

The diet of *Australopithecus sediba*

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Specimens of *Australopithecus sediba* from the site of Malapa, South Africa (dating from approximately 2 million years (Myr) ago)¹ present a mix of primitive and derived traits that align the taxon with other *Australopithecus* species and with early *Homo*². Although much of the available cranial and postcranial material of *Au. sediba* has been described^{3–6}, its feeding ecology has not been investigated. Here we present results from the first extraction of plant phytoliths from dental calculus of an early hominin. We also consider stable carbon isotope and dental microwear texture data for *Au. sediba* in light of new palaeoenvironmental evidence. The two individuals examined consumed an almost exclusive C₃ diet that probably included harder foods, and both dicotyledons (for example, tree leaves, fruits, wood and bark) and monocotyledons (for example, grasses and sedges). Like *Ardipithecus ramidus* (approximately 4.4 Myr ago) and modern savanna chimpanzees, *Au. sediba* consumed C₃ foods in preference to widely available C₄ resources. The inferred consumption of C₃ monocotyledons, and wood or bark, increases the known variety of early hominin foods. The overall dietary pattern of these two individuals contrasts with available data for other hominins in the region and elsewhere.

Early hominin diet is central to the study of human origins. Dietary data come from a variety of sources that provide different information about the foods consumed. Carbon isotopes indicate whether an animal ate C₃ resources (for example, trees, shrubs, some herbs, and animals eating these plants), C₄ resources (for example, most tropical grasses, sedges, and animals eating these plants) or a combination of these⁷. Chimpanzees consume C₃ plants such as fruits and leaves even when C₄ grasses are abundant^{8,9}. By contrast, isotopic evidence indicates that *Australopithecus*, *Paranthropus* and early *Homo* consumed variable amounts of C₄ foods, but their diets included more C₄ foods than the diets of modern chimpanzees, indicating that they probably used their environments in different ways than do living apes^{10–12}. Dental microwear provides information about the fracture properties of foods consumed shortly before the death of an animal¹³. Previous studies of *Australopithecus africanus*, and particularly of *Australopithecus afarensis* and *Paranthropus boisei*, suggest limited variance in food hardness, whereas *Homo erectus* and *Paranthropus robustus* have greater variance in texture complexity consistent with a more diverse or variable diet^{14–17}. Phytoliths are plant-produced silica bodies that take on taxon-specific morphology¹⁸. They can become trapped in dental calculus and can therefore provide a record of the plant foods an individual consumed. Phytoliths have been recovered from Neanderthal and modern human calculus¹⁹, but not yet from earlier hominins.

Palaeoenvironmental evidence from Malapa provides a context for interpreting the dietary proxy data. Pollen, phytoliths and wood fragments from *Podocarpus* trees and other woody taxa recovered from a probable carnivore coprolite indicate a forest or woodland

biome in the vicinity²⁰. Sediment samples from the hominin layer (Facies D²¹) preserve many grass phytoliths, predominantly long-necked bilobates and saddles typical of C₄ grasses in summer rainfall areas, consistent with a more open savanna or grassland biome (Supplementary Text, Supplementary Table 4 and Supplementary Fig. 6). The presence of grazers, including *Equus* and *Megalotragus*, supports the interpretation of abundant grass around Malapa²¹. The Malapa bovid fossils have carbon isotope compositions indicating nearly pure C₄ diets, and the rodent fossils have carbon isotope compositions demonstrating high C₄ consumption, as is common among extant rodents around the site (Table 1 and Supplementary Table 1). Thus, the palaeoenvironment probably included areas with abundant grass and woody vegetation.

