

1 **Dietary strategies of Pleistocene *Pongo* sp. and *Homo erectus* on Java (Indonesia)**

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27 **During the Early to Middle Pleistocene, Java was inhabited by hominid taxa of great diversity.**
28 **However, their seasonal dietary strategies have never been explored. We undertook the first**

29 **geochemical analyses of *Pongo* sp., *Homo erectus* and other mammalian Pleistocene teeth**
30 **from Sangiran. We reconstructed past dietary strategies at sub-weekly resolution and**
31 **inferred seasonal ecological patterns. Histologically-controlled spatially-resolved elemental**
32 **analyses by laser-based plasma mass spectrometry (LA-ICPMS) confirmed the preservation**
33 **of authentic biogenic signals despite the effect of spatially-restricted diagenetic overprint.**
34 **The Sr/Ca record of faunal remains is in line with expected trophic positions, contextualizing**
35 **fossil hominid diet. *Pongo* sp. displays marked seasonal cycles with ~3-month-long strongly**
36 **elevated Sr/Ca peaks, reflecting contrasting plant food consumption presumably during the**
37 **monsoon season, while lower Sr/Ca ratios suggest different food availability during the dry**
38 **season. In contrast, omnivorous *Homo erectus* shows low and less accentuated intra-annual**
39 **Sr/Ca variability compared to *Pongo* sp., with $\delta^{13}\text{C}$ data of one individual indicating dietary**
40 **adaptation from C₃ to C₄ plants through its lifetime. Our data suggest that *Homo erectus* on**
41 **Java was maximizing the resources available in more open mosaic habitats and was less**
42 **dependent on variations in seasonal resource availability. While still affected by seasonal**
43 **food availability, we infer that *Homo erectus* was affected to a lesser degree than *Pongo* sp.,**
44 **which inhabited monsoonal rainforests on Java. We suggest that *Homo erectus* maintained**
45 **a greater degree of nutritional independence by exploiting the regional diversity of food**
46 **resources across the seasons.**

47

48 The Pleistocene hominid fossil record from the Sangiran Dome in Central Java, Indonesia, is one of
49 the largest palaeoanthropological collections in Southeast Asia, evidencing an Early Pleistocene
50 expansion of *Homo erectus* onto the Sunda Shelf¹⁻⁴. The high morphodimensional variability of
51 Indonesian hominid specimens led in the past to the attribution of the fossils to a variety of taxa such
52 as *Homo erectus*, *Meganthropus palaeojavanicus*, *Pithecanthropus dubius* or *Pongo* sp. fuelled
53 taxonomic debates^{1,5-9}. Recently, a high level of Javanese hominid palaeodiversity was revealed,
54 which confirmed the taxonomic validity of the genus *Meganthropus*, a taxon that coexisted with *H.*
55 *erectus* and *Pongo*¹⁰. Although dental macrowear and enamel thickness broadly reflect different
56 dietary adaptations among these hominids¹⁰, little is known about their life history and ecological

57 niches. We used laser-based mass spectrometry to retrieve time-resolved information about dietary
58 diversity throughout the lives of individual early hominins from their dental enamel, in conjunction
59 with stable isotope analysis.

60 For decades, these geochemical analyses – primarily $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements – of tooth
61 enamel have been successfully used to retrieve palaeoenvironment, palaeodiet and life history
62 information of extinct hominins such as *Australopithecus*^{11,12}, *Paranthropus*¹¹ Wynn et al., 2020), and
63 Neanderthals^{13,14}. Nevertheless, many hominin species such as *Homo erectus* have not yet been
64 investigated. Consequently, we explored for the first time Sr/Ca and Ba/Ca ratios and other trace
65 element signals at high spatial/time-resolution in the dental enamel of premolars and molars, to
66 assess dietary and life history signals in Pleistocene *H. erectus* and *Pongo* sp. from the Sangiran
67 Dome. Tooth enamel – contrary to bone and dentine – is less prone to post-mortem diagenetic
68 alteration due to its highly mineralized nature^{15,16}. Moreover, it mineralizes sequentially *in utero* and
69 during infancy to early adolescence and, once fully mineralized, remains compositionally and
70 structurally stable during life. Consequently, enamel captures and preserves environmental and
71 dietary changes that occur during the enamel mineralization phases in an individual's life^{17–20}. The
72 incremental nature of tooth growth allows us to resolve shifts in chemistry that relate directly to life
73 history at near (sub) weekly resolution. Moreover, tooth tissues in themselves contain information of
74 potential taxonomic value. The longer period rhythms in dental enamel (striae of Retzius periodicity)
75 have been used to infer taxonomic affinity in certain Far Eastern fossil specimens. Indeed, elemental
76 and isotopic analysis by laser-ablation inductively-coupled-plasma mass spectrometry (LA-ICPMS)
77 across the incremental structures of sequentially secreted enamel provides a temporally and
78 spatially highly-resolved record of an individual's childhood. Such data allow the interpretation of
79 diet, health, growth rates, weaning, and mobility as well as changes of the environmental setting on
80 a seasonal to weekly scale^{13,14,21–23}. Trace element ratios strontium/calcium (Sr/Ca) and
81 barium/calcium (Ba/Ca) in dental enamel can record dietary signals due to the biopurification of Ca
82 in trophic chains^{24–26}. The higher the trophic level, the less [Sr] and [Ba] relative to [Ca] are
83 incorporated into enamel, resulting in higher values of trace element ratios in herbivore enamel than
84 that of omnivores or carnivores^{11,24,27}, though additional factors such as soil ingestion play a role²⁸.

85 For comparison and as a trophic level reference for the Sangiran hominids, we utilized isolated
86 premolars and molars of mammalian specimens belonging to different families (Felidae,
87 Rhinocerotidae, Suidae, Cervidae, Hippopotamidae; Table 1) from the Sangiran fossil assemblage
88 presumably co-existing with various hominid taxa such as *H. erectus*, *Meganthropus* and
89 *Pongo*^{10,29,30}.

90 All specimens were recovered from either the Early Pleistocene Sangiran Formation, or from the
91 later Early to initial Middle Pleistocene Bapang Formation, as both are fossiliferous and contain
92 distinct faunal assemblages and taxa^{4,31,32}. However, the *exact* stratigraphic allocation of all
93 specimens is not documented^{2,32}. The geological age of the specimens range between 1.4 to 1.0 Ma
94 and 1.0 to 0.7 Ma for specimens from the Sangiran and Bapang Formations, respectively⁴.

95 We focused our study on Sr/Ca (and to a lesser extent Ba/Ca) ratios as (relative) trophic level
96 proxies, including an assessment of how well biogenic geochemical information is preserved in
97 Pleistocene bioapatite from (sub)tropical contexts by utilizing elements Mn, Al, Y, Ce, U as tracers
98 of post-mortem alteration^{14,27,28,33-37}. Previous stable isotope analyses of *H. erectus* bone samples
99 from Sangiran were not successful in obtaining palaeoecological signals due to diagenetic alteration
100 of bone tissue³⁸. Here we include sequentially-microsampled carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$)
101 isotope analyses of dental enamel of one *H. erectus* permanent premolar (S7-37) in order to
102 contextualize our elemental results and obtain additional dietary/environmental information.

103

104 **Results**

105 In Table 2 we report Retzius periodicity (RP), laser track length and the corresponding time-span for
106 the analyzed samples. The RP of *Pongo* sp. SMF-8864 was obtained through direct counts of cross
107 striations between two adjacent Retzius lines. The RP of *Homo erectus* SMF-8865, given the section
108 thickness necessary for chemical analyses and the presence of some accentuated markings, was
109 calculated as the distance between adjacent Retzius lines divided by local daily secretion rate (DSR);
110 the latter directly measured in areas of the section where the cross striations were clearly visible.

