



Sr/Ca and early hominin diets revisited: new data from modern and fossil tooth enamel

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Abstract

A previous study of strontium/calcium (Sr/Ca) ratios in *Paranthropus* suggested that it consumed more animal foods than was previously believed. However, that study looked at Sr/Ca in fossil bone, which is known to be highly susceptible to diagenesis. Enamel, in contrast, is resistant to post-mortem alteration making it a more appropriate material for Sr/Ca analysis of Plio-Pleistocene fossils. Yet, we know virtually nothing about Sr/Ca in the enamel of modern African mammals, much less fossil taxa. To address this gap, we studied Sr/Ca in tooth enamel from modern mammals in the greater Kruger National Park, South Africa, as well as fossil fauna from the Sterkfontein Valley. Grazing herbivores have the highest Sr/Ca, followed by browsers and carnivores in both modern and fossil fauna. This similarity in ecological Sr/Ca patterning between modern and fossil fauna shows that diagenesis has not obscured the primary dietary signals. *Australopithecus* has significantly higher Sr/Ca than *Paranthropus*, and higher Sr/Ca than fossil papionins, browsers, and carnivores. *Paranthropus* has lower Sr/Ca than grazers, but its Sr/Ca is higher or equal to that of fossil papionins, browsers, and carnivores. Thus, Sr/Ca for both hominins is relatively high, and provides no direct evidence for omnivory in either taxon. The consumption of underground resources or insects are among the possible explanations for the highly elevated Sr/Ca in *Australopithecus*.

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Introduction

Strontium/calcium (Sr/Ca) ratio analysis of bones has long been used as a method for investigating paleodiets (e.g., Toots & Voorhies, 1965; Brown, 1974; Schoeninger, 1979; Sillen, 1981; Price & Kavanaugh, 1982; Sillen & Lee-Thorp, 1994; Burton & Wright, 1995; Balter et al., 2002). Mammals discriminate against dietary strontium (Kostial et al., 1969; Spencer et al., 1973), resulting in herbivores with lower Sr/Ca than the plants they consume. Faunivores, in turn, also discriminate against ingested strontium and thus have lower Sr/Ca than their herbivorous prey. Consequently, Sr/Ca ratios have been used as trophic level indicators within paleontological foodwebs. Most notably, this technique has been used to examine the trophic behavior of the early hominins *Paranthropus robustus* and *Homo ergaster* at Swartkrans (Sillen, 1992; Sillen et al., 1995). Sillen (1992) found that *Paranthropus* had similar Sr/Ca to carnivores, and lower Sr/Ca than primarily herbivorous taxa like *Papio* and *Procapra*. This, in conjunction with contextual data from dental microwear (Grine & Kay, 1988) and stable isotopes (Lee-Thorp, 1989), led him to conclude that this hominin was unlikely to be “purely herbivorous” as many believed. Unexpectedly, Sillen et al. (1995) found slightly lower Sr/Ca in *P. robustus* than in *Homo*, intimating that the latter might have relied heavily on strontium-rich underground storage organs.

These studies, like those carried out before them on less ancient material, were carried out on bone. A major drawback of bone, however, is that it is known to be particularly susceptible to post-mortem chemical alteration (Lee-Thorp & van der Merwe, 1991; Wang & Cerling, 1994; Michel et al., 1995, 1996) that could potentially obliterate its biological Sr/Ca signal. To address this problem, Sillen (1981, 1992) developed a “solubility profiling” technique based on the observation that fossil bone contains apatites having varying solubilities, and on the premise that diagenetic apatite would be likely to have differing solubility from biogenic apatites that remain in fossils. In this technique, highly-soluble and poorly-soluble diagenetic apatites are, in effect, stripped away from

