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Strontium–calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans

Strontium–calcium ratios (Sr/Ca) are normally reduced at higher trophic levels in foodwebs, due to discrimination against strontium in favour of calcium by animals. This phenomenon has not generally been applied to the study of fossil foodwebs and the diets of early hominids because of diagenetic changes which obscure or obliterate biological Sr/Ca. The examination of compartments of fossil apatite having differing solubility, however, is a promising method for independently measuring biological and diagenetic Sr/Ca. In this study, Sr/Ca in Member I fossils from the site of Swartkrans were examined using a solubility profile procedure. Sr/Ca relationships observed among Swartkrans fauna match those seen in modern African foodwebs, suggesting that biological Sr/Ca accounts for the observed variation.

When specimens of the fossil hominid *Australopithecus robustus* were examined, Sr/Ca values were inconsistent with that of a root, rhizome or seed-eating herbivore, suggesting that the diet of this species was more diverse than previously believed, and almost certainly included the consumption of animal foods.

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Introduction

Dietary reconstructions of *Australopithecus robustus* based on dental and cranial morphology have generally followed John Robinson's initial formulation that this species was primarily a herbivore (Robinson, 1954, 1956). While there has been considerable debate concerning the nature of *A. robustus* diets, this debate has been mainly limited to the amount of "hard objects", fibre, foliage and fruit within the context of herbivory (Grine, 1981; Pilbeam & Gould, 1974; Lucas *et al.*, 1985; Grine, 1986; Grine & Kay, 1988; Kay & Grine, 1988).

Exceptions to the idea of *A. robustus* herbivory exist in the literature. For example, it has been suggested that enamel chipping on the edge of occlusal surfaces in Swartkrans specimens is due to the consumption of bone (Tobias, 1967). One ecobotanical study has concluded that omnivory was a more plausible adaptation than herbivory for robust hominids in both East and Southern Africa (Peters, 1987), and a general caution has been proffered that all hominid diets were likely to have been extremely complex (Mann, 1981).

No firm archaeological data exist to support a herbivorous dietary adaptation for robust australopithecines. In both East and Southern Africa, these hominids occur at the same sites as early *Homo*, and given the resolution of the archaeological record in the period 1–2 million years ago (m.y.a.), it is not yet possible (except at the level of inference) to establish which hominid is responsible for stone tools and traces of carcass processing such as cut marks. The contextual issues regarding *Homo* sp., *A. robustus* and *Australopithecus boisei* in this period have recently been reviewed elsewhere (White, 1988).

Nevertheless, the notion that *A. robustus* was a herbivore has had a pervasive influence on the paleoanthropological literature. A recent study of robust australopithecine hand morphology, for example, concluded that these creatures were capable of making tools, but that "... it could well have been a toolmaking/-using vegetarian, while its less megadont hominid counterparts may have enjoyed a more omnivorous lifestyle ..." (Susman, 1988: 170). No alternative interpretations were considered. The prevalent view, based primarily

on microwear studies and East African cut-mark data, is that "the available evidence is consistent with a notion of hominine omnivory in contrast to 'robust' herbivory . . ." (Vrba, 1988:420). The available evidence is also consistent, however, with both hominine and "robust" omnivory.

The purpose of this study is to examine the judgment that *A. robustus* was a herbivore (as opposed to an omnivore) using the distribution of the trace element strontium (generally expressed as the strontium–calcium ratio, Sr/Ca) in foodwebs. For this purpose, hominid and faunal fossils from the South African Transvaal site of Swartkrans were analysed. This site was chosen because a well identified and carefully studied fauna was available (Brain, 1981), numerous specimens of *A. robustus* were similarly available, and initial study indicated that the fossil material from this site was amenable to such chemical analysis (Sillen & LeGeros, 1991).

Because Sr/Ca values are normally reduced at higher trophic levels in foodwebs, it has long been thought that they may provide key information into the diets of fossil humans (Mann, 1981; Walker, 1981). At the outset, however, it should be recognized that use of Sr/Ca to examine prehistoric diets is by no means straightforward. During the last decade two major areas of difficulty in using Sr/Ca for paleoanthropological study have been identified: the biological basis of the distribution of strontium in foodwebs, and diagenesis (the chemical and physical changes that bones undergo after interment). Since these issues bear directly on the design and interpretation of Sr/Ca studies on fossils, they warrant some initial discussion.

Sr/Ca in diet

While the theoretical basis for using Sr as a paleodietary indicator has been reviewed elsewhere (Sillen & Kavanagh, 1982; Price *et al.*, 1985), numerous developments during the past 5 years have prompted a reassessment of the models first proposed for using Sr/Ca to reconstruct human diets. Early models were based on the observation that, since relatively more dietary Ca than Sr is absorbed by animals, bone Sr/Ca is lower than that of the food an animal has consumed. It was thus recognized that, in theory, Sr/Ca should be reduced in high trophic-level organisms.

An important qualification was that such relationships could only be expected within circumscribed geographic regions having similar underlying geology and baseline levels of alkaline earths in soils (Sillen & Kavanagh, 1982). For example, no biologically meaningful relationships can be detected when species from different geographic regions are compared (Schoeninger, 1985). Moreover, wet, well drained soils generally have lower concentration of trace elements (including Sr) available to plants than do dry, poorly drained ones (Mitchell, 1955, 1957).

On the biological level, it was recognized that mammalian discrimination against Sr does not occur in juvenile animals (Lengemann, 1963; McClellan, 1964; Lough *et al.*, 1963; Rivera & Harley, 1965). The practical implications are that only adult animals are comparable to each other, and that bone, which is subject to turnover, is the tissue of choice for Sr/Ca (in preference to dental enamel, which is formed at a time when the individual may not be discriminating against Sr).

Because a reduction in Sr/Ca was demonstrated in animals from at least one such natural food web (Elias *et al.*, 1982), Sr/Ca was at first thought of principally as a trophic level indicator. When applied to humans, it was assumed to reflect inversely the contribution of meat to the diet (Brown, 1973; Schoeninger, 1979, 1982; Sillen, 1981a; Sillen & Kavanagh, 1982).

The Elias study, however, was not designed with the aim of providing background data for paleodietary research. One particular shortcoming is that it did not document the variability in Sr/Ca at each trophic level. Recent studies of both laboratory animals and natural foodwebs, conducted specifically as background research for using Sr/Ca as a paleodietary indicator, have made it necessary to qualify the biological model by which this measurement may be used to reconstruct human diets.

It is now known that considerable variability in Sr/Ca occurs within each trophic level (plants, herbivores and carnivores). Roots, rhizomes and edible grass parts (notably seeds) have been shown to have elevated Sr/Ca when compared with leaves, and to other vegetation in a given environment (Runia, 1987, 1988; see also Kuhnlein, 1990). Coupled with this, recent study of laboratory animals on controlled diets has shown that dietary fiber selectively binds Ca so that high fiber diets (e.g., consisting of seeds and storage organs) have relatively more available Sr/Ca than low-fiber diets (Lambert & Weydert, in press). This study also found an excellent correlation ($r=0.830$) between dietary and bone Sr/Ca.

These considerations explain why, among herbivores, animals feeding predominantly on leaves have been found to have relatively low Sr/Ca when compared to those feeding predominantly on high fiber plant parts. Two studies of African foodwebs which are particularly relevant, and provide further necessary background information, are from the Western Cape, South Africa (Sealy & Sillen, 1988), and from a hunting station in the region of Nagapande, Zimbabwe (Sillen, 1988). In the Nagapande study, warthogs whose stomach contents were almost exclusively roots of the grass *Loudetia superba* (Child, 1965) had significantly higher Sr/Ca than leaf and shoot eating kudu (Sillen, 1988). [Warthog diets may, however, vary considerably at other localities (Cumming, 1975; Smithers, 1983).] In the Western Cape, *Lepus capensis*, a hare which feeds on the leaves and new shoots of a variety of grasses (Smithers, 1983), had relatively low Sr/Ca for a herbivore when compared with hyraxes (*Procavia capensis*) (Sealy & Sillen, 1988). Relatively low Sr levels have similarly been reported in modern lagomorphs both from Africa (Schoeninger, 1985) and North America (Ezzo, 1992). Members of the genus *Procavia*, on the other hand, are mixed feeders who may graze or browse depending upon the seasonal availability of foods, and whose diet may include flowers, stems, bark, liverwort and lichens in addition to leaves (Olds & Shoshani, 1982; Hoeck, 1975; Walker *et al.*, 1978).

