

Evidence for dietary change but not landscape use in South African early hominins

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The dichotomy between early *Homo* and *Paranthropus* is justified partly on morphology^{1,2}. In terms of diet, it has been suggested that early *Homo* was a generalist but that *Paranthropus* was a specialist³. However, this model is challenged and the issue of the resources used by *Australopithecus*, the presumed common ancestor, is still unclear. Laser ablation profiles of strontium/calcium, barium/calcium and strontium isotope ratios in tooth enamel are a means to decipher intra-individual diet and habitat changes. Here we show that the home range area was of similar size for species of the three hominin genera but that the dietary breadth was much higher in *Australopithecus africanus* than in *Paranthropus robustus* and early *Homo*. We also confirm that *P. robustus* relied more on plant-based foodstuffs than early *Homo*. A South African scenario is emerging in which the broad ecological niche of *Australopithecus* became split, and was then occupied by *Paranthropus* and early *Homo*, both consuming a lower diversity of foods than *Australopithecus*.

The dietary specialization of *Paranthropus* is thought to have contributed to its demise because it was unable to adapt to the changing environmental conditions that took place approximately 1 million years ago¹. From an ecological point of view, a small dietary breadth is generally correlated with narrow habitat preferences³. The evaluation of the size of the home range area, in addition to the estimation of the dietary breadth, would provide a detailed picture of resource use by the hominins. Using tooth enamel, the present work investigates the dietary breadth and the home range area of South African hominins with strontium/calcium (Sr/Ca) and barium/calcium (Ba/Ca) ratios, and strontium isotope (⁸⁷Sr/⁸⁶Sr) compositions. Dietary Sr/Ca and Ba/Ca proxies are based on the biological discrimination of Sr and Ba relative to Ca (that is, Ca biopurification), resulting in predictably lower Sr/Ca and Ba/Ca in a consumer, relative to its diet⁴. In bones, Sr/Ca and Ba/Ca decrease concomitantly up trophic chains⁴, but in enamel, and for a reason that is not yet fully understood, only low Ba/Ca ratios are characteristic in carnivores⁵. Low Sr/Ca ratios are representative of browsers and carnivores⁵, whereas high Sr/Ca or Ba/Ca ratios in enamel are characteristic in grazers⁵. In contrast, the ⁸⁷Sr/⁸⁶Sr of a consumer is free of any trophic process⁶. It only reflects the ⁸⁷Sr/⁸⁶Sr composition of the bedrock (substrate) on which the consumer fed because the abundance of radiogenic ⁸⁷Sr is determined by normalization of the stable isotope variations relative to a reference ⁸⁶Sr/⁸⁸Sr ratio of 0.1194.

The Sr/Ca, Ba/Ca and ⁸⁷Sr/⁸⁶Sr ratios are assessed using laser ablation profiles in permanent molars from the dentine enamel junction to outer enamel following the direction of the enamel growth prism^{7–9}. The specimens include *Australopithecus africanus* ($n = 4$), *Paranthropus robustus* ($n = 7$) and early *Homo* ($n = 3$) from Sterkfontein, Swartkrans and Kromdraai B, South Africa (Supplementary Table 1). For comparison, we also measured the Sr/Ca, Ba/Ca and ⁸⁷Sr/⁸⁶Sr ratios in tooth enamel of grazers and browsers ($n = 3$) from Sterkfontein and Swartkrans. In most cases, several profiles were analysed for a given tooth to assess intra-tooth variability. The diagenetic effects on Sr/Ca,