The carbon isotope compositions of *Au. sediba* individuals MH1 and MH2 were measured using laser ablation isotope ratio mass spectrometry²². The $\delta^{13}\text{C}$ values of both individuals fall outside the range of all 81 previously analysed African early hominins, indicating a nearly pure C₃ diet (Fig. 1, Table 1 and Supplementary Tables 1 and 2)^{10–12,23–26}. The $\delta^{13}\text{C}$ values of MH1 and MH2 are more than two standard deviations below the mean of *Au. africanus*^{11,24}, and are closest to (but still below) the range of much older (4.4 Myr ago) *Ardipithecus ramidus*²⁶. Their values are comparable to those of savanna chimpanzees (corrected for anthropogenic changes in the $\delta^{13}\text{C}$ of atmospheric CO₂)^{8,9}, but higher than those of chimpanzees living in forest environments²⁷. Thus, the carbon isotope compositions of MH1 and MH2 are unusual for hominins, and more typical of C₃ specialists like giraffes (Supplementary Table 1)^{25,26}. If these individuals are representative of the species, *Au. sediba* had a diet that was different from those of most early African hominins studied so far.

Molars of both *Au. sediba* individuals were analysed using dental microwear texture analysis. Two measures of surface texture, area-scale fractal complexity and exact proportion length-scale anisotropy of relief, are useful for distinguishing a broad variety of mammals on the basis of food hardness and toughness, respectively¹⁴. The values for anisotropy are well within the ranges of most early hominins (Fig. 2 and Supplementary Table 3), but the complexity values are higher than those of most specimens of *Australopithecus* spp., *Homo habilis* and *P. boisei*. The complexity value for MH2 falls within the upper end of the *Au. africanus* range, but the juvenile male MH1 has a much higher value, within the range of only *P. robustus*, suggesting the consumption of hard objects before death. The complexity values for both *Au. sediba* specimens are between the medians for *H. erectus* and *P. robustus*, and the difference between them approximates the interquartile ranges of these two hominin taxa.

Thirty-eight phytoliths were recovered from dental calculus on two teeth of MH1, including 15 dicotyledon morphotypes, 9 monocotyledon morphotypes and 14 indeterminate forms (Table 2, Fig. 3 and Supplementary Table 5). This assemblage differs considerably from

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Table 1 | Stable carbon and oxygen isotope compositions of Malapa fauna, MH1 and MH2

Specimen	Taxon	$\delta^{13}\text{C}$ (‰, VPDB)	$\delta^{13}\text{C}$ adj* (‰, VPDB)	$\delta^{18}\text{O}$ (‰, SMOW)
MB1 analysis 1	Bovidae	0.3	0.8	26.0
MB1 analysis 2	Bovidae	0.4	0.9	26.4
MB1 mean	Bovidae	0.4	0.9	26.2
MB2 analysis 1	Bovidae	-0.7	-0.2	25.9
MB2 analysis 2	Bovidae	-0.9	-0.4	25.2
MB2 mean	Bovidae	-0.8	-0.3	25.6
Bovidae mean	Bovidae	-0.2	0.3	25.9
Bovidae s.d.	Bovidae	0.8	0.8	0.4
MR1	Rodentia	-4.5	-4.0	21.4
MR2 analysis 1	Rodentia	-5.4	-4.9	19.8
MR2 analysis 2	Rodentia	-5.7	-5.2	20.1
MR2 mean	Rodentia	-5.6	-5.1	20.0
MR3 analysis 1	Rodentia	-5.0	-4.5	18.8
MR3 analysis 2	Rodentia	-5.3	-4.8	18.9
MR3 mean	Rodentia	-5.2	-4.7	18.9
Rodentia mean	Rodentia	-5.1	-4.6	20.1
Rodentia s.d.	Rodentia	0.6	0.6	1.3
Modern <i>Otomys</i> mean**	Rodentia		-5.5	21.5
Modern <i>Otomys</i> s.d.**	Rodentia		2.0	4.9
MH1 analysis 1	<i>Au. sediba</i>	-12.8	-12.3	20.1
MH1 analysis 2	<i>Au. sediba</i>	-11.5	-11.0	20.6
MH1 mean	<i>Au. sediba</i>	-12.2	-11.7	20.4
MH2 analysis 1	<i>Au. sediba</i>	-12.5	-12.0	18.2
MH2 analysis 2	<i>Au. sediba</i>	-11.7	-11.2	18.4
MH2 mean	<i>Au. sediba</i>	-12.1	-11.6	18.3
<i>Australopithecus sediba</i> mean	<i>Au. sediba</i>	-12.2	-11.7	19.4
<i>Australopithecus sediba</i> s.d.	<i>Au. sediba</i>	0.1	0.1	1.5

