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1 **The origin of placental mammal life histories**

2

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16 After the end-Cretaceous extinction, placental mammals quickly diversified<sup>1</sup>, occupied key  
17 ecological niches<sup>2,3</sup>, and increased in size<sup>4,5</sup>, but the latter was not true of other therians<sup>6</sup>.  
18 The uniquely extended gestation of placental young<sup>7</sup> may have factored in their success and  
19 size increase<sup>8</sup>, but reproduction style in early placentals remains unknown. Here, using  
20 palaeohistology and geochemistry, we present the earliest record of a placental life history,  
21 in a 62-million year old pantodont, the clade including the first mammals to achieve truly  
22 large body sizes. We extend the application of dental trace element mapping<sup>9,10</sup> by sixty  
23 million years, identifying chemical markers of birth and weaning, and calibrate these to a  
24 daily record of growth in the dentition. A long gestation (~7 months), rapid dental  
25 development, and short suckling interval (~30–75 days) show *Pantolambda bathmodon* was  
26 highly precocial, unlike non-placental mammals and known Mesozoic precursors. These  
27 results demonstrate *P. bathmodon* reproduced like a placental, and lived at a fast pace for  
28 its body size. Assuming *P. bathmodon* reflects close placental relatives, our findings suggest  
29 the ability to produce well-developed precocial young was established early in placental  
30 evolution, and that larger neonate sizes were a possible mechanism for rapid size increase  
31 in early placentals.

32

33

34 Placentals are the most diverse group of mammals, comprising >6,000 extant species<sup>11</sup> and the  
35 largest animals ever. Their success may relate to their derived life history<sup>8,12</sup>, with maternal  
36 investment shifted prenatally through extended gestation<sup>7,13</sup>. This adaptation allows placentals  
37 the unique capability among mammals to produce highly precocial young: typically single  
38 offspring born at larger masses with well-developed dentition, fur, and open eyes<sup>13,14</sup>. Extended

39 gestation may have released placentals from developmental constraints associated with  
40 prolonged lactation in other mammals<sup>8,15,16</sup>, enabling experimentation with new locomotor  
41 modes and habitats<sup>17,18</sup>. However, when extended gestation evolved in mammals remains  
42 unclear: Mesozoic eutherians (mammals more closely related to placentals than marsupials) did  
43 not grow like living placentals<sup>19–21</sup> and it has been hypothesized that ancestral placentals gave  
44 birth to altricial young<sup>21</sup>. Nonetheless, immediately after the end-Cretaceous extinction, early  
45 Palaeocene placentals emerged from a 100-Ma lineage of small-bodied ancestors and quickly  
46 achieved much greater masses as they diversified into a variety of niches<sup>4</sup>. Thus, the early  
47 Palaeocene was likely an important interval in the eutherian transition to placental-like growth  
48 strategies, but the life histories of these mammals remain unknown.

49         Among early placental clades, the Palaeocene–Eocene Pantodonta are a key group,  
50 because they were among the first large mammalian herbivores, becoming the largest mammals  
51 ever up to that point in time<sup>22</sup>. The early Palaeocene (~62 ma) *Pantolambda bathmodon* (~42 kg)  
52 is represented by multiple skeletons representing most of its ontogeny, including a small juvenile  
53 with deciduous dentition and unfused epiphyses (New Mexico Museum of Natural History and  
54 Science [NMMNH] P-27844; ~17 kg at death). As one of the largest mammals in its  
55 ecosystem<sup>23</sup>, its life history might provide insight into the relationship between life history and  
56 body size in Palaeocene eutherians.

57         Life histories of extinct animals can be reconstructed using incremental growth features  
58 of mineralized tissues like bones and teeth<sup>24–26</sup>. Bones preserve evidence of stress and annual  
59 cycles<sup>27,28</sup>, and they accurately reflect growth rate throughout life<sup>29,30</sup>, including changes  
60 associated with maturity<sup>31</sup>. In teeth, daily incremental lines in the dentine and enamel allow for  
61 precise chronologies and faithful recording of life history events such as birth and nutritional

62 stress like that experienced during weaning<sup>32,33</sup>, whereas cementum preserves annual growth  
63 cycles<sup>24,34</sup>. Chemical signals of birth and early-life diet are recorded in the developing teeth by  
64 the abundances of certain trace elements, like zinc (Zn), which is enriched at birth<sup>35,36</sup>, and  
65 barium (Ba), which varies according to bioavailability in the diet<sup>26</sup>. When integrated with daily  
66 growth increments, trace elements maps can reveal birth and the timing of weaning, a technique  
67 applied to primates up to 2.6 million years old<sup>9,10,26</sup>, but with unrealised potential in other fossil  
68 mammals.

69 Here we combine palaeohistological and geochemical evidence to reconstruct the life  
70 history of *P. bathmodon* on a daily scale and evaluate the physiology of a key group in the rise of  
71 mammals following the end-Cretaceous mass extinction. These data provide unprecedented  
72 insight into the life history of a fossil mammal, revealing that characteristic placental  
73 reproductive strategies were established early in their evolution.