In the modern Western Cape foodweb, the leaf eating animals steenbok (*Raphicerus* sp.) and duiker (*Sylvicapra grimmia*) were found to have relatively low Sr/Ca, and therefore were not distinguishable from carnivores (Figure 1). Porcupines (*Hystrix africae-australis*), whose diet consist largely of roots and rhizomes, were found to have elevated Sr/Ca which was clearly distinguished from carnivores. Thus, while the general trend of reduced Sr/Ca in higher trophic levels has been confirmed, the differences amongst herbivores causes considerable overlap in Sr/Ca when different trophic groupings are compared. Because of the difference among herbivores, the reduction in trophic level is reliably seen only when specific prey-predator pairs are compared (in the case of the Western Cape, leopards with hyraxes, and seals or cormorants with fish) (Sealy & Sillen, 1988).

Before such variability within trophic levels was appreciated, our ability to understand empirical data derived from fossils was seriously limited. For example, a previous study of fossils from the Omo Shungura Formation found that the extinct specialized sabre-tooth, *Homotherium*, had elevated Sr/Ca when compared to other less specialized carnivores in the study (Sillen, 1986). Indeed, *Homotherium* Sr/Ca was not significantly different from that of kudu (*Tragelaphus nakuae*). This seemed counter-intuitive at the time, and a number of

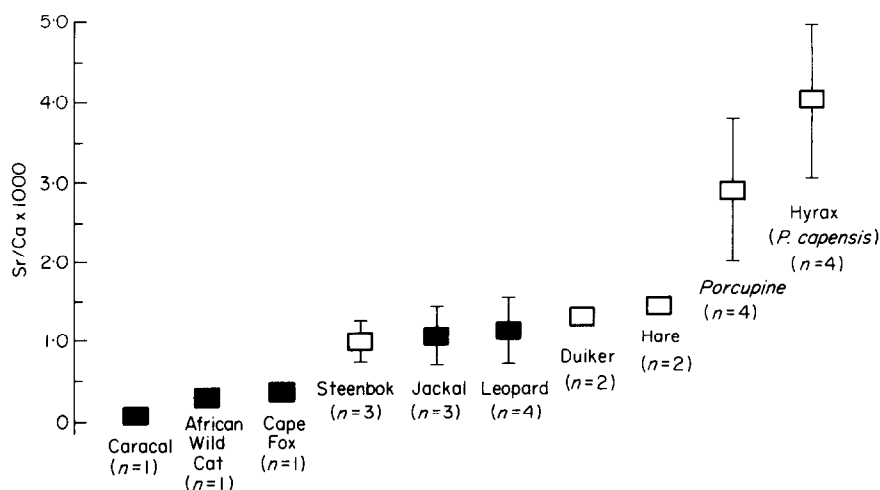


Figure 1. Sr/Ca of modern animals from the Western Cape (data from Sealy & Sillen, 1988). (■) Carnivores; (□) herbivores. There is considerable overlap between carnivores and folivorous herbivores.

diagenetic and/or biological explanations were explored, including the likely metabolic response to a specialized flesh diet. The one explanation which was not considered, however, was that *Homotherium* simply consumed herbivores with higher Sr/Ca than the herbivores consumed by the other carnivores. This explanation is entirely plausible given our current understanding of this measurement in foodwebs.

These observations imply that one must exercise care when comparing fossil species either with the aim of establishing whether biological Sr is recoverable at the outset, or with the aim of examining a species whose diet is unknown. Such studies have increased the likelihood, however, that with appropriate care, we may achieve these aims. For example, it is now possible to formulate specific predictions about Sr/Ca variability in fossil foodwebs based on investigations of modern ones. If a similar pattern of interspecific differences is observed, this would confirm the biological validity of the measurements. Moreover, since *A. robustus* was not likely to have been a specialized folivore, the discrimination against Sr which occurs in foodwebs remains a viable system for examining the trophic level of this species.

Diagenesis of Sr

It has been increasingly recognized that diagenetic alteration of bones after interment is a significant impediment to fossil studies (Sillen, 1981b, 1988; Nelson *et al.*, 1986; Lambert *et al.*, 1984; Pate & Brown, 1985; Klepinger *et al.*, 1986; Price, 1989; Ezzo, 1992). At least one study of a Plio-Pleistocene assemblage failed to find any biologically interpretable relationships in Sr/Ca (Boaz & Hampel, 1978).

A number of different techniques have been explored for dealing with diagenesis, ranging from mechanical cleaning and washing (Lambert *et al.*, 1990) to physical separation (Sillen, 1981c). One research avenue has been the investigation of fossil apatite solubility characteristics (Sillen, 1981a, 1986, 1988; Sealy & Sillen, 1988; Sealy *et al.*, 1991; Sillen & LeGeros, 1991). This research has suggested that some biologically meaningful Sr survives—and may be recovered—in mineral compartments of discrete solubility in Plio-Pleistocene fossils from both East and Southern Africa.

These studies have exploited the principle that diagenetic apatite is likely to have differing concentrations of carbonate and fluoride from biological apatites. Substitution of carbonate for phosphate ions result in increased solubility in apatites (LeGeros & Tung, 1983; Nelson *et al.*, 1983), while substitution of fluoride for hydroxyl ions result in decreased solubility (Moreno *et al.*, 1977; LeGeros & Tung, 1983). Therefore, the solubility of diagenetic apatite is expected to differ from any biological apatite crystallites which may remain in fossils.

The practical application of apatite solubility phenomena includes repetitively washing powdered fossil preparations in a weakly acidic buffer, and measuring Sr, Ca and PO_4 in successive washes (see methods). The most soluble mineral dissolves in the first washes; less soluble mineral in later washes. Concentrations of Sr and Ca are then measured in the washes, rather than in the powders. The effect is to create a curve of elemental concentrations in a profile of fossil mineral of decreasing solubility. There is strong evidence, discussed below, that in many fossils, a certain part of the curve represents the dissolution of biological mineral. A detailed rationale for the use of differential apatite solubility (or "solubility profiles") as a means of recovering biological Sr/Ca in fossils has been presented elsewhere (Sillen, 1986, 1989; Sillen & LeGeros, 1991).

One objection to the use of solubility profiles to recover biological Sr/Ca stems from a taphonomic study of decaying faunal material from the Amboseli basin (Tuross *et al.*, 1989). In this study, Sr/Ca in washes of 10-year-old rib specimens were never seen to recover to levels seen in less decayed controls from the same animal. The authors concluded that recovery of biologically interpretable values does not necessarily reflect biological reality. This study did not, however, attempt to determine whether biological relationships were actually obscured by the changes in Sr/Ca observed (Sillen, 1990). There are, presumably, many intermediate stages between unaltered natural values and complete obscuration. The question is not so much whether changes have taken place, but whether enough change has taken place to destroy the signal of interest.

Solubility profiles are effective in identifying diagenesis in fossils, based on a number of criteria including apatite solubility (measured as wash calcium), stoichiometry (measured as wash Ca/PO_4) and the shape of the Sr/Ca curve (Sillen, 1986; Tuross *et al.*, 1989). These criteria may also be used to suggest the presence of biological mineral, and a preliminary study of Swartkrans fauna was promising in that these indices were consistent with that of biological mineral (Sillen & LeGeros, 1991). Since this demonstration is so critical to any use of Sr/Ca to reconstruct prehistoric diets, however, a number of independent approaches have been devised.