the biogenic material (Sillen, 1981, 1992). While ingenious, this technique is technically challenging and extremely slow, greatly limiting its potential application. More significantly, several studies have shown that the biological signal of bone, even using “solubility profiling” or related methods, is sometimes irrevocably lost during fossilization (Sillen, 1981; Hoppe et al., 2003; Lee-Thorp & Sponheimer, 2003). In contrast, tooth enamel has been shown to be far less susceptible to diagenetic processes (Lee-Thorp & van der Merwe, 1991; Wang & Cerling, 1994; Sponheimer, 1999; Lee-Thorp & Sponheimer, 2003; Hoppe et al., 2003), although it is not completely immune from them (e.g., Kohn et al., 1999; Sponheimer & Lee-Thorp, 1999a; Schoeninger et al., 2003). This strongly suggests that enamel would provide more reliable Sr/Ca data than bone, especially for older material from the Plio-Pleistocene. Yet enamel is not routinely used to this end. The principle reason for this is that some enamel is formed partially during infancy when mammals may not have fully developed their capacity to discriminate against strontium (Lengeman, 1963; Lough et al., 1963; McClellan, 1964; Rivera & Harley, 1965). Nonetheless, this problem is easily avoided by analyzing late-developing teeth. Hence, there seems to be no clear reason why enamel should not be used to investigate paleodiets. Indeed, it might also be argued that analysis of enamel is necessary if we are to have full confidence in Sr/Ca data from Plio-Pleistocene fauna. We believe that this argument has considerable merit and that a reinvestigation of early hominin Sr/Ca using enamel is both timely and appropriate.

Our aims in this paper are three-fold. Firstly, we present novel data on Sr/Ca in the tooth enamel of African savanna mammals, as no such data are known to exist. These data then serve as an interpretive framework for our fossil study. Secondly, we establish that diagenesis has not obscured the ecological information we seek to retrieve by showing that the ecological patterning of Sr/Ca observed in modern African savanna fauna is retained in fossils from the Sterkfontein Valley. Lastly, we present data for *P. robustus*, *Australopithecus africanus*, and associated fauna and discuss the implications of these findings.

Methods

Modern samples from the greater Kruger National Park were obtained from collections housed at the Transvaal Museum and the Bernard Price Institute for Palaeontological Research in South Africa (Table 1). We focused on sampling three major groups of mammals, namely grazers,

browsers, and carnivores. This enabled us to look for differences in Sr/Ca within (grazers/browsers) and between (herbivore/carnivore) trophic levels. All fossil specimens were sampled at the Transvaal Museum. To ensure comparability with our modern dataset, we focused on the same groups (grazers, browsers, and carnivores) from Sterkfontein Member 4 (M4) and Swartkrans Member 1 (M1), which are dated to about 2.5 Ma and 1.8 Ma respectively (e.g., Vrba, 1985) (Table 2). We also sampled papionins and hominins from each site, as well as one hominin specimen from Kromdraai B Member 3 (Table 3). As this site is adjacent to the others (~1 km), on the same geologic substrate,

Table 1

Sr/Ca \times 1000 of modern browsers, carnivores, and grazers analyzed for this study. Specimen numbers with the prefixes BP and TM are from the Bernard Price Institute for Palaeontological Research and Transvaal Museum respectively

Specimen	Taxon	Sample	Sr/Ca
<i>Browsers</i>			
BP/4 27	<i>Giraffa camelopardalis</i>	M2	1.16
BP/4 332	<i>Giraffa camelopardalis</i>	dP4	0.80
BP/4 529	<i>Giraffa camelopardalis</i>	dP4	0.73
BP/4 38	<i>Tragelaphus scriptus</i>	M2	1.06
TM 13381	<i>Tragelaphus scriptus</i>	M3	1.51
TM 13098	<i>Tragelaphus strepsiceros</i>	M3	0.77
TM 13171	<i>Tragelaphus strepsiceros</i>	M3	0.90
TM 13266	<i>Tragelaphus strepsiceros</i>	M3	1.53
TM 16658	<i>Tragelaphus strepsiceros</i>	M3	1.58
Mean \pm SD			1.12 \pm 0.35
<i>Carnivores</i>			
BP/4 202	<i>Crocota crocuta</i>	P4	1.04
BP/4 203	<i>Crocota crocuta</i>	P4	1.40
TM 13273	<i>Crocota crocuta</i>	P4	2.07
TM 16703	<i>Crocota crocuta</i>	P4	2.02
BP/4 186	<i>Panthera leo</i>	Bone	1.18
TM 13924	<i>Panthera leo</i>	Bone	0.76
TM 4402	<i>Panthera leo</i>	P4	1.25
TM 4404	<i>Parahyaena brunnea</i>	P4	0.62
Mean \pm SD			1.29 \pm 0.53
<i>Grazers</i>			
BP/4 87	<i>Connochaetes taurinus</i>	M2	3.03
BP/4 89	<i>Connochaetes taurinus</i>	M2	2.49
TM 13159	<i>Connochaetes taurinus</i>	M3	1.93
BP/4 79	<i>Damaliscus lunatus</i>	M2	1.20
BP/4 80	<i>Damaliscus lunatus</i>	M2	1.82
BP/4 328	<i>Equus burchelli</i>	M2	4.91
BP/4 46	<i>Hippotragus niger</i>	M2	2.65
BP/4 51	<i>Kobus ellipsiprymnus</i>	M2	4.21
BP/4 52	<i>Kobus ellipsiprymnus</i>	M2	0.82
TM 16701	<i>Kobus ellipsiprymnus</i>	M3	2.36
BP/4 11	<i>Phacochoerus aethiopicus</i>	M2	2.88
BP/4 12	<i>Phacochoerus aethiopicus</i>	M3	2.47
BP/4 13	<i>Phacochoerus aethiopicus</i>	M2	3.01
TM 24005	<i>Phacochoerus africanus</i>	M3	2.72
Mean \pm SD			2.61 \pm 1.06

