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Elemental signatures in *Australopithecus africanus* teeth reveal seasonal dietary stress

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Author contributions RJB, JWA, CA, IM, MA, AIRH, LF, SB, ARE, OK and SW selected the sample, designed the project, and/or received funding for the research. RJB, CA and IM conceived and designed the experiments. RJB, CA, IM, MPT and AD conducted the analytical campaign on the different instruments and interpreted the data. RJB prepared the figures and wrote the manuscript, with extensive contribution from CA, MA, IM, LF, AIRH, JWA, MPT, SB, ARE, OK, AD and SW.

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Readers are welcome to comment on the online version of the paper.

Data availability - The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Abstract

Reconstructing the detailed dietary behaviour of fossil hominins is extremely challenging¹, particularly in a species such as *Australopithecus africanus* whereby a highly variable dental morphology suggests a diversity of sustenance^{2,3}. Dietary response to seasonal fluctuations in food availability remains poorly understood, and nursing behaviours are even more cryptic, with most of the direct information being obtained from high-resolution trace element geochemical analysis of *Homo sapiens* (modern and fossil), *Homo neanderthalensis*⁴ and living apes⁵. Here, we apply, for the first time a similar methodology to two 2.6–2.1 Ma *A. africanus* specimens from Sterkfontein Member 4 in South Africa. Elemental signals indicate that the diet of *A. africanus* infants was predominantly breast milk for the first year after birth. Furthermore, a cyclical elemental pattern following the nursing sequence, comparable to the seasonal dietary signal observed in wild primate and non-primate mammals, indicates irregular food availability. These results are also supported by isotopic evidence of a geographical range dominated by nutritionally depauperate areas. A new finding of cyclical lithium accumulation in teeth also supports fluctuating resources and physiological adaptations. This study provides insight into the previously unknown dietary cycles and ecological behaviours of *A. africanus* in response to food availability. This includes the potential cyclical resurgence of milk intake during challenging nutritional times, as observed in wild extant *Pongo*⁵. The new geochemical findings uncovered in ~2.6–2.1 million years old teeth of *A. africanus* reinforce the unique place of the species in the fossil record and indicate dietary stress in specimens that occur not long before the extinction of *Australopithecus* in South Africa at ~2 Ma.

Keywords

Australopithecus africanus; nursing; fossil teeth; geochemistry; trace elemental mapping; seasonal food stress

Australopithecus africanus is arguably one of the first known hominins to inhabit the South African landscape, living from 3.03–2.61 Ma until sometime between 2.3–2.1 Ma⁶. Decades of research on the diet^{7,8,9} and mobility³ of this species has suggested an unusually high degree of dietary variability (which probably included the consumption of fruits, leaves, grasses, sedges and roots) relative to other hominins, that has led to the interpretation that *A. africanus* lived in a complex range of environments, including open grassland and forest⁷. These interpretations are based principally on the broad range of morphology in *A. africanus*, which is tentatively attributed to the potential occurrence of more than one species¹⁰ within Sterkfontein Member 4 (2.61–2.07 Ma) and Makapansgat Limeworks (3.03–2.61 Ma) assemblages⁶ (ED Fig. 1) or substantial changes in diet over time in response to significantly changing South African ecosystems of the early Pleistocene (~2.3–2.1 Ma)^{11,12}. While seasonal changes in tropical grassland-dominated ecosystems

(frequently referred to as the savanna biome) are associated with only minor temperature variations, important oscillations in rainfall produce lengthy dry and wet periods¹³. This has considerable impact on food availability, leading to long alternating periods of abundance and scarcity of nutritious food. This cyclical rhythm of dry open grassland in winter and wet blooming woodland in summer prompted mammals to adapt either by undertaking long annual migrations to more clement regions, or, to adapt to seasonal food consumption, including the use of fall-back resources (those with poor nutritional values eaten only when preferred foods are scarce or unavailable)^{14,15}. This climatic cycle has consequences on the physiological (e.g. nursing, reproduction and infant development) and ecological behaviour (e.g. diet, grouping of individuals, territory size) of endemic species, particularly to non-migrating individuals^{13,14,15}.