SMOW, Standard Mean Ocean Water; VPDB, Vienna Pee Dee belemnite.

* $\delta^{13}\text{C}$ values obtained through laser ablation are lower than those obtained through conventional acid hydrolysis by about 0.5‰ (ref. 22). Values have been adjusted in this column accordingly.

** Modern values have been adjusted to compensate for the fossil-fuel effect. Five *Otomys* individuals (which are typically grass consumers and potential analogues for the fossil rodents analysed from Malapa) have been sampled from an active owl roost near the site. Most other modern rodents from the roost consumed far more C_3 vegetation, and as a result the overall roost mean ($n = 24$; $\delta^{13}\text{C}$, $-9.8 \pm 5.3\%$; $\delta^{18}\text{O}$, $19.8 \pm 4.3\%$) is much lower than that of the available fossil sample (Supplementary Table 1).

those recovered from the Facies D sediment, which contains abundant C_4 grass phytoliths, and from the breccia block containing MH1, in which no phytoliths were found (Supplementary Text, Supplementary Fig. 6 and Supplementary Table 4). Unlike the sediment, there were no distinctive C_4 monocotyledon morphotypes in the calculus. These monocotyledon phytoliths most probably represent the consumption of tropical shade- and water-loving C_3 grasses and sedges. The presence of fruit, leaf and wood or bark phytoliths suggests that all of these were consumed to some extent, although quantification of their relative importance is hampered by differences in phytolith density among taxa and plant parts¹⁹. Bark and woody tissues have

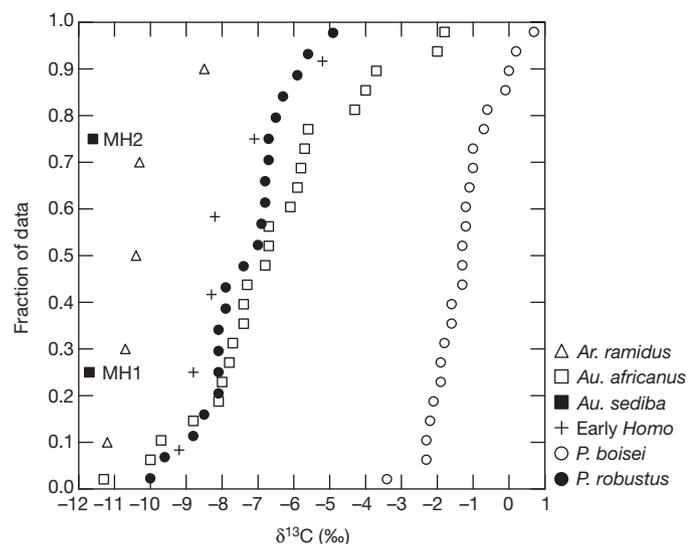


Figure 1 | $\delta^{13}\text{C}$ values for early hominins. *Au. sediba* individuals MH1 and MH2 have $\delta^{13}\text{C}$ values ($\delta^{13}\text{C} = (^{13}\text{C}/^{12}\text{C}_{\text{sample}} / ^{13}\text{C}/^{12}\text{C}_{\text{standard}} - 1) * 1000$) outside the range of previously sampled hominins, and indicate that these individuals consumed almost exclusively C_3 foods. Values for other hominin specimens have been collected from the literature and are presented alongside the data for the Malapa modern and fossil taxa in Supplementary Table 1.