One powerful demonstration that biological Sr/Ca may be recovered from fossils using solubility profiles is derived from recent studies of the Sr isotopic ratio $^{87}\text{Sr}/^{86}\text{Sr}$. Because these heavy isotopes undergo no measurable biological fractionation, bone $^{87}\text{Sr}/^{86}\text{Sr}$ reflects the $^{87}\text{Sr}/^{86}\text{Sr}$ of the underlying mineral substrates which form the ultimate source of Sr in a foodweb. In certain circumstances, biological and diagenetic Sr may have differing $^{87}\text{Sr}/^{86}\text{Sr}$; these circumstances are of special utility in exploring the technique. Modern marine $^{87}\text{Sr}/^{86}\text{Sr}$ has been measured to be 0.70923 (DePaolo & Ingram, 1985) and most terrestrial rocks and soils differ from this value. Thus, terrestrial animals buried under seawater, and marine animals buried in terrestrial sediments, should have different biological and diagenetic $^{87}\text{Sr}/^{86}\text{Sr}$. If biological Sr is recoverable in these specimens, the measurement should change in the course of a profile.

Indeed, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio has been shown to change in successive washes from specimens such as terrestrial animals which have been buried in marine sands, and marine animals which have been buried in terrestrial sediments (Sealy *et al.*, 1991). In the latter case, it was

possible to recover Sr having a marine $^{87}\text{Sr}/^{86}\text{Sr}$ signature, a result which unambiguously demonstrated the recovery of biological Sr.

It is necessary to keep in mind, however, that the mechanism of fossilization and diagenesis may differ from site to site; it is known, for example, that solubility profiles cannot be universally applied (Sillen, 1981a), and it is not yet possible to predict where solubility profiles will be successful in recovering biological Sr. A recent study of $^{87}\text{Sr}/^{86}\text{Sr}$ in Miocene fish skeletons using solubility profiles was unsuccessful at recovering biological Sr (Koch *et al.*, 1992). An earlier attempt using 50% (v/v) acetic acid (Nelson *et al.*, 1986) was also unsuccessful at recovering biologically meaningful $^{87}\text{Sr}/^{86}\text{Sr}$, although the method employed was substantially different from solubility profiles, and not directly comparable.

Sites at which dietary and diagenetic $^{87}\text{Sr}/^{86}\text{Sr}$ differ are the exception, rather than the rule, and therefore an isotopic approach is not usually open at the sites of paleontological interest. Where it is necessary to demonstrate the efficacy of the solubility profiles without reference to Sr isotopes, a comparative faunal approach must be employed.

This approach explores whether variation seen in a fossil fauna matches that which is known to occur in modern foodwebs. Provided that the biological relationships are carefully chosen, the advantages of this approach include: (a) it specifically addresses the fossil assemblage under investigation, and (b) no known mechanism of diagenesis could mimic such variation. Indeed the recovery of such relationships amongst Swartkrans fauna is the best possible criterion against which to judge diagenesis. No independent test, for example, would be credible if the biological relationships known to exist in modern foodwebs (and expected to exist in fossil foodwebs) were not observable in fossils. In the final analysis this empirical approach is the most powerful one.

In order to determine whether biologically meaningful Sr/Ca was recoverable from Swartkrans fossils, such a comparative faunal approach was employed in this study. A number of different phenomena may be examined in the search for biological Sr. First, variability in Sr/Ca within taxa can itself provide evidence of the presence of biological Sr/Ca (Toots & Voorhies, 1965). Diagenesis for Sr/Ca is generally characterized by a reduction in variability amongst fossils, as bones come into equilibrium with the matrix of interment (Sillen, 1981b, 1988, 1989). This phenomenon not only obscures the natural differences that exist between taxa, but also the natural variability that exists within them. Thus, the normal variation seen within a species should be maintained if biological Sr survives in fossils.

A second category is the differences in variability among species, where such differences are known to occur. A preliminary study using solubility profiles has already found that, in both the Nagapande foodweb and Swartkrans fossils, mid to large size migratory animals are more variable than territorial ones in Sr/Ca (Sillen, 1988; Sillen & LeGeros, 1991). This result cannot be attributed to diagenesis with parsimony.

Third, as mentioned previously, modern foodweb studies have shown that Sr/Ca is reduced in prey–predator pairs (Sealy & Sillen, 1988). Investigation of prey–predator pairs at Swartkrans was thus a primary objective of this study. Both baboons and hyraxes are well documented prey species of leopards in the Transvaal, both for modern animals (Rautenbach, 1982) and in Member I times (Brain, 1981). Baboon specimens chosen for this study were those designated *Papio robinsoni*, a possible ancestor of the modern chacma baboon (Freedman, 1957). Stable carbon isotope analysis of enamel apatite has also indicated that *P. robinsoni* was very likely a preferred prey species of the Swartkrans leopards (Lee-Thorp, 1989). Should biological Sr/Ca be recoverable from Swartkrans fossils, *Panthera* Sr/Ca should be considerably lower than both *Papio* and *Procavia* Sr/Ca.

Table 1 Swartkrans Member I faunal specimens used in this study

Species	English name	Number
<i>Tragelaphus strepsiceros</i>	kudu	4
<i>Papio robinsoni</i>	baboon	10
<i>Procavia antiqua</i>	hyrax	8
<i>Procavia transvaalensis</i>	hyrax	7
<i>Lepus</i> sp.	hare	5
<i>Panthera pardus</i>	leopard	9
Hyaenid (probably <i>Crocota</i> sp.)	hyaena	1
<i>Australopithecus robustus</i>		9
Total		53

Finally, since roots and rhizomes are higher in Sr/Ca than leaves in a given environment, and because of the effect of dietary fiber, folivores (eating either shrub or grass leaves) should have relatively low Sr/Ca among herbivores. In the Western Cape foodweb, duiker (*Sylvicapra grimmia*), for example, were found to have relatively low Sr/Ca, while the hyrax, *P. capensis*, had relatively high Sr/Ca (Sealy & Sillen, 1988). Similarly, in a study of a modern foodweb from Nagapande (Zimbabwe), kudu, a browser whose diet is largely confined to leaves and shoots, had relatively low Sr/Ca among herbivores (Sillen, 1988). If biological Sr survives, it should be possible to observe such relationships among Swartkrans herbivores as well.

In choosing the Swartkrans herbivore faunal sample, it was necessary to keep in mind that, due to differing substrate Sr/Ca, free-ranging animals are highly variable in Sr/Ca and may not be comparable to territorial ones at a given site. Kudu and most small mammals are satisfactory from this point of view, while most large grazers (e.g., wildebeest and equids) are migratory and thus highly variable in Sr/Ca. Therefore, they were excluded from this study. Instead, hyraxes (*Procavia antiqua* and *Procavia transvaalensis*) were chosen as examples of mixed feeders. Moreover, since hyraxes were included in the Western Cape foodweb study, it was possible to make specific predictions about the relationship of their Sr/Ca to that of other species. If biological Sr is recoverable, then hyraxes should have elevated Sr/Ca when compared not only to leopards, but also to kudu and hares.

In summary, any discussion of fossil hominid diets based on Sr/Ca requires that meaningful biological signals be recoverable from fossils. This study first sought to determine whether Sr/Ca data recovered from Swartkrans specimens were consistent with biological or geochemical (diagenetic) phenomena. This investigation takes three forms, including: (i) investigation of the stoichiometry and shape of solubility profile curves; (ii) measurement of the natural variability in Sr/Ca within taxa, both in modern foodwebs and at Swartkrans; and (iii) comparison of differences between taxa in modern foodwebs to that seen in Swartkrans fauna. Once it became clear that diagenesis could not explain the results, the study was extended to include specimens of *A. robustus*.

