Despite considerable advances in knowledge of the anatomy, ecology and evolution of early mammals, far less is known about their physiology. Evidence is contradictory concerning the timing and fossil groups in which mammalian endothermy arose. To determine the state of metabolic evolution in two of the earliest stem-mammals, the Early Jurassic *Morganucodon* and *Kuehneotherium*, we use separate proxies for basal and maximum metabolic rate. Here we report, using synchrotron X-ray tomographic imaging of incremental tooth cementum, that they had maximum lifespans considerably longer than comparably sized living mammals, but similar to those of reptiles, and so they likely had reptilian-level basal metabolic rates. Measurements of femoral nutrient foramina show *Morganucodon* had blood flow rates intermediate between living mammals and reptiles, suggesting maximum metabolic rates increased evolutionarily before basal metabolic rates. Stem mammals lacked the elevated endothermic metabolism of living mammals, highlighting the mosaic nature of mammalian physiological evolution.
Recent discoveries and analyses have revolutionized our knowledge of Mesozoic mammals, revealing novel aspects of their ecology, development, systematics and macroevolution. However, details of physiology are more difficult to determine from fossils, and our knowledge of physiological evolution remains comparatively poor. Living mammals are endotherms, possessing the ability to control and maintain metabolically produced heat and have a substantially higher capacity for sustained aerobic activity than ectothermic animals. The origin of endothermy is an important event in mammalian evolution, often noted as key to their success. There are a number of competing evolutionary hypotheses for the origin of endothermy: (a) selection for higher maximum metabolic rates (MMRs) enhanced sustained aerobic activity, (b) selection for higher basal metabolic rates (BMRs) enhanced thermoregulatory control, or (c) MMRs and BMRs evolved in lockstep with each other.

Direct evidence from living mammals to support these hypotheses is equivocal. Recent analyses find no long-term evolutionary trend in BMR contradicting earlier suggestions of increasing BMR throughout the Cenozoic and so implying that the Middle Jurassic (~170 Ma) most recent common ancestor (MRCA) of living mammals possessed a BMR within the range of present-day mammals. Several indirect indicators of metabolic physiology in fossil synapsids have been suggested but provide contradictory evidence for the timing of the origin of endothermy and its evolutionary tempo. These include: the presence of fibrolamellar long-bone histology, first seen in the Early Permian synapsid Ophiacodon (~300 million years (Ma) ago); the presence of an infraorbital canal and lack of parietal foramen, used to infer facial whiskers, fur, lactation and endothermy in the Late Permian (~255 Ma) therapsid Glanosuchus; and the mammaliaform (stem mammal sensu Rowe20) Morganucodon21,22; and acquisition of a parasagittal gait in the Early Cretaceous (~125 Ma) therian mammals Eomaia and Sinodelphys23. Several recent studies provide more quantitative links to physiological parameters. Oxygen isotopes were used to infer elevated thermometabolism in Middle–Late Permian (~270–255 Ma) eucynodonts24, red blood cell size diminution in Late Permian (~255 Ma) therapsid Glanosuchus, used to suggest that mammalian levels of endothermy evolved by the Late Triassic (~210 Ma)18; a trend towards increased relative brain size initiated in Late Triassic non-mammaliaform cynodonts19 and the mammaliaform (stem mammal sensu Rowe20) Morganucodon21,22; and acquisition of a parasagittal gait in the Early Cretaceous (~125 Ma) therian mammals Eomaia and Sinodelphys23. Several recent studies provide more quantitative links to physiological parameters. Oxygen isotopes were used to infer elevated thermometabolism in Middle–Late Permian (~270–255 Ma) eucynodonts24, red blood cell size diminution in Late Permian (~255 Ma) euatheriodontid therapsids was linked via two proxies to increased MMR25 and osteocyte lacuna shape correlations suggested “mammalian” resting metabolic rates in Permo-Triassic (~250 Ma) dicynodonts26.

However, the inconsistency of these characters, in time and with respect to phylogeny, along with re-assessments of function in relation to endothermy, limit their use as conclusive indicators of modern mammalian levels of endothermy in fossil taxa. Such temporal and phylogenetic heterogeneity suggests that the evolution of mammalian endothermy followed a complex, mosaic pattern with different physiological aspects likely evolving independently, and at separate rates, towards current mammalian levels. Additionally, few of these physiological proxies are directly related to measurable aspects of metabolic rate.

To address these issues, we use two proxies to improve understanding of physiology at one of the most important nodes along this transition. We do so by estimating BMR and growth rate, and calculating a known proxy for MMR, for two of the earliest known mammaliaforms, Morganucodon and Kuehnotherium31. Using cementochronology to estimate maximum lifespan by counting growth increments in synchrotron radiation-based micro-computed tomographic (µCT) data of fossil dental cementum, we estimate that both taxa had significantly longer lifespans than extant mammals of comparable size. By regressing lifespan against BMR and postnatal growth rate in extant mammals and reptiles, we in turn estimate significantly lower values for both of these metrics for the earliest mammaliaforms. However, when we compare the blood flow index (the ratio between femoral nutritive foramina area and femur length that serves as a proxy for MMR) of Morganucodon with those of extant taxa, we find that Morganucodon had an intermediate value between living mammals and reptiles. These results suggest that basal mammaliaforms occupied a metabolic grade similar to living reptiles and had yet to achieve the endothermic physiology of living mammals.