Ba/Ca and ⁸⁷Sr/⁸⁶Sr of the Sterkfontein Valley fossil material are negligible (Supplementary Information). Several lines of evidence support this conclusion. First, if a sizeable pool of biological Sr is exchanged with a diagenetic component, this would affect the Sr isotopic composition and the samples would fall on a Sr/Ca versus ⁸⁷Sr/⁸⁶Sr line representing the mixing between the biological and the diagenetic Sr components. Taking the whole data set into account, it is evident that Sr/Ca and ⁸⁷Sr/⁸⁶Sr ratios are not correlated ($R^2 = 0.008$, $P = 0.260$). As well as Ca, Sr and Ba, we also measured a suite of other trace elements (Mn, Zn, Rb, Y, La, Sm, Yb, Th and U), which are present at the sub-p.p.b. level in modern enamel, and which are taken up easily post mortem¹⁰. No co-variation between Ca, Sr or Ba and the diagenetic proxies was found for any of the profiles (Supplementary Information). Last, the concentrations of the diagenetic proxies are very low, typically at the p.p.b. level, which is characteristic of pristine enamel and in accordance with previous results obtained using solution inductively coupled plasma mass spectrometry (ICPMS)¹¹.

The ⁸⁷Sr/⁸⁶Sr ratio ranges from 0.7197 to 0.7412 for the hominins and the bovids, with a mean value of 0.7309 ± 0.0048 (± 1 s.d.) (Fig. 1 and Supplementary Table 1). Recently, a study¹² reported ⁸⁷Sr/⁸⁶Sr ratios in the enamel of hominins and animals from Sterkfontein and Swartkrans (min = 0.7197, max = 0.7454, mean = 0.7305 ± 0.0054 (± 1 s.d.)). The ⁸⁷Sr/⁸⁶Sr values of the two sets of data for hominins are indistinguishable (Fig. 1; Student's t -test, $P = 0.240$). However, the data sets differ in the variability of the intra-tooth ⁸⁷Sr/⁸⁶Sr ratio, which is provided by the coefficient of variation associated with the mean ⁸⁷Sr/⁸⁶Sr value for a given tooth. In this study, the mean ⁸⁷Sr/⁸⁶Sr values and their associated coefficients of variation are normally distributed (Shapiro–Wilk test, $P = 0.306$ and $P = 0.107$, for mean and standard deviation, respectively) and are not correlated ($R^2 = 0.007$, $P = 0.659$). In contrast, in the study mentioned above¹², the mean ⁸⁷Sr/⁸⁶Sr values are normally distributed (Shapiro–Wilk test, $P = 0.111$), whereas the coefficient of variation values are log-normally distributed (Shapiro–Wilk test, $P = 0.972$) and the mean ⁸⁷Sr/⁸⁶Sr values are positively correlated with their log-normalized coefficient of variation values ($R^2 = 0.546$, $P < 10^{-3}$). The two data sets were obtained using different laser-sampling strategies, and this probably explains the observed patterns of intra-tooth ⁸⁷Sr/⁸⁶Sr variability.

As in the majority of studies using laser-ablation ICPMS on tooth samples^{7,8,13–17}, we carried out laser sampling on flat enamel surfaces. To do this, we used naturally broken teeth or teeth that had already been cross-sectioned mechanically. However, in the study mentioned previously¹², sampling was carried out using laser scans on the external surface of the enamel of whole teeth, which is a curved surface. This would have inevitably resulted in the sampling of laser-unfocused areas, an analytical bias that is known to produce variations of the size of the ablated particles and instrumental isotopic fractionation during ionization, leading to artificially scattered isotopic ratios¹⁸. The sampling strategy that was used¹² could explain why the smallest teeth were found to exhibit the highest intra-tooth ⁸⁷Sr/⁸⁶Sr variability.