Methods

Swartkrans specimens housed at the Transvaal Museum and used in this study are shown in Table 1. Only specimens from Member I with satisfactory modern analogues were chosen for this study. (For example, among carnivores, leopards were chosen in preference to

sabre-tooths.) In each case, approximately 100–500 mg of non-diagnostic cortical bone was sampled from well identified specimens.

The laboratory procedures were similar to those described previously (Sillen & LeGeros, 1991). Whole cortical bone specimens were prepared by milling under liquid nitrogen using a Spex model 6700 freezer-mill. These powders were washed three times in acetone to remove any glyptol preservative. A 50 mg sample of each treated powder was placed in an Eppendorf microcentrifuge tube. One millilitre of 0.1 acetic acid/sodium acetate buffer adjusted to pH 4.5 was added to the powder, and the preparation was sonicated for exactly 1 min, then rapidly centrifuged in an Eppendorf microcentrifuge to separate the powder from the buffer. After centrifugation for 10 s, the buffer was decanted and the supernatant saved for elemental analysis. This extraction procedure was repeated 19 times on each powder, resulting in a series of 20 washes.

Concentrations of Sr and Ca were measured by furnace and flame atomic absorption spectroscopy respectively, using a GBC System 2000 AAS, according to methods described elsewhere (Sillen, 1986). Experiments to determine accuracy were conducted by adding 500 ng Sr and 1000 ng Sr (as strontium nitrate) to samples; the recovery was found to be 104%. These recovery experiments were confirmed by an independent method: samples measured in our laboratory were found to be 104–105% of the values obtained by isotope dilution (Sealy & Sillen, 1988). This minor systematic error was ignored. Concentrations of phosphate were measured colorimetrically using a modification of the method of Fiske & SubbaRow (1925) (Rouser *et al.*, 1970). Sr/Ca is expressed as the generally used formulation $(\text{Sr}/\text{Ca}) \times 1000$, and reported as mass ratios throughout. Similarly, Ca and Ca/PO_4 are reported as mass ratios.

Solubility of fossil powders was monitored using total Ca concentration of the washes (Sillen & LeGeros, 1991); stoichiometry was monitored by calculation of the mass Ca/PO_4 . Specimens in which the Ca/PO_4 of washes did not fall to a value consistent with apatite (~ 2.1) were discarded from the study. From the original sample of nine, one *A. robustus* specimen, SK 49, was discarded for this reason.

To estimate the precision of Sr, Ca and PO_4 measurements obtained by solubility profiles, one specimen of an organic rabbit bone was profiled 10 times, and the 10th wash of each profile compared. The solubility was found to vary by 7% ($\bar{X}=821$ ppm Ca; S.D. = 54); the Ca/P by 4% ($\bar{X}=2.01$; S.D. = 0.09); the Sr by 7% ($\bar{X}=518$; S.D. = 38); and the Sr/Ca by 8% ($\bar{X}=0.64$; S.D. = 0.05).

Results

Chemical aspects of solubility profiles

Figure 2 presents Sr/Ca in composite solubility profiles for Swartkrans Member I leopards and baboons. A number of features of these curves are consistent with the recovery of a biological “signal” in these specimens. First, the curves for both species are essentially flat, with the standard deviation for each species becoming somewhat lessened in the course of the profiles. Flat curves are typical of biological bone mineral, while changing Sr/Ca in the course of a profile is a clear sign of diagenesis (Sillen & LeGeros, 1991; Sealy *et al.*, 1991). This is not to say, however, that there is no diagenetic mineral in the first washes; only that the diagenetic mineral itself has low Sr/Ca. In most specimens, the Ca/PO_4 is high and variable in the first washes, and only descends to a value which is consistent with biological apatite by wash seven. (The high variability in the early washes is almost certainly due to variation in

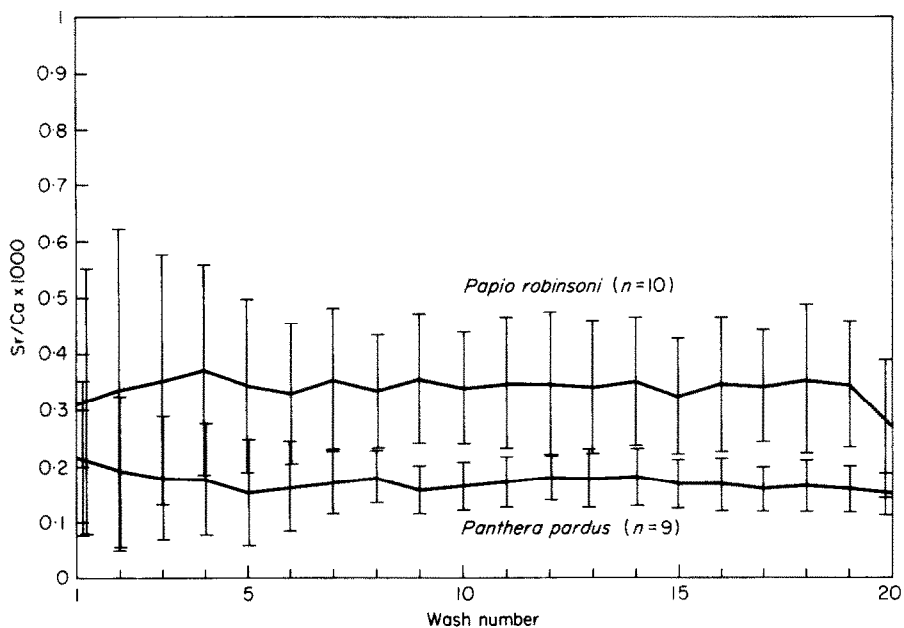


Figure 2. Sr/Ca in composite solubility profiles of Member I leopards (*Panthera pardus*, $n=9$) and baboons (*Papio robinsoni*, $n=10$). The lines shown with bars represent ± 1 S.D. The curves are flat, and there is no overlap in the distributions after wash six.

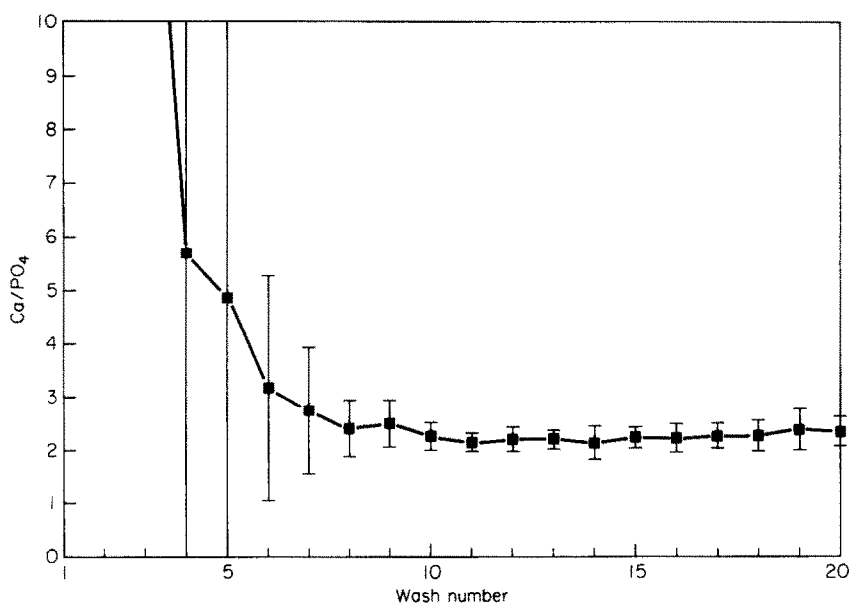


Figure 3. Mean Ca/PO₄ in leopards ± 1 S.D. ($n=9$). Ca/PO₄ are extremely high and variable in the first few washes, but descend to values consistent with apatite by wash six.