Table 2

Sr/Ca \times 1000 for fossil browsers, carnivores, and grazers in this study. Specimens with the prefixes SK and STS are from Swartkrans M1 and Sterkfontein M4 respectively

Specimen	Taxon	Sample	Sr/Ca
<i>Browsers</i>			
SK 14112	<i>Tragelaphus</i>	RM2	0.71
SK 2095	<i>Tragelaphus</i>	RM3	0.37
SK 2281	<i>Tragelaphus</i>	LM2	0.46
SK 3110	<i>Tragelaphus</i>	RM3	0.54
STS 2412	<i>Tragelaphus</i>	M3	0.36
STS 2561	<i>Tragelaphus</i>	M2	0.21
STS 793	<i>Tragelaphus</i>	M2	0.62
Mean \pm SD			0.47 \pm 0.17
<i>Carnivores</i>			
STS 133	<i>Chasmodon</i>	P4	0.50
SK 1807	<i>Crocota</i>	P3	0.46
SK 321	<i>Crocota</i>	P4	1.05
STS 129	<i>Hyaenid</i>	P4	0.60
STS 867	<i>Hyaenid</i>	P4	0.76
STS 880	<i>Hyaenid</i>	P4	0.58
SK 342	<i>Panthera</i>	RM1	0.72
SK 348	<i>Panthera</i>	LM1	0.62
Mean \pm SD			0.66 \pm 0.19
<i>Grazers</i>			
SK 2110	<i>Connochaetes</i>	LM3	1.14
SK 2483	<i>Connochaetes</i>	RM3	0.59
SK 3097	<i>Connochaetes</i>	LM3	0.56
STS 2061	<i>Connochaetes</i>	RM3	1.11
SK 4241	<i>Damaliscus</i>	LM3	0.86
SK 9897	<i>Damaliscus</i>	RM3	0.89
STS 1319	<i>Damaliscus</i>	LM3	0.76
STS 1696	<i>Damaliscus</i>	LM3	0.91
STS 2586	<i>Damaliscus</i>	LM3	1.46
Mean \pm SD			0.92 \pm 0.28

Table 3

Sr/Ca \times 1000 for fossil papionins and hominins in this study. Specimens with the prefixes SK and STS are from Swartkrans M1 and Sterkfontein M4 respectively. TM 1532 is from Sterkfontein M4 and TM 1603 is from Kromdraai B M3