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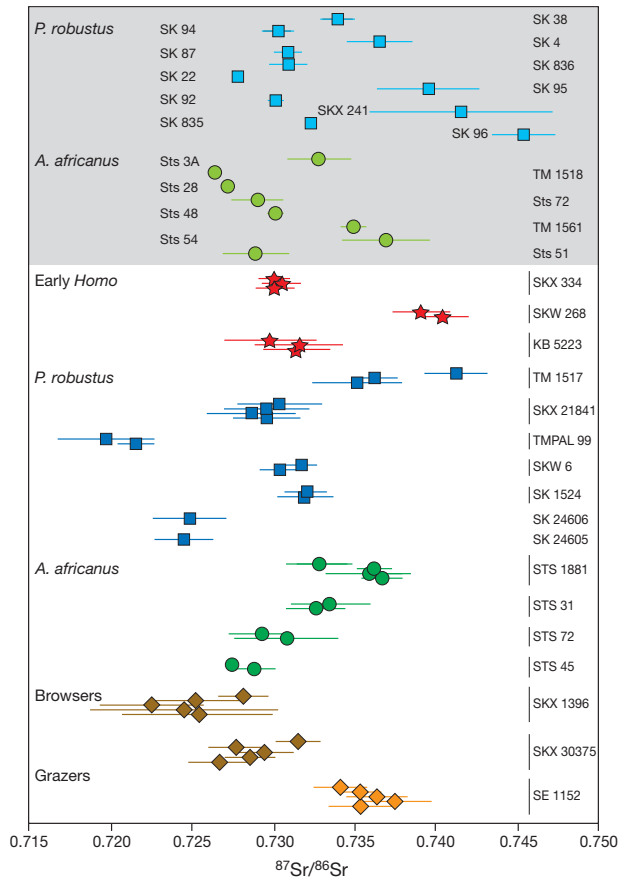


Figure 1 | $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of hominin and bovid enamel. The shaded area contains data from a previous study¹². Error bars are 2-sigma standard deviations of the mean.

Finally, we do not find statistically significant differences of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio between hominin groups (Kruskal–Wallis, $P = 0.266$), or between the hominin group as a whole and the fauna (Kruskal–Wallis, $P = 0.259$). Thus, the South African hominins do not show clear systematic variation of the enamel $^{87}\text{Sr}/^{86}\text{Sr}$ ratio, and we conclude, on the basis of present results, that the home range areas of the three hominins were of similar size and composed of identical geological substrates.

The Sr/Ca and Ba/Ca ratios tend to decrease from the enamel dentine junction to the outer enamel, in accordance with previous findings⁸ (Supplementary Data). These trends have been interpreted to result from a positive gradient of mineralization, which favours Ca against Sr and Ba during the enamel secretory and maturation phases. In contrast to the Sr isotopic data, the elemental Sr/Ca and Ba/Ca data in the enamel of South African hominins display differences between the three genera, with a certain degree of overlap (Figs 2 and 3). The Sr/Ca ratio of *A. africanus* is significantly higher than that obtained for other hominin taxa, and the Ba/Ca ratio of early *Homo* is significantly lower than that obtained for other hominin taxa (Supplementary Table 2). The *P. robustus* specimens are characterized by Sr/Ca and Ba/Ca values that are intermediate between those of *A. africanus* and early *Homo*. Compared to the fauna, and taking into account both the Sr/Ca and Ba/Ca ratios, early *Homo* and *P. robustus* are indistinguishable from carnivores and browsers, respectively (Supplementary Table 2). With regard to *A. africanus*, the Sr/Ca and Ba/Ca ratios are indistinguishable from grazers and browsers, respectively (Supplementary Table 3). A possible interpretation is that the diets of early *Homo* and *P. robustus* were typical of carnivores and browsers, respectively, whereas the diet of *A. africanus* was more complex.

Taking the intra-tooth variability of Sr/Ca and Ba/Ca into account gives a more complete picture of the dietary habits of hominins. The