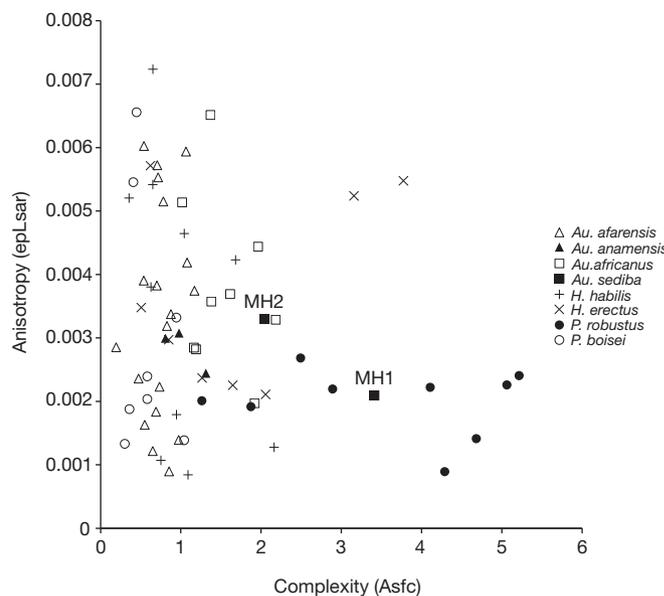


Figure 2 | Dental microwear patterns for individuals MH1 and MH2 compared to those of other fossil hominins. Area-scale fractal complexity and exact proportion length-scale anisotropy of relief typically differentiate diets based on food hardness and toughness, respectively. Although the anisotropy values of *Au. sediba* individuals MH1 and MH2 fall within the range of most early African hominins, the complexity values suggest MH1 and MH2 consumed hard foods, similar to *H. erectus* and *P. robustus*.

Table 2 | Counts of phytoliths recovered from the calculus of MH1

Tooth	Dicotyledon		Monocotyledon			Indeterminate	Totals
	Leaf	Fruit	Wood/Bark	Sedge	Grass		
LI ²	1	1	7	2	1	1	11
LP ³	2	-	4	2	3	-	3
Totals	3	1	11	4	4	1	14

LI², upper left second incisor; LP³, upper left first premolar

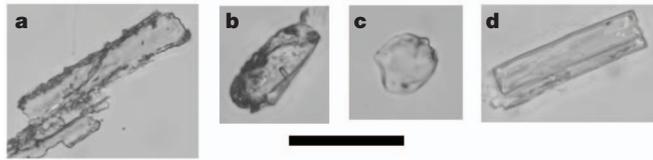


Figure 3 | Phytoliths from the dental calculus of MH1. **a**, A dicotyledon fruit phytolith. **b**, A dicotyledon wood or bark phytolith. **c**, A small bulliform phytolith from grass. **d**, A sedge phytolith. Scale bar, 50 μm .

not been documented previously as a dietary component for hominins, although these foods are consumed by many primates and contain proteins and soluble sugars^{28,29}. The diversity in phytolith types, despite the small available sample, suggests a varied diet.

The three lines of evidence suggest these two individuals had an unexpected diet compared to those of African hominins of a similar antiquity. Dental microwear texture analysis suggests consumption of at least some hard foods to an extent not previously seen in most *Australopithecus* spp. or in *P. boisei*, apparently more like that of *H. erectus* and *P. robustus*. Carbon isotope data indicate that these individuals were nearly exclusive C_3 feeders, much like today's savanna chimpanzees. The recovered phytoliths indicate that C_3 dicotyledons and monocotyledons were probably a considerable component of the diet, and the variety of morphotypes implies that MH1 consumed a wide variety of foods. Among the early African hominins, the closest match is arguably *Ar. ramidus* based on their similar carbon isotope compositions, although microwear texture data and phytoliths are unavailable for this taxon.

