



Strontium isotopic aspects of *Paranthropus robustus* teeth; implications for habitat, residence, and growth



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ABSTRACT

The strontium isotopic ratio $^{87}\text{Sr}/^{86}\text{Sr}$ has been studied in the Sterkfontein Valley of South Africa to infer both habitat usage and residence for a number of early hominins. This paper examines the existing $^{87}\text{Sr}/^{86}\text{Sr}$ data collectively derived from three studies of *Paranthropus robustus* teeth with the aim of exploring whether the dataset as a whole may provide deeper insight into habitat, mobility, and growth for this species. $^{87}\text{Sr}/^{86}\text{Sr}$ from seven Swartkrans Member I third molars varies in a well defined narrow range, and while some canines were consistent with this range, a number of *P. robustus* canines and first and second molars were not, and therefore represent individuals who had arrived from other localities. A first and third molar $^{87}\text{Sr}/^{86}\text{Sr}$ was found to differ in TM1517c, the holotype *P. robustus* specimen from Kromdraai, suggesting this individual had moved to the locality sometime after the first molar and before the third molar had completely mineralized. While early forming teeth vary widely, the relatively low variation and absence of exogenous $^{87}\text{Sr}/^{86}\text{Sr}$ in third molars suggest that these teeth mineralized relatively late when compared to life history events bearing on higher primate residence patterns. The implications for further study of habitat, residence, and growth are discussed.

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1. Introduction

Geographical variation in the $^{87}\text{Sr}/^{86}\text{Sr}$ of the Sterkfontein Valley presents unique opportunities for the study of early hominin behavior and biology. While the strontium ratio varies with the rubidium content and age of mineral substrates, it is not significantly fractionated by biological organisms (Graustein and Armstrong, 1983; Graustein, 1989; Kawasaki et al., 2002). Therefore, the $^{87}\text{Sr}/^{86}\text{Sr}$ of plants represents the available $^{87}\text{Sr}/^{86}\text{Sr}$ from substrates on which they grow. $^{87}\text{Sr}/^{86}\text{Sr}$ of animal calcified tissues reflects the circulating $^{87}\text{Sr}/^{86}\text{Sr}$, which are derived from dietary strontium. To the extent that individuals moved across differing geological substrates or localities—having different $^{87}\text{Sr}/^{86}\text{Sr}$ —during growth and development, the different $^{87}\text{Sr}/^{86}\text{Sr}$ in those habitats will be reflected in $^{87}\text{Sr}/^{86}\text{Sr}$ variation in mineralized tissues, such as enamel, that were calcifying at various periods of growth.

$^{87}\text{Sr}/^{86}\text{Sr}$ has been used in such diverse applications as source-tracing elephant ivory to specific African game reserves (van der Merwe et al., 1990), identifying the rearing streams of juvenile Atlantic salmon (Kennedy et al., 1997) and the preferred feeding habits of contemporary fauna of the Cape Fynbos region of South Africa (Radloff et al., 2010). The background to and growing applications of $^{87}\text{Sr}/^{86}\text{Sr}$ to source-tracing in ecological research have been extensively reviewed elsewhere (Bentley, 2006; Crowley et al., 2015).

Beginning with the work of Jonathan Ericson (1985), anthropologists have steadily expanded the use of $^{87}\text{Sr}/^{86}\text{Sr}$ to study paleontological, prehistoric, and historic human remains, and this has been reviewed extensively elsewhere (Bentley, 2006; Slovak and Paytan, 2011). The work has gone beyond comparison of different individuals to attempts to elucidate life-histories of individuals, both by sampling different teeth from the same skeleton (as in the case of the Alpine Iceman; Muller et al., 2003) and by examination of incremental structures within enamel (Dolphin et al., 2003; Kang et al., 2004; Richards et al., 2007).

$^{87}\text{Sr}/^{86}\text{Sr}$ of habitat, fauna, and hominins of the Sterkfontein Valley have so far been explored in at least four studies (Hall, 1994;

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Sillen et al., 1998; Copeland et al., 2011; Balter et al., 2012), which viewed together answer certain questions, pose new questions, and leave many questions unanswered regarding hominin habitat, mobility, and growth. In this article, we will (i) briefly review the data reported so far, (ii) clarify the state of our knowledge in the light of subsequent critique, (iii) identify new, previously undescribed patterns in the existing published data, and finally, (iv) outline some questions yet to be answered and that are likely to be answerable with further study. Although data have been reported for numerous hominin species (and other biological markers such as carbon isotopes and Sr/Ca), this paper focuses exclusively on $^{87}\text{Sr}/^{86}\text{Sr}$ data pertaining to *Paranthropus robustus*.

2. Background

Hominin-bearing sites such as Swartkrans, Kromdraai, and Sterkfontein are located on a narrow dolomite band that is part of the Malmani Subgroup, Chuniespoort Group of the Proterozoic Transvaal Sequence. To the northwest of the site, rocks of the Pretoria Group of the Transvaal Sequence consist predominantly of quartzite and shale, with a prominent volcanic unit, the Hekpoort Andesite Formation. Further to the northwest is the Daspoort Quartzite Formation, then alternating bands of diabase and undifferentiated surface deposits. To the southeast of the site, the dolomite gives way to rocks of the Witwatersrand Supergroup, which are underlain by Archaean Granite dated approximately 3 Ga (Geological Survey, SA, 1989). This granite is exposed to the east of

Swartkrans. Remaining areas of the Witwatersrand Supergroup are represented by the Krugersdorp Quartzite Formation, with occurrence of quartzites, shales, and conglomerates (Fig. 1).

Examination of $^{87}\text{Sr}/^{86}\text{Sr}$ patterns in the region showed very high variation in whole soil $^{87}\text{Sr}/^{86}\text{Sr}$ derived from these substrates, but somewhat less variation in available soil and plant $^{87}\text{Sr}/^{86}\text{Sr}$ (Hall, 1994; Sillen et al., 1998). In this system, highly radiogenic strontium from the ancient rocks and insoluble components of the dolomite mix with the relatively depleted strontium from soluble components of the dolomite. Given that this ratio is routinely measured to the 5th decimal place, the $^{87}\text{Sr}/^{86}\text{Sr}$ endmembers for this system are extraordinary for their wide divergence: 0.90060 for the Archaean granite at the high end and 0.70861 for the soluble components of the Malmani Formation dolomite at the low end. Because of mixing and heavy domination by the dolomitic soluble strontium, habitat and biome variation in Sterkfontein Valley $^{87}\text{Sr}/^{86}\text{Sr}$ generally lies between 0.72000 and 0.75000.

Since streams and their adjacent greenbelts are heavily dominated by the less radiogenic (soluble) strontium, wet streamside habitats have more depleted $^{87}\text{Sr}/^{86}\text{Sr}$ than upland, drier habitats (Sillen et al., 1998). This phenomenon similarly existed in the Pleistocene, as demonstrated by $^{87}\text{Sr}/^{86}\text{Sr}$ of carbonate from the Swartkrans Cave; Member I breccia was found to have $^{87}\text{Sr}/^{86}\text{Sr} = 0.7217 \pm 0.0009$, well within the range of modern Blaaubank stream water and nearly indistinguishable from modern water obtained at Swartkrans. Further study of the Sterkfontein Valley system confirmed relatively radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ in habitats