Results
Lifespan as a proxy for mammaliaform physiology. We used maximum lifespan (i.e. the single longest known lifespan of a taxon) estimates for fossil mammaliaform taxa as a proxy for both BMR and postnatal growth rate. In extant tetrapods, negative correlations exist between maximum lifespan and BMR and between maximum lifespan and growth rate. Growth rates have been shown to correlate strongly with metabolic power in extant vertebrates, with endotherms growing an order of magnitude faster than ectotherms. Maximum lifespan is an applicable value for fossil samples, as, unlike other metrics (e.g. 10% most long lived or mean lifespan of a cohort), it does not rely on cohort- or population-based statistics that fossil samples cannot fulfill. This value is also less susceptible to extrinsic population-level factors on lifespan, such as disease or predation, and relates most closely to the physiological limit of lifespan of an organism. An accurate assessment of maximum lifespan in fossil mammals can therefore be used to estimate their metabolic potential.

To estimate mammaliaform lifespans, we used cementochronology. This well-established technique, which counts annual growth increments in tooth-root cementum, has been used to record lifespans in extant mammals37 with >70 species aged using this technique. Cementum is a mineralized dental tissue surrounding the tooth root (Fig. 1a, b), attaching it to the periodontal ligament and anchoring the tooth within the alveolus. Growth of cementum is continuous throughout life in extant mammals and seasonally appositional in nature, forming a series of increments of differing thickness and opacity when viewed in histological thin sections under light microscopy. The correlation between increment count and chronological age is well documented, with one thick and one thin increment deposited every year. It has been shown that the thin, hyper-mineralized opaque increments record growth rate reduction in less favourable seasons. Despite this potential, cementochronology has not previously been attempted for fossil mammals older than the Pleistocene (2.6 Ma), because histological thin sections destroy fossils and provide only a restricted field of view. We overcame these problems by using propagation phase-contrast X-ray synchrotron radiation microtomography (PPC-µCT) to non-destructively image fossilized cementum increments. The sub-micrometre resolution, fast-throughput and three-dimensional (3D) nature of PPC-µCT allows for large sample sizes and for increments to be imaged along their entire transverse and longitudinal trajectories in volumetric PPC-µCT data sets. Cementum increments are known to occasionally split and coalesce, creating errors in counts based on single, or limited numbers of, two-dimensional thin sections created for each tooth (Supplementary Fig. 1). PPC-µCT imaging and 3D segmentation of individual increments across extensive vertical distances within
the cementum allowed us to confidently distinguish principal annual increments from any accessory increments created by lensing and coalescence (see “Methods”).

Morganucodon and Kuehneotherium are shrew-sized insectivores1, which co-existed on a small landmass during the Early Jurassic marine transgression (Hettangian-early Sinemurian, ∼200 Ma) in what is now Glamorgan, South Wales, UK45 (Supplementary Notes 1 and 2 and Supplementary Data 1 and 2). Thousands of their bones and teeth were washed into karst fissures that have subsequently been revealed by quarrying. This provides a rare opportunity to analyse large samples of fossil material needed for confident estimation of maximum lifespan. Importantly, these are the earliest diphyodont taxa (Fig. 2), with a single replacement of non-molar teeth and no molar tooth replacement31, and so estimates of lifespan are accurate to the time of the measured tooth-root formation.

The fossil sample studied included both isolated teeth and mandibles with multiple teeth or roots in situ. We applied PPC-SRµCT to 87 Morganucodon specimens (52 isolated teeth, 35 dentaries, all Morganucodon watsoni) and 119 Kuehneotherium specimens (116 isolated teeth, 3 dentaries) (see “Methods”). From these, 34 Morganucodon and 27 Kuehneotherium specimens were sufficiently well preserved for three observers to independently estimate lifespan from cementum increments. These estimates were compared to validate their accuracy and precision (see “Methods”; Supplementary Data 1). The remainder showed physical and/or diagenetic damage that prevented increment measurement (Supplementary Fig. 2).

The cementum of Morganucodon and Kuehneotherium (Fig. 1a, b) is distinguished from dentine in our PPC-SRµCT data by a distinct boundary layer separating the two tissues. This lies external to the granular layer of Tomes of the dentine and is interpreted as the hyaline layer of Hopewell-Smith (Fig. 1c–g). Synchrotron nanotomographic imaging (30 nm isotropic voxel size) highlights individual Sharpey’s fibre bundles (linking cementum to the periodontal ligament in extant mammals) visible in several exceptionally preserved specimens, which can be traced radially through the cementum (Fig. 1g). Across the tooth-root transverse axis, cementum is ∼10–70 µm radial thickness and displays a series of contrasting light and dark circumferential increments representing different material densities (Figs. 1e–g and 3a–d). Higher-density increments (represented by greater greyscale values) are on average 2–3 µm radial thickness, and lower density increments are 1–3 µm radial thickness (Fig. 1c–g and 3a–d). Individual increments can be followed continuously both longitudinally and transversely through the entire scanned volume of a tooth root (Fig. 3e, f).

Increment count accuracy, tooth eruption sequence and timing. We tested the accuracy of cementum increment counts for predicting lifespan in fossils by additional PPC-SRµCT imaging and counting of increments in the cementum of several teeth along the tooth row in eight dentulous Morganucodon specimens with a range of teeth in situ (Table 1) and of growth increments (lines of arrested growth (LAGs)) in the periostal region of the
dentary bone in two of these (Fig. 4). In both specimens where dentary LAGs are found, counts are identical with the cementum increments in the teeth (p3–m2; Fig. 4). Also, comparisons between counts of cementum increments are identical across all four premolars (p1–p4) and the anterior molars (m1–m2), in all specimens where they occur together (Table 1). This agreement between p1–m2 teeth and dentary increment counts indicates that growth in both teeth and jaws was following the same, circum-annual rhythm, as previously reported for multiple extant mammal species. We consider this to be strong support for the circum-annual rhythm, as previously reported for multiple extant mammals.