Here, we have undertaken elemental mapping of dental tissues of *Australopithecus africanus* (ED Fig. 1) to study the dietary intake of offspring during early stages of development. Teeth are particularly valuable for reconstructing the early-life history of ancient populations as they contain precise temporal and chemical records that are more resistant to post-burial diagenesis than bone (ED Fig. 2). Mineralisation of enamel and dentine occurs incrementally and thus retains a sequential record of an individual's early-life chemical exposure - both external and internal (e.g., metabolites). The well-preserved elemental and isotopic signals have been used to reconstruct trophic levels¹, diet^{1,2,8} and migration patterns³ of early hominins and even the breastfeeding history of late Pleistocene *Homo*⁴ and extant apes⁵. Understanding nursing history is extremely valuable in reconstructing the early life of extinct hominins, in particular for clarifying when the characteristic early weaning and late maturation of modern humans evolved. Our previous work identified barium (Ba) in teeth as a reliable marker of maternal milk intake⁴. Generally, Ba concentration in dental tissues formed prenatally is low due to restricted maternal transfer via the placenta¹⁶. It increases after birth with absorption from mother's milk and then slowly decreases with the weaning process to reach its lowest level when the infant's diet is based solely on solid food. The decrease in Ba with weaning, despite many plant foods having higher Ba concentrations, has been attributed to differences in the bioavailability of barium in milk compared with non-milk foods⁴. Biochemical processes that increase the bioavailability of calcium (Ca) in milk, likely effect Ba as well because of the chemical similarity between the two elements¹⁷, leading to greater absorption of Ba from milk compared to non-milk foods.

We estimate that mineralisation of an *A. africanus* molar (M1) in StS 28 and lower canine (LC) in StS 51 started soon after birth and about 3 months after birth respectively¹⁸. To preserve these rare samples, thin sections of the teeth were not created and developmental timing of the tooth samples were estimated using known values^{18,19}. Both teeth show increasing Ba/Ca from the start of mineralisation that peaks at 6–9 months (StS 28 M1 and StS 51 LC respectively), based on crown formation times^{18,19}. This indicates a predominately breastmilk diet (Fig.1) for a minimum of 6–9 months followed by increased supplementation with non-milk foods which peaks around 12 months. After the initial high Ba/Ca deposition, the elemental ratio increases and decreases in a cyclical pattern with a period of about 4–6 months for StS 51 and 6–9 months for StS 28 (see Fig. 1–2 and ED Fig. 3 for StS 28 and Fig. 1–3, ED Fig. 4 for StS 51). The cyclical signal is clearly visible in all

A. africanus teeth, with multiple occurrences from cusp to root that follow a pattern associated with tooth growth rather than diagenesis and are consistent across teeth from the same individual. Uranium, a marker of diagenesis, shows a markedly different diffuse pattern that does not follow tooth growth patterns. Although the presence of uranium indicates some post-burial alteration, the Ba, strontium (Sr) and lithium (Li) banding that follows the developmental architecture of dentinogenesis and amelogenesis, and the repetition of the pattern across teeth from the same individual confirm that the observed cyclical patterns are biogenic (see supplementary discussion & ED Fig. 3 & 4). The highly cyclical Ba/Ca pattern observed in permanent teeth from StS 28 and StS 51 indicates a repeated behaviour over time until at least ~4–5 years of age (Fig. 1–3, ED Fig. 3 & 4). This pattern is reinforced by Sr/Ca and Li/Ca signals that also occur cyclically along the growth axis of the tooth.

