

Author Accepted Manuscript

OSF DOI: <https://doi.org/osf.io/8sbwq>

Reference: Joannes-Boyau, R., Adams, J.W., Austin, C., Arora, M., Moffat, I., Herries, A.I.R., Tonge, M., Benazzi, S., Evans, A., Kullmer, O., Wroe, S., Doesseto, A and Fiorenza, L., 2019, *Cyclic elemental signatures suggest nursing adaptations to food stress in Australopithecus africanus*, Nature, 572: 112-115.

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

Authors: Renaud Joannes-Boyau, Justin W. Adams, Christine Austin, Manish Arora, Ian Moffat, Andy I.R. Herries, Matthew P. Tonge, Stefano Benazzi, Alistair R. Evans, Ottmar Kullmer, Stephen Wroe, Anthony Dosseto, Luca Fiorenza

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

3

4

5 AUTHORS

6

7 Renaud Joannes-Boyau^{1*#}, Justin W. Adams^{2,3#}, Christine Austin^{4#}, Manish Arora⁴,
8 Ian Moffat^{5,6}, Andy I.R. Herries^{7,3}, Matthew P. Tonge¹, Stefano Benazzi⁸, Alistair R.
9 Evans⁹, Ottmar Kullmer^{10,11}, Stephen Wroe¹², Anthony Dosseto¹³, Luca Fiorenza^{2,11}

10

11 ¹ Geoarchaeology and Archaeometry Research Group, Southern Cross University,
12 Military Road, Lismore, NSW, 2480

13

14 ² Department of Anatomy and Developmental Biology, Monash University,
15 Melbourne, VIC 3800 Australia

16

17 ³ Palaeo-Research Institute, University of Johannesburg, Auckland Park,
18 Johannesburg 2006, South Africa

19

20 ⁴ Department of Environmental Medicine and Public Health, Icahn School of
21 Medicine at Mount Sinai, New York, NY, 10029, USA

22

23 ⁵ Archaeology, College of Humanities, Arts and Social Sciences, Flinders University,
24 Adelaide, South Australia

25

26 ⁶ McDonald Institute for Archaeological Research, University of Cambridge,
27 Cambridge, UK

28

29 ⁷ Palaeoscience Labs, Dept. Archaeology and History, La Trobe University,
30 Melbourne Campus, Bundoora, 3086, VIC, Australia.

31

32 ⁸ Department of Cultural Heritage, University of Bologna, Via degli Ariani 1, 48121
33 Ravenna, Italy

34

35 ⁹ School of Biological Sciences, Monash University, Melbourne, VIC 3800, Australia;
36 Geosciences, Museums Victoria, Melbourne, VIC 3001, Australia

37

38 ¹⁰ Senckenberg Research Institute and Natural History Museum Frankfurt,
39 Senckenberganlage 25, 60325 Frankfurt am Main, Germany

40

41 ¹¹ Department of Paleobiology and Environment, Institute of Ecology, Evolution, and
42 Diversity, Johann Wolfgang Goethe University, Max-von-Laue-Str. 13, 60438
43 Frankfurt, Germany

44

45 ¹² Function, Evolution and Anatomy Research Laboratory, School of Environmental
46 and Rural Science, University of New England, Armidale, NSW 2351 Australia

47

48 ¹³ Wollongong Isotope Geochronology Laboratory, School of Earth and
49 Environmental Sciences, University of Wollongong, Northfields Avenue,
50 Wollongong, NSW 2522 Australia.

51
52 * Corresponding author
53 # Authors contributed equally

54
55 **Keywords:** *Australopithecus africanus*, nursing, fossil teeth, geochemistry, trace
56 elemental mapping, seasonal food stress.

57 **Running title:** Early-life history of *Australopithecus africanus*

58 **Manuscript information:** 3 figures

59 **Word and character counts:** 262 abstract words, 2156 words in the text not
60 including acknowledgements, references, and figure captions.