111 For *Homo erectus* S7-37 P⁴, we report the RP calculated in¹⁸ for the S7-37 M¹ belonging to the same
112 individual.

113 Elemental signals were retrieved within enamel close to the enamel-dentine-junction (EDJ; <100
114 μm) because it is where environmental signals are best captured topographically during secretion
115 and elemental overprint during enamel maturation has the least effect^{14,22,39–41}. For assessing post-
116 mortem diagenetic overprint, scatterplots of [Sr] or [Ba] vs. [Mn] or [U] at EDJ profiles of
117 representative samples of each trophic level were generated (Fig. 1 and Supplementary Fig. 1). All
118 cases show clearly positive correlations between trace elements and diagenesis-indicating element
119 concentrations. Even though multi-stage diagenetic histories may be indicated by different
120 trajectories (Fig. 1), uptake of Sr and Ba with increasing geochemical alteration is evident, which
121 implies that the best approximations of initial biogenic [Sr] or [Ba] (or expressed as Sr/Ca, Ba/Ca
122 ratios) can be found at lowest [Mn] or [U]. These plots also reveal that [Sr] increases by a maximum
123 of ~180%, while [Ba] is characterized by a threefold to tenfold increase, confirming the higher
124 susceptibility of Ba to post-mortem overprint. Repeat profiles at the EDJs of both tooth aspects and
125 along prism directions indicate greater consistency between corresponding Sr/Ca profiles, relative
126 to those of Ba/Ca (Supplementary Figs. 2-6). Using [Mn] and [U] thresholds of 400 and 1 ppm,
127 respectively, to screen Sr/Ca and Ba/Ca trophic level signals, revealed expected patterns for trophic
128 groups for Sr/Ca, but more ambiguous ones for Ba/Ca (Fig. 2; Supplementary Fig. 7). As a result,
129 we focus more on Sr/Ca results but also note that Ba/Ca can indicate reliable results in case of well-
130 preserved samples (e. g., *Pongo* SMF-8864, see below).

131 The Sr/Ca ratio boxplots of faunal and hominid specimens (Fig. 2) show carnivorous Felidae with
132 the lowest Sr/Ca ratio in the faunal assemblage ($\sim 8.4 \cdot 10^{-4}$), following the expected trophic level trend
133 towards lower Sr/Ca ratios relative to omnivores ($\sim 1.1 \cdot 10^{-3}$; represented by Suidae) and different
134 herbivore groups ($1.6 \cdot 10^{-3} - 4.0 \cdot 10^{-3}$). Rhinocerotidae exhibit a Sr/Ca level ~2 times higher than all
135 other herbivores and a broad Sr/Ca variability. The three *H. erectus* dental specimens yield Sr/Ca
136 ratios between those of the Felidae and Suidae. The *Pongo* sp. specimen SMF-8864 shows the
137 largest variation in Sr/Ca distribution among all taxa and has a large number of distributional outliers
138 toward higher Sr/Ca values (Fig. 2). Its median value fits well within the Hippopotamidae and

139 Cervidae central distributions. The peculiar distribution of Sr/Ca values in *Pongo* sp. SMF-8864 is
140 the result of distinct biogenic Sr/Ca peaks throughout the life of this individual and not of diagenetic
141 origin, as shown by the diagenetic indicators (see below).

142 The elemental ratio profiles in hominid tooth enamel were aligned with the individual
143 odontochronologies (see Figs. 3 and 4; Supplementary Figs. 2-6) on both lingual and buccal aspects
144 (except for S7-37 P⁴ where only the buccal aspect was available for analysis) to derive Sr/Ca (and
145 Ba/Ca) variation vs. time (secretion-days). Only for S7-37 P⁴ the life time referred to birth is available
146 following⁴² but not for molars with uncertain position such as S7-13, SMF-8864, SMF-8865, although
147 we tentatively attribute molar positions based on some diagnostic morphological features described
148 in the Supplementary Information and corresponding chemical signals. Figure 3a shows the Sr/Ca
149 and Ba/Ca EDJ profiles together with diagenesis-indicating [U] and [Mn] against time for the 1073
150 days (~2 years and 11 months) of the buccal aspect of the *Pongo* sp. SMF-8864 molar. EDJ (Fig.
151 3a) and corresponding prisms (P; Fig. 3b and Supplementary Fig. 4) Sr/Ca profiles for the buccal
152 enamel show good agreement but along the prisms invariably lower Sr/Ca values towards outer
153 enamel (Fig. 3b), as expected by the effect of maturation overprint²². The buccal and lingual Sr/Ca
154 EDJ profiles of *Pongo* sp. SMF-8864 are compared in Fig. 3c to assess the reproducibility of in-vivo
155 elemental signals. The time span covered by the lingual aspect is 1339 days (~3 years and 8 months;
156 Fig. 3c). Generally, [Mn] and [U] on both sides of the crown are at detection limit, with [U] rising to a
157 maximum of ~2 ppm for the final ~100 days of thin cervical enamel. Neither Sr/Ca nor Ba/Ca ratios
158 are strongly affected by these minor [U] increases confirming the biogenic nature of the signal; yet
159 we note that some smaller Ba/Ca-peaks co-occur with minor U-peaks (e.g., ~930 days; Fig. 3a).

160 The consistency of the chronologies is attested by the high correspondence of the Sr/Ca signals
161 between the two EDJ and prisms profiles. *Pongo* sp. SMF-8864 exhibits stark intra-tooth variability
162 with three distinct peaks characterized by up to sixfold Sr/Ca and ~eightfold Ba/Ca increases. This
163 sixfold Sr/Ca change for the first peak ($1.8 \cdot 10^{-3}$ to $10.7 \cdot 10^{-3}$) decreases for the second and third
164 peaks to threefold and twofold values, respectively. The influence of the Sr/Ca attenuation along
165 prisms towards outer enamel²² is discernible but partly compensated for in e. g. prism 3 by the strong
166 biogenic signal (Fig. 3b). On the buccal side, three hypoplastic defects and four accentuated lines

167 (AL) are present (Fig. 3c), yet these non-specific growth disturbances⁴² are not coincident with the
168 Sr/Ca (or Ba/Ca) trends. The interval between the midpoints of two consecutive peaks on the buccal
169 aspect approximates one year, namely 364 and 324 days between peaks 1₋2 and peaks 2₋3,
170 respectively. The duration of these peaks is 95, 118 and 90 relative days for the first, second and
171 third peak, respectively, approximating an overall duration of three months each.

172 The Sr/Ca-profiles of the three *H. erectus* samples display low [U] and [Mn] and thus acceptable
173 preservation, apart from localized peaks indicating spatially-restricted diagenetic alteration (Fig. 4).
174 Comparative elemental profiles for the lingual and buccal aspects of two *H. erectus* specimens
175 presented in Supplementary Figures 2 and 3 illustrate that enamel of the same tooth may be variably
176 preserved yet we utilized the better preserved domains. Limited inter-sample Sr/Ca-variation ranges
177 between $0.7 \text{ -- } 1.4 \cdot 10^{-3}$, while intra-profile Sr/Ca-variability is 20 -- 30%. These *H. erectus* Sr/Ca-
178 values are thus always below those in *Pongo* sp. SMF-8864, which is even more pronounced for the
179 intra-sample variability (20 -- 30 vs. 200 -- 600%). The temporal spacing between broad Sr/Ca
180 troughs and/or peaks in all samples lies between 340 -- 380 days, consistent with approximately
181 annual cyclicity. As it is uncertain which of the apparent minor Sr/Ca fluctuations are indicative of
182 variable food intake or minor cryptic diagenetic overprint, we refrain from attributing unwarranted
183 importance to small-scale variability. Despite the uncertain molar position for *H. erectus* SMF-8865,
184 the stability of the Sr/Ca ratio in the first 220 days of tooth formation suggests the absence of the
185 breastfeeding signal^{14,22}. Therefore, the tooth likely is not a first permanent molar, which starts to
186 form earlier in life.

187 We report sequentially-microsampled stable carbon and oxygen isotope compositions of enamel
188 derived from *H. erectus* S7-37 P⁴ ($n = 3$; Fig. 5; Supplementary Table 1). The samples correspond
189 to three distinct portions of the dental crown representing three partially overlapping life time
190 moments. $\delta^{13}\text{C}$ values range from -4.9 to -2.4 ‰ (average = -3.9 ± 1.4 ‰ (1s)), suggesting a diet
191 which ranged from a mixed C₃/C₄ plant consumption to dominated C₄ plant consumption (54 to 72
192 % C₄ fraction in the diet, calculated after⁴³). $\delta^{18}\text{O}$ values remain stable with only very little variation
193 between -6.7 and -5.9 ‰ (average = -6.3 ± 0.4 ‰).