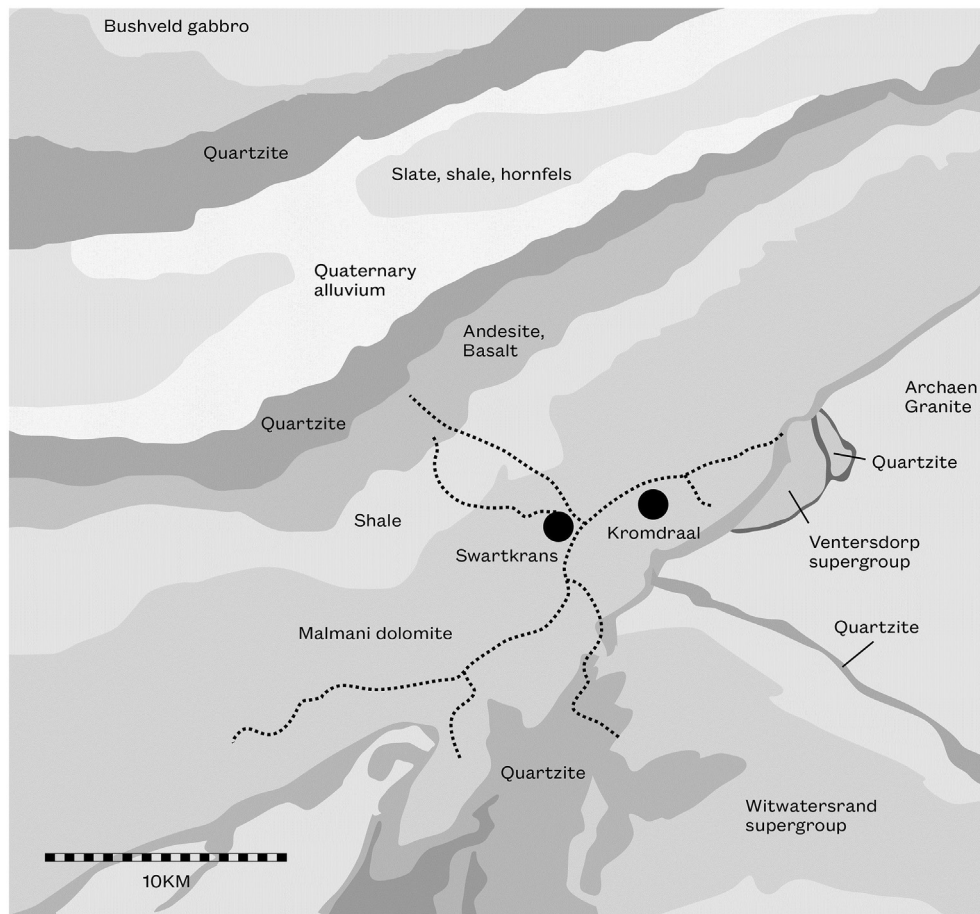


Figure 1. Sterkfontein Valley geology, showing the locations of Swartkrans and Kromdraai on the Malmani dolomite, and the course of the Blaaubank stream in the immediate vicinity of the sites.

distant to Swartkrans (as opposed to nearby habitats), which is consistent with both the geology and hydrology of the Valley (Copeland et al., 2011). When these datasets are viewed together, a clear pattern emerges of relatively radiogenic strontium in plants upland and distant from Swartkrans, as opposed to plants nearby, on the dolomite band (Fig. 2).

Even less radiogenic strontium is seen in the riparian habitat immediately adjacent to Swartkrans. In turn, the $^{87}\text{Sr}/^{86}\text{Sr}$ of plants in this habitat is consistent with $^{87}\text{Sr}/^{86}\text{Sr}$ of Blaaubank stream water (Sillen et al., 1998; Copeland et al., 2011). Put another way, plant $^{87}\text{Sr}/^{86}\text{Sr}$ increases sharply coming off the Blaaubank greenbelt and then continues to increase with distance from Swartkrans, over approximately 30 km, until relatively depleted $^{87}\text{Sr}/^{86}\text{Sr}$ is once again encountered in plants growing on Bushveld gabbro, some 30 km to the NW of Swartkrans (Copeland et al., 2011).

Using laser ablation mass spectrometry of *P. robustus* and *Australopithecus africanus* enamel specimens, Copeland et al. (2011) sought to establish landscape use by comparing the $^{87}\text{Sr}/^{86}\text{Sr}$ of relatively large versus relatively small hominin teeth, employing tooth size as a proxy for sex determination. Specifically for *P. robustus*, they reported that a higher proportion of small canines rather than large canines had non-local $^{87}\text{Sr}/^{86}\text{Sr}$. Ascribing the small tooth specimens to females, they concluded that the data indicated female exogamy and male philopatry, consistent with the behavior of modern chimpanzees.

At least three aspects of this study require further consideration in the effort to understand habitat use and mobility (which may be broadly grouped under the rubric 'landscape use') by *P. robustus*. First, it is useful to note that the *P. robustus* specimens analyzed included nine canines and two third molars. Since these teeth

mineralize at different periods of growth and development in both apes and humans, it seems logical to ask whether any additional information may be gleaned by comparing the $^{87}\text{Sr}/^{86}\text{Sr}$ of such teeth. While perhaps not possible with the small sample examined by Copeland et al. (2011), the question may indeed be explored in the light of the expanded sample size available when data from Balter et al. (2012) are taken into account (see below).

Second, are Copeland et al. (2011) correct when they describe all specimens having $^{87}\text{Sr}/^{86}\text{Sr}$ below approximately 0.733 as local and those above as non-local? To be sure, elevated values must be non-local, but it is not the case that all depleted values (i.e., below 0.726) are necessarily local as well. Two alternative sources of depleted $^{87}\text{Sr}/^{86}\text{Sr}$ exist in this region: the riparian habitat immediately astride the Blaaubank stream and distant localities beyond the quartzite bands to the NW. While the riparian habitat immediately adjacent to Swartkrans is also depleted, in the region of 0.722, it seems unlikely that any individuals of *P. robustus* would be exclusively obtaining dietary strontium from this biome, while others were not. Therefore, when relatively depleted $^{87}\text{Sr}/^{86}\text{Sr}$ is found in *P. robustus* teeth, a non-local origin may in fact be indicated. Indeed, it may be possible to move beyond a local/non-local dichotomy and deduce more than one non-local region of origin.

Third, inferences into female exogamy and male philopatry are necessarily dependent on sex assignment, and this has been challenged on the basis that hominins have relatively low sexual dimorphism when compared to apes, specifically for the measurement employed: canine measured basal area (mesiodistal \times buccolingual dimensions; Plavcan, 2012). Because the sex assignment of such teeth is uncertain, it was argued that it is impossible to conclude female exogamy and male philopatry from the analysis (Plavcan, 2012).

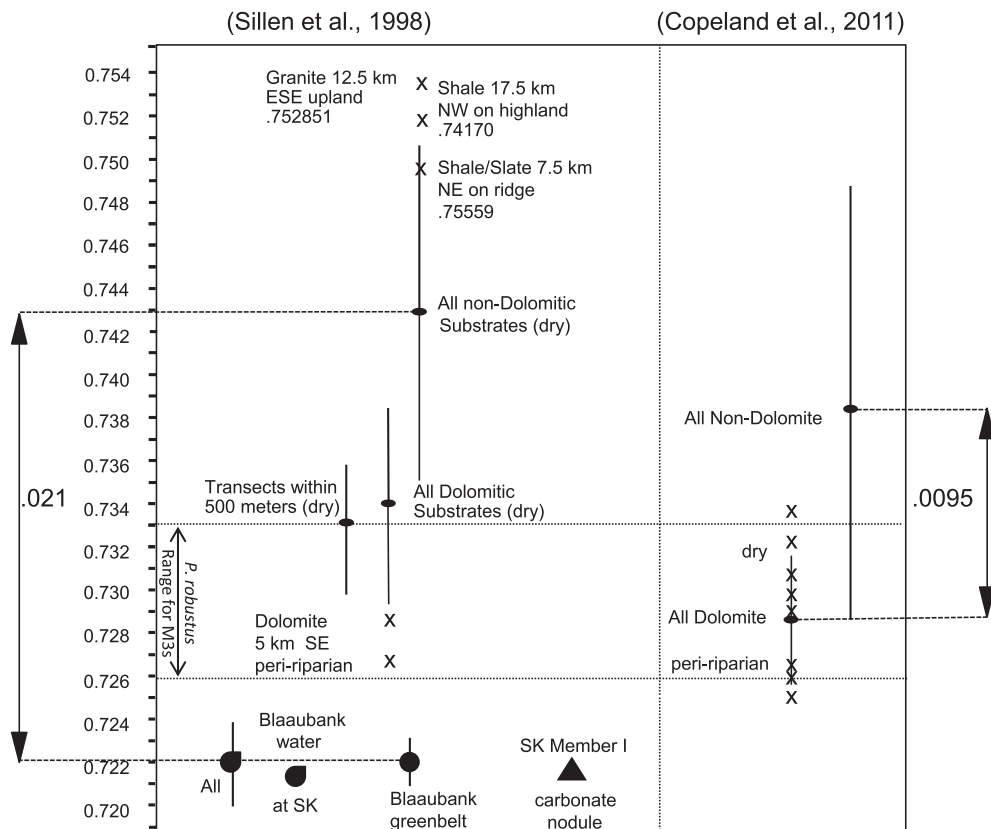


Figure 2. Both Sillen et al. (1998) and Copeland et al. (2011) report a difference between near and far $^{87}\text{Sr}/^{86}\text{Sr}$ increases substantially, from 0.0095 to 0.021. A picture emerges of depleted $^{87}\text{Sr}/^{86}\text{Sr}$ at the Swartkrans Cave and the Blaaubank greenbelt, increasing even on the dolomite with distance from water, and increasing further on surrounding substrates especially at higher elevations.