Specimen	Taxon	Sample	Sr/Ca
<i>Papionins</i>			
SK 508	<i>Papio</i>	RM3	0.72
SK 621	<i>Papio</i>	LM3	0.57
STS 454	<i>Parapapio</i>	M3	0.47
STS 510	<i>Parapapio</i>	M3	0.48
Mean \pm SD			0.56 \pm 0.11
<i>Hominins</i>			
STS 2218	<i>Australopithecus</i>	M	0.90
STS 31	<i>Australopithecus</i>	RM3	0.69
STS 32	<i>Australopithecus</i>	RM3	1.49
STS 45	<i>Australopithecus</i>	RM2	0.60
STS 61	<i>Australopithecus</i>	M	0.98
STS 72	<i>Australopithecus</i>	RM3	1.62
TM 1532	<i>Australopithecus</i>	LM3	1.39
Mean \pm SD			1.09 \pm 0.41
SK 14000	<i>Paranthropus</i>	LM3	1.20
SK 14132	<i>Paranthropus</i>	RM3	0.78
SK 1524	<i>Paranthropus</i>	LM3	0.74
SK 19	<i>Paranthropus</i>	RM3	0.90
SK 24606	<i>Paranthropus</i>	RM3	0.54
SK 35	<i>Paranthropus</i>	LM1	0.70
SK 41	<i>Paranthropus</i>	LM3	0.51
SK 57	<i>Paranthropus</i>	LM3	0.65
SK 831a	<i>Paranthropus</i>	LM2	1.08
SKW 3068	<i>Paranthropus</i>	LM2	0.87
SKW 4768	<i>Paranthropus</i>	LM2	0.89
SKW 6	<i>Paranthropus</i>	LM3	0.73
TM 1600	<i>Paranthropus</i>	M	0.48
Mean \pm SD			0.78 \pm 0.21

and from a similar time period as Swartkrans M1, we felt that its inclusion was warranted.

All specimens were visually inspected prior to sampling. We did not sample specimens that were highly stained or had mineral inclusions. About 2 mg of tooth enamel (see Tables 1, 2 & 3 for teeth sampled) was abraded from each tooth using a rotary drill with a diamond tipped burr (Sponheimer, 1999). In general, we endeavored to collect enamel over a large surface area, so as to avoid collecting enamel that was formed over a brief period. We also sampled, in the same way, two bones and two juvenile teeth for our modern study (Table 1). As Sr/Ca for these samples is not systematically different from that of late-forming

teeth (e.g., the dP4's did not have elevated Sr/Ca), and excluding them has little effect on the statistical significance of our results, we have included these data herein. All hominin teeth that were sampled had been previously fractured, enabling us to sample between the enamel-dentine junction and the outer surface, thus avoiding damage to the external surface of the teeth.

The enamel powder from each specimen was then treated with 0.1 M acetic acid for 10 minutes to remove contaminating carbonates, and then rinsed to neutrality with distilled, deionized water (Sponheimer, 1999). Following the standard practice in our ICP-MS laboratory, the remaining sample was then dissolved in 1 ml of HF:HNO₃ (4:1) in closed teflon beakers. After complete dissolution the beakers were opened and the samples evaporated to dryness on a hotplate. The residue was then dissolved in 0.5 ml of HNO₃ and evaporated to dryness. After further dissolution in 0.5 ml of HNO₃, the samples were dried and dissolved in 10 ml of 5% HNO₃ solution and finally analyzed for Sr and Ca on a Perkin-Elmer Elan 6000 ICP-MS. The precision of this instrument for these elements is better than 3%, and the coefficient of variation of an internal rhino apatite standard run concurrently with the samples in this study was 1% Sr/Ca is presented here as (Sr/Ca)*1000 as in Sillen (1992). We looked for differences in the Sr/Ca of grazers, browsers, carnivores, papionins and hominins using analysis of variance (ANOVA) and Fisher's FLSP. We also log-transformed the Sr/Ca data (e.g., Burton et al., 1999; Balter et al., 2002), but as this did not appreciably affect the results, we restrict discussion to the non-transformed dataset.

Results and discussion

Modern study

The modern data are provided in Table 1 and summarized in Fig. 1. Herbivore Sr/Ca ($x = 2.02$, s.d. = 1.13, $n = 23$) was higher, albeit not significantly higher than carnivore Sr/Ca ($x = 1.29$, s.d. = 0.53, $n = 8$) ($P = 0.08$). This lack of significance is largely due to the disparity between the