The increment counts along Morganucodon dentary toothrows can also provide information on eruption sequence and timing details. The ultimate incisor (i4), the canine and the third molar erupted in the following year. We do not have information on eruption timing of more anterior incisors, or the fourth molar, which was long lived relative to comparatively sized extant mammals (see below), this pattern of most of the adult tooth row being in place during the first 2 years of life is also supportive of a relatively short (compared with its total lifespan) juvenile stage and determinate growth. The absolute length of these stages in Morganucodon is, however, considerably longer than extant mammals of comparable body size. Unfortunately, dentulous specimens of Kuehneotherium are rare, and there are no tooth rows with cementum increment counts in our sample.

Long lifespans, low BMR and growth rates. Cementum increment counts provide a minimum estimate of maximum lifespan of 14 years for Morganucodon and 9 years for Kuehneotherium (Figs. 3 and 5a and Supplementary Data File 1). These may underestimate true maximum lifespan, as any damage to outer cementum increments would reduce estimated maximum lifespan. One-way analysis of variance (ANOVA) comparisons of mean intra-observer coefficient of variation (CV) between our study and ten previous cementochronological studies of different extant mammal species suggest that values for PPC-SRuCT data (Shapiro–Wilk W = 1) of Morganucodon (CV = 9.32) and Kuehneotherium (CV = 4.89) are significantly lower than previous thin section-based studies (W = 0.93; minimum extant CV = 14.2, mean CV = 21.8, standard deviation = 5.87; F = 11.12, p < 0.01; Supplementary Table 1).

We estimated body mass ranges of 10.7–25.0 g (mean 17.9 g) for Morganucodon and 14.9–32.7 g (mean 23.8 g) for Kuehneotherium (minimum mass estimates based on skull length and maximum mass estimates on dentary length; see “Methods”). Maximum lifespan and mean body mass for the mammaliaforms were compared with published data for large
samples of terrestrial, non-volant wild extant mammal \((n = 278)\) and non-avian reptile \((n = 256)\) species (“Methods”; Supplementary Data 3). Maximum wild lifespans of extant taxa were chosen for comparison with our fossil taxa, as these values are the closest analogue to our estimated lifespans, relative to captive lifespan values. To ensure robustness of our results, we additionally analysed maximum captive lifespans of extant taxa below 100 g, which show an average increase above maximum wild lifespans of approximately 3.43 and 4.38 years per taxon for mammals and reptiles, respectively (Supplementary Fig. 4). Broad results of statistical tests, and the overall conclusions of our study, are unchanged regardless of whether wild or captive data are used for analysis and comparisons between our fossil lifespans and the lifespans of extant taxa (see Supplementary Note 4 and Supplementary Figs. 1–6).

Phylogenetic generalized least squares (PGLS) regression of log10-transformed values shows that the fossil mammaliaforms fall within the range of extant reptiles and have longer maximum lifespans for their size and are further above the mammal regression mean, than all extant mammals under 4 kg (the long-lived and secondarily dwarfed mouse lemur Microcebus murinus is closest). Only the short-beaked echidna Tachyglossus aculeatus, a monotreme with long lifespan and low metabolic rate, exceeds the distance above the mammalian mean for Kuehneotherium, but not for Morganucodon (Fig. 5b). One-way phylogenetic analysis of covariance (ANCOVA) comparisons show that regression slopes for extant mammals and reptiles are statistically similar \((p = 0.35)\) but their means are significantly separated \((p = 0.036)\), with reptiles on average living 18.3 years longer than mammals of the same body mass.

To estimate BMR, we used PGLS and recovered significant correlations between log10-transformed values of maximum wild lifespan and mass-specific standard metabolic rate (msSMR; measured in mL O2 h\(^{-1}\) g\(^{-1}\) and analogous with BMR in extant mammals—SMR was used as BMR cannot be measured in reptiles\(^{50}\) from published data for 117 extant mammals and 55 extant reptiles (“Methods”; Supplementary Data 3 and Fig. 6a). Using the correlation between maximum wild reptile lifespan and msSMR and plotting our mammaliaforms directly onto this

Table 1 Cementum and dentary increment counts for each element of dentulous Morganucodon specimens.

| Specimen      | Element | Increments |
|---------------|---------|------------|
| NHMUK PV M 95790 | i4      | 7          |
| NHMUK PV M 95790 | c       | 7          |
| NHMUK PV M 95790 | p1      | 8          |
| NHMUK PV M 95790 | p2      | 8          |
| NHMUK PV M 95790 | p3      | 8          |
| NHMUK PV M 96413 | p3      | 5          |
| NHMUK PV M 96413 | p4      | 5          |
| NHMUK PV M 96413 | m1      | 5          |
| NHMUK PV M 96413 | Dentary | 5          |
| NHMUK PV M 96396 | p4      | 4          |
| NHMUK PV M 96396 | m1      | 4          |
| NHMUK PV M 96396 | m2      | 4          |
| NHMUK PV M 96396 | m3      | 3          |
| NHMUK PV M 96396 | Dentary | 4          |
| NHMUK PV M 95809 | m1      | 3          |
| NHMUK PV M 95809 | m2      | 3          |
| NHMUK PV M 104128 | m1     | 5          |
| NHMUK PV M 104128 | m2     | 5          |
| NHMUK PV M 96441 | m1      | 5          |
| NHMUK PV M 96441 | m2      | 5          |
| NHMUK PV M 104130 | m1   | 5          |
| NHMUK PV M 104130 | m2   | 5          |
| NHMUK PV M 104130 | m3   | 4          |
| NHMUK PV M 104129 | m1   | 9          |
| NHMUK PV M 104129 | m2   | 9          |
| NHMUK PV M 104129 | m3   | 8          |