61
62 **ABSTRACT**

63
64 Reconstructing the detailed dietary behaviour of fossil hominins is extremely
65 challenging¹, particularly in a species such as *Australopithecus africanus* whereby
66 a highly variable dental morphology suggests a diversity of sustenance^{2,3}. Dietary
67 response to seasonal fluctuations in food availability remains poorly understood,
68 and nursing behaviours are even more cryptic, with most of the direct
69 information being obtained from high-resolution trace element geochemical
70 analysis of *Homo sapiens* (modern and fossil), *Homo neanderthalensis*⁴ and living
71 apes⁵. Here, we apply, for the first time a similar methodology to two 2.6-2.1 Ma
72 *A. africanus* specimens from Sterkfontein Member 4 in South Africa. Elemental
73 signals indicate that the diet of *A. africanus* infants was predominantly breast
74 milk for the first year after birth. Furthermore, a cyclical elemental pattern
75 following the nursing sequence, comparable to the seasonal dietary signal
76 observed in wild primate and non-primate mammals, indicates irregular food
77 availability. These results are also supported by isotopic evidence of a
78 geographical range dominated by nutritionally depauperate areas. A new finding
79 of cyclical lithium accumulation in teeth also supports fluctuating resources and
80 physiological adaptations. This study provides insight into the previously
81 unknown dietary cycles and ecological behaviours of *A. africanus* in response to
82 food availability. This includes the potential cyclical resurgence of milk intake
83 during challenging nutritional times, as observed in wild extant *Pongo*⁵. The new
84 geochemical findings uncovered in ~2.6-2.1 million years old teeth of *A. africanus*
85 reinforce the unique place of the species in the fossil record and indicate dietary
86 stress in specimens that occur not long before the extinction of *Australopithecus*
87 in South Africa at ~2 Ma.

88
89 **MAIN**

90
91 *Australopithecus africanus* is arguably one of the first known hominins to inhabit the
92 South African landscape, living from 3.03-2.61 Ma until sometime between 2.3-2.1
93 Ma⁶. Decades of research on the diet^{7,8,9} and mobility³ of this species has suggested an
94 unusually high degree of dietary variability (which probably included the
95 consumption of fruits, leaves, grasses, sedges and roots) relative to other hominins,
96 that has led to the interpretation that *A. africanus* lived in a complex range of
97 environments, including open grassland and forest⁷. These interpretations are based
98 principally on the broad range of morphology in *A. africanus*, which is tentatively
99 attributed to the potential occurrence of more than one species¹⁰ within Sterkfontein
100 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.

151 1-3, ED Fig. 4 for StS 51). The cyclical signal is clearly visible in all *A. africanus*
152 teeth, with multiple occurrences from cusp to root that follow a pattern associated
153 with tooth growth rather than diagenesis and are consistent across teeth from the same
154 individual. Uranium, a marker of diagenesis, shows a markedly different diffuse
155 pattern that does not follow tooth growth patterns. Although the presence of uranium
156 indicates some post-burial alteration, the Ba, strontium (Sr) and lithium (Li) banding
157 that follows the developmental architecture of dentinogenesis and amelogenesis, and
158 the repetition of the pattern across teeth from the same individual confirm that the
159 observed cyclical patterns are biogenic (*see supplementary discussion & ED Fig. 3 &*
160 *4*). The highly cyclical Ba/Ca pattern observed in permanent teeth from StS 28 and
161 StS 51 indicates a repeated behaviour over time until at least ~4-5 years of age (Fig.
162 1-3, ED Fig. 3 & 4). This pattern is reinforced by Sr/Ca and Li/Ca signals that also
163 occur cyclically along the growth axis of the tooth.

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

188 In general, Sr/Ca banding was clearer across the teeth in *A. africanus* with additional
189 narrow lines that were not observable in the Ba/Ca images (ED Fig. 3 and 4). Yet, the
190 Sr/Ca and Ba/Ca patterns were largely synchronous indicating a common source of
191 exposure (ED Fig. 5 & 6). This is in contrasts with modern human samples that often
192 show asynchronous Ba/Ca and Sr/Ca patterns (ED Fig. 7). Li/Ca banding in teeth
193 from *A. africanus* was less frequent than other elemental patterns but occurred
194 predominantly just before the Ba/Ca intake episodes with the highest amplitudes (Fig.
195 2 & ED Fig. 8). Furthermore, a similar relationship between the two cycles was not
196 observed in other non-primate mammals analysed (ED Fig. 5), but was detected in
197 baboons and modern orangutans⁵. The presence of highly cyclical Ba/Ca and Li/Ca
198 banding in *A. africanus* likely reflects seasonal dietary shifts and perhaps also
199 physiological responses similar to those of modern wild *Pongo*⁵. It appears that *A.*

201 *africanus* was under seasonal food stress and had to adapt to changing resources and
202 food access²⁰. The analysis of the strontium isotope ratio (⁸⁷Sr/⁸⁶Sr) of *A. africanus*
203 from Sterkfontein shows that some specimens principally lived on the dolomite karst,
204 dominated by more open bushland and grassland rather than the closed woodland of
205 surrounding lithologies^{3,10,11}. Our present strontium isotope data (ED Fig. 9) are
206 consistent with both individuals analysed herein having spent the majority of their
207 time in the Malmani Dolomite Subgroup during amelogenesis. This specific
208 geological setting is severely depleted of many nutrients, thereby limiting plant
209 growth⁸.