74

## 75 **Dental development, birth, and weaning**

76 Incremental growth features are well preserved in the teeth, especially the enamel, and  
77 are clearly visible in histological thin sections (Fig. 1b–g; Extended Data Fig. 1). Daily  
78 laminations in the dentine and enamel<sup>37</sup> (Fig. 1b, c, e) track the successive growth of the tooth  
79 crown (Extended Data Table 1). High-resolution trace element mapping of several teeth  
80 (Extended Data Table 1; Figs. S1–7) reveals patterns in Zn and Ba that correspond to these  
81 incremental growth patterns and provide evidence of birth and weaning in *P. bathmodon* (Fig. 2),  
82 extending the viable window for dietary trace element mapping by roughly 60 million years  
83 compared to previous studies<sup>10</sup>. The most complete record of early life comes from a second

84 lower molar of an adult individual (NMMNH P-19541), where both the neonatal event and the  
85 weaning transition are preserved (Fig. 2).

86 Birth is recorded in the enamel by a prominent neonatal line (Fig. 1g; 2b), a discontinuity  
87 in the enamel prisms reflecting developmental disruptions in response to the physiological stress  
88 of birth<sup>38</sup>. The neonatal line is Zn-enriched (Fig. 2b; Extended Data Fig. 2), as observed in  
89 modern teeth, where this results from changing levels of Zn in serum over the birth interval and  
90 the ingestion of Zn-rich colostrum<sup>35,36</sup>. Importantly, the neonatal line is Zn-enriched in multiple  
91 cusps of the tooth, and no other accentuated lines in the enamel of this or other teeth are Zn-  
92 enriched (Fig. 2b, see Supplement). This suggests that analysis of Zn may be useful as an  
93 independent criterion for distinguishing neonatal lines from other accentuated lines in fossil  
94 mammals<sup>36</sup>.

95 Concentrations of Ba in the enamel are elevated postnatally, but decrease sharply after a  
96 short period (Fig. 2c). This pattern is present in both the protoconid and paraconid of the second  
97 lower molar, as well as in the first lower molar of the same individual (Fig. 2d), indicating that it  
98 represents a consistent biogenic signal. Temporary postnatal Ba enrichment in *P. bathmodon* is  
99 identical to that reported in modern and fossil primates<sup>9,10,26</sup>, where it reflects the increased  
100 bioavailability of Ba in breastmilk<sup>26</sup>. The decrease in Ba presumably marks the onset of weaning  
101 and indicates a minimum suckling period of about 31–56 days in *P. bathmodon*. Further  
102 independent evidence for a short suckling period also comes from mesowear and microwear in  
103 the dentition of a young juvenile (NMMNH P-27844; Extended Data Fig. 3), where growth  
104 increments in the dentine of the deciduous teeth are exceptionally well preserved (Fig. 1c;  
105 Extended Data Fig. 1). Like in the enamel, a birth signature appears to be recorded in the dentine  
106 by a neonatal line, and in this individual the postnatal dentine is Zn-enriched (Extended Data Fig.

107 4). Dentine continues to infill the pulp cavity throughout life, providing a record of growth both  
108 before and after eruption of the tooth and allowing precise estimation of age at death<sup>24</sup>.  
109 Approximately 75 daily growth increments separate the neonatal line and the pulp cavity in each  
110 tooth of this juvenile skeleton, indicating an age at death of ~2.5 months for this individual.  
111 Despite its young age, the presence of dental meso- and microwear<sup>39</sup> (Extended Data Fig. 3) in  
112 this individual shows that solid foods (not only milk) were being ingested, providing an upper  
113 constraint of 75 days on the onset of weaning.

114         Aligning daily growth records in the teeth based on the neonatal lines enables the  
115 reconstruction of a dental chronology (Fig. 11). Crown formation times in the teeth are rapid,  
116 ranging from 68 days to 183 days (~2–6 months; Extended Data Table 1). All of the deciduous  
117 teeth were complete and began erupting before birth, and the first and second adult molars had  
118 begun mineralizing. The adult molar crowns were completed within four months after birth and  
119 would have begun erupting in the first year. Based on eruption sequences in other pantodonts<sup>40–</sup>  
120 <sup>42</sup>, where the third molar erupts last, it is therefore likely that all of the adult teeth of *P.*  
121 *bathmodon* erupted within the first year (see Supplement).

122         In the permanent teeth of mammals, age at death can be estimated from annual bands in  
123 the cementum that anchors the tooth to the jaw<sup>24,34</sup>. Cementum annulations are clearly present in  
124 the acellular cementum of most teeth in our sample (Fig. 1d). Most individuals have between two  
125 and four annual pairs (Extended Data Table 1), but three individuals with highly worn dentitions  
126 compared to other Palaeocene pantodonts have five, seven and possibly as many as eleven pairs,  
127 respectively (Extended Data Figure 5; see Supplement).