Further detailed laser ablation work conducted by Balter et al. (2012) significantly expanded the data on individual *P. robustus* teeth, both by reporting $^{87}\text{Sr}/^{86}\text{Sr}$ on a number of new molar teeth and by reporting $^{87}\text{Sr}/^{86}\text{Sr}$ in laser transects of enamel from the dentino-enamel junction (DEJ) to the outer enamel (OE). That study focused on comparing *P. robustus* to *Australopithecus* and early *Homo*, but did not compare data to those of Sillen et al. (1998) and Copeland et al. (2011), nor did the analysis seek to interpret changes in the $^{87}\text{Sr}/^{86}\text{Sr}$ observed across the laser scans from the DEJ to the OE.

To be sure, limitations exist in our current ability to fully explore hominin movement and growth using strontium isotopes. Foremost among them, laser ablation instruments currently available have relatively small sample chambers, which make it impossible to routinely obtain measurements from different teeth in the same mandible with this technology. Nevertheless, in certain circumstances, it may be possible to examine different fractured teeth from the one individual, as in the case of TM1517c, a number of teeth associated with the holotype *P. robustus* specimen reported by Robert Broom in 1938 (Thackeray et al., 2001). Moreover, instruments with larger sample chambers are likely to be available in the near future, so it seems appropriate to explore the potential of the approach using individual teeth. An advantage of examining individual fractured teeth is that ablation scans may be conducted from the DEJ to the OE, providing a timeline of dietary or habitat changes during the period the individual tooth enamel was mineralizing.

Taken together, the Sillen et al. (1998), Copeland et al. (2011), and Balter et al. (2012) studies document the $^{87}\text{Sr}/^{86}\text{Sr}$ in the enamel of some twenty *P. robustus* teeth (of 19 individuals), including canines and first, second, and third molars. Furthermore, the teeth reported by Balter et al. (2012) have the additional nuanced information from the laser scans. In the current paper, this dataset will be examined as a whole.

3. Materials and methods

Reference plant $^{87}\text{Sr}/^{86}\text{Sr}$ for localities in the modern Sterkfontein Valley are those reported by Sillen et al. (1998) and Copeland et al. (2011); values for fossil fauna were also taken from Copeland et al. (2011) supplementary data. With regard to *P. robustus* dental enamel, data from three available published datasets were used. The first is the $^{87}\text{Sr}/^{86}\text{Sr}$ reported for SK 876; second molar enamel was obtained by conventional VG Sector 7-collector mass spectrometer in the Radiogenic Isotope Facility Department of Geological Sciences, University of Cape Town (Sillen et al., 1998). A second, larger dataset derives from the study of Copeland et al. (2011), who used laser ablation ICP-MS to measure $^{87}\text{Sr}/^{86}\text{Sr}$ in the permanent dentition of 19 hominin specimens from the Sterkfontein Valley, including 11 *P. robustus* individuals from Swartkrans (Member 1, 1.6–2.3 Ma; Brain, 1981; Pickering et al., 2011; Herries and Adams, 2013). The third dataset is from the study of Balter et al. (2012), which also used laser ablation technology to measure $^{87}\text{Sr}/^{86}\text{Sr}$ in transects of permanent enamel from seven *P. robustus* molar teeth from the DEJ to the OE. Of this set, three teeth (SK 24606, SK 1524, and SKW6) were third molars derived from Swartkrans Member 1 and, therefore, judged to be from the same population as the Member 1 teeth analyzed by Copeland et al. (2011). Canines and third molars examined in this study are listed in Figure 3.

Although provided results from a profile of $^{87}\text{Sr}/^{86}\text{Sr}$ along the width of the enamel, for the purpose of the statistical comparison, the reported mean $^{87}\text{Sr}/^{86}\text{Sr}$ of all values obtained from each profile was deemed representative. Where multiple profiles were reported for the same teeth, the average of the multiple scans was used.

Variation in $^{87}\text{Sr}/^{86}\text{Sr}$ in the laser ablation transects provided by Balter et al. (2012) may also contain meaningful individual life history information. In general, these transects were performed from the DEJ to the OE, which may broadly be interpreted as representing, for the transect in question, earlier-mineralizing enamel and later-mineralizing (not necessarily earliest and latest mineralizing) enamel at each respective end. No effort was made to report or follow incremental enamel structures however, so it may not be appropriate to interpret the transect line as a linear representation of $^{87}\text{Sr}/^{86}\text{Sr}$ changes during growth. Nevertheless, in three specimens (SKX 21841, SK2524, and SKW6), it is possible to identify relatively early mineralizing enamel for these M3s from the location of the transects, based on the specific location of the DEJ origin at the early apical cusp. It is also possible in some teeth to identify late forming enamel, such as the OE near the cervical margin in the TM1517c first molar. Finally, as mentioned previously, Balter et al. (2012) report data from transects on both an M1 and M3 from TM1517, the holotype specimen for *P. robustus* recovered from Kromdraai Member 3. This is the only instance where transects on different teeth from one individual were ablated.

For the statistical treatment of isolated teeth, because each $^{87}\text{Sr}/^{86}\text{Sr}$ measurement is associated with its own instrumental error, error propagation (Weisstein, 2016) was used to determine the difference or similarity between individual canines and third molars. Since each $^{87}\text{Sr}/^{86}\text{Sr}$ value has its own error, the error needs to be propagated to determine an error for the average. In error propagation, this is done by taking the square of each error value, then averaging the squares, and then finally taking the square root. This is also necessary for the four values that are integrated from different scans and then again with the main values.

To compare individual canines with the average of the third molars, the error interval around both of the values in each pair was considered. Since the values in the canines are larger, for each value it is necessary to subtract its error estimate first, and then subtract the error estimate from the average of the third molar values, before comparing to the third molar average. In other words, in order to conclude that one canine value is significantly larger than the average of the third molars, it is necessary to demonstrate that the confidence intervals around the compared values do not intersect.

4. Results

4.1. Comparison of individual canine and third molar $^{87}\text{Sr}/^{86}\text{Sr}$

Canine and third molar $^{87}\text{Sr}/^{86}\text{Sr}$ and their associated errors are presented in Figure 3. As a group, the $^{87}\text{Sr}/^{86}\text{Sr}$ for both canines and third molars are normally distributed (Shapiro-Wilk test $p = 0.385$ and 0.243 , respectively). The two random variables Y_1 and Y_2 have means $\bar{Y}_1 = 0.73606$ and $\bar{Y}_2 = 0.72979$, respectively, and standard errors $SE(Y_1) = 0.002612023$ and $SE(Y_2) = 0.00160087$, respectively. To determine whether $Y_1 - Y_2$ is significant, a third new random variable, Z , was defined as $Y_1 - Y_2$.

$$\text{Var}(Z) = \text{Var}(Y_1) + \text{Var}(Y_2) \quad (\text{plus not minus})$$

$$\text{SE}(Z) = 0.003064$$

The 95% confidence interval is $(Z - 2SE(Z), Z + 2SE(Z))$, because it is twice the standard error. Therefore, the 95% confidence interval for $Y_1 - Y_2$ is $0.00627 \pm 0.006128 = (0.000142, 0.012398)$, meaning there is a 5% chance that the actual difference is outside this interval and less than 2.5% chance the difference is less than or equal to 0. Therefore, taken together, the canine values are different from