The lower dental formula of Morganucodon is 4:1:4:4–51.
regression line, we estimated a reptile-derived msSMR of $0.055 \text{mL O}_2 \text{h}^{-1} \text{g}^{-1}$ (Morganucodon) and $0.08 \text{mL O}_2 \text{h}^{-1} \text{g}^{-1}$ (Kuehneotherium) (Fig. 6a). We additionally used the correlation between maximum wild mammal lifespan and msSMR and estimated a mammal-derived msSMR of $0.36 \text{mL O}_2 \text{h}^{-1} \text{g}^{-1}$ for Morganucodon and $0.46 \text{mL O}_2 \text{h}^{-1} \text{g}^{-1}$ for Kuehneotherium (Fig. 6a). When log$_{10}$ PGLS is used to regress these estimates against body mass, both mammaliaforms fall outside the 95% predictor interval (PI) of the mammalian data and within the reptile range of msSMR, regardless of whether mammaliaform msSMR is estimated from reptilian or mammalian data (Fig. 5c). This suggests that the mammaliaforms had significantly lower msSMR values when compared to extant mammals of similar size. The comparably sized mammal (<100 g) of lowest msSMR is

**Fig. 4** Shared increment patterns between m1 and m2 tooth-root cementum and the dentary of *Morganucodon* specimen NHMUK PV M 96413. a Four lines of arrested growth and a fifth incipient one are visible within the periosteal region of the dentary, each highlighted by three-dimensional segmented bands of differing colour corresponding to coloured arrows in the accompanying transverse PPC-SRµCT slice. Only LAGs persisting through the volume are segmented and highlighted. This pattern is mirrored in b the anterior root of the m1 tooth, c the posterior root of the same m1 tooth and d the anterior root of the m2 tooth. Scale bars represent 30 µm.
the marsupial *Dasycercus cristicauda*, with a maximum wild lifespan of 7 years and msSMR of 0.63 mL O2 h$^{-1}$ g$^{-1}$ (Fig. 5c).

We estimated growth rates using PGLS correlations between maximum wild lifespan and growth rate from published data from 115 extant mammals and 30 extant reptiles ("Methods"; Supplementary Data 3 and Fig. 6b). From mammal data, we...
estimate growth rate constants $K$ (days$^{-1}$—see “Methods”) of 1.085$^{-2}$ days$^{-1}$ (Morganucodon) and 1.474e$^{-2}$ days$^{-1}$ (Kuehneotherium). From reptile data, we estimated $K = 4.91^{-4}$ days$^{-1}$ (Morganucodon) and $K = 6.65^{-4}$ days$^{-1}$ (Kuehneotherium) (Fig. 6b). Log$_{10}$ PGLS regression against body mass again places both mammaliaforms outside the mammalian 95% PI and within the reptile growth rate range, whether estimated from mammalian or reptilian data (Fig. 5d). The lowest growth rate of any <100 g extant mammal is $K = 3.24e^{-2}$ days$^{-1}$ for the Mongolian gerbil Meriones unguiculatus.

In summary, our estimates of maximum lifespan provided by tomographic imaging of cementum increments in Morganucodon and Kuehneotherium are significantly longer than the maximum wild lifespan of any extant mammal of comparable body mass. These lifespans provide estimates of SMR/BMR and growth rate that are significantly lower than comparably sized extant mammals and instead correspond to those of extant reptiles.

**Femoral blood flow shows intermediate MMR.** To compare our fossil mammaliaform BMR estimates with MMR, we used a second proxy directly linked to MMR$^{31}$. The ratio between nutrient foramen area and femur length has been used as an index for relative blood flow ($Q_i$) through the femur during and after metabolically demanding exercise ($Q_i = r_i^2/L$, where $r_i =$ foramen radius and $L =$ femur length), previously shown to correlate well with MMR$^{31}$. From μCT data of the six most complete Morganucodon femoral diaphyses available, we segmented all nutrient foramina (Fig. 7a) and estimated their area by measuring their minimal radii (see “Methods”). Kuehneotherium could not be included as no suitable femoral specimens are known.