Table 2 Variation in Sr/Ca seen in modern herbivores

Modern species	<i>n</i>	CV (%)	Reference
White-tailed deer (<i>Odocoileus virginianus</i>)	53	35	Price <i>et al.</i> , 1985
Gazelle (<i>Gazella gazella</i>)	13	44	Sillen <i>et al.</i> , 1989
Reedbuck (<i>Redunca arundinum</i>)	10	37	Sillen, 1988
Kudu (<i>Tragelaphus strepsiceros</i>)	28	34	Sillen, 1988
Warthog (<i>Phacochoerus aethiopicus</i>)	31	34	Sillen, 1988
Zebra (<i>Equus burchelli</i>)	6	71	Sillen, 1988

the degree of acetic acid exposure during recovery of the fossils from breccia.) This is seen using the leopard sample as an example in Figure 3. Clearly, the early washes represent diagenetic mineral: the elevated Ca/PO₄ points to calcite and/or high carbonate apatite. The average Ca/PO₄ in washes 11–15 for this sample (*n*=9), however, is 2.18 (±0.04), a value consistent with apatite.

Stoichiometry in the region of Ca/PO₄=2.1 is a necessary but not sufficient indicator of biological mineral. Therefore, these results do not in themselves rule out the presence of diagenetic Sr/Ca in later washes of Swartkrans fossils examined. They do show, however, that clear diagenetic danger signals, such as unstable Sr/Ca curves and peculiar stoichiometry, are absent.

Variability within taxa

In all available studies of modern animals in the wild, the coefficient of variation (CV) of mid-sized, territorial herbivores is in the region of 30–45% (Table 2). Because diagenesis involves the equilibration of bones with the matrices in which they are interred, it is generally characterized by a reduction in CV as biologically-induced variability is obliterated. Not surprisingly, archaeological studies which did not employ solubility profiles generally report somewhat low CVs, and differences in trophic level have been shown to be totally obscured when diagenesis causes CV within taxa to drop below 10% (Sillen, 1981a).

In summarizing the Swartkrans data, Sr/Ca in washes 11–15 from each specimen were averaged and this value was used to generate one Sr/Ca number for each specimen. This method was acceptable since in all specimens the Sr/Ca curve is essentially flat in this region of the profile. Means, standard deviations and CVs were then calculated for each species.

The CV for mid-sized territorial species in the Swartkrans sample range between 25–35% (Table 3), somewhat lower than that seen for modern populations, but well within a range sufficient for paleodietary purposes. At this level of variation within taxa, Sr/Ca has been successfully employed in other archaeological contexts, since the basic relationships known to exist between faunal categories remain observable. Moreover, the CV seen in smaller species, the lagomorphs and hyraxes are high and similarly inconsistent with diagenetic equilibration with matrix. The high CV for modern and fossil *Procavia* is perhaps related to the seasonal variability in the diet of this genus (Hoeck, 1975).

Differences between taxa

As can be seen in Figure 2, Sr/Ca is significantly reduced in Swartkrans leopards (*n*=9, \bar{X} =0.17, S.D.=0.04) when compared with baboons (*n*=10, \bar{X} =0.35, S.D.=0.11)

Table 3 Sr/Ca in Swartkrans Member I fauna by specimen*

Species	n	\bar{X} Sr/Ca	S.D.	CV (%)
<i>Tragelaphus</i> sp.	4	0.20	0.05	25
<i>Papio robinsoni</i>	10	0.35	0.11	31
<i>Procavia antiqua</i>	8	0.56	0.30	53
<i>Procavia transvaalensis</i>	7	0.76	0.35	46
<i>Lepus</i> sp.	5	0.32	0.11	34
<i>Panthera pardus</i>	9	0.17	0.04	24
Hyaenid	1	0.22		
<i>Australopithecus robustus</i>	8	0.26	0.03	13

*Averages of washes 16–20.

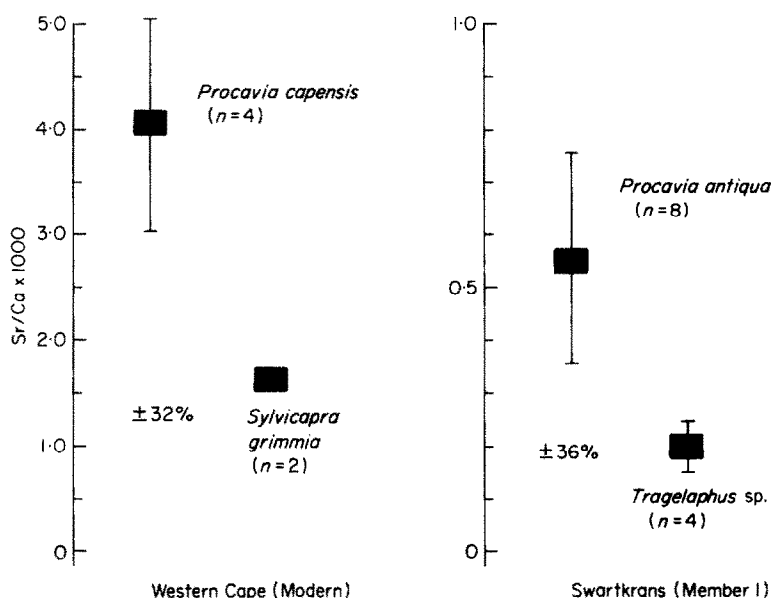


Figure 4. Comparison of the difference between *Procavia* sp. and browsing herbivores from the Western Cape study (Sealy & Sillen, 1988) and Swartkrans Member I fossils. Although absolute amounts of Sr differ in these regions, the spacing between the two categories is the same.

($p = < 0.001$; $t = 4.6302$; $df = 17$), and the ranges do not overlap. Moreover, hyraxes (*P. antiqua*) were found to have significantly elevated Sr/Ca ($n = 5$, $\bar{X} = 0.55$, S.D. = 0.19) when compared to both baboons ($p = < 0.05$; $t = 2.6159$; $df = 13$) and kudu ($p = < 0.01$; $t = 3.5419$; $df = 7$) (Table 3).

The relationships seen among modern and fossil taxa, insofar as it is currently possible to describe them, are remarkably similar. For example, in the Western Cape modern foodweb, browser Sr/Ca was approximately 38% of that seen in hyraxes (Sealy & Sillen, 1988); at Swartkrans, kudu Sr/Ca was on average 36% of that of the hyrax *P. antiqua* (Figure 4). In other words, the relative difference between the two categories is the same. In the Western

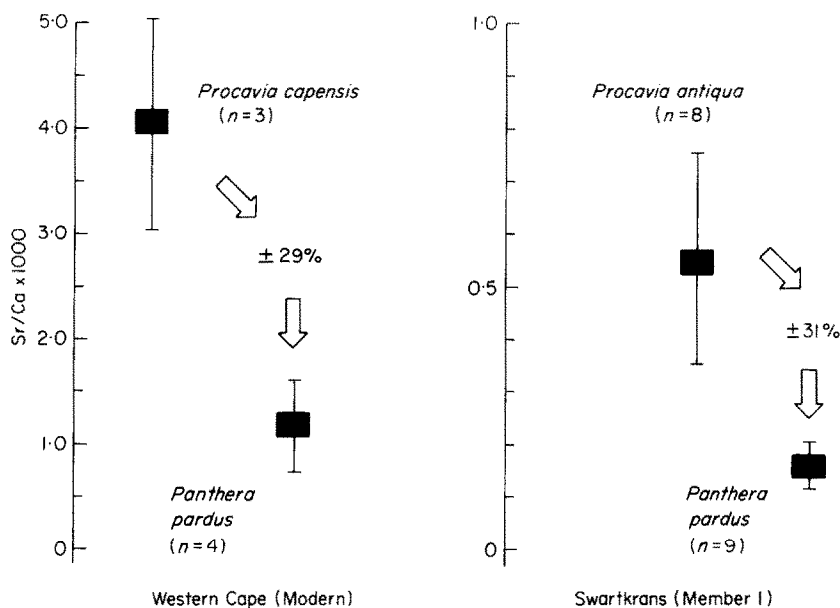


Figure 5. Comparison of the biomineralization of Sr/Ca seen in the prey-predator pair *Procavia* sp./*Panthera pardus* from the Western Cape study (Sealy & Sillen, 1988) and from Swartkrans Member I fossils. The reduction in Sr/Ca seen in the predator is clearly evident in the Swartkrans fossils.