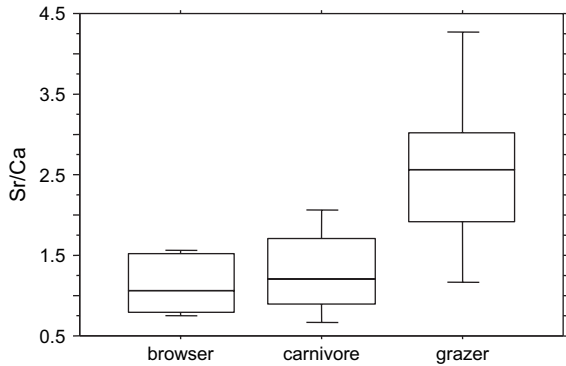


Fig. 1. Sr/Ca \times 1000 for browsers (*Tragelaphus strepsiceros*, *T. scriptus*, *Giraffa camelopardalis*), grazers (*Kobus ellipsiprymnus*, *Hippotragus niger*, *Connochaetes taurinus*, *Damaliscus lunatus*, *Equus burchelli*, *Phacochoerus africanus*) and carnivores (*Panthera leo*, *Crocota crocuta*, *Parahyaena brunnea*) from greater Kruger National Park. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles.

browsers ($x = 1.12$, s.d. = 0.35, $n = 9$) and grazers ($x = 2.61$, s.d. = 1.06, $n = 14$) ($P < 0.001$) that comprise the herbivore group. While this difference between grazers and browsers has not been reported outside the African continent (e.g., Burton et al., 1999; Balter et al., 2002), it is consistent with work on African mammals showing that grazers like warthogs (*Phacochoerus africanus*) have higher Sr/Ca than browsers like kudu (*Tragelaphus strepsiceros*) and steenbok (*Raphicerus campestris*) (Sillen, 1988, 1992; Sealy & Sillen, 1988). The low Sr/Ca in browsers may be driven by the low Sr/Ca of their leaf diets compared to other plant foods (see Bowen & Dymond, 1955; Menzel & Heald, 1959; Alexahin & Ravikovich, 1967; Wallace & Romney, 1971; Iserman, 1981; Runia, 1987 for discussions of Sr/Ca in plants). Grazers and carnivores, in contrast, were highly different ($P < 0.001$). Thus, it is clear that, from an African perspective at least, the term herbivore is of limited utility, and that mammals should be broken down into more specific dietary groups such as grazers, browsers, and carnivores for statistical analysis. In fact, given the variation present in the grazers, it might be appropriate to break them down into more specific ecological categories such as fresh grass grazers and secondary grassland grazers in certain instances. We do

not do so here, as our main goal was to demonstrate that there are strong differences in enamel Sr/Ca between mammals with different diets, and in so doing establish the viability of enamel for paleoecological study.

Fossil study

Swartkrans versus Sterkfontein

There are no systematic differences in Sr/Ca between the fauna from Sterkfontein M4 and Swartkrans M1, as was expected given their proximity (1 km) and identical local geology. For instance, carnivores at Sterkfontein M4 ($x = 0.61$, s.d. = 0.11, $n = 4$) and Swartkrans M1 ($x = 0.71$, s.d. = 0.25, $n = 4$) are statistically indistinguishable ($P = 0.48$). The same is true for grazers ($P = 0.39$) and browsers ($P = 0.39$). Consequently, dietary groups (browsers, grazers, and carnivores) cluster together regardless of site. We therefore pool samples from both sites (hereafter Sterkfontein Valley fauna) for statistical analysis.

Diagenesis and ecological patterning

The Sr/Ca patterning of the Sterkfontein Valley fauna is very similar to that observed for the modern mammals (Table 2 & Fig. 2). Browsers ($x = 0.47$, $n = 7$, s.d. = 0.17) have the lowest Sr/Ca, followed by carnivores ($x = 0.66$, $n = 8$,

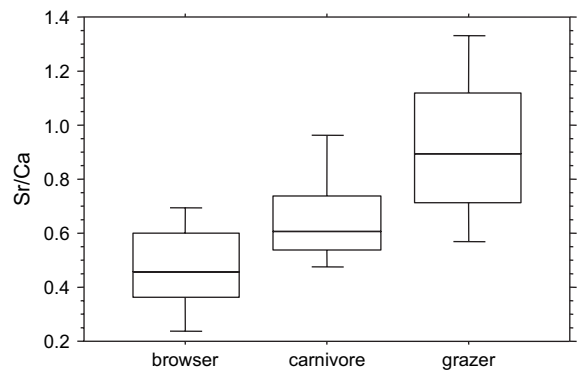


Fig. 2. Sr/Ca \times 1000 for browsers (*Tragelaphus*), grazers (*Connochaetes*, *Damaliscus*), and carnivores (*Crocota*, *Chasmodon*) from Swartkrans M1 and Sterkfontein M4. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles.