We estimated a $Q_i$ of 3.829e$^{-7}$ mm$^3$ for Morganucodon and compared this with published and new data (“Methods”) for extant mammals ($n = 69$) and reptiles ($n = 30$). The latter includes varanids ($n = 8$), which in the absence of mammalian predators fill an active hunting niche and tend to have mammalian MMR levels while retaining reptilian BMR levels$^{31}$ (Supplementary Table 2). One-way ANCOVA comparisons show that means of GLS regression slopes for extant mammals and non-varanid reptiles are significantly different ($p < 0.01$) while the slopes are similar ($p = 0.16$). Log$_{10}$ GLS regression of body mass and $Q_i$ shows that Morganucodon is further above (higher $Q_i$ for its mass) the non-varanid reptile mean than all non-varanid reptiles (phylogenetically informed statistical comparisons were not used here due to the non-significant lambda values showing no phylogenetic signal in the taxa used, see “Methods”). However, Morganucodon is also slightly further from the mammalian mean than the non-varanid reptile mean and considerably closer to small non-varanid reptile species data points than those of small mammalian species (Fig. 7b). This intermediate $Q_i$ and so inferred intermediate MMR, suggests that, while retaining typical reptilian BMR and growth rates, Morganucodon had MMR above non-varanid reptiles but not as high as mammals or actively foraging varanid reptiles.

**Discussion**

We have used two quantitative proxies to determine the metabolic status of early mammaliaforms. Relatively long lifespans for both Morganucodon and Kuehneotherium result in SMR/BMR and growth rate estimates equivalent to modern reptiles of comparable size and indeed at the higher lifespan/lower BMR/slower growth end of the reptile scale for the femur data on Morganucodon. This is true whether we compare our fossil estimates to wild lifespans of extant taxa or estimate fossil “captive” lifespans and compare them to captive values for extant taxa. In contrast, femoral blood flow estimates ($Q_i$) suggest that the MMR of Morganucodon was intermediate between extant non-varanid reptiles and mammals. We therefore infer that in Morganucodon increased MMR (and so also absolute aerobic capacity (AAC) = MMR – BMR) was initially selected for before BMR and that the MMR-first hypothesis is the best-supported model for the evolution of mammalian endothermy. We suggest that at least Morganucodon, if not also Kuehneotherium, occupied a metabolic grade approaching extant varanids: able to undergo longer bouts of aerobically demanding activity than non-varanid reptiles but not capable of sustaining either mammalian levels of aerobic activity or the elevated thermometabolism exhibited by living endotherms.
Evidence from non-mammalian synapsids (including changes in gait\(^2\), long bone histology\(^{15}\) and development of secondary osteological features correlated with increased metabolic rate\(^{17,18}\)) indicate unquestionable changes in physiology from pelycosaurs to mammaliaform-grade taxa. Determine growth\(^7\) and reduction of dental replacement (diphyodonty) in basal mammaliaforms permitted more precise occlusion\(^5\), which has been considered a key innovation in the development of mammalian endothermy by enabling increased assimilation and higher metabolism\(^{53}\). However, determinant growth and diphysodonty appear to have preceded the appearance of modern mammalian levels of endothermy, at least in *Morganucodon* and *Kuehneotherium*. We therefore suggest that the development of precise occlusion in basal mammaliaforms\(^6\) may be more associated with dietary specialization and niche partitioning\(^1\).

Comparison of our results to those of other recent studies of physiology in fossil synapsids supports the hypothesis of a complex, mosaic pattern for the evolution of endothermy, with different characters being selected for at different rates through time, and with respect to phylogeny. For example, the size diminution associated with plesiomorphic mammaliaform transition\(^54\) may have reversed the evolutionary trajectory of some previous histological proxies for endothermy\(^35\), contributing to the complex, contradictory patterns observed. Our study also suggests that more work is needed to compare fossil and extant ectothermic and endothermic taxa directly in order to better understand their relative metabolic properties. Many previous studies rely on simple binary divisions, such as the presence/absence of fibrolamellar bone and/or respiratory nasal turbinates. These proxies cannot represent accurately the complex series of physiological characteristics that range between “ectothermy” and “endothermy” and are frequently distributed homoplastically across the synapsid phylogeny, individually and with respect to each other. Other studies provide relative data such as preserved apatite oxygen isotopes\(^{24}\) that allow comparisons with co-habiting ectothermic taxa but cannot be directly compared to extant data and so do not suggest where the studied fossil tax fall in the metabolic spectrum of extant vertebrates. However, our results are compatible with recent work on living mammals, suggesting that the BMR of the Middle Jurassic (~170 Ma) mammalian MRCA was comparable to present-day values\(^{13}\). This indicates that evolution towards modern-day mammalian endothermy occurred during the 25 million year-long Early Jurassic and suggests that the mammalian mid-Jurassic adaptive radiation\(^{45}\) was driven by this or vice versa.

In conclusion, our data offer a direct link to measurable aspects of endothermy, such as BMR and MMR, at a key point in mammalian evolution. Further work applying these methods to additional Mesozoic mammaliaforms and mammals, and comparison with evidence from other physiological characters, will allow the evolutionary tempo and mode of multiple aspects of mammalian physiology to be determined. The early mammaliaforms *Morganucodon* and *Kuehneotherium* possessed surprisingly low, reptile-like metabolic rates plus a mixture of plesiomorphic and derived characters\(^7\) relating to life history and physiology. Ultimately, we can no longer assume that the endothermic metabolism of living mammals had evolved in the earliest mammaliaforms.