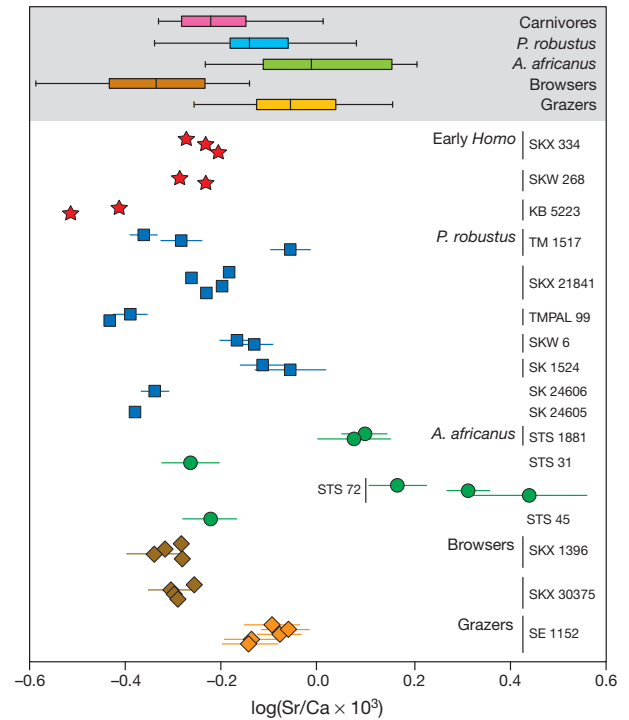


Figure 2 | Sr/Ca ratios of hominin and bovid enamel. For both ratios, error bars are 2-sigma standard deviations of the mean, and the shaded areas contain data from a previous study²⁰.

variability of intra-tooth Sr/Ca ratios provided by the coefficient of variation of the mean Sr/Ca value for a given sample is higher for *A. africanus* ($29.5 \pm 11.3\%$ (± 1 s.d.)) than for the other hominin groups (*P. robustus*, $13.8 \pm 7.6\%$; early *Homo*, $8.6 \pm 2.7\%$; Supplementary Table 3). This is also the case for the variability of the intra-tooth

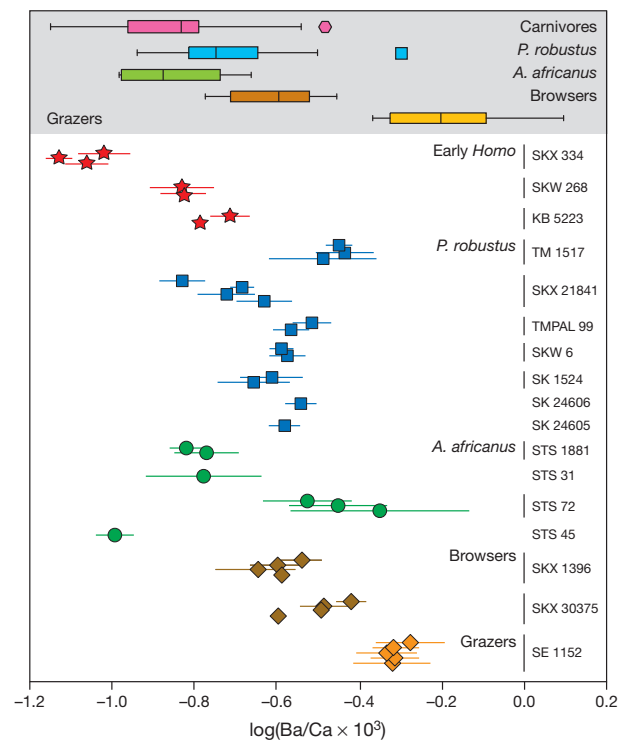


Figure 3 | Ba/Ca ratios of hominin and bovid enamel. For both ratios, error bars are 2-sigma standard deviation of the mean, and the shaded areas contain data from a previous study²⁰.

Ba/Ca ratio (*A. africanus*, $47.7 \pm 25.6\%$; *P. robustus*, $26.0 \pm 12.5\%$; early *Homo*, $23.8 \pm 8.0\%$; Supplementary Table 3).