s.d. = 0.19) and grazers ($x = 0.92$, $n = 9$, s.d. = 0.28). Like the modern fauna, there is no significant difference between carnivores and herbivores ($P = 0.63$), but grazer Sr/Ca is significantly higher than browser ($P < 0.001$) and carnivore ($P = 0.04$) Sr/Ca. Furthermore, in both the modern and fossil datasets browser Sr/Ca is about half of that in grazers (43% modern, 51% fossil). This finding, that the modern and fossil fauna have the same Sr/Ca patterning, demonstrates that biogenic signals are retained in fossil enamel from these sites. It should be noted, however, that we are not arguing that the fossil enamel has undergone no chemical change, but only that the ecological patterning of concern here has not been obscured by diagenesis. This result is not surprising given recent studies showing that, unlike bone, very little diagenetic strontium remains in enamel after appropriate pretreatment (Hoppe et al., 2003; Lee-Thorp & Sponheimer, 2003).

Hominins and papionins

The hominin and papionin data proved surprising on three counts (Table 3 & Fig. 3). Firstly, *Australopithecus* ($x = 1.10$, $n = 7$, s.d. = 0.41) has higher Sr/Ca than *Paranthropus* ($x = 0.78$, $n = 13$, s.d. = 0.21) ($P = 0.01$). Although previous dental microwear studies found evidence of dietary differences between these taxa, they suggested

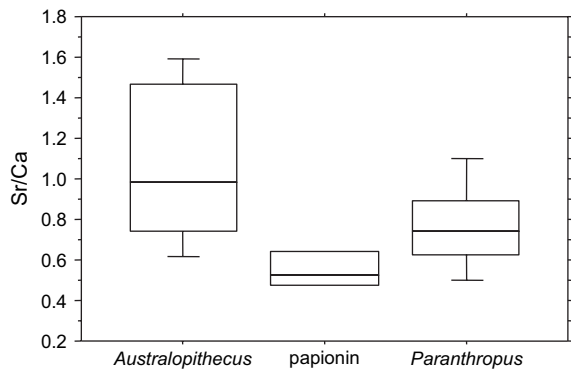


Fig. 3. Sr/Ca $\times 1000$ of *Australopithecus*, *Paranthropus*, and fossil papionins from the Sterkfontein Valley. The box represents the 25th–75th percentiles (with the median as a horizontal line) and the whiskers show the 10th–90th percentiles.

diets of hard, brittle foods for *Paranthropus* and fleshy fruits and leaves for *Australopithecus* (Grine, 1986; Grine & Kay, 1988), and it was not at all clear that these diets should have dissimilar Sr/Ca. Furthermore, studies of the carbon isotopes locked in the tooth enamel of these hominins were unable to document any dietary differences (Sponheimer & Lee-Thorp, 1999b, 2003; van der Merwe et al., 2003). Thus, Sr/Ca appears to provide evidence of a dietary differentiation that other chemical techniques could not. This might also be seen to strengthen the observation that *Homo* has higher Sr/Ca than *Paranthropus* (Sillen et al., 1995), but as only two specimens of *Homo* have been analyzed, the evidence for this difference remains weak and requires further sampling and analysis to be substantiated.

The second surprise is that neither hominin species has particularly low Sr/Ca ratios. Indeed, in contrast to Sillen (1992), we found that *Paranthropus* Sr/Ca is higher than that of the Sterkfontein Valley's papionins ($x = 0.56$, $n = 4$, s.d. = 0.12), although the difference is not significant ($P = 0.14$). Moreover, *Australopithecus* Sr/Ca is significantly higher than that of the papionins ($P < 0.01$). Together with the higher Sr/Ca of both hominins compared to the Sterkfontein Valley browsers and carnivores ($P \leq 0.01$ except *Paranthropus*/carnivore pairing ($P = 0.31$)), these data indicate that the australopiths have relatively high, rather than low, Sr/Ca. Sillen (1992) argued that the relatively low Sr/Ca in *Paranthropus* was best interpreted as evidence of an omnivorous diet; however, these new Sr/Ca data provide no direct evidence for omnivory in *Paranthropus* or *Australopithecus*. This does not mean that these taxa did not consume significant proportions of animal foods, but only that there is no evidence of such trophic behavior to be found in the Sr/Ca data themselves.