Cape study, leopards were found to have Sr/Ca values approximately 29% that of hyraxes; keeping in mind that Transvaal leopards also consume baboons, at Swartkrans the value is marginally higher (31%), but clearly represents a similar pattern (Figure 5). Finally, as in the Western Cape, *Lepus* Sr/Ca is also lower than that seen in *Procavia*.

In summary, these results match those which are to be expected given what is currently known of modern African foodwebs, and are inconsistent with those to be expected from diagenesis. The data thus suggest that biological, rather than diagenetic phenomena account for the variation observed. On this basis, it was judged appropriate to proceed with sampling and analysis of hominid specimens.

Australopithecus robustus Sr/Ca

When the study was extended to hominids, isolated or morphologically undiagnostic fragments from nine clearly identified specimens of *A. robustus* were selected and analysed (see Table 4). Because of the destructive nature of the analyses, special care was taken when planning the hominid sample to identify samples of no morphological value. In most cases previously existing fragments which could not be incorporated into reconstructions were used (Table 4). Where samples were taken from specimens or breccia, a photographic record (before and after) was kept of the effect of the sampling procedure.

Apatite solubility, measured as wash calcium for the *A. robustus* specimens is presented in Figure 6. Solubility is extremely high in the first wash (also pointing to the dissolution of calcite), but levels off by wash five. As with the faunal sample, Ca/PO₄ is very high in the first washes, but is reduced to a value consistent with that of apatite ($\bar{X}=2.15$, S.D.=0.07) by wash five (Figure 7).

Table 4 Swartkrans Member I *Australopithecus robustus* specimens sampled for this study

Specimen	Age (years)	Description	Sample
SK 858/883/861	19 ± 2	Mandible	Fragment taken from base of mandible near interior aspect of symphysis
SK 1588	13 ± 1	Mandible fragment	Isolated chip in tray
SK 10/1648	29 ± 2	Mandible fragment	Isolated chip in tray
SK 876	28 ± 4	Crushed mandible	Alveolar cortical bone 1 cm posterior and lateral to left M ₃
SK 46	34 ± 3	Crushed cranium	Isolated fragment in tray
SK 57	25 ± 2	Fragmentary palate	Isolated bone chip from breccia at lateral margin of palate (left side)
SK 49	19 ± 2	Crushed cranium	Fragment taken from posterior portion of right parietal
SK 54	Immature	Calotte	Isolated fragment from bottle
SK 14248	Adult	Crushed cranium	Isolated fragments in tray

See Brain, 1981, for Member I catalogue.

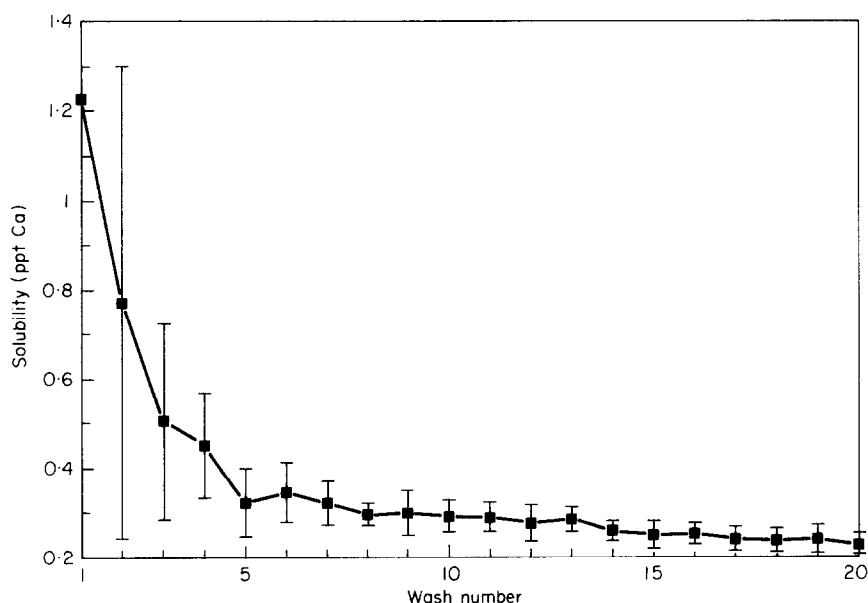


Figure 6. Mean apatite solubility (composite profile), measured as the total wash calcium concentration, in specimens of *A. robustus* ± 1 S.D. ($n = 8$). A highly soluble phase, presumably containing calcite, disappears after wash five.

A composite Sr/Ca curve for the *A. robustus* specimens with the exception of SK 49, is presented in Figure 8 [SK 49 was rejected on the basis of its Ca/PO₄ values, which averaged 3.50 in washes 11–16 (Table 5)]. With regard to Sr/Ca in the remainder of the specimens, the curves for *A. robustus* profiles are (as with the other fauna) essentially flat. The mean Sr/Ca in

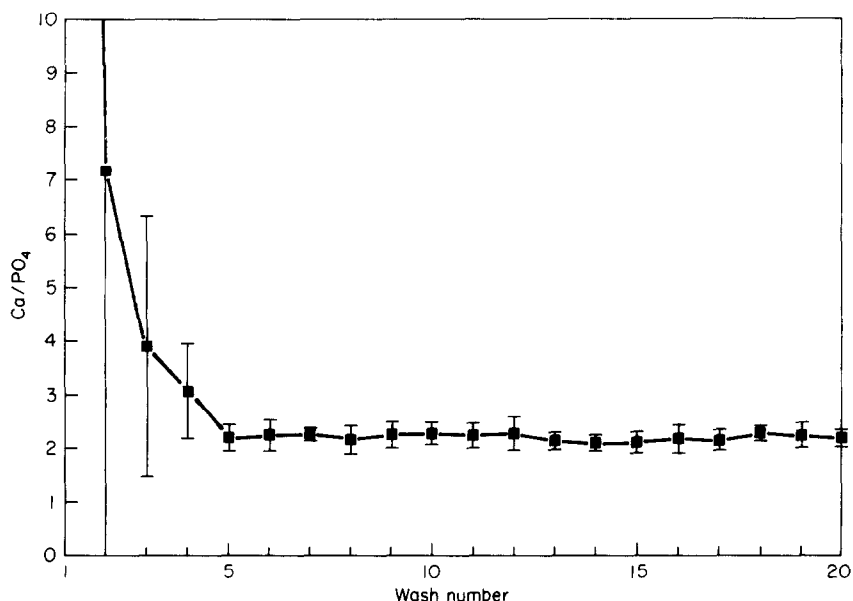


Figure 7. Mean Ca/PO_4 (composite profile) in specimens of *A. robustus* ± 1 S.D. ($n=8$). As with the faunal specimens, an apatitic signal is clearly discernible after the first few washes.