The diet of *A. africanus* has a high Sr/Ca and a low Ba/Ca ratio, but a monotonous consumption of a Sr-enriched and Ba-depleted diet would not have produced the observed high intra-tooth Sr/Ca and Ba/Ca variability of *A. africanus*. It is more likely that the diet of *A. africanus* resulted from the combination of two distinct dietary sources. An association of woody plants represented by leaves and fruits of trees and bushes, which are Sr-enriched and Ba-depleted⁴, and meat, which is both Sr- and Ba-depleted, could explain the enamel Sr/Ca and Ba/Ca patterns of *A. africanus*. Woody plants and meat products could have been consumed alternately by *A. africanus* on a seasonal scale. This is regarded as the most probable dietary association for the genus *Australopithecus* because it is the only way to reconcile conflicting results based on tooth morphology¹⁹, dental microwear² and carbon isotope ratios²⁰. This scenario is compatible with the idea of fallback resource use, by which it is proposed that food items of poor nutritional quality become an increasing food component as preferred foods become rare^{21,22}. However, at this stage, it is not possible to state whether the fallback food was the woody plant or the meat component.

The diet of *P. robustus* seems to have been less variable than that of *A. africanus* and was mainly based on woody plant foodstuffs. This is consistent with the measured average Sr/Ca and Ba/Ca ratios, which are indistinguishable from browsers, the reduced intra-tooth Sr/Ca and Ba/Ca ratio variability, and with dental microwear and tooth morphology data^{2,23}. Similar to *P. robustus*, the diet of early *Homo* was less variable than that of *A. africanus*, but contrary to the diet of *P. robustus*, it was based more on meat products. Our results support the idea that the degree by which woody plants and underground storage organs²¹ were consumed by *A. africanus* was reduced in the *Homo* lineage, whereas the more specialized masticatory apparatus of the robust australopithecines enabled them to have subsisted mostly on this type of food. However, this constitutes a South African scenario for which the diet of the *Homo*-like australopithecine *A. sediba* remains to be tested²⁴.

METHODS SUMMARY

The analysed tooth samples were housed at the Transvaal Museum (Ditsong National Museum of Natural History) in Pretoria, South Africa. The hominid teeth that were selected were naturally broken or already cut for microstructural studies purposes. This strategy of sampling enables chemical variations to be measured along profiles from the enamel dentin junction to the outer enamel. Sintered standard SRM-1400 ('Bone Ash') was used as a bracketing reference, both for elemental and isotopic measurements, to correct for instrumental biases. A quadrupole-ICPMS (ThermoElement X7) was used for the measurement of trace elements concentrations. Selected monitored elements were Ca, Mn, Zn, Rb, Sr, Y, Ba, La, Sm, Yb, Th and U. The ⁸⁷Sr/⁸⁶Sr ratio was measured on a Nu-HR (Nu-instrument) multicollector-ICPMS. The laser is a 157-nm F₂/He excimer laser LPF202 of Lambda Physik⁹. Contrary to our previous study⁷, we did not measure trace element concentrations and isotopic ratios on the same laser spot, because the Sr concentrations were too low in some of the samples, resulting in poor signal intensity on the multicollector-ICPMS. The trace elements and the isotopic ratios were therefore measured separately in two different sessions. The main operational conditions are summarized in Supplementary Table 1. The standard bone ash SRM-1400, which is certified to contain 250 p.p.m. of Sr, produces typical signals of ⁸⁸Sr of approximately 5×10^4 counts per second (c.p.s.) on the quadrupole-ICPMS and approximately 700 mV on the multicollector-ICPMS. We obtain an average Sr/Ca $\times 10^3$ value of 0.668 ± 0.042 (± 2 s.d.) and an average Ba/Ca $\times 10^3$ value of 0.578 ± 0.054 (± 2 s.d.) for the standard SRM-1400 ($n = 16$). These numbers are close to the certified values of 0.652 and 0.629, respectively²⁵. We obtain an average ⁸⁷Sr/⁸⁶Sr value of 0.713068 ± 0.000728 (± 2 s.d.) for the standard SRM-1400 ($n = 17$), which is close to a thermal ionization mass spectrometry (TIMS) value of 0.713104 ± 0.000019 (± 2 s.d.) that was reported previously²⁶. The method is described fully in the Supplementary Information.

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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 V.B., J.B. and J.F.T. designed the study, V.B. and P.T. carried out the analysis, V.B. wrote the manuscript with J.B. and J.F.T. All authors discussed the results.

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