All three lines of evidence are consistent with *Au. sediba* having made use of habitats in which C_3 dicotyledons and monocotyledons grew within a regional environment with abundant C_4 grasses, similar to a gallery forest. Like *Ar. ramidus* and savanna chimpanzees, MH1 and MH2 seem to have consumed C_3 foods in preference to widely available C_4 resources, and they probably included bark and other fracture-resistant foods as at least a seasonal part of their diet. This interpretation is consistent with postcranial evidence suggesting that *Au. sediba* was a facultative tree climber⁶, possibly indicating a reliance on arboreal resources. However, our results raise several questions about other aspects of *Au. sediba* behaviour. For example, the carbon isotope data suggest that these individuals were limited to C_3 resources, which could indicate that these individuals required large home ranges to acquire preferred fruit resources, like savanna chimpanzees. However, if they consumed a wider variety of C_3 resources during periods of fruit scarcity, as evinced by the phytoliths, this might have reduced the need for larger home ranges.

Previous analyses have shown that *Au. sediba* has an unusual suite of morphological features^{2–6}, and our results present new oddities and questions. This work and other recent studies suggest that the diets of australopiths were diverse³⁰ (both within and between most species), which mirrors recently recognized morphological diversity among the australopiths². Nevertheless, our interpretations of the diet of *Au. sediba* must be tempered by the small sample that is available. We expect that studying additional individuals from the site will provide a better understanding of the dietary ecology of *Au. sediba*.

METHODS SUMMARY

Carbon and oxygen isotope ratios of the specimens (upper right first incisor (RI¹) of MH1 and upper right second molar (RM²) of MH2) were determined using laser ablation–gas chromatography–isotope ratio mass spectrometry following established methods (ref. 22, Supplementary Text, Supplementary Table 1, and Supplementary Figs 1 and 2). When necessary, sample surfaces were cleaned using abrasional removal of surface layers, treatment in 10% hydrogen peroxide or treatment in ethanol, or a combination of these. Data were normalized to CO_2 reference gas aliquots calibrated to NBS-19 (TS-Limestone). Accuracy and precision were also monitored through repeated analyses of an internal tooth enamel standard calibrated to NBS-19.

Microwear data were collected following established protocols (refs 15, 18, Supplementary Text and Supplementary Figs 3 and 4). Specimens (RM² of MH1 and lower right second molar (RM₂) of MH2) were cleaned with alcohol and cotton swabs, moulded using a polyvinylsiloxane impression material and cast in high-resolution epoxy. Point clouds with 0.18- μm lateral spacing were generated using a white-light scanning confocal profiler representing four adjoining surfaces on facet 9, each measuring 102 \times 138 μm . Scale-sensitive fractal complexity and length-scale anisotropy data were computed using Toothfrax software for each surface, and median values were calculated for each specimen.

Calculi from the buccal surfaces of the LI² and LP³ (upper left second incisor and upper left anterior premolar) of MH1 were collected using an established protocol (ref. 19, Supplementary Text and Supplementary Fig. 5) and analysed using transmitted light microscopy at $\times 400$ magnification. The samples were then processed further with hydrochloric acid to remove calcite crystals and then re-examined. Sediment from the breccia block encasing MH1 was examined to test for potential contamination (Supplementary Text). Sediment samples from the site were examined to provide an environmental baseline (ref. 19, Supplementary Text, Supplementary Table 4 and Supplementary Fig. 6). Phytoliths were identified based on comparison to modern plant reference collections.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions A.G.H., P.S.U., M.S., D.J.d.R. and L.B. conceived the project. A.G.H. collected and processed sediment and calculus samples. P.S.U. performed the dental microwear analysis. B.H.P., M.S. and P.S. performed isotopic analyses. L.R. identified grass phytoliths in the calculus and examined grass silica short cells (GSSCs) in Facies D sediment sample. M.B. identified the non-grass phytoliths in the calculus and analysed sediment samples. All authors contributed to the paper.

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