195 **Discussion**

196 **Hominid Retzius periodicity.** Retzius periodicities of 7 to 9 days for our sample of *H. erectus* teeth
197 are typical of these Pleistocene hominins. They are similar to the periodicities reported previously
198 for *Homo erectus/ergaster* molars and premolars (7-8 and 9 days, respectively)⁴⁴, but this apparent
199 tighter distribution of values differs from the wider range of periodicities between 6 to 12 days
200 characteristic of larger samples of living humans⁴⁵. An 8-day periodicity for the *Pongo* sp. lower molar
201 SMF-8864 is slightly lower than the 9 to 12-day periodicity reported for fossil *Pongo* from Sumatra
202 and mainland Asia⁴⁶ but lies within the range of values (8–11 days) reported for living *Pongo*⁴⁷.

203

204 **Hominid trophic levels at Sangiran.** Trophic levels portray the relative position of species in a food
205 web and are important for ecosystem functioning⁴⁸. Fossil teeth of Carnivora (Felidae),
206 Perissodactyla (Rhinocerotidae), and Artiodactyla (Suidae, Cervidae, Hippopotamidae) from the
207 Sangiran Dome with known trophic levels were used to establish an underlying relative trophic level
208 framework for Sangiran. The ordering of fossil faunal taxa from Sangiran according to their enamel
209 Sr/Ca ratios ($Sr/Ca_{\text{carnivores}} < Sr/Ca_{\text{omnivores}} < Sr/Ca_{\text{herbivores}}$) reflects trophic level differences that are in
210 good agreement with their expected dietary habits (Fig. 2)^{11,49}, suggesting reliable trophic level
211 determination based on enamel Sr/Ca.

212 The *Pongo* sp. lower molar SMF-8864 exhibits a high intra-tooth variability, caused by cyclical Sr/Ca
213 peaks (Fig. 3) along the EDJ profile covering the whole range of other herbivorous specimens in this
214 study. The average Sr/Ca ratios between the peaks is closer to the Sr/Ca ratio of herbivorous
215 animals such as *Hexaprotodon* sp. and *Axis lydekkeri*^{50–53}. The maximum Sr/Ca values for the first
216 and second peaks are exceeding those of the rhinocerotids (for whom soil or dust ingestion might
217 additionally lead to elevated Sr/Ca)²⁸. The lowest Sr/Ca values in SMF-8864 overlap with those of
218 suids and with the higher values of felids. This fits well with the known versatile diet of living
219 orangutans, which includes fruits, flowers, bark, insects, eggs and occasionally meat^{54,55}. The *H.*

220 *erectus* lower molar SMF-8865 shows Sr/Ca ratios similar to *H. erectus* individuals S7-13 and S7-
221 37. All *H. erectus* specimens in this study group with omnivorous (Suidae) and carnivorous (Felidae)
222 mammals from Sangiran (Fig. 2), suggesting an omnivorous diet with a certain degree of meat
223 consumption for *H. erectus* on Java.

224

225 **Comparison of Sr/Ca patterns in *Homo erectus* and *Pongo* sp.** The biogenic Sr/Ca peaks in
226 *Pongo* sp. SMF-8864 occur nearly annually (Fig. 3). The Sr/Ca variation in *H. erectus* SMF-8865
227 also shows cyclical pattern: the duration of the cycle is approximately 345 days. *H. erectus* S7-13
228 shows a complete cycle of 347 days and a partial cycle of 148 days. The preserved portion of the
229 crown ends before the end of the cycle. *H. erectus* S7-37 also shows two cycles with a duration of
230 375 relative days and 383 relative days. The second cycle is marked by two smaller Sr/Ca decreases
231 within the cycle. Uranium does not follow the annual cycle trend in any of the samples, thus
232 suggesting negligible influence of diagenetic imprint (Fig. 4a-c). In summary, all *H. erectus*
233 individuals demonstrate low-amplitude Sr/Ca cycles with a duration of approximately one year,
234 whereas *Pongo* sp. SMF-8864 demonstrates two cycles with sharp peaks that last 3–4 months.

235

236 **Diet of *Pongo* sp. reflects high seasonal food variability.** The cyclical pattern of Sr/Ca and Ba/Ca
237 peaks in *Pongo* sp. SMF-8864 with higher ratios occurring on an essentially annual basis gradually
238 decreases within the ~3 years of life represented by the tooth (Fig. 3). The repeatedly high Sr/Ca
239 and Ba/Ca signals in this sample likely reflect annual periods with an increased intake of plant-based
240 food resources, probably linked to a higher food availability during monsoonal periods, with a
241 variation of the peak heights also linked to different food intake⁵⁶.–The duration and availability of
242 food resources during the monsoon can fluctuate from season to season depending on monsoon
243 intensity. This might be the reason of the oscillation of the amplitude and height of the Sr/Ca and
244 Ba/Ca peaks.–Studies of palaeosols and the occurrence of palaeovertisols in the Sangiran Dome
245 strongly suggest that Java was a monsoon region in the Early Pleistocene, with an annual dry
246 season³. Monsoonal rain forest was likely the preferred habitat of *Pongo* sp. on Java. Indeed,

247 palaeoenvironmental reconstructions propose that Java was dominated by a mix of savannah, open
248 woodlands and monsoonal rain forests during the Early to Middle Pleistocene^{3,57-59}.

249 Besides differences in food intake the gradual decrease in Sr/Ca amplitude across the lifetime of the
250 individual might also be influenced by the geometry of the tooth cusp to cervix which might alter the
251 expression of Sr and Ba relative to Ca. Increased maturation overprint, which is inversely
252 proportional to enamel thickness, where Sr and Ba signals reduce towards the thinner cervical
253 enamel of the tooth, was observed in a previous study²². One recent study suggested a causal
254 relationship to a cyclical nursing pattern, resulting in a cyclical increase of Ba concentration in teeth
255 (i.e., through the increased intake of mothers' milk)⁶⁰. However, the synchronous up to sixfold
256 increase in Sr/Ca and up to eightfold increase in Ba/Ca are unlikely to reflect a breastmilk signal
257 because breastmilk is Sr-depleted through epithelial discrimination within the mammary
258 glands^{14,22,61,62}. Recent studies on dentine and cementum in *Pongo* revealed that regions of [Sr]
259 enrichment and depletion relate to both regular and irregular fluctuations in diet and Sr ingestion
260 rather than to cyclical breastfeeding and may continue for as long as twenty years into permanent
261 canine tooth formation^{63,64}. Caloric intake in orangutans is 2-3 times greater during supra-annual
262 masting events where several fruit and other plant food sources happen to ripen at the same time⁵⁶.
263 Masting events are often then followed by periods of low fruit availability during dry periods,
264 compensated in turn by orangutans burning fat reserves stored during mast-feeding⁶⁵. Sr/Ca and
265 Ba/Ca signals might also be enhanced during episodes of mast-feeding because of geophagic
266 behaviour, i.e. the deliberate ingestion of soils enriched in trace elements, which absorb toxins and
267 tannins and which appear to alleviate gastrointestinal upsets⁶⁴. This behaviour was previously
268 observed to be 'routine' in free-living orangutans⁶⁶. The sharp and relatively higher Sr/Ca and Ba/Ca
269 signal of the first peak may perhaps represent an occasion where the supra-annual masting event
270 coincided with the monsoon.

271 It has been shown that non-specific stress enamel markers (accentuated lines, ALs) can be
272 correlated to variations in barium concentrations in dental tissues of primates⁶⁷. In *Pongo* sp. SMF-
273 8864 four ALs, occurring between the first and the second peaks (Fig. 3c), show a weak or absent
274 correlation with elemental variations. However, the ALs' position outside of the peaks' regions

275 provide possible evidence of seasonal effects, as they might reflect stress events occurring during
276 the first identified dry season. Hypoplastic defects on the tooth crown as a further sign of
277 physiological stress do not correlate with elemental variations too (Fig. 3c) and indicate more
278 complex, still-to-be-defined developmental deficiencies^{14,42}.