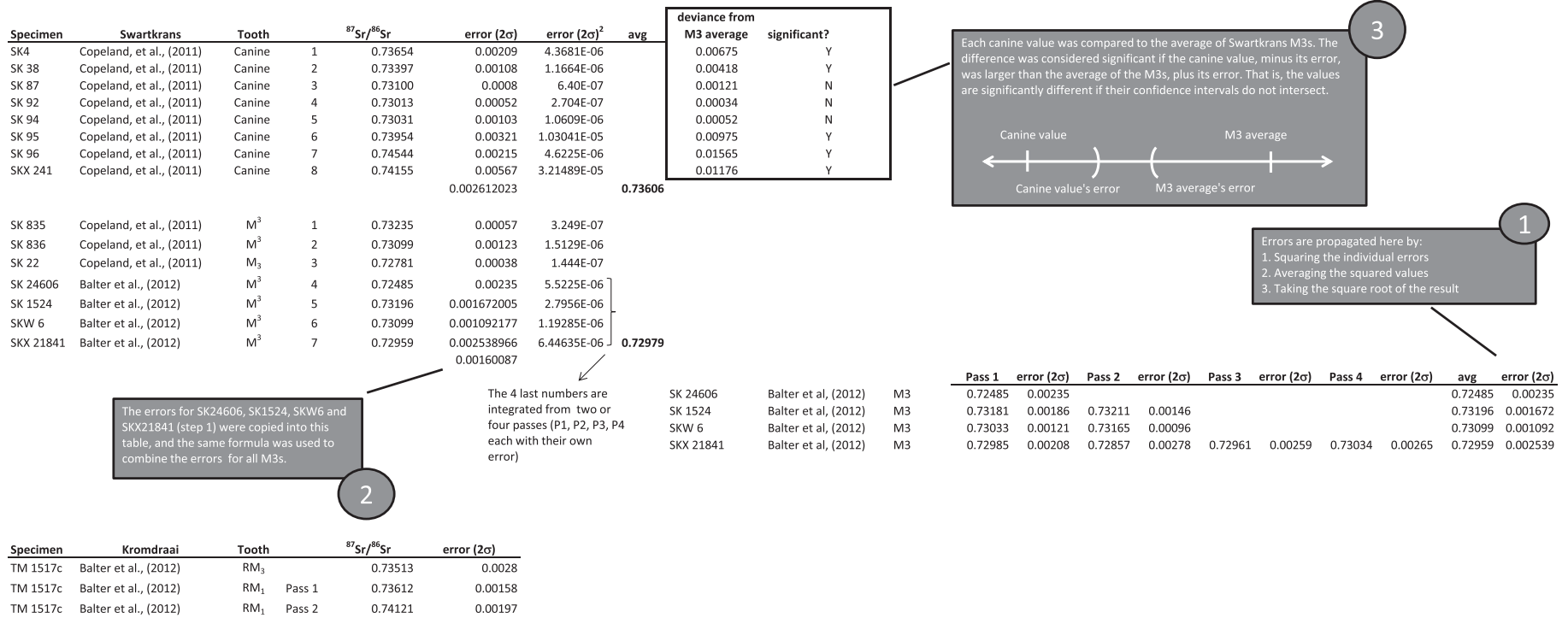


Figure 3. ⁸⁷Sr/⁸⁶Sr for all canines and third molars examined in this study, with standard errors, error propagation, and inferential statistics.

the M3 values with at least 95% confidence. However, this is not to say that all canines are different from all third molars. On the contrary, when comparing individual canines to the average of third molars using error propagation, it is possible to conclude that SK 4, SK 38, SK95, and SKX 241 are significantly more radiogenic than third molars, while SK87, SK92, and SK94 are not (Fig. 3).

In Figure 4, the $^{87}\text{Sr}/^{86}\text{Sr}$ of canines, M2s, and M3s is graphically represented, along with the trajectory of $^{87}\text{Sr}/^{86}\text{Sr}$ values in enamel from the DEJ to the OE in the teeth reported by Balter et al. (2012). Assuming that, for any given transect, OE is mineralizing later than enamel close to the DEJ, it is clear that all M3s examined exhibit $^{87}\text{Sr}/^{86}\text{Sr}$ in a narrow band from 0.72650 to 0.73450, and are either within this band or gravitating towards it during mineralization. In contrast, four canine specimens (SK 4, SK 95, SKX 241, and SK 96) show a relatively radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ inconsistent with the dolomite substrate in the immediate vicinity, as do one first molar and one second molar.

4.2. Detailed examination of TM1517c

The specimens grouped under TM1517c are unique in this dataset for representing two different teeth from one individual. Two scans were conducted on a fractured right lower M₁ and one scan on a right lower M₃. With regard to the M₁, the locations of the scans are of special interest because they sample enamel that is mineralizing in different periods over the life history of the tooth. From Figure 5, it can be seen that pass 1 begins at the base of a crown cusp, a region of early forming enamel that in human first molars enamel forms at age 0.1 ± 0.1 (summarized in Hillson, 2014). Pass 2, on the other hand, ends at the OE close to the cervical

margin, which is relatively late forming enamel. By reference to perikymata maps of human lower first molars (Reid and Dean, 2006; Hillson, 2014), it may be estimated the end of this scan roughly conforms to enamel mineralizing from 2.5 to 3.0 years of age. $^{87}\text{Sr}/^{86}\text{Sr}$ measurements associated with the laser ablation scans are also shown in Figure 5.

Late forming M₁ enamel has a strikingly different $^{87}\text{Sr}/^{86}\text{Sr}$ signature from the M₃ (Fig. 6). In scan MC-P2, $^{87}\text{Sr}/^{86}\text{Sr}$ ranges from a low of 0.7385 to a high of 0.7435, with an average of 0.74121 and a 2σ error of 0.00197. In contrast, the $^{87}\text{Sr}/^{86}\text{Sr}$ reported for M₃ enamel ranges from a high of 0.738 to a low of 0.733, with an average of 0.73513 and a SD 2σ of 0.00280. It is of interest that the scan of this tooth presents as a unidirectional decline in $^{87}\text{Sr}/^{86}\text{Sr}$ from the DEJ to the outer enamel — the latest mineralizing enamel has the most depleted strontium. The $^{87}\text{Sr}/^{86}\text{Sr}$ of the M₁ is well outside of the range reported for M₃ teeth from Swartkrans, although within the range reported for canines; however, the outer, presumably late forming M₃ enamel is within the range for Swartkrans third molars.

4.3. Detailed examination of SKX 21841, SK 1524, and SKW6

SKX 21841, a *P. robustus* RM³ from Swartkrans Member 3, SK 1524, a *P. robustus* LM³ from Member I, and SKW6, a *P. robustus* LM³, are of special interest because, among all the teeth reported by Balter et al. (2012), scans of these teeth originate at the DEJ beneath a cusp, thereby sampling enamel that formed at an early stage of third molar mineralization. Thus scans of these teeth are most likely to correspond to the mineralization that might overlap with canine or second molar mineralization in apes. Balter et al. (2012)

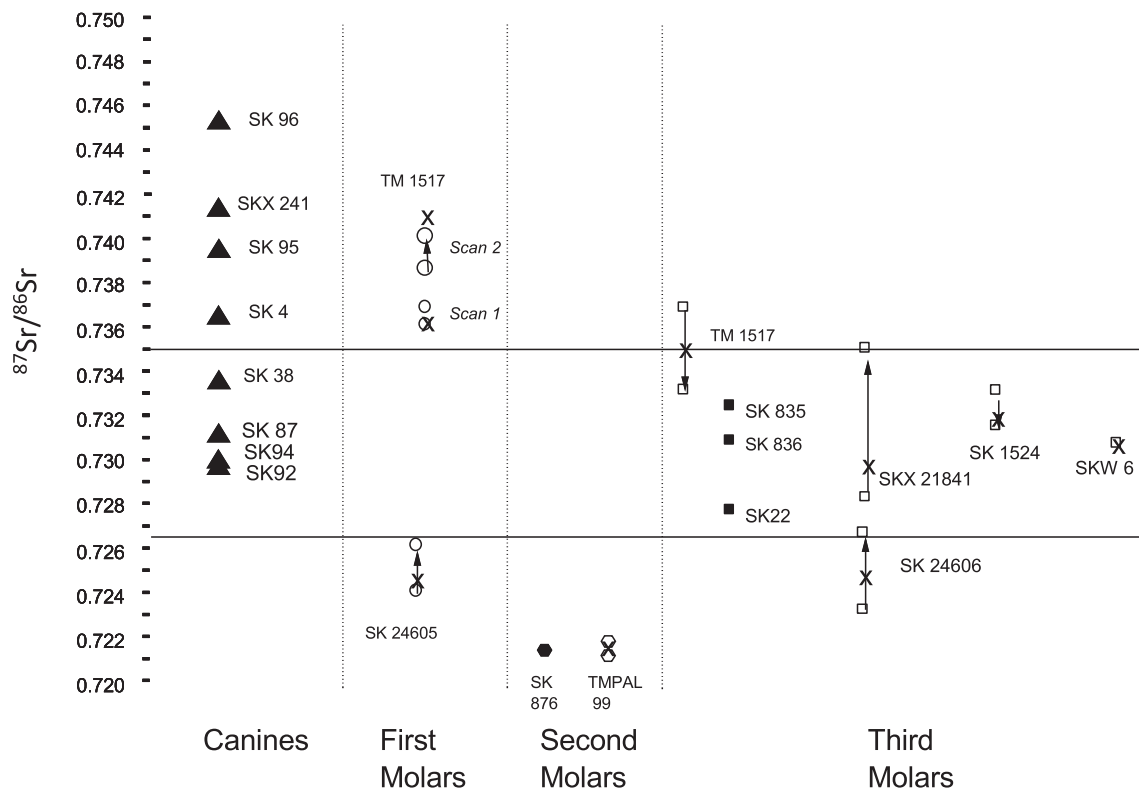


Figure 4. $^{87}\text{Sr}/^{86}\text{Sr}$ of all *Paranthropus robustus* teeth considered in this analysis. All teeth are derived from Swartkrans with the exception of TM1517, the holotype specimen from Kromdraai Member 3. Solid symbols represent summary reported data; open symbols represent the endpoint $^{87}\text{Sr}/^{86}\text{Sr}$ of reported transects from the dentino-enamel junction to outer enamel in the direction of arrows. \times = mean reported values for ablation transects; \blacktriangle = canines; \circ = first molars; \bullet = second molars; \blacksquare = third molars. All third molars exist in, or gravitate to, a narrow range from approximately 0.72600 to 0.73300. On the other hand, canines vary widely from 0.73000 to 0.74600 with five individuals outside of the M3 range. First molar and second molar teeth also fall outside the range for third molars. All data from Sillen et al. (1998); Copeland et al. (2011); Balter et al. (2012).