210
211 Some primate species opportunistically adapted their physiology to cope with
212 seasonal food availability due to specific environmental pressures²¹. Immature
213 baboons in high-altitude environments, a challenging setting for offspring, have been
214 reported to extend nursing cycles, decrease foraging time, wean later and engage in
215 lower-energy activity than lowland *Papio*²¹. Varying milk intake can compensate for
216 periods of extreme and unpredictable oscillations in food availability. This adaptation
217 allows the survival of immature individuals, who are particularly vulnerable to
218 fluctuations in food accessibility because of lower fat reserves and weaker muscle
219 tissues. During periods of abundance, the infant can rely more heavily on solid food,
220 thus allowing the mother to replenish large energetic and calcium reserves to support
221 an increase in lactation during periods of food scarcity. Previous reports suggested
222 that wild *Pongo* (*Pongo abelii* and *Pongo pygmaeus*) females adapted to seasonal
223 variation by increasing the weaning period until a late offspring age of 8-9 years old⁵.
224 This ecological exigency has forced orangutan females to lower their metabolic
225 requirements²⁰, increase their aptitude to rapidly build energetic reserves²² and to
226 catabolise fat reserves and muscle tissue faster during periods of nutrient
227 insufficiency²³. Elemental mapping of a tooth from a captive orangutan receiving a
228 constant supply of food showed a different pattern that lacked the imprints of cyclical
229 dietary intake (ED Fig. 10). Narrow bands of increased Ba and Sr were observed in
230 this animal and attributed to acute stress events²⁴. Intense, narrow Ba and Sr bands
231 were also observed in teeth from *A. africanus*, baboons and other savannah mammals,
232 however, these bands overlap with broader dietary bands indicating a co-occurrence
233 of stress and seasonal dietary changes. The overlap of possible cyclical nursing and a
234 stressful environment due to changing food availability make it difficult to interpret
235 accurately the underlying cause of the banding pattern (ED Fig. 6A).

236
237 Likewise, the Li/Ca banding pattern, also found in modern *Pongo* and baboons (to a
238 lesser extent) but rarely observed in modern *Homo* samples (ED Fig. 7) nor in the
239 non-primate mammals analysed here, suggests complex physiological adaptations to
240 cyclical periods of abundance and starvation. Lithium, while not directly incorporated
241 within the fatty tissues, has been shown to vary in concentration with body mass²⁵.
242 However, the exact relationship between weight gain and Li storage remains unclear
243 with a possible link to psychological factors in modern humans (*supplementary
244 discussion*). Another explanation could be the role of Li in preventing protein
245 deficiency during low caloric intake²⁶. Primates are known to switch to higher-protein
246 fallback foods during low resource seasons to maintain strength^{20,22}. Moreover, Li
247 concentration varies greatly between plants or parts of the same plant and was
248 reported to transfer to breast milk (*supplementary discussion*). While the evidence of
249 an adaptive shift to fall-back resources in *A. africanus* has been questioned^{8,9,27}, the
250 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.

272

273

274

275 FIGURE LEGENDS

276

FIG. 1: Breastfeeding period of *A. africanus*: (A) section of enamel lower canine of StS 51 and associated ¹³⁸Ba/⁴³Ca elemental mapping. (B) section of enamel upper first molar of StS 28 and associated ¹³⁸Ba/⁴³Ca 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 µm/d)^{16,17,18}

285

286

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 ⁷Li/⁴³Ca (B) StS 28 and (C) StS 51 and ¹³⁸Ba/⁴³Ca (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.

295

296

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 ⁷Li/⁴³Ca and (C) ¹³⁸Ba/⁴³Ca. 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

300

301 temporal periodicity of Ba/Ca (black line and diamonds) and Li/Ca (red line and Xs)
302 accentuated lines 1, 2, 3 and 4, along the transect (A). Li/Ca recurrence shows a slight
303 temporal offset compared to Ba/Ca periodicity.