279 Orangutans have the slowest life histories of any non-human primate with the latest weaning age of
280 any mammal at around 7 years, but with relatively low levels of nutrient transfer during breast-
281 feeding^{60,68,69,70}. Consequently, solid foods are supplemented in the infant's diet between 1 and 1.5
282 years of age, to compensate additional nutritional demands^{60,69}. Infants can forage solid foods
283 independently from the age of ~1.5 years, whilst the mother is not decreasing her lactation efforts⁶⁹.
284 Dry seasons with low food availability are compensated by extending weaning ages for infants
285 leading to low growth and reproduction rates and solitary lifestyles^{65,71-73}.

286

287 **Dietary strategy of *Homo erectus*.** The three *H. erectus* specimens show distinct Sr/Ca cycles with
288 a duration of approximately one year (Fig. 4). In contrast to the results from *Pongo* sp., the yearly
289 Sr/Ca cycles in *H. erectus* are of low amplitude (20 - 30 %), which are much smaller than the
290 seasonal changes observed in *Pongo* sp. SMF-8864. For *H. erectus*, these might reflect the
291 consumption of specifically selected animal or plant resources, which were available in the regional
292 context of a highly diverse ecosystem. Our $\delta^{13}\text{C}$ data show that the analyzed *H. erectus* individual
293 consumed a C_4 -dominated diet at the start of P^4 mineralization, and then changed to a consumption
294 of a mix of C_3 and C_4 biomass in the later stages of tooth development (Fig. 5). *H. erectus* probably
295 inhabited an open, mosaic setting with the C_3 signal indicating use of woodland/forest-edge habitats
296 or gallery forests along rivers. The more C_4 -dominated diet suggests a tendency towards grasslands
297 in the earlier life stages, possibly reflecting seasonal adaptations. The small variation of the relatively
298 low $\delta^{18}\text{O}$ values (Fig. 5) of the analyzed *H. erectus* indicates that the individual had access to a water
299 source with only small fluctuations in $\delta^{18}\text{O}$ during the whole time of P^4 tooth formation. Therefore, *H.*
300 *erectus* possibly have exploited regionally available resources and consumed water and/or aquatic
301 foods from e.g., rivers. Nearly 70 km east of Sangiran, at the site of Trinil where *H. erectus* was first

302 discovered and described^{74,75}, it was suggested that members of this species likely consumed
303 aquatic resources like shellfish, indicating a high level of food resilience⁷⁶. In general, a high adaptive
304 versatility is assumed for early members of the genus *Homo*⁷⁷ and dental microwear traits in
305 Sangiran *H. erectus* teeth also confirm an opportunistic omnivorous dietary strategy^{78,79}.

306 **Conclusions**

307 The main outcome of the present study is the demonstration that both *Pongo* sp. and *H. erectus* at
308 Sangiran had cyclical food resource availability with an annual periodicity. However, distinct
309 differences in their chemical patterns point to dietary and life history differences of Pleistocene
310 Southeast Asian *Pongo* sp. and *H. erectus*, both reacting to seasonal resource variations differently.
311 While *Pongo* sp. consumed contrasting plant-based food resources during the wet (monsoonal)
312 season presumably available in monsoonal rain forests, *H. erectus* was more versatile and exploited
313 a broader range of high diversity food resources along open mosaic habitats possibly with a tendency
314 towards grasslands as suggested by the carbon isotopic data.

315 We demonstrate the effective use of histologically-controlled time-resolved LA-ICPMS elemental
316 analyses of hominid dental fossils to retrieve biogenic signals at sub-weekly time resolution. Our
317 results show the first time-resolved geochemical analyses on *Homo erectus* from the Sangiran
318 Dome, which showcases the importance of geochemical analysis of fossil dental enamel of early
319 humans to reconstruct past dietary behaviours and life histories in an evolutionary-developmental
320 perspective.

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322

323

324 **Methods**

325 Overall the methodologies employed here follow those in Nava et al. 2020¹⁴ and Müller et al.
326 2019²² and only a brief summary is given here below.

327 **Enamel thin sections.** Preparation, imaging and histological analysis of enamel thin sections^{80,81}
328 were carried out at the Museo delle Civiltà in Rome. Sectioning was performed using a Leica high
329 precision diamond blade (Leica AG) and IsoMet low speed diamond blade microtome (Buehler Ltd).
330 Sections were ground with Minimet 1000 Automatic Polishing Machine (Buehler Ltd) using silicon
331 carbide grinding papers with two grits (1000 and 2500; Buehler Ltd). Sections were polished using
332 a Minimet 1000 Automatic Polishing Machine (Buehler Ltd) with a micro-tissue damped with distilled
333 water and diamond paste (Diamond DP-suspension M, Struers) containing 1 µm sized
334 monocrystalline diamonds. Thickness of the faunal thin sections was 130–150 µm depending on the
335 preservation and visibility of the enamel microstructure. The hominid section thickness varied
336 between 250 and 400 µm, thus facilitating the geochemical analysis but ensuring sufficient
337 readability of the enamel microstructures.

338

339 **LA-ICPMS analyses.** LA-ICPMS analyses were carried out at the Frankfurt Isotope and Element
340 Research Centre (FIERCE), Goethe University (Frankfurt am Main). Histologically-controlled tracks
341 were determined on the enamel micrographs with Photoshop (Adobe Inc.). Sampling included
342 continuous laser ablation tracks in enamel <100µm parallel to the EDJ following the tooth growth
343 direction²².

344 The LA-ICPMS system includes an 193nm ArF excimer laser (RESOLUTION S-155; now Applied
345 Spectra, Inc. (ASI), USA) coupled to a two-volume laser ablation cell (Laurin Technic, Australia)^{22,82}.
346 The laser ablation system is connected to an ICPMS Element XRTM (Thermo Fisher Scientific) using
347 nylon6-tubing. Thin sections were ultrasonically cleaned with methanol and fixed in the sample
348 holder together with a series of primary and secondary standards. The micrographs with pre-marked
349 laser tracks were uploaded in GeoStar µGIS Software (Norris Scientific, Australia) and retraced
350 before LA-analyses. LA-ICPMS data acquisition was performed in continuous path mode due to the
351 benefits of a two-volume LA cell with fast signal washout and constant signal response^{22,82}.

352 Prior to analysis, laser tracks were cleaned with a bigger spot size (40 μm), higher repetition rate (20
353 Hz) and scan speed (varying between 16.7-30 $\mu\text{m}/\text{s}$ depending on the size of teeth) to remove
354 surface residues, which could alter the results⁸³. Analyses were carried out with a spot size of 18
355 μm , scan speed of 10 $\mu\text{m}/\text{s}$ and a repetition rate of 15 Hz. The time signal obtained from the ICPMS
356 can be directly transferred to distance along the LA tracks via the constant scan speed of the laser
357 X-Y stage; no time delays of the X-Y stage exist at waypoints of composite tracks²². Between the LA
358 system and the ICPMS, a signal smoothing device ("squid") was included⁸².

359 The ICPMS (Element XR) detected the following isotopes from the ablated sample material
360 (m/z): ²⁵Mg, ²⁷Al, ⁴³Ca, ⁴⁴Ca, ⁶⁶Zn, ⁸⁶Sr, ⁸⁸Sr, ⁸⁹Y, ¹³⁸Ba, ¹⁴⁰Ce, ²⁰⁸Pb, ²³⁸U. For calibration purposes
361 (following Longerich et al. 1996⁸⁴), NIST612 as a primary external standard and ⁴⁴Ca as internal
362 standard were used. In bioapatite, Ca is commonly used as an internal standard, which is set at
363 37%^{22,85,86}, but for elemental ratios no prior knowledge of the sample [Ca] is necessary. For NIST
364 612 the following preferred values (\pm 2SD (in %)) were used (from GeoREM website
365 <http://georem.mpch-mainz.gwdg.de>): CaO: $11.9 \pm 0.4\%$ m/m; Zn: 38 ± 4 , Sr: 78.4 ± 0.2 , Y: 38 ± 2 ,
366 Ba: 39.7 ± 0.4 , Ce: 38.7 ± 0.4 , Pb: 38.57 ± 0.2 , U: 37.38 ± 0.08 $\mu\text{g}/\text{g}$.