128

129 **Skeletal growth**

130           The bone microstructure of the juvenile skeleton (NMMNH P-27844) exhibits densely  
131 vascularized fibrolamellar bone, indicating relatively rapid growth (Fig. 1i–k). No annual growth  
132 marks are present, consistent with its dental age of ~2.5 months, but a band of more organized,  
133 slowly-growing parallel-fibered bone occurs towards the outer surface of the radius and tibia  
134 (Fig. 1i; Extended Data Fig. 6), at an estimated mass of 9 kg (see Supplement). External to this  
135 band, the bone shows reduced vascularity and relatively slower growth, based on a higher  
136 proportion of parallel-fibered matrix (Fig. 1j,k), although laminations in this tissue are not as  
137 well developed as in the lamellar bone of the adult individual. This transition likely corresponds  
138 to changes in growth rate associated with weaning, as in living ungulates a similar transition  
139 occurs in some individuals over this interval<sup>43</sup> (see Supplement). The position of this transition  
140 partway through the cortex provides evidence for weaning in this individual prior to death at 2.5  
141 months of age, supporting the 1–2 month suckling period suggested by dental trace elements and  
142 tooth wear.

143           In a skeletally mature adult (NMMNH P-22012), seven annual growth marks are  
144 discernible in the exterior cortical bone, matching the number of cementum annulations in its  
145 teeth and demonstrating that it was seven years old when it died. The exterior cortex is formed of  
146 highly organized lamellar bone, indicating slow growth (Fig. 1h). The earliest annual growth  
147 mark is within the slowly-growing exterior cortex (Extended Data Fig. 7), indicating that growth  
148 rate decreased significantly before the end of the first year of life. This likely corresponds to the  
149 achievement of sexual maturity<sup>31</sup>, suggesting that *P. bathmodon* likely reached sexual maturity  
150 and approached maximum body size in its first year.

151

152 **Life history in *Pantolambda bathmodon***



153           Correcting for the onset of tooth mineralization partway through fetal development (see  
154 Supplement), the prenatal growth record in the deciduous teeth indicates a gestation period of  
155 roughly 207 days or 29.5 weeks. This is an order of magnitude longer than in marsupials or  
156 monotremes, but falls close to extant placentals of similar body size (Fig. 3b). Within placentals,  
157 gestation length is dichotomous between species that give birth to single or multiple young in  
158 each litter<sup>44</sup> (Fig. 3c). The long gestation period in *P. bathmodon* suggests it was likely (posterior  
159 probability = 0.96) to have given birth to singleton offspring (see Supplement).

160           Multiple independent lines of evidence from two individuals indicate the onset of  
161 weaning between 1–2 months after birth in *P. bathmodon*. Postnatal enrichment in enamel Ba for  
162 1–2 months after birth in an adult individual (Fig. 2c, d) is consistent with the development of  
163 abrasive microwear and mesowear on the dentition of the 2.5-month old juvenile (Extended Data  
164 Fig. 3) and with the transition recorded in its limb bones (Extended Data Fig. 6), identical to  
165 weaning transitions recently described on the basis of fluorescent labelling<sup>43</sup>. Together, these  
166 lines of evidence constrain weaning in *P. bathmodon* to between 31 and 75 days after birth, with  
167 the weight of evidence supporting cessation of suckling by 2 months after birth. The age (31–75  
168 days) and mass (9 kg) at weaning in *P. bathmodon* were shorter and smaller than expected for a  
169 placental of its adult body mass, but its gestation period (207 days) was slightly longer (Fig. 3a,  
170 b). This indicates greater prenatal than postnatal investment in the young, characteristic of  
171 placental mammals<sup>7</sup>, but also suggests a distinct life history for these early Palaeocene  
172 placentals, consistent with other unusual aspects of their biology<sup>45</sup>.

173           Most individuals within our sample died between 2–5 years of age (Fig. 11), suggesting  
174 high mortality rates in young animals. The oldest specimen in our sample (estimated to be ~11  
175 years old) lived only half the expected lifespan for a mammal of its body mass (20 years; Fig.

176 3d). This high mortality rate, in conjunction with its short suckling period and rapid onset of  
177 sexual maturity (Fig. 3a, e), suggest a fast pace of life in *P. bathmodon*, despite its relatively  
178 large size (42 kg).

179 Combined with its rapid dental and skeletal development, these life history parameters  
180 indicate a highly precocial lifestyle in *P. bathmodon*, comparable to the most precocial extant  
181 mammals (e.g., deer, giraffes, sheep), which give birth to young with hair and open eyes<sup>13,14</sup>.  
182 After a long gestation—the hallmark of the typical placental reproductive mode—a mother *P.*  
183 *bathmodon* likely gave birth to a single, haired offspring with open eyes and well-developed  
184 dentition, which nursed for 1–2 months. At ~62 Ma, this constitutes the earliest example of a  
185 placentalian-grade physiology in the fossil record.