**Methods**

**Choice of fossil specimens.** All *Morganucodon* and *Kuehneotherium* specimens are from the Early Jurassic St Brides Island fissure suite, from Glamorgan, South Wales (UK)\(^{1,6,37}\). *Morganucodon* specimens used for the cementum analysis are from the collections of the Natural History Museum, London, UK (NHMUK), *Kuehneotherium* specimens are from the collections of the NHMUK and University Museum of Zoology Cambridge, UK (UMZC) and the *Morganucodon* femora specimens are from the collections of UMZC. The *Morganucodon* specimens are all one species, *M. watsoni*, from Pontalun 3 fissure, excavated in 1962–1963 in Pontalun quarry (now known as Lithalun)\(^{15,36}\). *Kuehneotherium* is a senior junior of *Morganucodon* from Pontalun 3 fissure and the specimen analysis is from three Glamazon fissures in Pontalun and Pant quarries: Pontalun 3, Pant 2, and Pant 4. Pontalun 3 and Pant 2 fissures have a relatively impoverished fauna, and Pant 4 has a more diverse biota\(^{47}\) (Supplementary Data 2). *Kuehneotherium* from Pontalun 3 fissure is *Kuehneotherium prae-cursoris*, but those from the scissurals are considered to be different species, based on small molar differences\(^88\). All specimens from Pontalun 3 fissure in the NHMUK (*Morganucodon* and *Kuehneotherium*) were prepared by immersing dried blocks of clay matrix in hot tap water, with the addition of dilute hydrogen peroxide (3%) and sodium hexametaphosphate (Calgon) in very small quantities. The UMZC collection were prepared with 10% acetic acid. *Kuehneotherium* specimens from Pant quarry (Pant 2 and Pant 4) were collected by the Kermack team from University College London, between 1955 and 1978, and are from a harder matrix, which was prepared with 15% acetic acid\(^{10}\).

The *Morganucodon* and *Kuehneotherium* specimens used for cementum analysis are either isolated teeth or dentary specimens with a range of teeth in situ. The lower dental formula of *Morganucodon* is 1:1:1:2–5 and for *Kuehneotherium* it is 1:1:1:2–6\(^5\). In *Morganucodon*, the majority of isolated teeth measured were lower second molars (m2) since they are easily identified, are relatively large, have robust separated roots and, as anterior diphysodont molars, they should erupt relatively early and are not replaced, therefore offering a near-complete record of life history. However, i4, c3, p3, p4, m1, m3 and m4 teeth were also studied in dentulous *Morganucodon* specimens. Dentulous *Kuehneotherium* specimens are extremely rare and so isolated teeth were scanned in almost all cases. For *Kuehneotherium*, all appropriate teeth were chosen; the distinctive p5 and p6, and a range of lower and upper molars, which can be identified to anterior, mid or posterior tooth row on the degree of triangulation\(^58\).

**Tomographic imaging of cementum.** Pilot scans of two *Morganucodon* lower second molars (NHMUK PV M 104131 and NHMUK PV M 104132) were carried out in 2011 on the nanotomographic imaging beamline ID22 at the European Synchrotron Radiation Facility (ESRF), Grenoble, France (project EC 1064). For ID22, we used the following experimental settings for computed tomographic (CT) imaging: X-ray energy of 29.6 keV, 1999 projections over a 180° rotation, 0.5 ms exposure time, 321 nm voxel size, 405 mm sample-to-detector distance, diamond windows (for the p5–p6), a 20-µm-thick LSQ scintillator doped with Tb, and 1.35 µm Al filter, single propagation distance tomography.

During a 4-day experiment at the ID19 beamline of the ESRF (18/04/2014-22/04/2014), 71 additional *Morganucodon* specimens (52 isolated teeth and 19 dentaries) and 2 pilot *Kuehneotherium* specimens were scanned (project ES 152). A single harmonic U13 undulator was used as the X-ray source, delivering a pink X-ray beam with peak energy at 26.5 keV, with a 1.4 mm Al filter used to cut the background lower energies. The detector was a microscop optic system coupled to a sCMOS sensor (PCO edge 5.5), mounted with a 10-µm thick GGG:Eu scintillator. Scans were performed using single propagation distance tomography (15 mm propagation distance, detector propagation distance), an exposure time of 2499 angular projections over a 360° scan and at voxel sizes of 280, 347 and 700 nm.

Subsequently, 117 additional *Kuehneotherium* specimens (116 isolated teeth and one dentary) and 12 additional *Morganucodon* dentary specimens were scanned during a 3-day experiment at the TOMCAT tomographic beamline of the Swiss light source (SLS), Villigen, Switzerland (13/04/2015-16/04/2015). The beam was set at an energy of 20 keV using a double multilayer monochromator, a LSO: Tb scintillator and a pco.EDGE 5.5 detector. Samples were scanned using single propagation distance tomography (14 mm sample-to-detector propagation distance), an exposure time of 150 ms and 1500 angular projections over a 180° scan at a voxel size of 330 nm. A *Kuehneotherium* lower molar (UMZC Sy 141) was imaged at 1.2 µm voxel size (with an exposure time of 150 ms and 1500 angular projections over 180°) to provide the 3D volume presented in Fig. 1b.

Three juvenile *Morganucodon* dentary specimens, with roots from final deciduous premolars (NHMUK PV M 27312, NHMUK PV M 27474 and NHMUK PV M 27465) and an older individual with extensive wear (NHMUK PV M 27465), were scanned during a 3-day experiment at the TOMCAT beamline of the SLS (07/03/2016-10/03/2016). The beam energy was set at 21 keV using a double multi-layer monochromator. Samples were scanned using single propagation distance tomography (14 mm sample-to-detector propagation distance), an exposure time of 200 ms and 1601 angular projections over a 180° scan at a voxel size of 330 nm.