Lastly, one of the enigmas of the previous *Paranthropus* dataset was its virtual lack of variability. The coefficient of variation (CV) for Sr/Ca in modern African mammals tends to range between 22% and 37% (Sillen, 1988), while the CV for the previously sampled *Paranthropus* specimens was only 13% (s.d = 0.03) (Sillen, 1992). This oddity led Thackeray (1995) to hypothesize

that the *Paranthropus* specimens analyzed were all males, thereby reducing variability. However, the CV for *Paranthropus* in this study is 28%, evidence of far greater variability than was previously reported, and much more in line with other modern and fossil taxa. Hence, the anomalously low CV for *Paranthropus* is no longer a problem. The question now becomes why did we observe so much more variability than did Sillen (1992)? There are a number of possible explanations for this finding. For one, the sample size in this study (13) is larger than the previous sample (8). Thus, we may have captured variation that was masked by Sillen's smaller sample size. Another possible explanation is that because the prior study relied on bone rather than enamel, Sr/Ca variability was reduced due to diagenetic phenomena (despite "solubility profiling") (Sillen, 1996). The increased variability here might also be the result of sampling enamel, which provides information about a discrete period of an individual's life, as opposed to bone which represents more of a lifetime average (Sealy et al., 1995; Lowenstam & Weiner, 1989; Aiello & Dean, 2002). At present, we cannot determine which of these possibilities is most likely to explain the increased variation in this study. Indeed, it is possible that all three, as well as other factors, contributed in some way.

Dietary interpretations

So what does this exercise tell us about early hominin diets? Of particular note, the data suggest that unlike carbon isotopes (Sponheimer & Lee-Thorp, 1999, 2003; van der Merwe et al., 2003), Sr/Ca can distinguish between the diets of *Australopithecus* and *Paranthropus*. We can also say that there is little reason to argue for omnivory based upon Sr/Ca in either taxon, as both have higher Sr/Ca than contemporaneous browsing herbivores and papionins. The fact that *Paranthropus* has somewhat lower Sr/Ca than grazing herbivores is certainly not sufficient to make a case for omnivory. It is particularly salient that *Paranthropus* Sr/Ca cannot be distinguished statistically from that of the Sterkfontein Valley's papionins; therefore, there is no reason to believe that *Paranthropus* consumed greater amounts of animal foods than contemporaneous baboons. In

addition, even if the Sr/Ca of one or both of these australopith species was low, it would still provide only limited support for omnivory given our nascent understanding of Sr/Ca throughout African foodwebs. For instance, diets rich in leaves also lead to low Sr/Ca, and while a diet rich in leaves is unlikely for the australopiths (given their extremely low shearing crests) (Kay, 1985; Ungar, 2004), we cannot rule out the consumption of other low Sr/Ca foods. We know very little about the Sr/Ca of different kinds of African fruits, for example, and it is possible that some have low Sr/Ca. Consequently, our limited knowledge of Sr/Ca in plant foods, and even African savanna mammals, makes further dietary interpretation from Sr/Ca data problematic.

Nevertheless, the very high Sr/Ca of *Australopithecus* observed here remains intriguing and demands at least some tentative explanation. Could it be that *Australopithecus* ate large quantities of grass (like grazers do), leading to their elevated Sr/Ca? There is strong evidence that *Australopithecus* ate about 33% C₄ grasses, C₄ sedges, or perhaps animals that ate these foods (Sponheimer & Lee-Thorp, 1999b, 2003; van der Merwe et al., 2003), so this idea merits consideration. However, preliminary evidence from a study of barium in *Australopithecus* militates against this interpretation. *Australopithecus*' Ba/Ca is very low ($x = 0.15$, s.d. = 0.05, $n = 7$), and quite unlike contemporaneous grazers ($x = 0.68$, s.d. = 0.25, $n = 9$) ($P < 0.001$), which have high Sr and Ba concentrations (Fig. 4). Thus, the incorporation of above-ground grass products alone does not appear to be the best explanation for the elevated Sr/Ca of *Australopithecus*.