186

### 187 **Growth in early placentals**

188 The growth pattern and rate of *P. bathmodon* differs from both those of Mesozoic  
189 mammaliaforms<sup>19,34</sup> and other Cenozoic mammals<sup>46,47</sup>. The mammaliaform *Morganucodon* grew  
190 at a much slower rate and for longer period, evidence of a protracted life history more like that of  
191 reptiles than mammals<sup>19,34</sup>. Late Cretaceous multituberculates and some eutherians had faster  
192 growth rates than *Morganucodon*, but these were still not as rapid as extant mammals<sup>19</sup>. In  
193 contrast, *P. bathmodon* exhibits fast growth rates and a rapid developmental schedule, more  
194 similar to living precocial placentals. Nonetheless, *P. bathmodon* lived and died faster than  
195 expected for a mammal of its body size, outpacing extant mammals and even other extinct  
196 mammals from later in the Cenozoic<sup>46,47</sup>. The closest living analogues for *Pantolambda*,  
197 independent of mass (Extended Data Fig. 8a), are small antelope, like the neotragines *Madoqua*  
198 (Dik-dik) and *Raphicerus* (Steenbok). However, when adult body mass is considered,

199 *Pantolambda* is unique among terrestrial mammals (Extended Data Fig. 8b). This life history  
200 strategy would have enabled *P. bathmodon* to proliferate at a rapid rate for an animal of its size,  
201 which may have been advantageous in the recovering ecosystems of the Palaeocene. Perhaps, as  
202 was the case with locomotion<sup>45</sup> and brain size<sup>48</sup>, placental life history strategies became limited  
203 to their modern range later, as ecosystems saturated.

204 In contrast to its distinctly rapid pace of life, the gestation period of *P. bathmodon* is  
205 remarkably similar to living placentals of its body mass (Fig. 3b; Extended Data Fig. 8),  
206 suggesting a more constrained relationship between size and gestation. Indeed, neonate weight  
207 and adult body mass are more tightly correlated than other life history parameters in extant  
208 placentals (Extended Data Fig. 9), suggesting that neonate weight drives and/or is constrained by  
209 adult body mass. As longer gestation enables the larger neonate sizes required for larger adults  
210 (Extended Data Fig. 9c), extended gestation periods like that in *P. bathmodon* may have  
211 contributed to the rapid increase in body mass in early Palaeocene placentals. The option of  
212 extended gestation may have reduced developmental constraints on body size and allowed  
213 placentals to expand into vacant niches after the extinction of the non-avian dinosaurs, reaching  
214 larger sizes than any Mesozoic mammal<sup>22</sup>, and culminating in the largest animals ever<sup>49</sup>.

215 The excellent preservation of daily incremental structures and dietary trace element  
216 signatures in a ~62 million year old fossil unlock a new perspective for studying the life history  
217 of extinct mammals. Our results suggest that biogenic trace element signals can be retained much  
218 longer than previously realized, providing new tools for inferring birth and early-life diet in  
219 ancient fossil mammals. Rather than being a limitation for studying reproduction, the  
220 abundantly-preserved isolated teeth of Mesozoic mammals may enable combined  
221 palaeohistological and geochemical approaches to directly address the evolution of reproduction

222 in mammals, including its role in their survival at the end-Cretaceous extinction and their  
223 radiation thereafter. Indeed, the highly precocial life history of *P. bathmodon* shows that the  
224 physiology of at least some close placental relatives had diverged from other mammals by at  
225 least the Palaeocene, early in their evolutionary history<sup>21</sup>, and suggests that the capacity to  
226 increase body size played a role in their ascent from humble Mesozoic beginnings to the  
227 dominant role they play in global ecosystems today.

228

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354 **Figure Captions:**

355

356 **Fig. 1.** Palaeohistology of *Pantolambda bathmodon*. (a) Skeletal reconstruction of adult with  
357 sampled elements in blue; boxes show representative locations of palaeohistological images,  
358 silhouette shows relative size of juvenile NMMNH P-27844. (b–g) dental features used for  
359 reconstruction of life history (all coronal sections): (b) enamel cross-striations (arrows) in second  
360 lower molar of NMMNH P-19541; (c) lines of von Ebner in deciduous ultimate upper premolar  
361 of NMMNH P-27844, white dots mark five lines and arrows show orientation of lines; (d)  
362 cementum annulations (one light + one dark band) in first lower premolar of NMMNH P-69919;  
363 (e) daily laminations (arrows) in lower incisor of NMMNH P-69918; (f) neonatal line in dentine  
364 of deciduous ultimate upper premolar of NMMNH P-27844; and (g) neonatal line (arrow) in  
365 enamel of second lower molar of NMMNH P-19541. (h–k), osteohistological features used for  
366 reconstruction of life history (all transverse midshaft diaphysis sections): (h) lines of arrested  
367 growth (arrows) in outer cortex of rib of NMMNH P-22012; (i) annulus (orange arrow) at  
368 weaning transition in radius of NMMNH P-27844; (j–k) weaning transition (arrows and yellow  
369 line) in outer cortex of tibia of NMMNH P-27844 under plane polarized light (j) and cross-  
370 polarized light with a lambda filter (k). Images (b–g, i) under cross-polarized light, (h) under  
371 cross-polarized light with a lambda filter. (l) life history chronology of *P. bathmodon* showing  
372 crown formation times for deciduous (blue) and adult (green) teeth, life history events, and  
373 mortality. Daggers indicate ages at death, youngest and oldest specimens highlighted in blue.  
374 **Abbreviations:** CCCB, compact coarse cancellous bone; DEJ, dentinoenamel junction; WB,  
375 woven-fibered bone; **glg**, growth layer group; **LB**, lamellar bone; **NNL**, neonatal line; **PFB**,

376 parallel-fibered bone. Scale bars: 10 cm (a), 25  $\mu\text{m}$  (b), 50  $\mu\text{m}$  (e), 100  $\mu\text{m}$  (c, d), 200  $\mu\text{m}$  (f–h),  
377 500  $\mu\text{m}$  (i–k).