CT reconstructions of the above tomographic data were generated using a filtered back-projection algorithm coupled with “Paganin-style” single distance phase retrieval\(^3\) algorithms developed in-house at the respective beamlines\(^{66,61}\). For data from ID19, β = 8.1 × 10\(^{-9}\), γ = 9.8 × 10\(^{-9}\). For data from ID22, β = 3.7 × 10\(^{-8}\), γ = 1.7 × 10\(^{-10}\).

Of the 71 *Morganucodon* molar specimens imaged at beamline ID19 in 2014, 4 were additionally imaged at the nano-imaging beamline ID16A of the ESRF synchrotron (project ES 152). These were imaged using holotomography\(^{68}\) from four different propagation distances. Here, a commercially available self-suspended device detector with an effective pixel size of 3 µm and a 23-µm-thick GGG:Eu scintillator at both 17 keV and 33.6 keV. The selected voxel sizes were 10, 25, 30...
and 130 nm. The number of angular projections recorded over 180° varied between 1200 and 2000 and the exposure times were set at 250–800 ms. To generate the image containing the virtual section in Fig. 1g with 30 nm voxel size, the four focus-to-sample distances were 2.65, 13.19, 15.36 and 19.87 mm and the sample-to-detector distance was 1.2684 m. To produce the 3D model presented in Fig. 1a, a *Morganucodon* lower molar (NHMUK PV M 104134) was imaged using µCT at the University of Helsinki in March 2013. µCT was performed using a Nano MX180 NE (Phoenix X-ray Systems & Services GmbH) with a CMOS detector (Hamamatsu Photonics) and a high-power transmission-type X-ray nanofocus source with a tungsten anode. A total of 900 angular projections were collected for a 180° rotation, at an exposure time of 500–900 ms at a pixel size of 2 x 2 μm². The raw projection data were reconstructed using filtered back-projection by the reconstruction software dátos rec supplied by the system manufacturer.

**Increment counting and creation of virtual thin sections.** Cementum increments were counted in CT data using modifications to the techniques suggested by the Cementochronology Research Program56 to take into account the 3D nature of the PPC-SRµCT cementum data. First, the cementum was visually inspected throughout the entire volume of each scan, in transverse PPC-SRµCT slices using ImageJ/Fiji63 to distinguish between specimens that could be confidently interpreted as preserving cementum increments or those that were too badly affected by diagenesis for increment counting. Phase-contrast imaging of incremental features is understood to recruit destructive interference patterns from Fresnel diffraction that create periodic blurring at differing frequencies when they are scanned using inappropriate experimental parameters (principally X-ray energy, sample-to-detector propagation distance and voxel size). However, our parameters produce blurring frequencies that are too narrow (approximately 500–900 nm) to significantly affect the contrast between cementum increments (1–3 μm radial thickness) (Tafforeau, personal observation). Therefore, no significant masking of increments from Fresnel diffraction blurring should be expected in our data. In specimens that preserved increments, volumes were inspected by eye to identify regions of highest increment contrast with no lensing and/or evidence between increments. Increments identified in these regions were followed by eye throughout the entire cementum tissue surrounding these regions, both longitudinally and transversely through the root, in order to distinguish between principal increments and accessory increments formed by lensing and coalescence of primary increments in discrete portions of the tissue (Supplementary Fig. 1). Primary increments were distinguished as those that persisted vertically through the entire scanned region of cementum, whereas accessory increments lasted only for short periods before coalescing into neighbouring increments (Supplementary Fig. 1).

Once regions of highly contrasting principal cementum increments had been identified, virtual thin sections of these regions were created. This was performed by isolating ten transverse PPC-SRµCT slices through each region and summing their greyscale values using the "Sum slices" option of the "Z projection" tool in ImageJ/Fiji to create a new image of increased contrast between dark and light cementum increments and reduced image noise. Between three and five virtual thin sections were recorded from specimens with the highest documented age. For each virtual thin section, increments were counted manually by three different observers: Observer One (E.N.) who had considerable experience in counting cementum increments (>100 specimens studied); Observer Two (K.W.) who had training in counting cementum increments (30 specimens studied under guidance from Observer One) and experience in studying growth patterns in PPC-SRµCT data of long-bones; Observer Three (C.N.) who had no prior experience in counting cementum increments (>100 specimens studied); Observer Two (K.W.) had training in identifying Fig. 1). Primary increments were distinguished as those that persisted vertically through the entire scanned region of cementum, whereas accessory increments lasted only for short periods before coalescing into neighbouring increments (Supplementary Fig. 1).

Once regions of highly contrasting principal cementum increments had been identified, virtual thin sections of these regions were created. This was performed by isolating ten transverse PPC-SRµCT slices through each region and summing their greyscale values using the "Sum slices" option of the "Z projection" tool in ImageJ/Fiji to create a new image of increased contrast between dark and light cementum increments and reduced image noise. Between three and five virtual thin sections were recorded from specimens with the highest documented age. For each virtual thin section, increments were counted manually by three different observers: Observer One (E.N.) who had considerable experience in counting cementum increments (>100 specimens studied); Observer Two (K.W.) who had training in counting cementum increments (30 specimens studied under guidance from Observer One) and experience in studying growth patterns in PPC-SRµCT data of long-bones; Observer Three (C.N.) who had no prior experience in counting increments or studying growth patterns. Each observer studied virtual thin sections blind, after collection of virtual thin sections were numbered and randomized between observers. Each observer had counted increments in every virtual thin section (Supplementary Fig. 3 and Supplementary Data 1) and the precision between their counts and counted in every virtual thin section (Supplementary Table 1):
per subset, birth-death node-dated completed tree distribution for mammas) representing the phylogenetic relationships of every taxon in the respective branch. For crocodilian taxa, a phylogeny was manually constructed in R following the time-calibrated phylogeny of Oaks73 (using node mean age values from the species tree/90 My maximum analysis) and added to the base of the squamate phylogeny to produce a reptile clade. Each subset was investigated to find the tree that produced the highest PGLS values and this tree was then input into the “corPagel” covariance structure for the “gls” function to produce a phylogenetically informed regression model between the respective metrics.