367 Secondary standards with known concentrations and a matrix broadly similar to apatite (STDPx
368 glasses) were analyzed to assess accuracy and precision: STDP3-150, STDP3-1500, STDP5 (Ca-
369 P-(Si) glass standards)⁸⁷, KL2-G (basalt glass)⁸⁸, MAPS5 (phosphate pellet) and MACS3
370 (Microanalytical Carbonate Standard; United States Geological Survey USGS: preliminary
371 Certificate of Analysis by Steve Wilson), both available as 'nano'pellets from D. Garbe-
372 Schönberg^{89,90}. MACS3 was used for Zn accuracy because no reported Zn values are available for
373 the Ca-P-(Si) glass standard²². Comparisons between measured secondary standard concentrations
374 and reported concentrations revealed that the most accurate results with the lowest average bias
375 were produced using the combination of NIST612 with ⁴⁴Ca. Average relative biases of all three
376 STDPx standards and MAPS5 were (in %): Al: -2.87 ± 3.26 , Ca: 2.62 ± 1.72 , Rb: 2.14 ± 20.47 , Sr:
377 2.57 ± 4.98 , Y: 5.85 ± 3.11 , Ba: 0.68 ± 5.23 , Ce: -1.31 ± 3.46 , Pb: -2.88 ± 10.33 , U: 2.80 ± 5.48
378 (average bias of all standards \pm 1SD in %).

379 The compositional profiles displaying the concentration of elements relative to distance/days along
380 the EDJ profile were smoothed with a locally weighted polynomial regression fit, with its associated
381 standard error range (± 2 SE) for each predicted value⁹¹. The software R (ver. 4.0.4; R-Core-Team,
382 2021) and the packages “lava”, “readxl”, “shape” and “tidyverse” were used for all statistical
383 computations and generation of graphs.

384 Elemental data was matched with odontochronologies of the *H. erectus* and *Pongo* sp. Specimens
385 by determining the chronology of each EDJ track after LA-ICPMS analysis (Supplementary Fig. 8),
386 and directly assessing the enamel daily secretion rates (DSR). DSR i. e. the speed at which the
387 ameloblast - the enamel forming cells - move towards the outer surface of the tooth is expressed in
388 $\mu\text{m day}^{-1}$ along the prisms^{92,93}, in the 100 μm region close to the EDJ. Carefully chosen histologically-
389 defined (EDJ) profiles facilitate the correlation between odontochronological and geochemical
390 signals at a very high time resolution (<1 week).

391 **Isotopic ratio mass spectrometry (IRMS) analyses.** Stable carbon and oxygen analyses of S7-37
392 (right P⁴) were performed at the Goethe University-Senckenberg BiK-F Joint Stable Isotope Facility
393 Frankfurt, Germany. 2.9 to 3.8 mg of enamel powder was retrieved for each sample with a hand-
394 held diamond tip dental drill. To produce sufficient sample material, drill holes were expended along
395 to the growth axis of the enamel.

396 To remove organic matter and potential diagenetic carbonate, enamel was pretreated with 2 %
397 NaOCl solution for 24 hours followed by 1 M Ca-acetate acetic acid buffer solution for another 24
398 hours and thoroughly rinsed with deionized water (modified after Koch et al., 1997). Typically,
399 enamel pre-treatment resulted in ~60 % mass loss. Then, 950 to 1100 μg of pretreated enamel
400 powder were reacted with 99% H₃PO₄ for 90 min at 70 °C in continuous flow mode using a Thermo
401 Finnigan 253 mass spectrometer interfaced to a Thermo GasBench II. Analytical procedure followed
402 the protocol of Spötl and Vennemann (2003)⁹⁴. Final isotopic ratios are reported versus VPDB
403 (Vienna Pee Dee Belemnite); overall analytical uncertainties are better than 0.3 ‰ for $\delta^{13}\text{C}$ and 0.05
404 ‰ for $\delta^{18}\text{O}$.

405 **References**

- 406 1. von Koenigswald, G. H. R. Fossil hominids from the Lower Pleistocene of Java. in
407 *Rep. 18th Internat Geological Congress* 59–61 (1948).
- 408 2. Grine, F. E. & Franzen, J. L. Fossil hominid teeth from the Sangiran Dome (Java,
409 Indonesia). *Cour. Forsch. Inst. Senckenberg* **171**, 75–103 (1994).
- 410 3. Bettis, E. A. *et al.* Way out of Africa: Early Pleistocene paleoenvironments inhabited
411 by *Homo erectus* in Sangiran, Java. *J. Hum. Evol.* **56**, 11–24 (2009).
- 412 4. Matsu'ura, S. *et al.* Age control of the first appearance datum for Javanese *Homo*
413 *erectus* in the Sangiran area. *Science* **367**, 210–214 (2020).
- 414 5. Weidenreich, F. Giant early man from Java and South China. *Anthropol. Pap. Am.*
415 *Mus. Nat. Hist.* **40**, 1–134 (1945).
- 416 6. von Koenigswald, G. H. R. *Pithecanthropus*, *Meganthropus* and the
417 Australopithecinae. *Nature* **173**, 795–797 (1954).
- 418 7. Franzen, J. L. What is “*Pithecanthropus dubius* Koenigswald, 1950”? In *Ancestors:*
419 *The Hard Evidence* (ed Delson, E.) 221–226 (Alan R. Liss, Inc., New York, 1985).
- 420 8. Tyler, D. E. Sangiran 5, (“*Pithecanthropus dubius*”), *Homo erectus*, “*Meganthropus*,”
421 or *Pongo*? *Hum. Evol.* **18**, 229–241 (2003).
- 422 9. Tyler, D. E. An examination of the taxonomic status of the fragmentary mandible
423 Sangiran 5, (*Pithecanthropus dubius*), *Homo erectus*, ‘*Meganthropus*’, or *Pongo*?
424 *Quat. Int.* **117**, 125–130 (2004).
- 425 10. Zanolli, C. *et al.* Evidence for increased hominid diversity in the Early to Middle
426 Pleistocene of Indonesia. *Nat. Ecol. Evol.* **3**, 755–764 (2019).
- 427 11. Balter, V., Braga, J., Télouk, P. & Thackeray, J. F. Evidence for dietary change but
428 not landscape use in South African early hominins. *Nature* **489**, 558–560 (2012).

- 429 12. Joannes-Boyau, R. *et al.* Elemental signatures of *Australopithecus africanus* teeth
430 reveal seasonal dietary stress. *Nature* **572**, 112–115 (2019).
- 431 13. Smith, T. M. *et al.* Wintertime stress, nursing, and lead exposure in Neanderthal
432 children. *Sci. Adv.* **4**, 9483–9514 (2018).
- 433 14. Nava, A. *et al.* Early life of Neanderthals. *Proc. Natl. Acad. Sci. USA* **117**, 28719–
434 28726 (2020).
- 435 15. Hoppe, K. A., Koch, P. L. & Furutani, T. T. Assessing the preservation of biogenic
436 strontium in fossil bones and tooth enamel. *Int. J. Osteoarchaeol.* **13**, 20–28 (2003).
- 437 16. Hinz, E. A. & Kohn, M. J. The effect of tissue structure and soil chemistry on trace
438 element uptake in fossils. *Geochim. Cosmochim. Acta* **74**, 3213–3231 (2010).
- 439 17. Bromage, T. G., Hogg, R. T., Lacruz, R. S. & Hou, C. Primate enamel evinces long
440 period biological timing and regulation of life history. *J. Theor. Biol.* **305**, 131–144
441 (2012).
- 442 18. Lacruz, R. S., Dean, M. C., Ramirez-Rozzi, F. & Bromage, T. G. Megadontia, striae
443 periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *J.*
444 *Anat.* **213**, 148–158 (2008).
- 445 19. Lacruz, R. S., Habelitz, S., Wright, J. T. & Paine, M. L. Dental enamel formation and
446 implications for oral health and disease. *Physiol. Rev.* **97**, 939–993 (2017).
- 447 20. Dean, M. C. Tooth microstructure tracks the pace of human life-history evolution.
448 *Proc. R. Soc. B* **273**, 2799–2808 (2006).
- 449 21. Müller, W. & Anczkiewicz, R. Accuracy of laser-ablation (LA)-MC-ICPMS Sr isotope
450 analysis of (bio)apatite—a problem reassessed. *J. Anal. At. Spectrom.* **31**, 259–269
451 (2016).