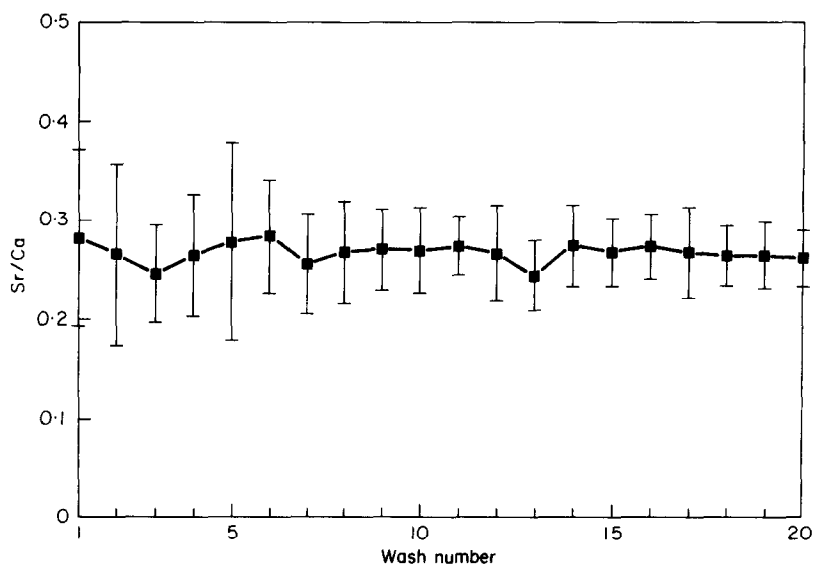


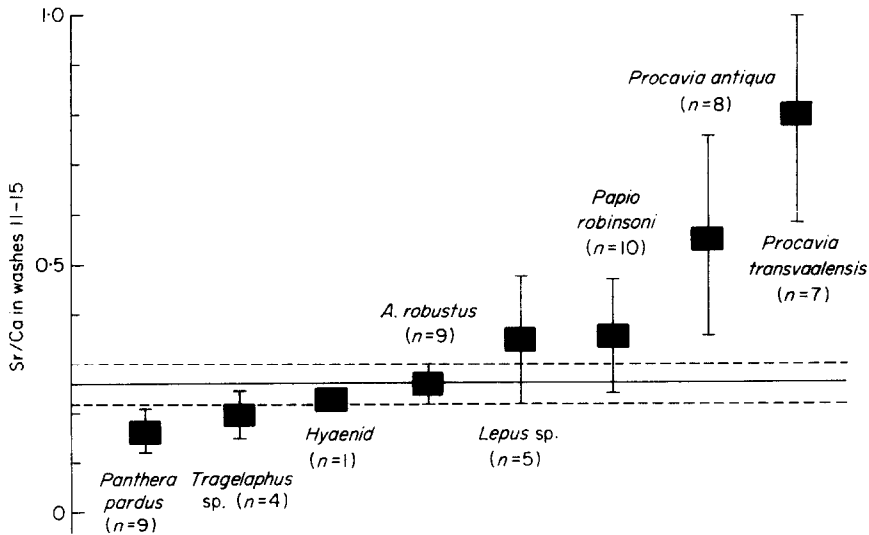
Figure 8. Mean Sr/Ca (composite profile) ± 1 S.D. of *A. robustus* ($n=8$).

washes 11–16 was 0.26 (S.D.=0.04); it is of interest that this value is midway between that obtained for leopards and baboons, and considerably lower than that obtained for hyraxes. The *A. robustus* sample was significantly different from both leopards ($p=0.0001$; $t=5.4808$; $\text{df}=15$) and *Papio* baboons ($p<0.05$; $t=2.2401$; $\text{df}=16$). A ranked comparison

Table 5 **Sr/Ca and Ca/P of *Australopithecus robustus***

Specimen	Sr/Ca	Ca/P
SK 858 (White, 1975)	0.20	1.76
SK 1588	0.24	2.38
SK 10/1648	0.28	2.27
SK 876	0.26	2.13
SK 46	0.28	2.27
SK 57	0.28	2.06
SK 54	0.30	2.25
SK 14248	0.27	2.17
SK 49 (rejected)	0.20	3.50

Averages of washes 11-15.

**Figure 9.** Mean Sr/Ca \pm 1 S.D. for Swartkrans Member I species examined in this study, based on the average of washes 11-16 in individual specimens. (---) \pm 1 S.D. around the *A. robustus* mean.

of Sr/Ca in the *A. robustus* sample to that of the other fauna analysed in this study is presented in Figure 9.

Among *A. robustus*, there was no detectable relationship between Sr/Ca and any other identifiable variable, with the possible exception of age. SK 54, clearly a juvenile, had the highest Sr/Ca amongst the specimens in this study (Table 5).

Discussion

Two main reasons exist for analysing faunal specimens when attempting to reconstruct hominid diets using trace elements or isotopes. The first reason is to help establish whether the technique is capable of detecting biologically meaningful information to begin with. Once

that is established, a second reason for using animals whose diets are well established is to help in the interpretation of data on species whose diets are essentially unknown.

In the preceding section, it has been shown that diagenesis cannot explain the variability seen in Swartkrans fauna. Since the variability is consistent with what is known from modern foodwebs, this fauna may also be used as a guide against which to interpret the hominid data. Interpretation of the Sr/Ca values for *A. robustus* depends upon the considerations, outlined in the beginning, that this measurement is affected by age, by geographic region, by trophic level and by consumption of plant parts having especially elevated Sr/Ca, notably roots, rhizomes and seeds. Before addressing these issues, however, it would first be useful to discuss what may be learned directly from the *A. robustus* data set itself. The discussion will then be extended to include the entire faunal set.

The observation that SK 54 has the highest Sr/Ca among the *A. robustus* specimens studied is not surprising given its age, listed as "immature" (Mann, 1975; Brain, 1981). Several studies, reviewed previously, have documented a lessened discrimination against strontium in young animals (Sillen & Kavanagh, 1982). Moreover, the age range 5–12 years, within which this specimen almost certainly falls, is known to be characterized by very high variability in humans (U.K. Medical Research Council, 1959–1970). Therefore, the data cannot be taken to show that this child's diet was any different from that of the adult sample. The high value for this specimen, however, reinforces the conclusion that a biological signal is present.

One striking feature of the *A. robustus* data is the low CV, in the order of 11–15%. This low value could be taken either as an indication of diagenesis or it may have some behavioral or biological basis. All other species examined in this and previous Swartkrans studies have CVs which, given the considerations discussed above, are consistent with their known modern counterparts. Therefore, although low CVs are often a feature of diagenetically altered samples, it is unlikely that diagenesis would selectively affect the *A. robustus* sample to the exclusion of all the other fauna. Herbivores may indeed be the wrong category for comparison to begin with, and sufficient data do not yet exist on natural variability in Sr/Ca in carnivore species. Since there is no known counterpart against which to compare *A. robustus* CV, a biological explanation merits serious consideration.

While it is not possible on the basis of this study to arrive at a firm explanation for the low CV of the *A. robustus* sample, one possibility may be explored in a speculative way. We know that modern free-ranging animals tend to be highly variable in Sr/Ca. This phenomenon also characterizes Swartkrans fossil fauna such as wildebeest (Sillen & LeGeros, 1991). Given the diversity of soils and underlying geology in the region of Swartkrans (South African Committee for Stratigraphy, 1980), and the low variability for *A. robustus* Sr/Ca, it thus seems unlikely that these animals had a very wide home range.

The hypothesis that they did not range widely is, in fact, amenable to study at Swartkrans using bone $^{87}\text{Sr}/^{86}\text{Sr}$. Within 20 km of Swartkrans are not only soils derived from the Malmani Supergroup dolomite, but also Swazium sediments and igneous rocks from the Randium and Vaalian Erathems [Geological Survey (SA), n.d.]. Since these rocks, the soils derived from them, and the organisms living on these soils are likely to have differing $^{87}\text{Sr}/^{86}\text{Sr}$, such a study is a logical next step.

Comparison of A. robustus to the other fauna

As can be seen in Figure 9, Sr/Ca of *A. robustus* is relatively low in the context of the Member I fauna examined to date. Given our current understanding of how this measurement varies in

foodwebs, outlined in the beginning of this article, a number of possibilities may explain this observation.