378

379 **Fig. 2.** Trace element distributions in the enamel of the first and second lower molars (NMMNH  
380 P-19541; also see Figs. S1–3). (a) Thin section under cross-polarized light shows clear daily  
381 laminations and the neonatal line (dotted line) in the enamel of the paraconid of the second lower  
382 molar. (b) Trace element map of Zn shows enrichment at the neonatal line. (c) Barium is  
383 enriched in early postnatal enamel (also see Supplementary Fig. S8), but decreases gradually  
384 between 31–56 days after birth (dashed lines). (d) The transition between high and low Ba is  
385 clearer in the paraconid of the first lower molar of the same individual, where older enamel  
386 including the neonatal line has been worn away. (e,f) overview images showing position of  
387 images within first (f) and second (e) lower molars. Scale bars: 500  $\mu\text{m}$  (a–d), 1 mm (e, f).

388

389 **Fig. 3.** Comparison of the reconstructed life history of *Pantolambda bathmodon* (black  
390 diamonds) to extant mammals using the PanTheria Dataset<sup>50</sup>. Suckling period, showing the range  
391 (31–75 days) estimated for *P. bathmodon* based on dental trace elements, bone histology, and  
392 dental wear (a); gestation period (b), violin plot of gestation period sorted by litter size (c),  
393 maximum lifespan, showing data from PanTHERIA (grey, solid line) and from the wild-only  
394 lifespan dataset of Newham et al.<sup>34</sup> (orange, dashed regression line) (d), and age at sexual  
395 maturity (e) for living mammals (green: placentals; blue: marsupials; purple: monotremes)  
396 plotted against adult body mass ( $\log_{10}$  g). Trendlines show generalized linear model regressions  
397 for placentals, marsupials, and monotremes, with 95% confidence intervals for the regression  
398 indicated by shaded envelopes. Horizontal lines show untransformed values. Silhouettes for each

399 panel show living taxa similar in the reconstructed parameter to the estimate for *P. bathmodon*.  
400 Silhouette of *Pantolambda bathmodon* created by SLS. Silhouettes of *Acinonyx*, *Antilocapra*,  
401 *Lycaeon*, *Orycteropus*, *Pan*, *Priodontes* have been adapted from Phylopic images (CC0 1.0  
402 <https://creativecommons.org/publicdomain/zero/1.0/>), silhouette of *Litocranius* is original  
403 artwork by GFF, and all others were generated from public domain images (CC0 1.0  
404 <https://creativecommons.org/publicdomain/zero/1.0/>).

405  
406

#### 407 **Methods:**

408 We prepared thin sections (see Supplementary Information) of the teeth and bones of 12  
409 specimens of *Pantolambda bathmodon*, including two partial skeletons and totalling 45 elements  
410 (23 bones and 22 teeth), collected from the Torrejonian NALMA of the Nacimiento Formation in  
411 the San Juan Basin of New Mexico, USA<sup>51</sup>. The specimens were selected to represent as much of  
412 the skeleton and as many tooth positions as possible and to capture varying degrees of dental  
413 wear, presumably attributable to individuals of different ages. The minimum number of  
414 individuals based on skeletal overlap *a priori* was three, but age variation indicates a minimum  
415 of seven individuals in our palaeohistological sample.

416 Incremental marks in the cementum, dentine, and enamel were counted from thin-  
417 sections to assess the timing and pace of tooth development. Cementum annulations, lines of von  
418 Ebner in the dentine, and cross-striations in the enamel were each clearly visible under cross-  
419 polarized light. Pairs of one light and one dark band in the acellular extrinsic fiber cementum  
420 near the cervix of the tooth were counted as growth layer groups representing annual growth  
421 cycles<sup>24,52,53</sup>. Lines of von Ebner in the dentine, clearly distinct from more broadly spaced

422 Andresen lines<sup>24,54</sup>, were counted from high-magnification photomontages as daily increments of  
423 growth. Likewise, cross-striations in the enamel were interpreted as daily increments of  
424 growth<sup>54,55</sup>. In every specimen, enamel cross-striations were aligned into clearly visible growth  
425 laminations, which have a daily periodicity<sup>37,56</sup>. The neonatal line in the enamel was identified as  
426 a prominent, Zn-enriched<sup>35</sup> accentuated line formed by discontinuities in the enamel prisms. In  
427 the dentine of the deciduous teeth, the earliest accentuated stress line was identified as the  
428 neonatal line<sup>24</sup>, which was supported by consistent changes in Zn concentration across the  
429 neonatal boundary<sup>35,57</sup> (Extended Data Fig. 4). The neonatal line was used to demarcate pre- and  
430 post-natal developmental periods, and to align sequences from different tooth positions within  
431 and between individuals. Daily growth increments in the enamel were traced from high-  
432 resolution photomontages to create temporal maps of daily dental development for each tooth.  
433 Enamel secretion, crown extension, and crown formation rates were estimated using the methods  
434 of Dirks et al.<sup>47</sup>