A similar recurring pattern in Li/Ca, Ba/Ca and Sr/Ca was observed in modern wild orangutans (*Pongo abelii* and *Pongo pygmaeus*)⁵ up to 9 years of age. This pattern was interpreted as seasonal dietary adaptation where Ba/Ca in teeth increased when infants relied more heavily on mother's milk during periods of low food availability. To investigate further we analysed teeth from several modern mammals from a similar ecological landscape (ED Fig. 5) to that of *A. africanus*. All mammal teeth also showed cyclical Ba/Ca signals. While no reliable crown formation times could be sourced for all mammals (Table S1), these specimens are reported to wean at a young age (2–9 months and up to 12 months for baboons)¹⁵. This suggests that the cyclical pattern of the mammals living in grassland-dominated ecosystem reflects seasonal dietary adaptations and later periods of higher Ba/Ca may indicate increased consumption of another, non-milk source of highly bioavailable Ba. The recurring pattern was least noticeable in carnivores, suggesting less variation in diet. A cycle of about 8 months was estimated in the baboon that is strikingly similar to that observed in *A. africanus* (ED Fig. 6A). Additionally, the Ba/Ca value measured in the modern baboon first molar is higher than for the third molar, supporting a mixture of seasonal and milk intake signal in the M1 compare to only seasonal dietary oscillation in the M3 (ED Fig. 6B). Yet, it cannot be excluded that the difference in mineralisation and physiological cycle during the amelogenesis could have also played a role for the difference in values. While the Ba/Ca banding in *A. africanus* appears to have greater regularity compared to the other mammals (in particular for StS 28 M1), the number of samples and lack of accurate tooth age estimates limits further analysis of any variation in seasonal regularity between modern and early Pleistocene eras.

In general, Sr/Ca banding was clearer across the teeth in *A. africanus* with additional narrow lines that were not observable in the Ba/Ca images (ED Fig. 3 and 4). Yet, the Sr/Ca and Ba/Ca patterns were largely synchronous indicating a common source of exposure (ED Fig. 5 & 6). This is in contrast with modern human samples that often show asynchronous Ba/Ca and Sr/Ca patterns (ED Fig. 7). Li/Ca banding in teeth from *A. africanus* was less frequent than other elemental patterns but occurred predominantly just before the Ba/Ca intake episodes with the highest amplitudes (Fig. 2 & ED Fig. 8). Furthermore, a similar relationship between the two cycles was not observed in other non-primate mammals analysed (ED Fig. 5), but was detected in baboons and modern orangutans⁵. The presence of highly cyclical Ba/Ca and Li/Ca banding in *A. africanus* likely reflects seasonal dietary

shifts and perhaps also physiological responses similar to those of modern wild *Pongo*⁵. It appears that *A. africanus* was under seasonal food stress and had to adapt to changing resources and food access²⁰. The analysis of the strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) of *A. africanus* from Sterkfontein shows that some specimens principally lived on the dolomite karst, dominated by more open bushland and grassland rather than the closed woodland of surrounding lithologies^{3,10,11}. Our present strontium isotope data (ED Fig. 9) are consistent with both individuals analysed herein having spent the majority of their time in the Malmani Dolomite Subgroup during amelogenesis. This specific geological setting is severely depleted of many nutrients, thereby limiting plant growth⁸.

Some primate species opportunistically adapted their physiology to cope with seasonal food availability due to specific environmental pressures²¹. Immature baboons in high-altitude environments, a challenging setting for offspring, have been reported to extend nursing cycles, decrease foraging time, wean later and engage in lower-energy activity than lowland *Papio*²¹. Varying milk intake can compensate for periods of extreme and unpredictable oscillations in food availability. This adaptation allows the survival of immature individuals, who are particularly vulnerable to fluctuations in food accessibility because of lower fat reserves and weaker muscle tissues. During periods of abundance, the infant can rely more heavily on solid food, thus allowing the mother to replenish large energetic and calcium reserves to support an increase in lactation during periods of food scarcity. Previous reports suggested that wild *Pongo* (*Pongo abelii* and *Pongo pygmaeus*) females adapted to seasonal variation by increasing the weaning period until a late offspring age of 8–9 years old⁵. This ecological exigency has forced orangutan females to lower their metabolic requirements²⁰, increase their aptitude to rapidly build energetic reserves²² and to catabolise fat reserves and muscle tissue faster during periods of nutrient insufficiency²³. Elemental mapping of a tooth from a captive orangutan receiving a constant supply of food showed a different pattern that lacked the imprints of cyclical dietary intake (ED Fig. 10). Narrow bands of increased Ba and Sr were observed in this animal and attributed to acute stress events²⁴. Intense, narrow Ba and Sr bands were also observed in teeth from *A. africanus*, baboons and other savannah mammals, however, these bands overlap with broader dietary bands indicating a co-occurrence of stress and seasonal dietary changes. The overlap of possible cyclical nursing and a stressful environment due to changing food availability make it difficult to interpret accurately the underlying cause of the banding pattern (ED Fig. 6A).