Another potential explanation for the high Sr/Ca of *Australopithecus*, and to a lesser extent *Paranthropus*, is insectivory. A recent pilot study discovered that modern insectivores (*Orycteropus afer*) have much higher Sr/Ca than carnivores (Sponheimer, unpublished data). Thus, not all faunivores are equivalent from the perspective of Sr/Ca. This possibility is particularly intriguing given recent evidence that Plio-Pleistocene bone tools in the Sterkfontein Valley were used to dig for termites (Backwell & d'Errico, 2001). Yet, these pilot data also show that, unlike the

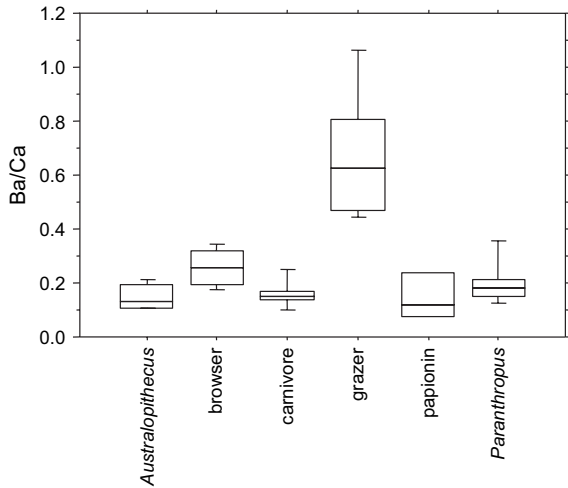


Fig. 4. Ba/Ca \times 1000 of *Australopithecus*, *Paranthropus*, papionins, browsers, carnivores, and grazers from the Sterkfontein Valley. The box represents the 25th-75th percentiles (with the median as a horizontal line) and the whiskers show the 10th-90th percentiles.

hominins, insectivores have high Ba/Ca, making it less likely that the elevated hominin Sr/Ca results from insectivory. At present, however, we have sampled far too few insectivores to seriously address this possibility.

There is, however, a somewhat more promising alternative. We have noticed that among the modern fauna that have the unusual combination of high Sr/Ca and low Ba/Ca are warthogs (*Phacochoerus africanus*) and mole rats (*Cryptomys hottentotus*) (Sponheimer, unpublished data), both of which eat diets rich in underground resources such as roots and rhizomes. Thus, the possibility of greater exploitation of underground resources by *Australopithecus* compared to *Paranthropus* requires consideration. In addition, the slightly enriched Sr/Ca of *Paranthropus* compared to papionins might also be evidence of increased utilization of underground resources. Thus, the consumption of underground resources seems to be a reasonable hypothesis to explain the Sr/Ca of South African hominins in general, and the very high Sr/Ca of *Australopithecus* in particular. Indeed, Sillen et al. (1995) have argued that the consumption of underground resources (e.g., *Hypoxis*) led to relatively high

Sr/Ca in early *Homo*. Underground resources are not consumed by either *Pan* or *Gorilla* to any significant degree (e.g., McGrew et al., 1982). It could be that the consumption of such foods, at least seasonally, was an important hominin adaptation that allowed exploitation of increasingly arid and seasonal environments so inimical to extant African apes (Hatley & Kappelman, 1980; Conklin-Brittain et al., 2002). We stress, however, that the consumption of underground foods is only one possible explanation for the Sr/Ca patterning observed herein.

Although interpretation of the data offered here remains difficult, Sr/Ca analysis of tooth enamel shows much promise. It is clear that the Sr/Ca of fossil enamel does preserve ecological information. Moreover, as enamel does not require a time-consuming pretreatment procedure and is more resistant to diagenesis than bone, it should prove an invaluable tool for investigating the ecology of Plio-Pleistocene fauna. However, truly fruitful application of this tool requires large scale, systematic investigation of Sr/Ca in plants and mammals. While promising work of this sort has been carried out in North America (see Burton et al., 1999), very little such work has been completed on the very different plant and faunal communities that abound in southern African savannas. Finally, we stress that paleoecological reconstruction is a tricky business, and that individual techniques (e.g., Sr/Ca, dental microwear, ecomorphology, carbon isotopes) all have strengths and limitations. We believe that only a concerted effort to integrate these disparate techniques will provide us with a better glimpse into the lives of our forebears.

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