435 Dietary trace element concentrations were assessed using laser-ablation inductively  
436 coupled-plasma mass spectroscopy (LA-ICP-MS) at the University of Edinburgh and the  
437 University of St. Andrews Isotope Geochemistry (STAiG) lab. After pilot runs using an ATLEX-  
438 I-LR Analyte Excite 193 nm ArF excimer coupled to an Attom ICPMS, Nu Instrument at the  
439 University of Edinburgh, to assess the suitability of the material for analysis, a broad array of  
440 trace element concentrations (<sup>11</sup>B, <sup>23</sup>Na, <sup>25</sup>Mg, <sup>27</sup>Al, <sup>31</sup>P, <sup>43</sup>Ca, <sup>46</sup>Ca, <sup>55</sup>Mn, <sup>59</sup>Co, <sup>60</sup>Ni, <sup>63</sup>Cu, <sup>66</sup>Zn,  
441 <sup>88</sup>Sr, <sup>89</sup>Y, <sup>138</sup>Ba, <sup>208</sup>Pb, and <sup>238</sup>U) in the enamel and dentine of six teeth were mapped using LA-  
442 ICP-MS on an Agilent 8900-QQQ at the STAiG lab. Entire enamel sequences of three teeth (the  
443 paraconid of a lower first molar [NMMNH P-19541], the protoconid of a lower second molar  
444 [NMMNH P-19541], and the labial enamel of an incisor [NMMNH P-69918]) were scanned at

445 high resolution (20  $\mu\text{m}$  spot size, 10  $\mu\text{m s}^{-1}$  scanning speed, ICP cycle time 0.2889 s), with an  
446 effective pixel size of 60  $\mu\text{m}^2$  (Figs. S1–4). Small regions of interest in the deciduous teeth  
447 (NMMNH P-27844) were also scanned at high resolution (38  $\mu\text{m}$  spot size, 38  $\mu\text{m s}^{-1}$  scanning  
448 speed; Figs. S5–7). LA-ICP-MS data were processed and rasterized in Iolite v4.5.5.4<sup>58</sup>.  
449 Concentrations were normalized to and drift-corrected by a NIST 612 glass standard after gas  
450 blank subtraction, and standardized to ~40% Ca. Elemental maps and transects were registered to  
451 temporal maps of dental development to evaluate daily changes in diet.

452 Dental microwear was evaluated using scanning electron microscopy (SEM) using a Carl  
453 Zeiss SIGMA DH VP field emission SEM at the University of Edinburgh operated at 15 kV for  
454 secondary electron imaging of the fine-scale features of the occlusal surface of the first upper  
455 molar of NMMNH P-27844.

456 Reconstructed life history parameters for *P. bathmodon* were plotted alongside data from  
457 the PanTHERIA dataset<sup>50</sup> for comparison. Because the PanTHERIA dataset includes mostly  
458 captive individuals, which are likely to have greater maximum lifespans than wild individuals,  
459 the estimated maximum lifespan of *P. bathmodon* was also compared to a recent wild-only  
460 dataset of mammal maximum lifespan<sup>34</sup>. Relative importance of life history parameters for  
461 predicting body size was evaluated using multiple regression, and litter size was predicted using  
462 linear discriminant analysis based on gestation period. Principal components analysis was used  
463 to identify the closest living analogues of *P. bathmodon*.

464

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- 488
- 489

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497

498 **Author contributions** G.F.F. designed the study, made the thin sections, conducted the  
499 histological, life history, and statistical analyses, prepared the figures, and wrote the manuscript;  
500 P.E.dP. contributed to the study design, identification of the material, morphological analyses,  
501 and the drafting of the manuscript; J.T.S. and M.D. conducted the LA-ICP-MS analyses at  
502 STAiG and contributed to figures and drafting the manuscript; S.L.S. created the skeletal  
503 reconstruction of *P. bathmodon* and contributed to discussion and drafting the manuscript; L.E.P.  
504 conducted the LA-ICP-MS analyses at the University of Edinburgh and contributed to drafting  
505 the manuscript; N.J.C. conducted the SEM analyses; J.R.W. contributed to drafting the  
506 manuscript; T.E.W. oversaw the collection and curation of the material, provided stratigraphic  
507 data and contributed to drafting the manuscript; J.W.B.R. supervised the LA-ICP-MS analyses;  
508 S.L.B. coordinated the project and contributed to study design and drafting the manuscript.

509

510 **Competing interests** The authors declare no competing interests.