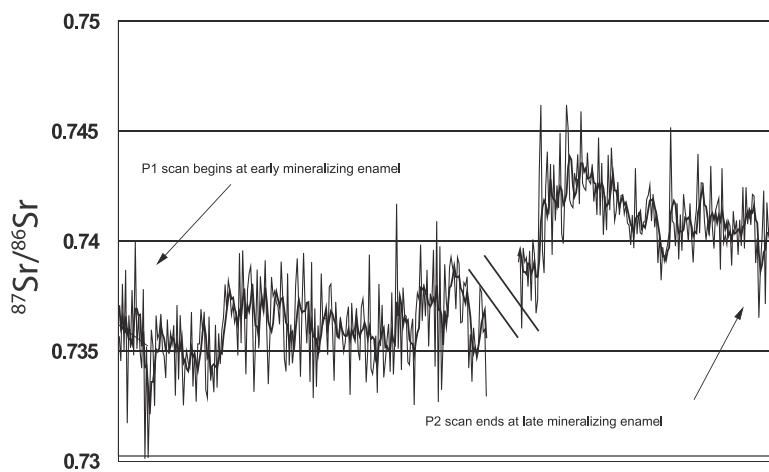
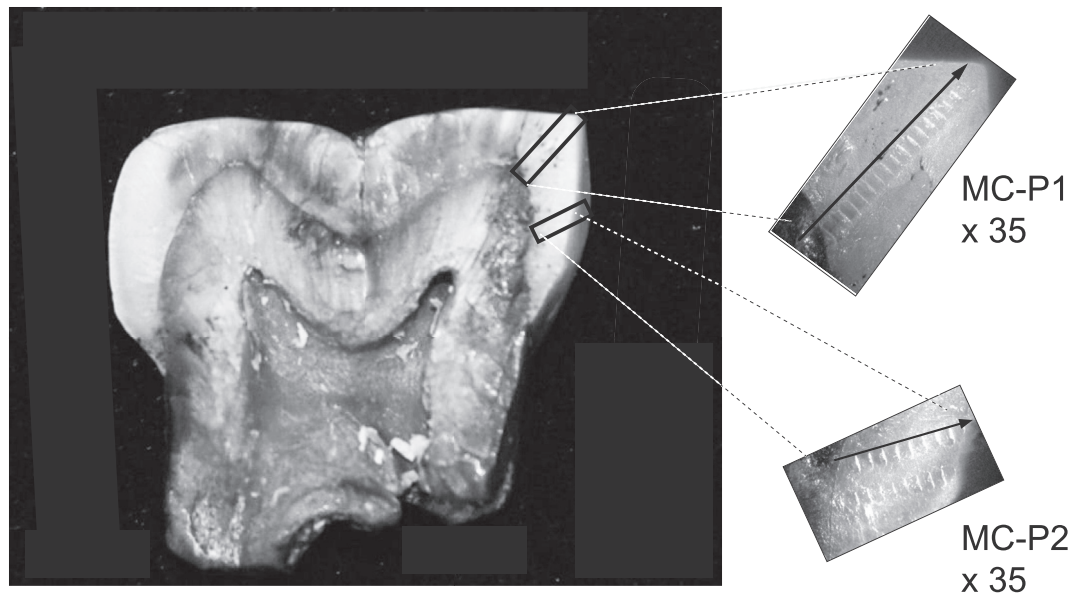


Figure 5. Location of laser ablation scans and their associated $^{87}\text{Sr}/^{86}\text{Sr}$ in the M_1 of TM1517c from Kromdraai. Scan P1 begins at early mineralizing enamel, at the base of a cusp near the DEJ, while scan P2 ends at late forming enamel, at the OE near the cervical margin. $^{87}\text{Sr}/^{86}\text{Sr}$ is more radiogenic in late forming enamel in this tooth.

report the average $^{87}\text{Sr}/^{86}\text{Sr}$ for SK 21841 is 0.72958, with a SD 2σ of 0.00208. For SK 1524, the average $^{87}\text{Sr}/^{86}\text{Sr}$ for SK 21841 is 0.73181, with a SD 2σ of 0.00186. From Figure 7, it is clear that the $^{87}\text{Sr}/^{86}\text{Sr}$ of the early mineralizing enamel from these teeth are consistent with the average figures for third molars. This indicates that either the individuals did not arrive from another locality, or if they did, third molar mineralization commenced after arrival in the locality.

5. Discussion

5.1. Habitat

Excellent modern reference values have been reported for plants from a variety of localities in the Sterkfontein Valley. Such data provide reference points for individual localities for the simple reason that plants are not mobile. In animals, on the other hand skeletal $^{87}\text{Sr}/^{86}\text{Sr}$ represents a mixing of all dietary strontium, which may itself be derived from more than one habitat, and in a ranging species, more than one locality.

This can be seen by reference to Figure 8, in which the $^{87}\text{Sr}/^{86}\text{Sr}$ of *P. robustus* teeth are compared to both the plant data and the available $^{87}\text{Sr}/^{86}\text{Sr}$ of faunal teeth. From this, we may conclude that *P. robustus* specimens, having a third molar $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.72650–0.73450, exploited a landscape consistent with the peri-riparian habitat and dry dolomite within five km from Swartkrans. Indeed the range is quite close to the midpoint for all measured dolomite localities: more radiogenic than immediate peri-riparian habitats, but not as radiogenic as the upland ones. However, these results do not imply that *P. robustus* exclusively exploited foods on the dolomitic substrate. For example, the *Papio robinsoni* specimens reported by Copeland et al. (2011) have $^{87}\text{Sr}/^{86}\text{Sr}$ comparable with *P. robustus*, but when the average home range of modern *Papio* (*P. cynocephalus*) is projected onto a geologic map with Swartkrans at the center, it has been estimated that 65–70% of the area exploited would be on a dolomitic substrate, with shales, quartzites, and mafic rocks forming the remaining area (Hall, 1994). Therefore it is more likely that such $^{87}\text{Sr}/^{86}\text{Sr}$ values reflect a mixing of (i) dolomitic substrate, (ii) radiogenic, non-

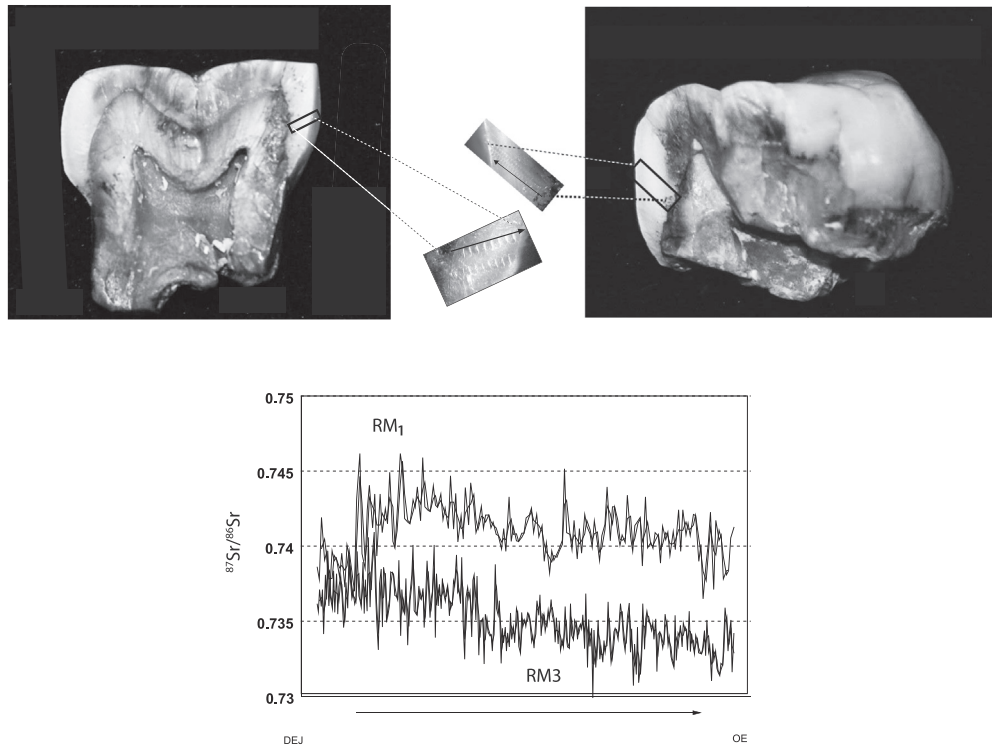


Figure 6. $^{87}\text{Sr}/^{86}\text{Sr}$ from laser ablation scans of RM₁ and RM₃ from TM1517c, the holotype *Paranthropus robustus* specimen from Kromdraai. $^{87}\text{Sr}/^{86}\text{Sr}$ for the RM₃ gravitate to the range for other *P. robustus* M3s reported, whereas the RM₁ values do not. Values for the RM₁ are consistent with the radiogenic canine teeth reported by Copeland et al. (2011).

dolomite substrate, and (iii) depleted riparian dolomitic substrate habitats.