Leaf eating herbivore. At first glance, the Sr/Ca values for *A. robustus* are consistent with that of a folivorous browser. For example, the *A. robustus* Sr/Ca values are not much different from those of kudu. Kudu, however, are ruminants who prefer the leaves and shoots of forbs and woody plants (Novellie, 1983; Smithers, 1983), organs which are all low in Sr/Ca. Such an interpretation of *A. robustus* diets is unlikely in light of the dental microwear evidence for consumption of hard objects by this species (Grine, 1981, 1986; Kay, 1985).

Specialization for wet microhabitat. Wet, well drained soils tend to have low background levels of many trace elements, including strontium (Sillen & Kavanagh, 1982); animals who derive all of their food from such soils may have low Sr/Ca for this reason. It is thus worth asking whether such a phenomenon could explain the low Sr/Ca of *A. robustus*.

While the area surrounding Swartkrans probably included a nearby stream, it is by no means certain that such a stream existed year-round. All who have studied the faunal assemblage, however, agree that it represents a predominantly arid, open grassland environment (Vrba, 1975, 1980, 1988; Shipman & Harris, 1988). Indeed, one hypothesis that has been proposed for further study is that *A. robustus* might have existed in open, arid habitats in preference to closed, wet ones (in contrast to East African *A. boisei*) (Shipman & Harris, 1988).

While the subject of the occurrence and/or preference of robust australopithecines in various habitats is the subject of continuing debate, there is no dispute that closed/wet environments were unlikely to have been the predominant habitat of *A. robustus*. The possibility that a localized wet habitat existed near Swartkrans, and that this species fed there exclusively, should not be ignored, but the scenario seems unlikely.

Omnivory. The Sr/Ca of *A. robustus* falls exactly midway between that of the leopards and *P. robinsoni* in this study. Modern baboons are omnivorous (Strum, 1987), and there is no reason to believe that *P. robinsoni* was any different. Therefore, the observation that *A. robustus* Sr/Ca is lower than that of *Papio* is a key observation of this study. *Papio* also feeds heavily on the roots and rhizomes of C₃ plants, which explains why the Sr/Ca of *P. robinsoni* is so much greater than that of kudu. Thus, were these items to have exclusively comprised the *A. robustus* diet, Sr/Ca for this species should be considerably higher than that recorded in this study. A diet consisting exclusively of seeds, roots and rhizomes can be ruled out.

If such foods did comprise a significant part of robust australopithecine diets, the low Sr/Ca values reported here can only be accounted for if a considerable portion of the diet also was made up of items with very low Sr/Ca. Given our current knowledge of Sr/Ca in foodwebs, the best candidate for this is high trophic level foods derived from animals.

Recent study of dental enamel stable isotopes of Swartkrans fauna, including *A. robustus* bear on this issue. Preliminary reports indicate that apatite $\delta^{13}\text{C}$ for this species is intermediate, in the region of -8‰ (Lee-Thorp, 1989). Browsers such as kudu have more negative $\delta^{13}\text{C}$ ($-11.1 \pm 0.8\text{‰}$), while specialized grazers, e.g., wildebeest, are considerably more positive, in the region of -1‰ (Lee-Thorp & van der Merwe, in press). The intermediate values for *A. robustus* indicate that this species depended predominantly on C₃ foods, but included a significant C₄ contribution which must have derived either directly from C₄ grasses or indirectly from animals eating C₄ grass (grazers) (Lee-Thorp, 1989). Member I

herbivores with $\delta^{13}\text{C}$ comparable to *A. robustus* were hyraxes (*P. antiqua*) ($-8.7 \pm 1.6\text{‰}$) (Lee-Thorp & van der Merwe, in press). This is not to say that their diet was similar to that of hyraxes, but that like hyraxes, *A. robustus* included some carbon ultimately derived from C_4 grass species in its diet (either directly from C_4 grasses, or from grazing animals). However, *A. robustus* Sr/Ca is considerably lower than that seen in these hyraxes (Figure 9).

The low Sr/Ca for *A. robustus* indicate either the consumption of leaves or high trophic level foods. Grass leaves are an extremely unlikely diet for hominids, leaving the consumption of grazing animals as the one plausible explanation for low Sr/Ca and intermediate $\delta^{13}\text{C}$. Thus, one interpretation which fits the carbon, Sr/Ca and environmental data is that the small hard objects pointed to by microwear studies were the seeds, roots and rhizomes of C_3 plants and/or the nuts of C_3 trees, and *A. robustus* attained its intermediate carbon values and relatively low Sr/Ca from the consumption of grazing animals.

Conclusion

Dietary reconstruction of early hominids using Sr/Ca have only just become possible because diagenesis has ceased to be an insurmountable impediment. While our understanding of how this measurement varies in foodwebs has improved during the past decade, definitive studies of foodwebs planned specifically for the purposes of paleodietary research remain to be conducted. As a result, reconstructions of early hominid diets must, for the time being, remain constrained. On the other hand, we can look forward to considerably better resolution in the years ahead.

As the fossil faunal sample from Swartkrans increases, and as results of further studies on modern foodwebs become available, the scenarios discussed above may well need revision. An obvious area for future study is expansion of the carnivore sample to include *Dinofelis*, *Megenteron* and the hyaenas *Crocota* sp. and *Hyaena* sp. Taking into account our understanding of the paleoecology and dental microanatomy of *A. robustus*, however, the results reported here indicate that a purely herbivorous dietary adaptation for this species is unlikely.

This is not to say that these animals did not themselves fall prey to carnivores, as has been suggested by Brain (1981). In fact, the data support Brain's suggestion that leopards were unlikely to have been a specialized predator of *A. robustus*, and concentrated instead on smaller animals. Apatite $\delta^{13}\text{C}$ in carnivores is very similar to that of their prey species (Lee-Thorp *et al.*, 1989) and more reduced in Sr/Ca. At Swartkrans, leopard enamel $\delta^{13}\text{C}$ values are more similar to those of *P. robinsoni* than *A. robustus* (Lee-Thorp & van der Merwe, in press). Future $\delta^{13}\text{C}$ and Sr/Ca studies should make it possible to test Brain's hypothesis that *Dinofelis* preyed more heavily upon *A. robustus* than did leopards, and to further clarify other predator-prey relationships in fossil assemblages.

The suggestion of omnivory does not rule out the consumption of small, hard objects suggested by microwear studies. In fact, the interpretation offered above depends upon it. Taken by themselves, however, microwear studies can only address those items which leave wear traces on teeth; they do not address the universe of potential food items, many of which may leave no such traces. While bone crunching may leave a characteristic wear or chip pattern, consumption of meat would be invisible to such analysis. The absence of occlusal pits may thus suggest the absence of hard objects in the diet, but their presence does not suggest absence of meat. For this reason, perhaps it is more appropriate to characterize robust australopithecine diets as including hard objects, rather than "consisting" of them (see for example, Kay & Grine, 1988:441).

In conclusion, the Sr/Ca data are inconsistent with the predominant view that *A. robustus* was a herbivore. Rather, the data suggest that this species' dietary adaptation was that of an omnivore. These results do not directly address whether these creatures may have eaten bone or flesh, although they do suggest that the causes of enamel chipping on *A. robustus* teeth might bear closer examination. Certainly the results do not address the diets of robust hominids elsewhere on the continent, namely *A. boisei* in East Africa.

It has been suggested that, given the multiplicity of environments in which robust australopithecines have been found, they should be viewed as "quite adaptable creatures" (Brown & Feibel, 1988). In Southern Africa, this adaptability seems to include the consumption of high trophic level foods. Therefore, that paleoecological models characterize niche differentiation amongst contemporary hominids on the basis of trophic level—i.e., *A. robustus* = herbivore *vs.* *Homo* sp. = omnivore—are oversimplified; the differences in diet which may have existed between these species are not adequately described by this terminology.

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