306 REFERENCES

- 308 1. Balter, V., Braga, J., Télouk, P. & Thackeray, JF. Evidence for dietary change
309 but not landscape use in South African early hominins. *Nature* **489**, 558-562
310 (2012).
- 312 2. Ungar, P.S. & Sponheimer, M. The Diets of Early Hominins. *Science* **334**,
313 190-3 (2011).
- 315 3. Copeland, S. R. *et al.* Strontium isotope evidence for landscape use by early
316 hominins. *Nature* **474**, 76–78 (2011).
- 318 4. Austin, C. *et al.* Barium distributions in teeth reveal early-life dietary
319 transitions in primates. *Nature* **498**, 216–219 (2013).
- 321 5. Smith, T.M., Austin, C., Hinde, K., Vogel, E.R. & Arora, M. Cyclical nursing
322 patterns in wild orang-utans. *Science Advances* **3** (5), e1601517 (2017).
- 324 6. Herries, A.I.R. *et al.*, 2013. *A multi-disciplinary perspective on the age of*
325 *Australopithecus in southern Africa*. In: Reed, K.E., Fleagle, J.G., Leakey, R.
326 (Eds.) *Paleobiology of Australopithecus*. *Vertebrate Paleobiology and*
327 *Paleoanthropology series*. 21-40. (2013)
- 329 7. Peterson, A., Abella, E.F., Grine, F.E., Teaford, M.F. & Ungar, P.S.
330 Microwear textures of *Australopithecus africanus* and *Paranthropus robustus*
331 molars in relation to paleoenvironment and diet. *J Hum Evol.* **119**, 42-63
332 (2018).
- 334 8. Sponheimer, M. & Lee-Thorp, J.A. Isotopic evidence for the diet of an early
335 hominid, *Australopithecus africanus*. *Science* **283** (5400), 368-70 (1999).
- 337 9. Strait, D. S. *et al.* The feeding biomechanics and dietary ecology of
338 *Australopithecus africanus*. *Proc. Natl Acad. Sci. USA* **106** (7), 2124-2129
339 (2009).
- 341 10. Dupont, L.M., Donner, B., Vidal, L., Pérez, E.M. & Wefer, G. Linking desert
342 evolution and coastal upwelling: pliocene climate change in Namibia. *Geology*
343 **33**, 461-464 (2005).
- 345 11. Pickering, R. & Herries, A.I.R. *A new multidisciplinary age of 2.61 – 2.07 Ma*
346 *for the Sterkfontein Member 4 Australopiths*. In: Ward CV, Zipfel B, editors.
347 Hominin postcranial remains from Sterkfontein, South Africa. Oxford: Oxford
348 University. (2018).

- 350 **12.** Clarke R. *Australopithecus from Sterkfontein Caves, South Africa*. In: Reed
351 K., Fleagle J., Leakey R. (eds) *The Paleobiology of Australopithecus*.
352 Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht
353 (2013).
- 354
- 355 **13.** Ecker, M., Brink, J., Kolska-Horwitz, L., Scott, L., Lee-Thorp, J.A. A 12,000
356 years record of changes in herbivore niche separation and palaeoclimate
357 (Wonderwerk Cave, South Africa). *Quaternary Science Reviews* **180**, 132-144
358 (2018).
- 359
- 360 **14.** Caley, T., Extier, T., Collins, JA., Schefuß, E., Dupont, LM., et al. A two-
361 million-year-long hydroclimatic context for hominin evolution in southeastern
362 Africa. *Nature* **560**, 76-79 (2018).
- 363
- 364 **15.** Shorrocks, B. *The biology of African savannas*. New York: Oxford
365 University Press (2007)
- 366
- 367 **16.** Krachler, M., Rossipal, E. & Micetic-turk, D. Concentrations of trace elements
368 in sera of newborns, young infants, and adults. *Biol. Trace Elem. Res.* **68**,
369 121–135 (1999).
- 370
- 371 **17.** Bouhallab, S. & Bougle, D. Biopeptides of milk: caseinophosphopeptides and
372 mineral bioavailability. *Reprod. Nutr. Dev.* **44**, 493-498 (2004).
- 373
- 374 **18.** Smith TM, Tafforeau P, Le Cabec A, Bonnin A, Houssaye A, Pouech J, et al.
375 (2015) Dental Ontogeny in Pliocene and Early Pleistocene Hominins. PLoS
376 ONE **10** (2): e0118118.
- 377
- 378 **19.** Lacruz, R.S., Dean, M.C., Ramirez-Rozzi, F., Bromage, T.G. Megadontia,
379 striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil
380 hominins. *J Anat* 213: 148–158. (2008).
- 381
- 382 **20.** Pontzer, H., Raichlen, D. A., Shumaker, R. W., Ocobock, C. & Wich, S. A.
383 Metabolic adaptation for low energy throughput in orangutans. *Proc. Natl
384 Acad. Sci. USA* **107**, 14048–1405 (2010).
- 385
- 386 **21.** van Noordwijk, M.A., Willemse, E.P., Utami Atmoko, S.S., Kuzawa, C.W. &
387 van Schaik, C.P. Multi-year lactation and its consequences in Bornean
388 orangutans (*Pongo pygmaeus*). *Behav. Ecol. Sociobiol.* **67**, 805–814 (2013).
- 389
- 390 **22.** Vogel, E. *et al.* Bornean orangutans on the brink of protein bankruptcy. *Biol.
391 Lett.* **8**, 333–336 (2012).
- 392
- 393 **23.** Harrison, M.E., Morrogh-Bernard, H.C. & Chivers, D.J. Orangutan energetics
394 and the influence of fruit availability in the nonmasting peat-swamp forest of
395 Sabangau, Indonesian Borneo. *Int. J. Primatol.* **31**, 585–607 (2010).
- 396
- 397 **24.** Austin, C., Smith, T.M., Farahani, R., Hinde, K., Carter, E., Lee, J., et al.
398 Uncovering system-specific stress signatures in primate teeth with
399 multimodal imaging. *Scientific Reports* **6**, 18802 (2016).