511



512 **Data availability** Fossil specimens in this study are housed at the New Mexico Museum of  
513 Natural History and Science, and the palaeohistological thin sections underlying the analyses are  
514 accessioned at the University of Edinburgh but will be returned to the NMMNH for permanent  
515 curation upon completion of our research. The living mammal datasets are available from Jones  
516 et al.<sup>50</sup> (<https://doi.org/10.6084/m9.figshare.c.3301274.v1>) and Newham et al.<sup>34</sup>  
517 (<https://www.nature.com/articles/s41467-020-18898-4#Sec18>). Overview images of  
518 palaeohistological slides and LA-ICP-MS data are deposited at Figshare (doi:  
519 10.6084/m9.figshare.20272737).

520

521 **Code availability** No custom code or software was used in the study.

522

### 523 **Additional information**

524 **Supplementary information** Supplementary Information is available for this paper.

525 **Correspondence and requests for materials** should be addressed to G.F.F.

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### 528 **Peer review information**

529 **Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints)

530

531 **Extended Data Captions:**

532

533 **Extended Data Fig. 1.** Incremental features of the teeth of *Pantolambda bathmodon*. (a)

534 Overview of coronal section of deciduous ultimate upper premolar of NMMNH P-27844 under

535 plane-polarized light (left) and cross-polarized light with a lambda filter (right), showing

536 locations of inset images. (b,c) Photomontages of the protocone exposed for the enamel (b) and

537 the dentine (c), showing excellent preservation of incremental features, neonatal line (dashed

538 line), and locations of close-up images. (d) Contrast-enhanced close-up of lines of von Ebner

539 preserved in the dentine (arrows), extending parallel to the dentinoenamel junction and

540 perpendicular to dentine tubules, and neonatal line (large arrow). (e) Contrast-enhanced close-up

541 of enamel cross-striations and daily laminations (arrows) in the enamel, extending sub-parallel to

542 the dentinoenamel junction and perpendicular to the enamel prisms. **Abbreviations:** NNL,

543 neonatal line. Scale bars: 1 mm (a), 200  $\mu\text{m}$  (b, c), 100  $\mu\text{m}$  (d, e).

544

545 **Extended Data Fig. 2.** Zn-enrichment of the neonatal line in the enamel of lower second molar

546 of NMMNH P-19541. (a, c) coronal sections of enamel of paraconid (a) and protoconid (c) under

547 cross-polarized light. Insets show location on coronal sections of entire tooth. (b, d), LA-ICP-MS

548 trace element maps, showing higher concentrations of Zn in discrete areas corresponding to the

549 neonatal line (white arrows). **Abbreviations:** DEJ, dentinoenamel junction; NNL, neonatal line;

550 OES, outer enamel surface. Scale bars: 1 mm (insets), 100  $\mu\text{m}$  (a–d).

551

552 **Extended Data Fig. 3.** Microwear on the dentition of NMMNH P-27844. (a) Right maxilla with

553 three deciduous premolars and adult first molar in occlusal view, showing location of scanning

554 electron microscopy (SEM) scan. (b) Overview secondary electron (SE) image of protocone of  
555 adult first molar, showing development of mesowear and location of close-up image. (c) Close-  
556 up SE image of scratches and gouges attributable to abrasive microwear; black arrows highlight  
557 curved scratches resulting from chewing motion. White arrows in (a) and (b) indicate lingual  
558 direction. **Abbreviations:** **d**, deciduous; **M**, upper molar; **P**, upper premolar.

559

560 **Extended Data Fig. 4.** Changes in zinc associated with birth in the deciduous upper premolars  
561 of NMMNH P-27844. Postnatal dentine is enriched in Zn in the deciduous upper ultimate  
562 premolar (a, b) and the deciduous upper second premolar (c, d). (a) Overview of thin section  
563 showing location of close-up image. (b) Mosaic image showing protocone in cross-polarized  
564 light, with trace element map overlain, showing change at histologically-inferred neonatal line  
565 (dashed line; NNL). (c) Overview image of embedded block showing location of trace element  
566 map. (d) Trace element map showing increased postnatal Zn. Scale bars: 1 mm (a, c), 500  $\mu\text{m}$  (b,  
567 d). **Abbreviations:** NNL, neonatal line.

568

569 **Extended Data Fig. 5.** Dental wear, cementum annulations, and maximum lifespan in the oldest  
570 sampled individuals. (a) Right first upper molar of NMMNH P-19625, showing extensive wear  
571 and erosion of enamel in most areas of the crown. (b) Anterior root of lower molar (tooth  
572 position unknown) from another individual of NMMNH P-19625, showing the location of the  
573 thin sections. (c) Overview transverse section of cervical root area, showing clear demarcation of  
574 cementum and dentine, and location of close-up. (d) Close-up of acellular extrinsic-fiber  
575 cementum in transverse section, showing six pairs of dark and bright bands comprising annual  
576 growth layer groups and alteration of external cementum; bright bands indicated with blue

577 arrows. (e) longitudinal section of the same tooth, showing thick external layer of cementum,  
578 continuity of growth layer groups, and location of close-up. (f) close-up image of acellular  
579 extrinsic-fiber cementum in longitudinal section, showing six annual growth layer groups and  
580 alteration of external cementum; bright bands indicated with orange arrows. Images c–f under  
581 cross-polarized light. Scale bars: 1 mm (a–c, e), 200  $\mu\text{m}$  (d, f).

