measure carbon and nitrogen isotopes in the amino acids of these enamel organic fractions which can reveal trophic levels and differentiate food types that are indistinguishable from bulk analysis alone (e.g. CAM versus C_4 vegetation), and can potentially be informative without extensive baseline work.[92] Still, nitrogen isotope differences between source and trophic amino acids (β) can differ by more than $5^o/_{oo}$ between species and plant parts, and diet quality and other factors impact fractionation among trophic-sensitive amino acids[19,99], so interpretation of compound-specific isotope data is not without complications.

We would urge too, given the results from the earlier (essentially) pilot work on trace element compositions of plants and animals, that the patterns of [Sr/Ca] and [Ba/Ca] compositions should be revisited. They seem to offer unique perspectives on the consumption of different plant forms (underground storage organs, leafy material, fruits, etc.) not available by other means.[67] The existing data for *A. africanus* and *P. robustus* suggest distinctions in the consumption of USOs and this approach may be appropriate for addressing the difficult questions about plant use in the fossil record. We are less sanguine about the prospects of such work at eastern African sites, however, given evidence of diagenetic increases in Sr and Ba.[87]

Given the above, there is still much to do if we are to improve our understanding of early hominin diets and, in turn, the ways that hominins competed with each other and other mammals in the context of climatic and environmental change since the Pliocene. There remains some low-hanging fruit for future study, much in the spirit of the work at UCT described above. One is to take a much deeper dive into the plants and mammals of modern African ecosystems to better understand how we can, and cannot, use emerging isotopic dietary proxies. To be clear, this should start with systematic surveys of plants in African ecosystems where, at the bare minimum, many species (including multiple growth forms like trees, grasses, sedges, forbs, and shrubs) are analysed across a series of microhabitats. Existing data make it clear that there should be great variability between such samples[19,91,99], but those data sets are as yet typically small, unsystematic, and not necessarily relevant from the perspective of African palaeodietary research.

The long history of work on carbon and oxygen isotopes shows that it is a long-term effort (~4 decades in the research reviewed above) to understand elemental and isotopic pathways within ecosystems. It has also shown that we underestimate at our peril the importance of plants – their distributions and processes of incorporation of nutrients from soil to plant tissues to animal digestive systems and finally calcified tissues. We suggest proceeding cautiously towards application in hominins, via careful selection of test applications from the present and more recent sites, and then proceeding to work with early hominins. As Nietzsche once noted, "He who would learn to fly one day must first learn to walk and run and climb and dance; one cannot fly into flying."[100] South African scholars are especially well placed to lead us towards such flight, given their history, proximity to materials, and technical capabilities.

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Data availability

Available from the original cited publications.

Declarations

We have no competing interests to declare. We have no AI or LLM use to declare.

Authors’ contributions

J.L-T.: Conceptualisation, writing – the initial draft, writing – revisions. M.S.: Writing – the initial draft, writing – revisions. Both authors read and approved the final manuscript.

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