Likewise, the Li/Ca banding pattern, also found in modern *Pongo* and baboons (to a lesser extent) but rarely observed in modern *Homo* samples (ED Fig. 7) nor in the non-primate mammals analysed here, suggests complex physiological adaptations to cyclical periods of abundance and starvation. Lithium, while not directly incorporated within the fatty tissues, has been shown to vary in concentration with body mass²⁵. However, the exact relationship between weight gain and Li storage remains unclear with a possible link to psychological factors in modern humans (supplementary discussion). Another explanation could be the role of Li in preventing protein deficiency during low caloric intake²⁶. Primates are known to switch to higher-protein fallback foods during low resource seasons to maintain strength^{20,22}. Moreover, Li concentration varies greatly between plants or parts of the same plant and was reported to transfer to breast milk (supplementary discussion). While the evidence of an adaptive shift to fall-back resources in *A. africanus* has been questioned^{8,9,27},

the periodic Li signal which is compatible with seasonal changes²⁸ could suggest such an adaptive trait. During periods of severe food shortage immature australopiths might have developed physiological adaptations to compensate for low caloric intake from fallback resources, including perhaps a long weaning sequence. Undoubtedly, high Ba/Ca and Li/Ca bands in *A. africanus* dental tissues attest to strong seasonal oscillation of food access, which would have had a substantial impact on australopith development. This interpretation is also reinforced by the characteristic high frequency of developmental defects in enamel of the species' dentition as a result of nutritional deficiencies²⁹.

With a short period of predominant breastfeeding not exceeding a year, *A. africanus* shows a very different sequence to extant great apes and instead has a timing comparable with modern *Homo* species^{4,30}. Yet, since nursing and seasonal dietary banding cannot be precisely disentangled, it remains possible that the species retained a lengthy weaning sequence well into an advanced age of the offspring to overcome seasonal food shortage, similar to modern day great apes^{5,30}. Our results identified important dietary cycles and physiological adaptations in response to food access, which would have had important repercussions on social structures and ecological behaviours adopted by *A. africanus* groups. These adaptations in response to seasonal variability and resource scarcity, would have extracted a toll on the resilience to other environmental pressures, thus possibly playing a role in the disappearance of the genus from the fossil record at ~2 Ma⁶.

Extended Data

Extended data Figure 1 - The Sterkfontein surface excavation and fossil teeth specimen.

Plan view of the Sterkfontein surface excavation adapted from Kuman, K., and Clark, R. J.³⁵, showing the association between the Type Site excavation and Member 4 deposits. (B) Photo of fossil teeth specimen StS 28; (C) upper first molar (M1) StS 28B; (D) permanent lower first molar (M1) StS 28C after being sectioned in two with a diamond low speed high precision rotary saw. (E) Photo of fossil teeth specimen StS 51; (F) permanent premolar (P3) StS 51A; (G) permanent canine (LC) StS 51B after being sectioned in two with a diamond low speed high precision rotary saw. The two teeth still embedded in the breccia were not sectioned.

Extended data Figure 2 - Elemental mapping by LA-ICPMS protocol:

(A) Sketch of a fossil *Pongo sp.* second molar tooth dentine and enamel section with indication of biogenic accentuated lines (green); Elemental mapping of both dental tissues using laser ablation-inductively coupled plasma-mass spectrometry shows (B) strontium distribution following the incremental growth pattern of the tooth, typical of biogenic signals, contrary to post-mortem diagenetic processes (C) (uranium diffusion during burial).

Extended data Figure 3 - Elemental mapping of *A. africanus* StS 28.

Elemental mapping of (top) upper first molar cusp (StS 28B); and (middle and bottom) lower first molar (StS 28C) showing records of cyclical banding between 0 and 7 years at crown completion. The broad repeated banding pattern is attributed to seasonal dietary shifts and potentially to cyclical nursing during long weaning periods. The identical elemental banding pattern found in both StS 28B and StS 28C first permanent molars confirm beyond any doubt the biogenic nature of the signal observed (compare B, C and D with G, H and I respectively). The typical patchy and spreading diffusion pathways of uranium in the dentine and the enamel can be observed (E, J, O) with characteristic accumulation or depletion in cracks and at the enamel-dentine junction, very different to the biogenic Li, Sr and Ba banding.