Clearly, the faunal dataset is yet too limited to provide meaningful references about range and diet: a variety of species with quite different dietary and behavioral patterns all provide $^{87}\text{Sr}/^{86}\text{Sr}$ values consistent with the *P. robustus* third molar range. For example, the browsers *Connochaetes* sp. and *Tragelaphus* sp. are not demonstrably different in $^{87}\text{Sr}/^{86}\text{Sr}$ from the grazers *Equus capensis*, *Antidorcas recki*, and *Hippotragus gigas*. Nor are water-independent species *A. recki* and *Raphicerus* sp. demonstrably different from water-obligate ones, notably *Tragelaphus* sp. and *Hippotragus* sp. Similar results have been obtained from modern herbivores moving across multiple substrates in southern Africa (Radloff et al., 2010).

None of these species are so intensely limited in habitat and range that we might expect anything other than mixing reflecting integration of the wet and dry places of the Sterkfontein Valley. Perhaps one exception is *Damaliscus* sp., a specimen with depleted $^{87}\text{Sr}/^{86}\text{Sr}$ consistent with riparian strontium, which is of interest since modern tsessebes demonstrate a distinct preference for swampy grasslands (Rautenbach, 1982; Skinner and Chimimba, 2005; Dörgeleh, 2006).¹ (However, with a sample size of one, and no species designation, this explanation is speculative at best.) Based on a study of cattle teeth from West Yorkshire, UK, it has been estimated that strontium is incorporated into cattle third molars over a period of at least one year, even at the level of Striae of Retzius and perikymata (Montgomery et al., 2010). While this may

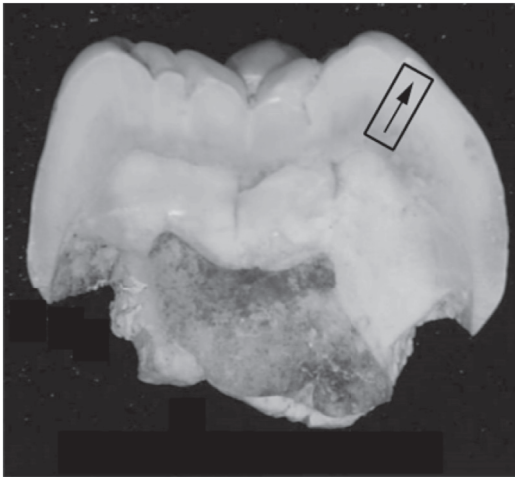
make it seem unlikely that seasonal movement of large herbivores could be tracked, the exceptionally large difference between $^{87}\text{Sr}/^{86}\text{Sr}$ endmembers in the Sterkfontein Valley system may yet make higher temporal resolution in large herbivore teeth possible. Therefore, carefully planned dissection and analysis of herbivore teeth is likely to materially advance our understanding of the isotopic ecology of the region.

Although some *P. robustus* first molar and second molar teeth exhibit a depleted $^{87}\text{Sr}/^{86}\text{Sr}$ consistent with the Blaauwbank riparian habitat, it is difficult to imagine that some individuals exclusively exploited this habitat — it seems more likely that these individuals arrived from somewhere else. In the future, this might be resolved by adding another isotopic or trace elemental parameter to the analysis.

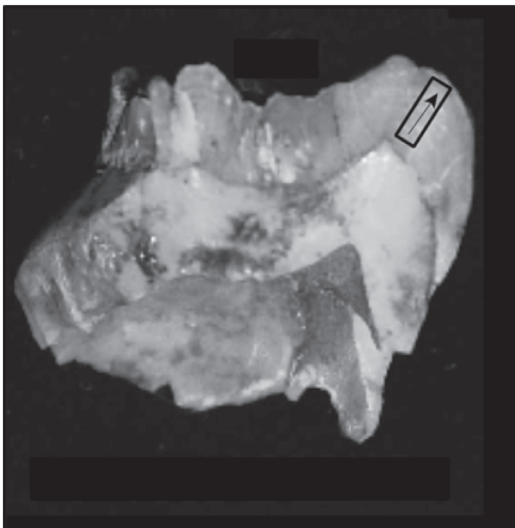
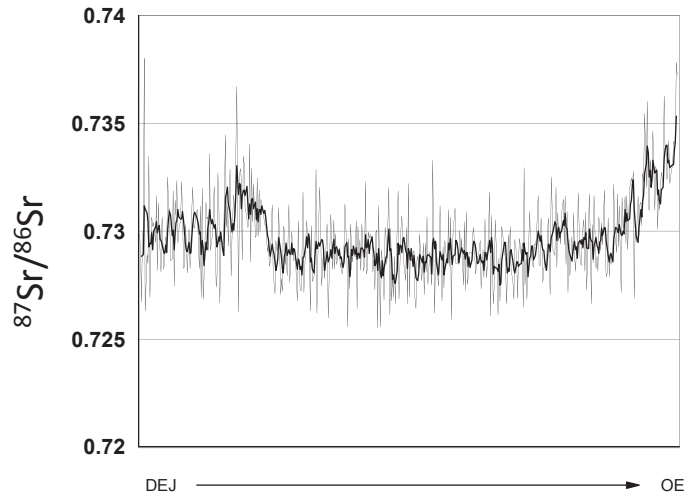
5.2. Residence

Copeland et al. (2011) interpreted their data to suggest a chimpanzee-like residence pattern, female exogamy and male philopatry, in which adolescent females emigrate from their natal groups (Goodall, 1986; Nishida et al., 2003). Subsequently, their work was challenged on the basis that the sex assignments of the canine teeth they analyzed were not sufficiently secure (Plavcan, 2012). Therefore, all we can say at this point is that some individuals, perhaps male or perhaps female, moved from their place of childhood to their place of demise. We can also say that some did not. Importantly, no individuals in the Copeland et al. (2011) and Balter et al. (2012) datasets show late forming third molar enamel $^{87}\text{Sr}/^{86}\text{Sr}$ inconsistent with the immediate locality, so there is as yet no positive indication of fully mature adults moving into the Swartkrans locality from elsewhere. Obviously, we cannot determine from the datasets whether any individuals moved away while juvenile, adolescent, or adult. An additional insight, from examination of the entire suite of specimens available, is that individuals

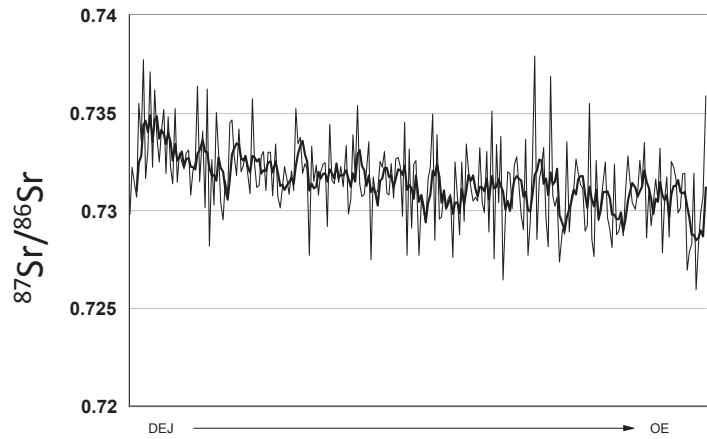
¹ This result is consistent with $^{87}\text{Sr}/^{86}\text{Sr}$ of bone from *Mystromis*, the white-tailed mouse (Sillen et al., 1998). This dominant microfaunal species at Swartkrans is today associated with particularly dense grass in the Transvaal (Rautenbach, 1982), and has been used as a representative indicator of waterside habitat in a general survey of southern African fossil sites (Avery, 1995).