582

583 **Extended Data Fig. 6.** Weaning transition recorded in the postcranial bones of NMMNH P-  
584 27844. (a) Transverse section of right humerus diaphysis under cross-polarized light, showing  
585 arrangement of tissues and large medullary cavity and location of close-up image. (b) Close-up  
586 of cortex of right humerus under cross-polarized light, showing increase in proportion of  
587 parallel-fibered bone (brighter tissues) later in growth (arrow), indicative of a decrease in growth  
588 rate. (c) Transverse section of right tibia diaphysis under plane polarized light, showing location  
589 of close-up image. (d) Close-up of cortex of right tibia under cross-polarized light with a lambda  
590 filter, showing transition (arrow) from highly-vascularized fibrolamellar bone with a high  
591 proportion of woven-fibered matrix (upper right) to more slowly-growing parallel-fibered bone  
592 with reduced vascularity (lower left). (e) Transverse section of right radius diaphysis under  
593 cross-polarized light, showing location of close-up image. (f) Close-up image of cortex of right  
594 radius under cross-polarized light with a lambda filter, showing annulus of parallel-fibered bone  
595 (arrow) separating region of highly-vascularized fibrolamellar bone (lower right) from region of  
596 less-vascularized fibrolamellar bone with a higher proportion of parallel-fibered bone (upper  
597 left). Scale bars: 1 mm (a, c, e), 500  $\mu\text{m}$  (b, d, f).

598

599 **Extended Data Fig. 7.** Transition to slower growth likely reflecting sexual maturity. (a) Coronal  
600 section of posterior dentary of NMMNH P-22012 under cross-polarized light with a lambda  
601 filter, showing locations of close-up images. Dark regions have been diagenetically altered by  
602 the deposition of opaque minerals. (b, c) Close-up of transition (dashed line) between faster-  
603 growing fibrolamellar bone (flb) and slower-growing lamellar bone (lb), indicative of sexual  
604 maturity, under cross-polarized light (b) and cross-polarized light with a lambda filter (c).  
605 Arrows indicate first line of arrested growth, deposited after the transition to slower growth.  
606 Scale bars: 1 mm (a), 200  $\mu$ m (b, c).

607

608 **Extended Data Fig. 8.** Life history of *P. bathmodon* compared to living mammals. (a, b)  
609 principal components analyses using the PanTHERIA dataset (placentals, green; marsupials,  
610 blue; monotremes, purple) incorporating suckling interval, gestation period, maximum lifespan,  
611 and age at sexual maturity, with adult body mass excluded (a) or included (b) as a variable; close  
612 living analogues to *P. bathmodon* indicated by silhouettes. (c–f) regressions of life history  
613 variables in placental mammals with 95% confidence intervals (thin black lines) centred on the  
614 generalized linear model regression trendline for suckling interval (c), gestation period (d),  
615 maximum lifespan (e), and age at sexual maturity (f), showing that *P. bathmodon* is within the  
616 95% confidence interval of placentals in all parameters. Silhouette of *Pantolambda bathmodon*  
617 created by SLS. Silhouettes of *Orycteropus* and *Priodontes* adapted from Phylopic images (CC0  
618 1.0 <https://creativecommons.org/publicdomain/zero/1.0/>), silhouette of *Leptonychotes* is original  
619 artwork by GFF, silhouette of *Phoca* was generated from a photograph taken by GFF, and all  
620 others were generated from public domain images (CC0 1.0  
621 <https://creativecommons.org/publicdomain/zero/1.0/>).

622

623 **Extended Data Fig. 9.** Relationship between neonate mass and adult body mass in extant  
624 mammals. (a) Generalized linear model regression of neonate body mass against adult body mass  
625 for all species in the PanTheria dataset, showing clear separation of placental mammals (green,  
626  $p\text{-value} < 2.2 \times 10^{-16}$ ) from non-placental mammals ( $p\text{-value}: 4.07 \times 10^{-6}$ ); 95% confidence interval  
627 for regression slope shown as shaded envelope. (b) Neonate body mass plotted against adult  
628 body mass for placental species, showing tight correlations of neonate mass and adult mass ( $p$   
629 values both  $< 2.2 \times 10^{-16}$ ); 95% confidence interval for generalized linear model regression slope  
630 shown as shaded envelope. (c) Gestation period plotted against neonate body mass; 95%  
631 confidence interval for generalized linear regression slope shown as shaded envelope. (d)  
632 Relative importance of multiple regression of adult body mass against neonate weight, gestation  
633 period, maximum lifespan, time to sexual maturity, and suckling period, showing relative  
634 contribution of factors to adult body mass; confidence intervals derived from 1000 replicates of  
635 bootstrapping.

636

637

638 **Extended Data Table 1. Quantitative dental histological data for *Pantolambda bathmodon*.**

639 Note: \*estimate, see Supplement for further details. For teeth with a neonatal line, † prenatal, ‡  
640 postnatal. §, counted as a pair of light and dark bands; - inapplicable or not available;

641