- 400
401 **25.** Gitlin, M. Lithium side effects and toxicity: prevalence and management
402 strategies. *Int J Bipolar Disord.* **4** (1), 27 (2016).
403
404 **26.** Tandon, A., Bhalla, P., Nagpaul, J.P., & Dhawan, D.K. Effect of lithium on rat
405 cerebrum under different dietary protein regimens. *Drug Chem Toxicol.*
406 **29**(4):333-44 (2006).
407
408 **27.** Wood, B. & Schroer, K. Reconstructing the diet of an extinct hominin taxon:
409 the role of extant primate models. *Int J Primatol.* **33**, 716–742 (2012).
410
411 **28.** Potts, R. Paleoenvironmental basis of cognitive evolution in great apes. *Am. J.*
412 *Primatol.* **62**, 209–228 (2004).
413
414 **29.** Guatelli-Steinberg, D. Macroscopic and microscopic analyses of linear enamel
415 hypoplasia in Plio-Pleistocene South African hominins with respect to aspects
416 of enamel development and morphology. *Am J Phys Anthropol.* **120** (4), 309-
417 22 (2003).
418
419 **30.** Kennedy, G.E. From the ape's dilemma to the weanling's dilemma: early
420 weaning and its evolutionary context. *J Hum Evol.* **48**, 123-145 (2005).
421
422

423 **Supplementary Information** is available in the online version of the paper.
424

425 **Acknowledgments** Part of this study was funded by Monash University seed grant to
426 LF, JWA, ARE, AIRH, SW, SB, OK and RJB. AIRH, JWA and RJB received
427 funding by the Australian Research Council Discovery Grant DP170100056. CA is
428 supported by NICHD award R00HD087523. IM is supported by an Australian
429 Research Council DECRA Fellowship (DE160100703), a Commonwealth Rutherford
430 Fellowship from the Commonwealth Scholarship Commission and a Research
431 Associate position from Homerton College. MA is supported by US National
432 Institutes of Environmental Health Grants 4R00ES019597 and 1DP2ES025453. We
433 would like to thank the South African Heritage Resources Agency (SAHRA), Dr
434 Bernhard Zipfel from the Evolutionary Studies Institute of the University of
435 Witwatersrand and Dr Mirriam Tawane from the Ditsong National Museum of
436 Natural History for granting the export permit of the valuable samples for analyses.
437 We would also like to thank Caroline Lawrence and Kate Simon-Menasse from Perth
438 Zoo who provided access to modern orangutan dental material. We also would like to
439 express our gratitude to Dr Kai Schultz for valuable comments on this manuscript.
440 The authors declare no competing interests.
441
442

443 **Author contributions** RJB, JWA, CA, IM, MA, AIRH, LF, SB, ARE, OK and SW
444 selected the sample, designed the project, and/or received funding for the research.
445 RJB, CA and IM conceived and designed the experiments. RJB, CA, IM, MPT and
446 AD conducted the analytical campaign on the different instruments and interpreted
447 the data. RJB prepared the figures and wrote the manuscript, with extensive
448 contribution from CA, MA, IM, LF, AIRH, JWA, MPT, SB, ARE, OK, AD and SW.
449