SKX 21841



SK 1524



SKW6

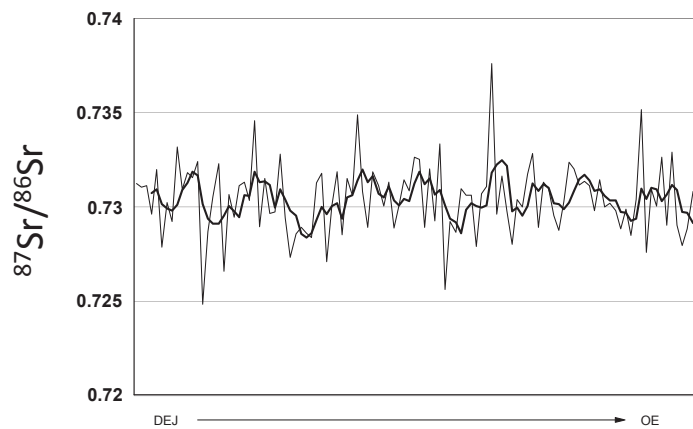


Figure 7. SKW6 $^{87}\text{Sr}/^{86}\text{Sr}$ from laser ablation scans of SKX 21841, RM^3 from Swartkrans Member 3; SK 1524, LM^3 from Member 1; and SKW6, LM^3 from Member 1. The origin of these scans conforms to the site of earliest mineralizing enamel. The values, in the region of 0.73–0.734, are consistent with M^3 $^{87}\text{Sr}/^{86}\text{Sr}$ for all teeth reported by Balter et al. (2012) and Copeland et al. (2011).

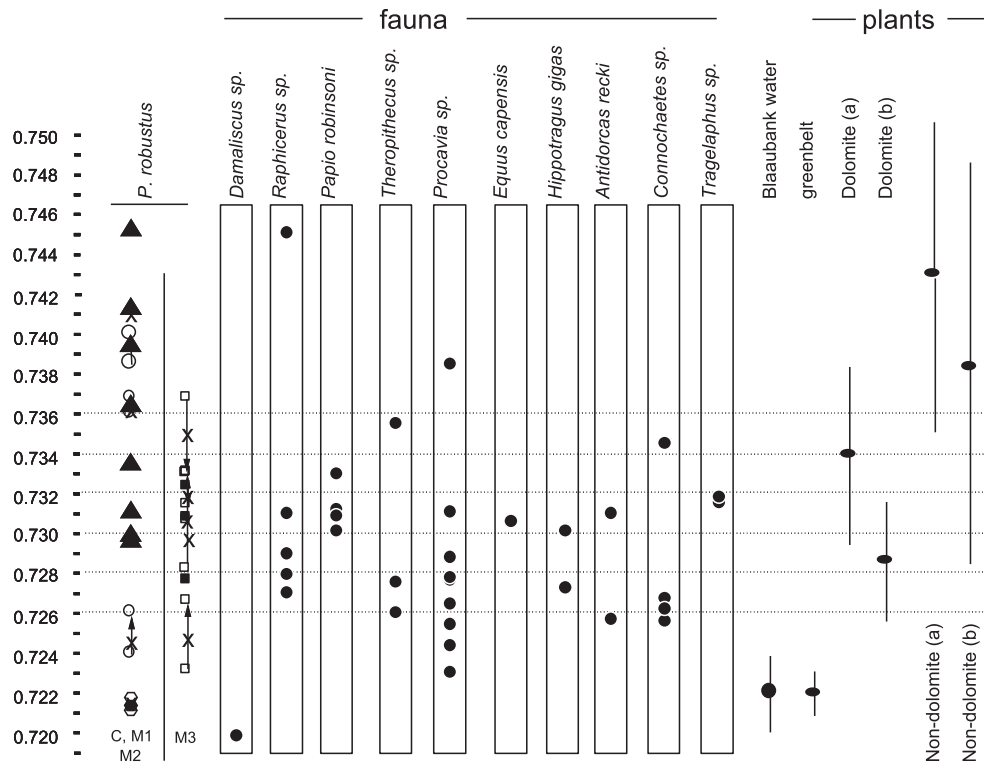


Figure 8. Summary of available $^{87}\text{Sr}/^{86}\text{Sr}$ data from Sterkfontein Valley *Paranthropus robustus*, fauna and plants. × = mean reported values for ablation transects; ▲ = canines; ○ = first molars; ● = second molars; ■ □ = third molars. Plant values bracketed (a) are taken from Sillen et al. (1998); values bracketed (b) are taken from Copeland et al. (2011).

may have moved into the Sterkfontein Valley from at least two different distant locations: one having a relatively radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ and one having a relatively depleted $^{87}\text{Sr}/^{86}\text{Sr}$. Addition of another trace elemental or isotopic parameter might in the future resolve these different locations.

The question remains of exactly how sensitive enamel $^{87}\text{Sr}/^{86}\text{Sr}$ is to dietary or habitat fluctuation, given (i) the lag time between deposition of the enamel matrix and mineralization, (ii) the size of the exchangeable skeletal reservoir or strontium and its relative contribution to the mineralizing fluids, and (iii) the distance between the $^{87}\text{Sr}/^{86}\text{Sr}$ endmembers in the system, and therefore the sensitivity of the analysis to changes in dietary strontium. With regard to the first, mineral deposition in the secretory phase of enamel maturation in a variety of species has been shown to be relatively minimal when compared to a dramatic increase at the onset of the maturation phase; the lag time may be on the order of weeks or months (Balasse, 2002; Hoppe et al., 2004; Robinson, 2014), but certainly not on the order of years. Strontium has been shown to be incorporated in human enamel even during the secretory phase, so evidence of dietary or habitat transitions occurring during this period of enamel deposition may also be recorded (Humphrey et al., 2008). As for the exchangeable skeletal reservoir, it is well to remember that when looking at canines and first molars, we are examining the tissue of rapidly growing children in which, under normal circumstances, there is a significant net retention of alkaline earths in bone. That said, the Total Exchangeable Pool (TEP) of skeletal strontium is relatively high in infants (Abrams, 2010), and this is likely to buffer any precursor (dietary or habitat) signal somewhat. A more significant consideration is likely to be the incorporation of the maternal skeletal $^{87}\text{Sr}/^{86}\text{Sr}$ given the well established mobilization of maternal skeletal minerals during pregnancy and lactation, as any such

maternal contribution will end with weaning. Finally, it has been pointed out that the greater the distance between $^{87}\text{Sr}/^{86}\text{Sr}$ endmembers in any given study, the greater the sensitivity of the analysis (Montgomery et al., 2010). As previously discussed, the Sterkfontein Valley is exceptional in this regard, and therefore the parameter is likely to be highly sensitive when compared to most other landscapes where the approach is employed.

Because first molar and anterior permanent teeth are mineralizing before weaning, the $^{87}\text{Sr}/^{86}\text{Sr}$ of the forming enamel will reflect that of maternal milk; that is to say, the radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ seen in some individuals represented by isolated canines (SK 96C, SKX 241, SK95C, SK4, SK24605) and first molars (SK24605, TM1517) of this species reflects both juvenile and maternal residence. These teeth tell us that some mothers of individuals represented by radiogenic teeth were resident in a different locality.

In the current analysis, although no assumptions are made or inferred about the sex assignment of the specimens examined, it is nevertheless of interest, and worthy of further study, that two of the most radiogenic canines reported, SK 96 and SK 241, are also the smallest. It is also important to note, however, that a relatively large second molar generally thought to be male (SK876) is also likely to be a migrant from another locality. Taken together, and with the rest of the sex designations of the canine teeth in doubt, the data do not yet support a conclusion regarding female exogamy (as in chimpanzees), male and female exogamy (as in gorillas), or for that matter, some other pattern novel to hominins. The question could be resolved, however, with a larger sample focusing on specimens with clear sex assignments and selection of appropriate teeth. Moreover, since some first molar enamel records maternal $^{87}\text{Sr}/^{86}\text{Sr}$, the question of female residence might be addressed in the future without any consideration of the sex-attribution of the tooth under examination.