Extended data Figure 4 - Elemental mapping of *A. africanus* StS 51.

Elemental mapping of (A) permanent premolar (StS 51A) (B) Li/Ca banding, (C) Sr/Ca banding, (D) Ba/Ca banding and (E) U/Ca diffusion; (F) permanent canine (StS 51B) (G) Li/Ca banding, (H) Sr/Ca banding, (I) Ba/Ca banding and (J) U/Ca diffusion; The strontium signal shows additional discrete lines most likely associated stress episodes compared to Li/Ca and Ba/Ca. Uranium distribution shows a typical and rather uniform diffusion pattern with enrichment close to the EDJ and in fractures and cracks.

Extended data Figure 5 - LA-ICPMS trace element mapping of primate and non-primate mammals:

All teeth specimens are from the grassland-dominated ecosystem of South Africa (frequently referred as savanna) and were recovered from wild modern animals. (A) *Antidorcas marsupialis* (M2) - Herbivore; (B) *Caracal caracal* premolar (P4) - Carnivore; (C) *Papio ursinus* third molar (M3) – Omnivore/opportunistic; (D) *Potamochoerus porcus* first premolar (P3) - Omnivore; (E) *Otocyon megalotis* second molar (M2) - Carnivore; (F) *Papio ursinus* first molar (M1) - Omnivore/opportunistic. All mammals exhibit Ba/Ca and Sr/Ca banding (except for (E) where no Sr lines can be observed). Li/Ca banding is absent from animal teeth except from the two Baboon teeth (C and F) and perhaps the hog tooth (D). In fact, the Ba/Ca banding pattern in *Papio* is very similar to the one observed in *A. africanus*, apart from the lack of clear periodicity, the baboon teeth are comparable to those of the australopiths. Baboons have a unique nursing cycle and an opportunistic seasonal feeding habit.

Extended data Figure 6 - $^{138}\text{Ba}/^{43}\text{Ca}$ and $^{88}\text{Sr}/^{43}\text{Ca}$ distribution in the enamel parallel to the Dentine-Enamel Junction (DEJ).

(A) StS 51 canine: The Ba/Ca and Sr/Ca ratios comparison show an inverse correlation towards the end of exclusive breastfeeding [A]. This pattern is repeated at [B] and [C] approximately 6 months apart, which may indicate cyclical milk intake. The concurrent increase in Sr/Ca with decreasing Ba/Ca at [A] indicates an increase in the predominance of solid food in the diet and indicates a food source with more bioavailable Sr than milk. Timing for the tooth development was approximated using estimated *A. africanus* species values^{17,18} and assuming linear growth rate of the enamel. (B) modern baboon molars: The Ba/Ca and Sr/Ca ratios along the DEJ of a first (left and ED Fig. 5F) and a third molar (right and ED Fig. 5C) of a modern baboon was compared giving several years of record. While both teeth had clear banding, the M1 display more intense fluctuations compare to the pattern observed in the third molar, potentially attributed to an additional nursing signal in

M1, with exclusive breastfeeding for the first 4–6 months until being completely weaned just after a year.

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Extended data Figure 7 - LA-ICPMS trace element mapping of modern humans:

The $^7\text{Li}/^{43}\text{Ca}$, $^{88}\text{Sr}/^{43}\text{Ca}$ and $^{138}\text{Ba}/^{43}\text{Ca}$ for each modern human specimen (*Homo sapiens*) HT01 (UM1), HT02 (LM1) and HT03 (UM1) (left to right respectively). The distribution pattern of all three elements is notably different to the signal observed in *A. africanus*, with an enrichment towards the pulp cavity for both $^{88}\text{Sr}/^{43}\text{Ca}$ and $^{138}\text{Ba}/^{43}\text{Ca}$, likely associated with blood flow. An important difference is the absence of a repeated pattern observable for all three elemental ratios. While some features could be interpreted as banding, such as the $^{88}\text{Sr}/^{43}\text{Ca}$ root signal of HT03, the isolated pattern is not mirrored in the other elemental distribution.

Extended data Figure 8 - Comparison of temporal occurrence of Li and Ba banding in StS 28C upper first molar.