- 452 22. Müller, W. *et al.* Enamel mineralization and compositional time-resolution in human
453 teeth evaluated via histologically-defined LA-ICPMS profiles. *Geochim. Cosmochim.*
454 *Acta* **255**, 105–126 (2019).
- 455 23. Li, Q. *et al.* Spatially-resolved Ca isotopic and trace element variations in human
456 deciduous teeth record diet and physiological change. *Environ. Archaeol.* 1–10
457 (2020). doi:10.1080/14614103.2020.1758988
- 458 24. Elias, R. W., Hirao, Y. & Patterson, C. C. The circumvention of the natural
459 biopurification of calcium along nutrient pathways by atmospheric inputs of industrial
460 lead. *Geochim. Cosmochim. Acta* **46**, 2561–2580 (1982).
- 461 25. Burton, J. H., Price, T. D. & Middleton, W. D. Correlation of bone Ba/Ca and Sr/Ca
462 due to biological purification of Calcium. *J. Archaeol. Sci.* **26**, 609–616 (1999).
- 463 26. Balter, V. *et al.* Ecological and physiological variability of Sr/Ca and Ba/Ca in
464 mammals of West European mid-Würmian food webs. *Palaeogeogr. Palaeoclimatol.*
465 *Palaeoecol.* **186**, 127–143 (2002).
- 466 27. Pate, F. D. Bone chemistry and paleodiet. *J. Archaeol. Method Theory* **1**, 161–209
467 (1994).
- 468 28. Kohn, M. J., Morris, J. & Olin, P. Trace element concentrations in teeth - a modern
469 Idaho baseline with implications for archeometry, forensics, and palaeontology. *J.*
470 *Archaeol. Sci.* **40**, 1689–1699 (2013).
- 471 29. de Vos, J. Faunal Stratigraphy and Correlation of the Indonesian Hominid Sites. In
472 *Ancestors: The Hard Evidence* (ed Delson, E.) 215-220 (Alan R. Liss, Inc., New York,
473 1985).
- 474 30. de Vos, J. *et al.* The *Homo* bearing deposits of Java and its ecological context. *Cour.*
475 *Forsch. Inst. Senckenberg* **171**, 129–140 (1994).

- 476 31. Leinders, J. J. M. *et al.* The age of the hominid-bearing deposits of Java: State of the
477 art. *Geol. Mijnbouw* **64**, 167-173 (1985).
- 478 32. Sondaar, P. Faunal evolution and the mammalian biostratigraphy of Java. In *The*
479 *Early Evolution of Man* (eds Andrews, P. & Franzen, J.) *Cour. Forsch. Inst.*
480 *Senckenberg* **69**, 219-235 (1984).
- 481 33. Peek, S. & Clementz, M. T. Sr/Ca and Ba/Ca variations in environmental and
482 biological sources: A survey of marine and terrestrial systems. *Geochim. Cosmochim.*
483 *Acta* **95**, 36–52 (2012).
- 484 34. Reynard, B. & Balter, V. Trace elements and their isotopes in bones and teeth: Diet,
485 environments, diagenesis, and dating of archeological and paleontological samples.
486 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **416**, 4–16 (2014).
- 487 35. Jacques, L. *et al.* Implications of diagenesis for the isotopic analysis of Upper
488 Miocene large mammalian herbivore tooth enamel from Chad. *Palaeogeogr.*
489 *Palaeoclimatol. Palaeoecol.* **266**, 200-210 (2008).
- 490 36. Brumfitt, I. M., Chinsamy, A. & Compton, J. S. Depositional environment and bone
491 diagenesis of the Mio/Pliocene Langebaanweg bonebed, South Africa. *S. Afr. J. Geol.*
492 **116**, 241-258 (2013).
- 493 37. Decrée, S. *et al.* The post-mortem history of a bone revealed by its trace element
494 signature: the case of a fossil whale rostrum. *Chem. Geol.* **477**, 137-150 (2018).
- 495 38. Janssen, R. *et al.* Tooth enamel stable isotopes of Holocene and Pleistocene fossil
496 fauna reveal glacial and interglacial paleoenvironments of hominins in Indonesia.
497 *Quat. Sci. Rev.* **144**, 145–154 (2016).
- 498 39. Blumenthal, S. A. *et al.* Stable isotope time-series in mammalian teeth: In situ $\delta^{18}\text{O}$
499 from the innermost enamel layer. *Geochim. Cosmochim. Acta* **124**, 223–236 (2014).

- 500 40. Zazzo, A., Balasse, M. & Patterson, W. P. High-resolution $\delta^{13}\text{C}$ intratooth profiles in
501 bovine enamel: Implications for mineralization pattern and isotopic attenuation.
502 *Geochim. Cosmochim. Acta* **69**, 3631–3642 (2005).
- 503 41. Deutsch, D. & Pe'er, E. Development of enamel in human fetal teeth. *J. Dent. Res.*
504 **61**, 1543–1551 (1982).
- 505 42. Dean, C. *et al.* Growth processes in teeth distinguish modern humans from *Homo*
506 *erectus* and earlier hominins. *Nature* **414**, 628–631 (2001).
- 507 42. Guatelli-Steinberg, D., Ferrell, R. J. & Spence, J. Linear enamel hypoplasia as an
508 indicator of physiological stress in great apes: Reviewing the evidence in light of
509 enamel growth variation. *Am. J. Phys. Anthropol.* **148**, 191–204 (2012).
- 510 43. Cerling, T. E. *et al.* Woody cover and hominin environments in the past 6 million
511 years. *Nature* **476**, 51–56 (2011).
- 512 44. Lacruz, R. S., Dean, M. C., Ramirez-Rozzi, F. & Bromage, T. G. Megadontia, striae
513 periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *J.*
514 *Anat.* **213**, 148–158 (2008).
- 515 45. Reid, D. J. & Dean, M. C. Variation in modern human enamel formation times. *J.*
516 *Hum. Evol.* **50**, 329–346 (2006).
- 517 46. Smith, T. M. Dental development in living and fossil orangutans. *J. Hum. Evol.* **94**,
518 92–105 (2016).
- 519 47. Schwartz, G. T., Reid, D. J. & Dean, C. Developmental aspects of sexual dimorphism
520 in hominoid canines. *Int. J. Primatol.* **22**, 837–860 (2001).
- 521 48. Bonhommeau, S. *et al.* Eating up the world's food web and the human trophic level.
522 *Proc. Natl. Acad. Sci. USA* **110**, 20617–20620 (2013).

- 523 49. Sponheimer, M. & Lee-Thorp, J. A. Enamel diagenesis at South African australopith
524 sites: Implications for paleoecological reconstruction with trace elements. *Geochim.*
525 *Cosmochim. Acta* **70**, 1644–1654 (2006).
- 526 50. Eltringham, S. K. The pygmy hippopotamus (*Hexaprotodon liberiensis*). in *Pigs,*
527 *Peccaries and Hippos* (ed Oliver, W.) 55–60 (International Union for the Conservation
528 of Nature and Natural Resources, Gland, 1993).
- 529 51. Jablonski, N. G. The hippo's tale: How the anatomy and physiology of Late Neogene
530 *Hexaprotodon* shed light on Late Neogene environmental change. *Quat. Int.* **117**,
531 119–123 (2004).
- 532 52. Hendier, A. Diet determination of wild pygmy hippopotamus (*Choeropsis liberiensis*).
533 (University of Neuchâtel, Switzerland, 2019).
- 534 53. Klein, I. Ernährung und ökologisches Profil von *Axis lydekkeri*. (Goethe University
535 Frankfurt, 2020).
- 536 54. Russon, A. E. *et al.* Geographic variation in orangutan diets. In *Orangutans:*
537 *Geographic variation in behavioral ecology and conservation* (eds Wich, S. A., Suci
538 Utami Atmoko, S., Mitra Setia, T. & van Schaik, C. P.) 135-156 (Oxford University
539 Press, Oxford, 2009).
- 540 55. Kanamori, T. *et al.* Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*)
541 in Danum Valley, Sabah, Malaysia: a 3-year record including two mast fruitings. *Am.*
542 *J. Primatol.* **72**, 820–840 (2010).
- 543 56. Kanamori, T., Kuze, N., Bernard, H., Malim, T. P. & Kohshima, S. Fluctuations of
544 population density in Bornean orangutans (*Pongo pygmaeus morio*) related to fruit
545 availability in the Danum Valley, Sabah, Malaysia: a 10-year record including two
546 mast fruitings and three other peak fruitings. *Primates* **58**, 225–235 (2017).