5.3. Residence and growth

From Kromdraai TM1517c, it is clear that habitat and/or diet experienced by the individual while the first molar was mineralizing was different from that when the third molar was mineralizing. In apes, the gap between the end of M1 mineralization and the beginning of M3 mineralization is some two and a half years (between 2.5 and 5 years of age); in humans, the gap averages some seven and a half years (between 2.0 and 9.5 years, reviewed in Mann et al., 1990). Detailed examination of the scans shows that the radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ for the M1 pertains even to the later mineralizing enamel. $^{87}\text{Sr}/^{86}\text{Sr}$ for the earlier mineralizing enamel for the M3 is somewhat lower and continues to decline towards the outer enamel. Although this result does not itself provide any insight into the timing of M3 eruption, it suggests that it was entirely discrete in timing from first molars, and that at least this individual moved from another locality sometime after M1 mineralization ended and before or contemporaneous with M3 mineralization. Taken together, the data suggest that there is no overlap in first molar and second molar mineralization on the one hand, and third molar mineralization on the other. In terms of growth, these data accord with the prevailing view that *P. robustus* follows an analogous (if not similar) pattern to *Homo*, in which third molar enamel mineralization does not overlap with that of the second molar (Beynon and Dean, 1988; Simpson et al., 1990; Dean, 2010). With regard to timing, however, the result of the current analysis seems difficult to reconcile with a relatively abbreviated span of growth on an apelike model. Interest in the evolution of early hominin dental growth stems from the observation that prolonged growth, and by extension a prolonged childhood dependency period, is a basic human adaptation (Gould, 1976; Lovejoy, 1981), and whether early hominin species exhibited ape-like or human-like timing of dental eruption has been explored at least since Mann (1975).

Mann (1975) used the sequence of eruption and dental wear patterns to argue that the robust southern African hominin *P. robustus* exhibited extended timing of growth. Subsequently, this conclusion was challenged using a number of different lines of evidence, including the pattern of dental maturation (Smith, 1986, 1987), external dental microstructure (perikymata; Bromage and Dean, 1985; Dean, 1987), internal dental microstructure (Striae of Retzius, cross striations; Beynon and Wood, 1987), and root development (Dean, 1985; Dean and Cole, 2013). In turn, the use of incremental structures has been questioned on the basis of growth irregularity (Mann et al., 1990) and human variation (Smith et al., 2015). Specifically with regard to the timing of third molar mineralization, Mann (1975) noted that in *P. robustus* a delayed appearance of the third molars suggested a pattern of dental development similar to that of modern humans and distinct from the African apes. The view has been challenged based on incremental markings: it has been calculated that *P. robustus* third molar enamel mineralized between the ages of approximately five to seven years (Beynon and Dean, 1988).

The observation that no individuals moved into the Swartkrans locale after their third molars completed mineralization seems difficult to reconcile with both abbreviated growth and African great ape residence patterns. Chimpanzees and gorillas generally do not move from their natal groups until they reach sexual maturity.

For chimpanzees in the wild, menarche is usually seen in females between 10 and 11 years of age (although it has been observed as early as age 8; Wallis, 1997; Boesch and Boesch-Achermann, 2000; Nishida et al., 2003; Sugiyama, 2004; Brewer Marsden et al., 2006; Emery Thompson and Wrangham, 2008; reviewed in Atselis and Videan, 2009), and a subsequent period of adolescent infertility usually coincides with permanent emigration from their natal groups (Goodall, 1986; Nishida et al., 2003). Yet

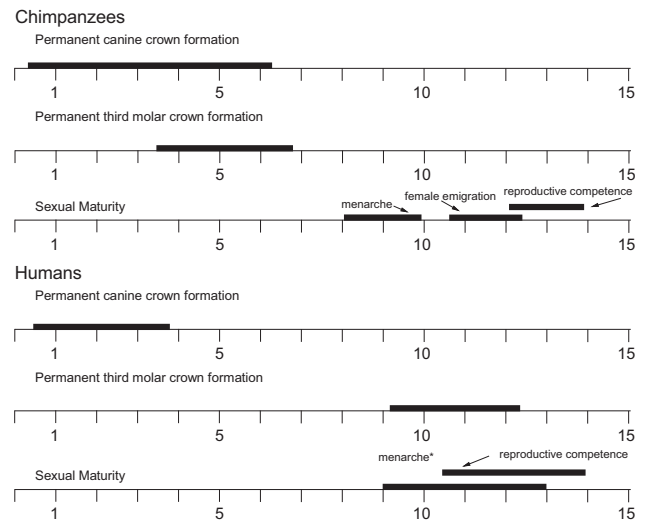


Figure 9. Tooth crown formation compared to initiation of sexual maturity in chimpanzees and humans. Data on chimpanzee third molar crown formation from Kuykendall (1996), Machanda et al. (2015); wild chimpanzee sexual maturity from Wallis (1997); Bosch and Bosch-Achermann (2000); Wrangham (2002); Nishida et al. (2003); Sugiyama (2004); Brewer Marsden et al. (2006); Emery Thompson and Wrangham (2008); Atselis and Videan (2009). *The range for human age at menarche is taken from what is considered clinically 'normal' in modern populations (Hillard, 2008).

permanent third molar formation is completed well before this, by 7.5 years. Bonobo females have been observed to migrate at adolescence, at around age 8 (Furuichi et al., 1998). With gorillas, males emigrate from their natal groups at or before the age of 15, and the average age of female emigration is 9 (Yamagiwa and Kahekwa, 2001; Yamagiwa et al., 2003). But third molar formation for this species is initiated at 4.9 years (Beynon et al., 1991) and is similarly completed about 2.5 years thereafter.

Thus, it is striking that no *P. robustus* third molars exhibit a distal locality $^{87}\text{Sr}/^{86}\text{Sr}$ in their late forming enamel. If *P. robustus* had anything like a chimpanzee- or gorilla-like growth timing, and individuals moved into the Swartkrans locality from elsewhere, there should be some third molars with exclusively exogenous $^{87}\text{Sr}/^{86}\text{Sr}$, but this is not the case: either every individual was local in origin (which we know is not the case from SK 24606, as well as TM1517 from Kromdraai), or some individuals moved as juveniles, or they had delayed third molar mineralization relative to the onset of sexual maturity.

The average age of menarche varies widely in humans, but it is currently approximately 12.5 years in the U.S. (Anderson et al., 2003), with anything between age 9 and 15 considered normal (Hillard, 2008). Although there is no direct evidence, even earlier menarche has been proposed for prehistoric populations (Gluckman and Hanson, 2006a, b).

In humans, the third molar calcifies between the ages of 9 and 12 years (summarized in Hillson [2014]). Thus, unlike African great apes, the onset of menarche overlaps with third molar calcification. Since mobility in *P. robustus* seems to be timed to a period before and during the mineralization of third molars, if *P. robustus* individuals did not move from their natal localities before the onset of sexual maturation, these data suggest that, in contrast to the conclusions based on incremental structures third molar mineralization was somewhat delayed in this species (Fig. 9).

6. Conclusion

Existing $^{87}\text{Sr}/^{86}\text{Sr}$ data for teeth from the Sterkfontein Valley provide intriguing glimpses into *P. robustus* behavior and biology.

Although it is not presently possible to conclusively determine residence patterns, the issue of exogamy and philopatry may be further addressed in the future, by study directed specifically to teeth with unquestioned sex assignments. An even more productive approach however, may be analysis of appropriately selected fractured teeth that reflect pre-weaning (maternal) $^{87}\text{Sr}/^{86}\text{Sr}$, since this will address female residence in a manner that does not depend on the sex assignment of the individual tooth analyzed.

In relation to habitat, specific focus on water dependent species (such as tsessebes), habitat specific species (such as white-tailed rats), and water-independent species, such as steenbok, may provide further reference points against which to compare hominin values. Isotopic dissection of the teeth of ranging and territorial species is necessary to further clarify how movement across landscapes affects the enamel $^{87}\text{Sr}/^{86}\text{Sr}$ of individual animals in the Sterkfontein region. Although they are yet to be conducted, multiple isotopic analyses and trace element analysis on the same anatomical locations in individual faunal teeth of known species designation would vastly improve our ability to reconstruct landscape use. Specifically, it would enable us to distinguish between multiple possible sources of depleted $^{87}\text{Sr}/^{86}\text{Sr}$.

With regard to growth timing, it is unclear why the enamel $^{87}\text{Sr}/^{86}\text{Sr}$ data suggest a relatively late initiation of third molar mineralization, in contrast to the conclusions of micro-anatomical analyses. Inevitably, more samples of fractured teeth will become available for $^{87}\text{Sr}/^{86}\text{Sr}$ analysis and it will be interesting to see if the patterns identified in this study continue to hold. It would also be most useful to identify fractured second molars that might provide more data on movements during childhood—especially without the complication of maternal $^{87}\text{Sr}/^{86}\text{Sr}$ that applies to first molars.

In theory, deeper insight into life history events such as birth and the timing of weaning may be possible from both $^{87}\text{Sr}/^{86}\text{Sr}$ and Sr/Ca observation of carefully prepared and landmarked microstructures, similar to that conducted for Sr/Ca in modern teeth (Humphrey et al., 2008). With current technology, however, that would entail destructive interventions that for the time being are not possible to contemplate. In the meantime, continued examination of isotopic phenomena in fractured teeth presents a viable way forward for examining early hominin life histories in this region.

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