The Li/Ca banding (A) when placed over the Ba/Ca bands (B) shows (C) a slight offset of the lithium banding. The lighter element (red dotted line marking the start of the Li deposition) appears to occur immediately before and during the deposition of Ba/Ca (blue shading lines). It is hypothesised that Li location in the hydrosphere of the bone is more rapidly reabsorbed and transported into the bloodstream than Ba.

Extended data Figure 9 - Strontium isotopic ratio distribution:

Location of the laser ablation spot (150 microns) along the enamel and dentine for StS 51A (A) and StS 28C (B). Circles with red filling correspond to the first point (1) and yellow filling to the last point (9 for enamel and 6 for dentine). The table below shows the $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic ratio and associated errors for each laser ablation spot measured above. All values measured in both teeth (including Dentine 6 of StS 28 with associated error) correspond to the Malmani dolomite values surrounding Sterkfontein ($^{87}\text{Sr}/^{86}\text{Sr}$ $0.723 < \text{Malmani dolomite} < 0.734$)³, showing limited mobility for both specimens.

Extended data Figure 10 - Permanent second molar of a modern *Pongo* specimen from the Perth Zoo.

The animal was born in captivity in 1975 in the Singapore Zoo, and join the Perth zoo later still as an immature individual. There appears to be no Ba/Ca banding pattern indicating cyclical milk consumption during crown completion. The captive orangutan Hsing Hsing, was born in captivity in 1975 at Singapore Zoo and was parent raised (although additional human feeding cannot be definitively excluded) before being relocated to Perth Zoo in 1983. His diet would have been significantly different to orangutans living in the wild, with limited seasonal influence and no periods of food scarcity. It is expected that the animal and his parents would have had abundant and guaranteed access to food, which would likely have led the specimen to be prematurely weaned compare to wild *Pongo*. On this basis, it is unlikely that Hsing Hsing would have had recurrent breastfeeding cycles and therefore the absence of Ba banding in this specimen is expected. The discreet banding observed for the Sr/Ca and the two Ba/Ca are likely stress related accentuated lines. No clear banding was observed in the enamel of this specimen.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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FIG. 1: Breastfeeding period of *A. africanus*:

(A) section of enamel lower canine of StS 51 and associated $^{138}\text{Ba}/^{43}\text{Ca}$ elemental mapping. (B) section of enamel upper first molar of StS 28 and associated $^{138}\text{Ba}/^{43}\text{Ca}$ elemental mapping. The dotted lines indicate the beginning of enamel calcification, the time at which the breastfeeding peaked and the date at which the infant *A. africanus* breast milk intake decreased in profit to solid food. A period of approximately ~12 months and ~13 months for StS 51 and StS 28 of predominant breastfeeding was estimated using the distance between the identified lines and the average rate of calcification of the species ($5.5 \mu\text{m}/\text{d}$)^{16,17,18}

FIG. 2: Elemental mapping of *A. africanus* StS 28 and StS 51 fossil teeth:

Micrograph ($\times 10$) of (A) StS 28C permanent first molar and (B) StS 51A permanent first premolar (P3). Associated elemental mapping of $^7\text{Li}/^{43}\text{Ca}$ (B) StS 28 and (C) StS 51 and $^{138}\text{Ba}/^{43}\text{Ca}$ (E) StS 28 and (F) StS 51. Assuming similar timing in *A. africanus* and in *Homo*, crown formation of the permanent first molar would correspond to an early-life record from birth to about 7 years of age, while crown formation of the permanent first premolar (P3) would correspond to an early life record from 1.5 years to about 5 years of age.

FIG. 3: Elemental mapping of StS 51 A. africanus canine:

(A) Micrograph ($\times 10$) of StS 51B permanent lower canine. (B) Associated elemental mapping of $^7\text{Li}/^{43}\text{Ca}$ and (C) $^{138}\text{Ba}/^{43}\text{Ca}$. Permanent canine teeth develop only a few months after birth, with completion of the crown between 3 and 4 years of age¹⁸. (D) Comparison of the temporal periodicity of Ba/Ca (black line and diamonds) and Li/Ca (red line and Xs) accentuated lines 1, 2, 3 and 4, along the transect (A). Li/Ca recurrence shows a slight temporal offset compared to Ba/Ca periodicity.