- 547 57. Sémah, A.-M., Sémah B, F., Djubiantono, T. & Brasseur, B. Landscapes and
548 hominids' environments: Changes between the Lower and the early Middle
549 Pleistocene in Java (Indonesia). *Quat. Int.* **4**, 451 (2009).
- 550 58. Sémah, A. M. & Sémah, F. The rain forest in Java through the Quaternary and its
551 relationships with humans (adaptation, exploitation and impact on the forest). *Quat.*
552 *Int.* **249**, 120–128 (2012).
- 553 59. Brasseur, B., Sémah, F., Sémah, A.-M. & Djubiantono, T. Approche
554 paléopédologique de l'environnement des hominidés fossiles du dôme de Sangiran
555 (Java central, Indonésie). *Quaternaire* **22**, 13–34 (2011).
- 556 60. Smith, T. M., Austin, C., Hinde, K., Vogel, E. R. & Arora, M. Cyclical nursing patterns
557 in wild orangutans. *Sci. Adv.* **3**, e1601517 (2017). (57)
- 558 61. Humphrey, L. T. Isotopic and trace element evidence of dietary transitions in early
559 life. *Ann. Hum. Biol.* **41**, 348–357 (2014).
- 560 62. Widdowson, E. M. Absorption, excretion and storage of trace elements: studies over
561 50 years. *Food Chem.* **43**, 203-207 (1992).
- 562 63. Dean, C., Le Cabec, A., Spiers, K., Zhang, Y. & Garrevoet, J. Incremental distribution
563 of strontium and zinc in great ape and fossil hominin cementum using synchrotron X-
564 ray fluorescence mapping. *J. R. Soc. Interface* **15**, (2018).
- 565 64. Dean, M. C., Le Cabec, A., Van Malderen, S. J. M. & Garrevoet, J. Synchrotron X-ray
566 fluorescence imaging of strontium incorporated into the enamel and dentine of wild-
567 shot orangutan canine teeth. *Arch. Oral Biol.* **119**, 104879 (2020).

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569

- 570 65. Pontzer, H., Raichlen, D. A., Shumaker, R. W., Ocobock, C. & Wich, S. A. Metabolic
571 adaptation for low energy throughput in orangutans. *Proc. Natl. Acad. Sci. USA* **107**,
572 14048–14052 (2010). (60)
- 573 66. Mahaney, W. C., Hancock, R. G. V., Aufreiter, S., Milner, M. W. & Voros, J. Bornean
574 orangutan geophagy: analysis of ingested and control soils. *Environ. Geochem.*
575 *Health* **38**, 51-64 (2016).
- 576 67. Austin, C. *et al.* Uncovering system-specific stress signatures in primate teeth with
577 multimodal imaging. *Scientific Reports* **6**, 1-11 (2016).
- 578 68. Humphrey, L. T. Weaning behaviour in human evolution. *Semin. Cell Dev. Biol.* **21**,
579 453–461 (2010).
- 580 69. van Noordwijk, M. A., Willems, E. P., Utami Atmoko, S. S., Kuzawa, C. W. & van
581 Schaik, C. P. Multi-year lactation and its consequences in Bornean orangutans
582 (*Pongo pygmaeus wurmbii*). *Behav. Ecol. Sociobiol.* **67**, 805–814 (2013). (55)
- 583 70. Galdikas, B. M. F. & Wood, J. W. Birth spacing patterns in humans and apes. *Am. J.*
584 *Phys. Anthropol.* **83**, 185–191 (1990).
- 585 71. van Noordwijk, M. A. & van Schaik, C. P. Development of ecological competence in
586 Sumatran orangutans. *Am. J. Phys. Anthropol.* **127**, 79–94 (2005).
- 587 72. Leuser National Park, G., Sugardjito, J., te Boekhorst, J. A. & van Hooff, J. A. R. A.
588 M. Ecological constraints on the grouping of wild orang-utans (*Pongo pygmaeus*) in
589 the Gunung Leuser National Park, Sumatra, Indonesia. *Int. J. Primatol.* **8**, 17–41
590 (1987).
- 591 73. Wich, S. A. *et al.* Life history of wild Sumatran orangutans (*Pongo abelii*). *J. Hum.*
592 *Evol.* **47**, 385–398 (2004).
- 593 74. Dubois, E. Palaeontologische onderzoekingen op Java. Extra bijvoegsel der
594 Javasche Courant, Verlag van het Mijnwezen over het 3e kwartaal pp. 12–14 (1891).

- 595 75. Dubois, E. *Pithecanthropus erectus*, einen menschenaehnliche Uebergangsform aus
596 Java. Landesdruckerei, Batavia (1894).
- 597 76. Joordens, J. C. A. *et al.* *Homo erectus* at Trinil on Java used shells for tool production
598 and engraving. *Nature* **518**, 228–231 (2015).
- 599 77. Ungar, P. S., Grine, F. E. & Teaford, M. F. Diet in early *Homo* : A review of the
600 evidence and a new model of adaptive versatility. *Annu. Rev. Anthropol.* **35**, 209–228
601 (2006).
- 602 78. Tausch, J. A New Method for Examining Hominin Dietary Strategy: Occlusal
603 Microwear Vector Analysis of the Sangiran 7 *Homo erectus* Molars. (Goethe
604 University Frankfurt, 2011).
- 605 79. Tausch, J., Kullmer, O. & Bromage, T. G. A new method for determining the 3D
606 spatial orientation of molar microwear. *Scanning* **37**, 446–457 (2015).
- 607 80. Caropreso, S. *et al.* Thin sections for hard tissue histology: A new procedure. *J.*
608 *Microsc.* **199**, 244–247 (2000).
- 609 81. Bondioli, L., Nava, A., Rossi, P. F., & Sperduti, A. Diet and health in Central-Southern
610 Italy during the Roman Imperial time. *Acta IMEKO* **5**, 19-25 (2016).
- 611 82. Müller, W., Shelley, M., Miller, P. & Broude, S. Initial performance metrics of a new
612 custom-designed ArF excimer LA-ICPMS system coupled to a two-volume laser-
613 ablation cell. *J. Anal. At. Spectrom.* **24**, 209–214 (2009).
- 614 83. Evans, D. & Müller, W. LA-ICPMS elemental imaging of complex discontinuous
615 carbonates: An example using large benthic foraminifera. *J. Anal. At. Spectrom.* **28**,
616 1039–1044 (2013).
- 617 84. Longerich, H. P., Jackson, S. E. & Günther, D. Laser ablation inductively coupled
618 plasma mass spectrometric transient signal data acquisition and analyte
619 concentration calculation. *J. Anal. At. Spectrom.* **11**, 899–904 (1996).