450 **Author Information** Reprints and permissions information is available at
451 www.nature.com/reprints. The authors declare no competing financial interests.
452 Readers are welcome to comment on the online version of the paper. Publisher's note:
453 Springer Nature remains neutral with regard to jurisdictional claims in published
454 maps and institutional affiliations. Correspondence and requests for materials should
455 be addressed to R. J-B (renaud.joannes-boyau@scu.edu.au)

456

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

459

460

461 EXTENDED DATA

462

463 **Extended data Figure 1 - The Sterkfontein surface excavation and fossil teeth**
464 **specimen.** Plan view of the Sterkfontein surface excavation adapted from Kuman, K.,
465 and Clark, R. J. ³⁵, showing the association between the Type Site excavation and
466 Member 4 deposits. (B) Photo of fossil teeth specimen StS 28; (C) upper first molar
467 (M1) StS 28B; (D) permanent lower first molar (M1) StS 28C after being sectioned in
468 two with a diamond low speed high precision rotary saw. (E) Photo of fossil teeth
469 specimen StS 51; (F) permanent premolar (P3) StS 51A; (G) permanent canine (LC)
470 StS 51B after being sectioned in two with a diamond low speed high precision rotary
471 saw. The two teeth still embedded in the breccia were not sectioned.

472

473 **Extended data Figure 2 - Elemental mapping by LA-ICPMS protocol:** (A) Sketch
474 of a fossil *Pongo sp.* second molar tooth dentine and enamel section with indication of
475 biogenic accentuated lines (green); Elemental mapping of both dental tissues using
476 laser ablation-inductively coupled plasma-mass spectrometry shows (B) strontium
477 distribution following the incremental growth pattern of the tooth, typical of biogenic
478 signals, contrary to post-mortem diagenetic processes (C) (uranium diffusion during
479 burial).

480

481 **Extended data Figure 3 - Elemental mapping of *A. africanus* StS 28.** Elemental
482 mapping of (top) upper first molar cusp (StS 28B); and (middle and bottom) lower
483 first molar (StS 28C) showing records of cyclical banding between 0 and 7 years at
484 crown completion. The broad repeated banding pattern is attributed to seasonal
485 dietary shifts and potentially to cyclical nursing during long weaning periods. The
486 identical elemental banding pattern found in both StS 28B and StS 28C first
487 permanent molars confirm beyond any doubt the biogenic nature of the signal
488 observed (compare B, C and D with G, H and I respectively). The typical patchy and
489 spreading diffusion pathways of uranium in the dentine and the enamel can be
490 observed (E, J, O) with characteristic accumulation or depletion in cracks and at the
491 enamel-dentine junction, very different to the biogenic Li, Sr and Ba banding.

492

493 **Extended data Figure 4 - Elemental mapping of *A. africanus* StS 51.** Elemental
494 mapping of (A) permanent premolar (StS 51A) (B) Li/Ca banding, (C) Sr/Ca banding,
495 (D) Ba/Ca banding and (E) U/Ca diffusion; (F) permanent canine (StS 51B) (G) Li/Ca
496 banding, (H) Sr/Ca banding, (I) Ba/Ca banding and (J) U/Ca diffusion; The strontium
497 signal shows additional discreet lines most likely associated stress episodes compared
498 to Li/Ca and Ba/Ca. Uranium distribution shows a typical and rather uniform
499 diffusion pattern with enrichment close to the EDJ and in fractures and cracks.

500

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.

515

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.

531

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.

541

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.

549

550 **Extended data Figure 9 - Strontium isotopic ratio distribution:** Location of the
551 laser ablation spot (150 microns) along the enamel and dentine for StS 51A (A) and
552 StS 28C (B). Circles with red filling correspond to the first point (1) and yellow filling
553 to the last point (9 for enamel and 6 for dentine). The table below shows the $^{87}\text{Sr}/^{86}\text{Sr}$
554 isotopic ratio and associated errors for each laser ablation spot measured above. All
555 values measured in both teeth (including Dentine 6 of StS 28 with associated error)
556 correspond to the Malmani dolomite values surrounding Sterkfontein ($^{87}\text{Sr}/^{86}\text{Sr}$ 0.723
557 < Malmani dolomite < 0.734)³, showing limited mobility for both specimens.
558