- 620 85. Retief, D. H., Cleaton-Jones, P. E., Turkstra, J. & De Wet, W. J. The quantitative
621 analysis of sixteen elements in normal human enamel and dentine by neutron
622 activation analysis and high-resolution gamma-spectrometry. *Arch. Oral Biol.* **16**,
623 1257–1267 (1971).
- 624 86. Lacruz, R. S. Enamel: Molecular identity of its transepithelial ion transport system.
625 *Cell Calcium* **65**, 1–7 (2017).
- 626 87. Klemme, S. *et al.* Synthesis and preliminary characterisation of new silicate,
627 phosphate and titanite reference glasses. *Geostand. Geoanalytical Res.* **32**, 39–54
628 (2008).
- 629 88. Jochum, K. P. *et al.* Accurate trace element analysis of speleothems and biogenic
630 calcium carbonates by LA-ICP-MS. *Chem. Geol.* **318–319**, 31–44 (2012).
- 631 89. Garbe-Schönberg, D. & Müller, S. Nano-particulate pressed powder tablets for LA-
632 ICP-MS. *J. Anal. At. Spectrom.* **29**, 990–1000 (2014).
- 633 90. Jochum, K. P. *et al.* Nano-powdered calcium carbonate reference materials:
634 significant progress for microanalysis? *Geostand. Geoanalytical Res.* **43**, 595–609
635 (2019).
- 636 91. Cleveland, W. S., Grosse, E. & Shyu, W. M. Local regression models. In *Statistical*
637 *Models in S* (eds Chambers, J. M. & Hastie, T.) 309–376 (Chapman and Hall/CRC,
638 New York, 1992).
- 639 92. Guatelli-Steinberg, D., Floyd, B. A., Dean, M. C. & Reid, D. J. Enamel extension rate
640 patterns in modern human teeth: Two approaches designed to establish an integrated
641 comparative context for fossil primates. *J. Hum. Evol.* **63**, 475–486 (2012).
- 642 93. Birch, W. & Dean, M. C. A method of calculating human deciduous crown formation
643 times and of estimating the chronological ages of stressful events occurring during
644 deciduous enamel formation. *J. Forensic Leg. Med.* **22**, 127–144 (2014).

645 94. Spötl, C. & Vennemann, T. W. Continuous-flow isotope ratio mass spectrometric
646 analysis of carbonate minerals. *Rapid Commun. Mass Spectrom.* **17**,1004–1006
647 (2003).

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665 **Author contributions**

666 The study was initiated by W. M., F. S. and J. K. and forms part of J. K.'s MSc research project
667 completed under the supervision of W. M., L. B. and A. N. J. K., W. M., A. N., L. B., F. S. and O. K.
668 designed research, J. K., W. M., A. N., L. B., B. P., T. L. and R. A. performed research, J. K., W. M.,
669 A. N., T. L. and L. B. analyzed data, J. K., W. M., A. N., L. B., F. S., O. K., C. Z., T. L. and C. H. wrote
670 the manuscript with contributions from all other authors.

671

672 **Data availability**

673 The raw data of element analyses used in this study are available as a separate Excel file.

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675 **Competing interests**

676 The authors declare no competing interests.

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678 **Additional Information**

679 **Supplementary information** is available in the online version of the paper.

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683 [frankfurt.de](http://www.uni-frankfurt.de)).

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685

686 **Table 1 | List of specimens from the GHR v. Koenigswald Collection used in the present study.**

687 The specimens are housed in the Department of Palaeoanthropology, Senckenberg Research
688 Institute and Natural History Museum Frankfurt, Frankfurt a. M., Germany.

689

	Catalogue number	Taxonomic identification	Dental elements
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PRIMATES	S7-13	Hominidae/ <i>Homo erectus</i>	upper left M
	S7-37	Hominidae/ <i>Homo erectus</i>	right P ⁴
	SMF-8865	Hominidae/ <i>Homo erectus</i>	lower left M
	SMF-8864	Hominidae/ <i>Pongo</i> sp.	lower right M
CARNIVORA	SMF/PA/F6664	Felidae/ <i>Panthera tigris</i>	right P ₄
	SMF/PA/F6666	Felidae/ <i>Panthera tigris</i>	right M ₁
PERISSODACTYLA	SMF/PA/F5941	Rhinocerotidae/ <i>Rhinoceros sondaicus</i>	left M ₁
	SMF/PA/F5950	Rhinocerotidae/ <i>Rhinoceros sondaicus</i>	left M ₂
ARTIODACTYLA	SMF/PA/F738	Suidae/ <i>Sus</i> sp.	right M ³
	SMF/PA/F869	Suidae/ <i>Sus</i> sp.	right M ³
	SMF/PA/F5077	Cervidae/ <i>Axis lydekkeri</i>	left M ₂
	SMF/PA/F5258	Cervidae/ <i>Axis lydekkeri</i>	right P ³ , M ¹ , M ² , M ³
	SMF/PA/F6	Hippopotamidae/ <i>Hexaprotodon</i> sp.	right M ²
	SMF/PA/F53	Hippopotamidae/ <i>Hexaprotodon</i> sp.	left M ₂

690

691 **Table 2 | Track lengths and Retzius Periodicity of the hominid sample.**

Catalogue number	Taxon	Tooth type	Cusp/aspect	Track length [µm]	Track length [years]	Retzius Periodicity [days]
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S7-13	<i>Homo erectus</i>	upper left M	paracone/buccal	4303	1.9	7 or 8*
S7-13	<i>Homo erectus</i>	upper left M	protocone/palatal	3629	1.8	
S7-37	<i>Homo erectus</i>	right P ⁴	protocone/palatal	6470	2.9 ⁺	7***
SMF-8865	<i>Homo erectus</i>	lower left M	protoconid/buccal	6252	3.1	8 or 9*
SMF-8865	<i>Homo erectus</i>	lower left M	metaconid/lingual	3906	-****	
SMF-8864	<i>Pongo sp.</i>	lower right M	protoconid/buccal	6009	2.9	8***
SMF-8864	<i>Pongo sp.</i>	lower right M	metaconid/lingual	5660	3.7	

692 *based on local DSRs between adjacent Retzius lines and not direct counts of cross striations due
693 to section thickness; ** reported in Lacruz et al 2008¹⁸ for S7-37 M¹; ***direct counts of cross
694 striations; ****section plane off centre, cervical portion damaged; ⁺Track length in years derived
695 from the revised crown formation time, which is slightly longer than reported in Lacruz et al. 2008¹⁸.

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698

699 Fig. 1 | Scatter plots of [Sr] or [Ba] vs. [Mn], respectively, for representative examples of each faunal
700 group, to illustrate the diagenesis assessment of the fossil assemblage. See Supplementary Figure
701 1 for equivalent plots relative to [U]. For simplicity, data are here shown as concentrations, whereas
702 elsewhere they are displayed as E/Ca to facilitate comparison.

703

704 Fig. 2 | Sr/Ca ratios. Box plot comparing *H. erectus* and *Pongo sp.* specimens to other taxa with
705 known trophic levels, all displayed after diagenesis filtering, i.e. [U]<1 ppm and [Mn]<400 ppm (µg/g)

706 (see Supplementary Fig. 7). Colour dots outside the whiskers represent outliers, lower whisker are
707 equal to minimum value (excluding outliers), lower hinge equals to first quartile, thick line represents
708 the median value, upper hinge equals to third quartile and upper whisker to maximum value
709 (excluding outliers). The numerous outliers in *Pongo* sp. SMF-8864 correspond to biogenic peaks
710 explained in Fig. 3.

711

712 Fig. 3 | Time-resolved compositional profiles for *Pongo* sp. SMF-8864 molar. a) Sr/Ca, Ba/Ca, [U]
713 and [Mn] along the EDJ plotted against relative days. Apart from isolated [U] peaks, only minor
714 diagenetic overprint is discernible for thin enamel from ~925 days. b) Comparative Sr/Ca, [U] and
715 [Mn] profiles along EDJ vs. corresponding prism orientations (Supplementary Fig. 4), plotted against
716 relative days; while data agree well overall, towards outer enamel the latter show lower Sr/Ca values
717 relative to corresponding EDJ positions due to maturation overprint. c) Elemental profiles for both
718 mesiolingual and mesiobuccal cusp showcase the remarkable similarity of Sr/Ca on both enamel
719 sides. Accentuated lines (A. L.) and hypoplastic defects are highlighted. See text for details.

720

721 Fig. 4 | Time-resolved compositional EDJ profiles for all investigated *H. erectus* specimens plotted
722 against their individual relative dental chronologies except for S7-37 where P⁴ where
723 odontochronology in life time is known¹⁸. a) SMF-8865. b) S7-13. c) S7-37. See text for details.

724

725 Fig. 5 | Carbon and oxygen isotope data of enamel from *H. erectus* S7-37 P⁴ plotted against life time
726 in relative days and years. Length of coloured bars indicate possible formation times of enamel used
727 for analyses, and thickness indicates 1sd of isotope data (0.03 ‰ for $\delta^{13}\text{C}$ and 0.05 ‰ for $\delta^{18}\text{O}$,
728 respectively).

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