559 **Extended data Figure 10 - Permanent second molar of a modern *Pongo* specimen**
560 **from the Perth Zoo.** The animal was born in captivity in 1975 in the Singapore Zoo,
561 and join the Perth zoo later still as an immature individual. There appears to be no
562 Ba/Ca banding pattern indicating cyclical milk consumption during crown
563 completion. The captive orangutan Hsing Hsing, was born in captivity in 1975 at
564 Singapore Zoo and was parent raised (although additional human feeding cannot be
565 definitively excluded) before being relocated to Perth Zoo in 1983. His diet would
566 have been significantly different to orangutans living in the wild, with limited
567 seasonal influence and no periods of food scarcity. It is expected that the animal and
568 his parents would have had abundant and guaranteed access to food, which would
569 likely have led the specimen to be prematurely weaned compare to wild *Pongo*. On
570 this basis, it is unlikely that Hsing Hsing would have had recurrent breastfeeding
571 cycles and therefore the absence of Ba banding in this specimen is expected. The
572 discreet banding observed for the Sr/Ca and the two Ba/Ca are likely stress related
573 accentuated lines. No clear banding was observed in the enamel of this specimen.
574
575
576
577
578
579
580
581

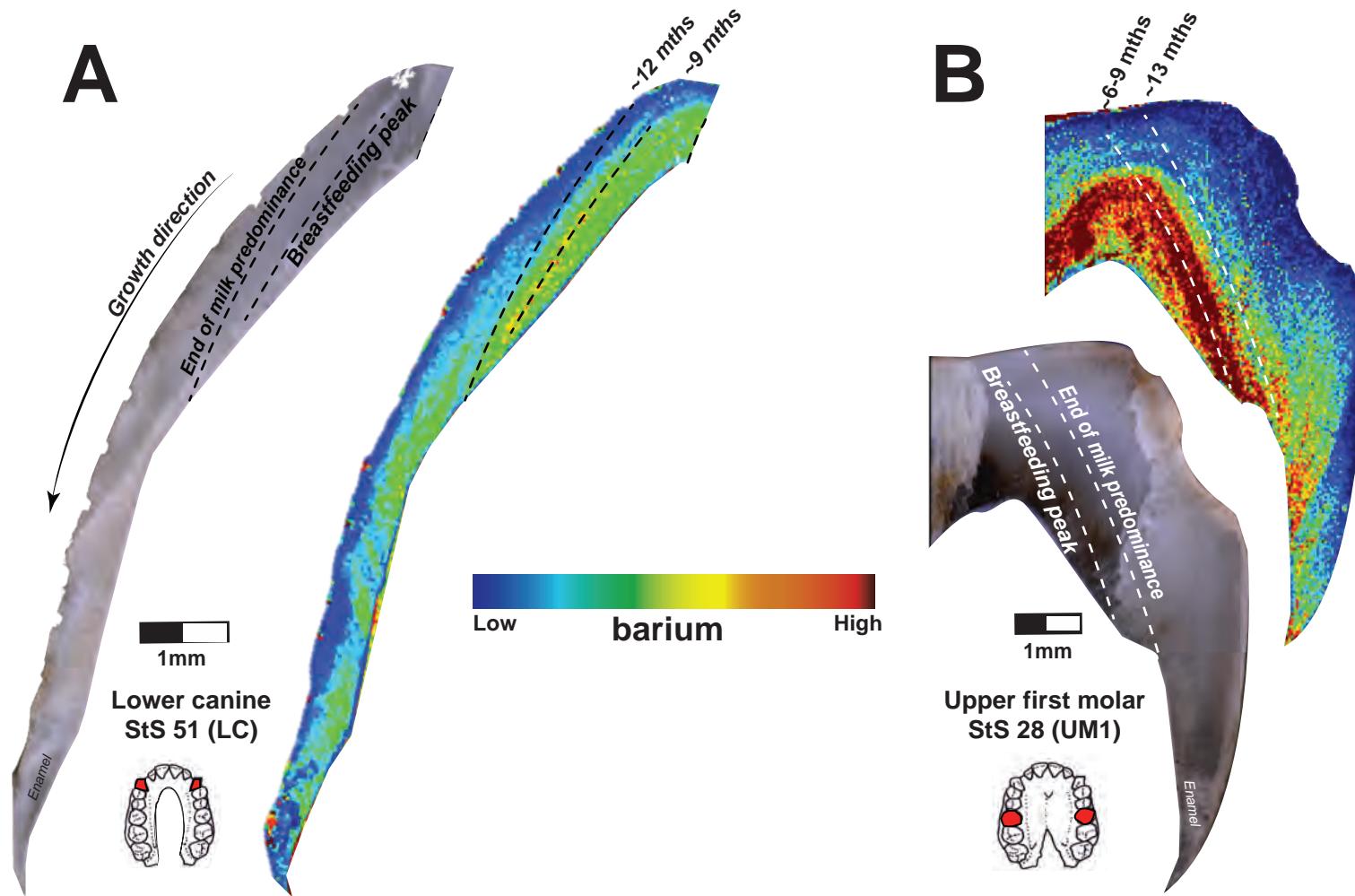


Figure 1: Joannes-Boyau et al.,

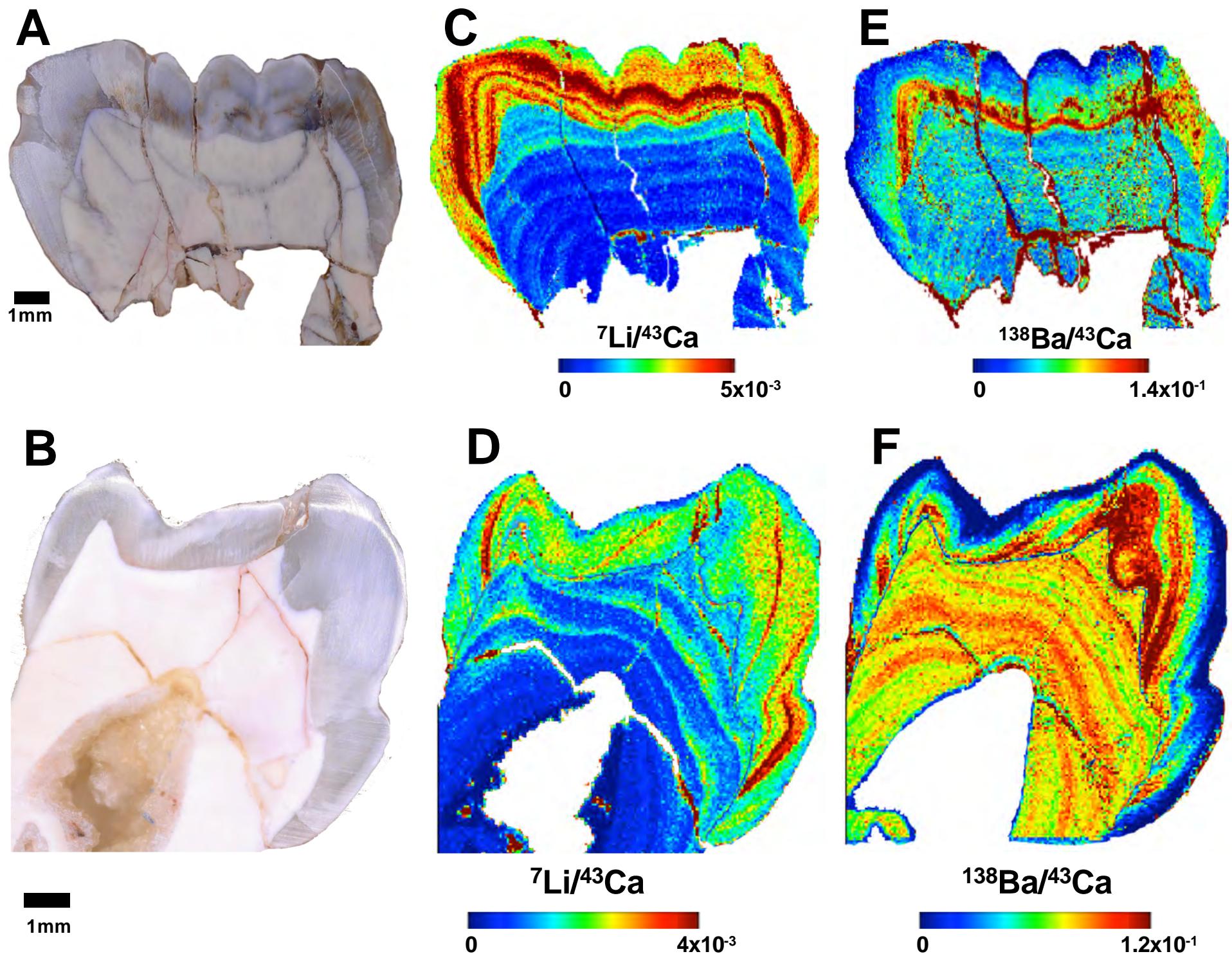


Figure 2: Joannes-Boyau et al.,