The relationships between body mass and maximum lifespan were compared between extant mammals and extant reptiles using phylogenetic ANCOVA following the method outlined in Seymour et al.51. If multiple foramina were used by Seymour et al.51, in the study of foramina in small mammals, and bone increment counts are available at the University of Southampton repository as data number D1506 (https://doi.org/10.5258/SOTON/D1506).

Phylogenetic and phylogenetic data are from online databases of the Max Planck Institute (https://www.demogr.mpg.de/longevityrecords/0203.htm), an online Ecological Archives database (http://www.esapubs.org/archive/ecd/084/094/metadata.htm), the AnAge database (https://genomics.senescence.info/species/), the VerteLife online project (https://vertlife.org) and the literature (references in Supplementary Data file 3) and are provided in Supplementary Tables, as Supplementary Data files, and as a part of the Source data provided with this paper.

Received: 1 November 2019; Accepted: 11 September 2020; Published online: 12 October 2020

References
1. Gill, P. G. et al. Dietary specializations and diversity in feeding ecology of the earliest stem mammals. Nature 512, 303–305 (2014).
2. Luo, Z. X. Transformation and diversification in early mammalian evolution. Proc. Natl Acad. Sci. U.S.A. 110, 719–725 (2013).
3. Penny, D. W. Maximizing differences among species for a reconstructed European stem mammal tree. J. Vert. Paleontol. 10, 490–501 (1990).
4. Han, G., Mao, F., Bi, S., Wang, Y. & Meng, J. A Jurassic gliding euharamiyidian mammal with an ear of five auditory bones. Nature 551, 451–456 (2017).
5. Wilson, G. P. et al. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483, 457–460 (2012).
6. Close, R. A., Friedman, M., Lloyd, G. T. & Benson, R. B. Evidence for a mid-Cretaceous adaptive radiation of mammalian diversity. Curr. Biol. 25, 2137–2142 (2015).
7. Bennett, A. F. & Ruben, J. A. Endothermy and activity in vertebrates. Science 206, 649–654 (1979).
8. Kemp, T. S. The origin of mammalian endothermy: a paradigm for the concept of the Last Common Ancestors (LCAs) of the crocodilian, squamate and mammal lineages. Proc. R. Soc. B 267, 483–490 (2010).
9. Koteja, P. Energy assimilation, parental care and the evolution of endothermy. Nature 267, 488–490 (1977).
10. Clarke, A. & Pörtner, H. O. Temperature, metabolic power and the evolution of endothermy. Biol. Rev. 85, 703–727 (2010).
11. Koteja, P. Energy assimilation, parental care and the evolution of endothermy. Proc. R. Soc. B 267, 479–484 (2000).
12. Hooper, J. A. The role of foraging mode in the origin of therapsids: implications for the origin of mammalian endothermy. Fieldiana Life Earth Sci. 49, 126–149 (2012).
13. Farmer, C. G. Reproduction: the adaptive significance of endothermy. Am. Nat. 162, 826–840 (2003).
14. Lovegrove, B. G. The evolution of endothermy in Cenozoic mammals: a pleiomorphic-apomorphic continuum. Biol. Rev. 87, 128–162 (2012).
15. Cavalli-Sforza, L. L., Lafore, R. J., Herring, C. E. & Borst, G. The decoupled nature of basal metabolic rate and body temperature in endotherm evolution. Nature 572, 651–654 (2019).
16. Gross, W. Die typen des mikroskopischen knochenauses bei fossilien stegoccephalen und reptilien. Anat. Embryol. 103, 731–764 (1934).
17. Ray, S., Boitha, J. & Chinsamy, A. Bone histology and growth patterns of non-mammalian therapsids. J. Vert. Paleontol. 24, 634–648 (2004).

Statistics. One-way ANOVA comparison of intra-observer CV between cementoarcheontological studies; Shapiro–Wilk normality test: PPC-SRμCT data

\[
W = I, \quad p = 1, \quad \text{histological data} \quad W = 0.93, \quad p = 0.41; \quad \text{test statistics} \quad F = 11.12, \quad \text{degrees of freedom (df) = 10, \quad Cohen’s effect size d = 3.13, \quad p = 0.00728. Phylo-

genic ANCOVA comparison of PGLS regression slopes for lifespan against body mass in mammals (log₁₀ lifespan = 0.26(log₁₀ body mass) + 0.16; 95% confidence interval (CI) = 0.05; r² = 0.69 and reptiles (log₁₀ lifespan = 0.26 (log₁₀ body mass) + 0.60; 95% CI = 0.08; r² = 0.46); slopes are statistically similar (F = 0.868, p = 0.352) while means are significantly separated (F = 4.44, df = 529, partial eta squared effect size = 0.32, p = 0.036). PGLS regression of mammalian lifespan against msSMR: log₁₀ msSMR = -0.237(log₁₀ lifespan) – 0.083; 95% CI = 0.07; r² = 0.59, p < 0.001. PGLS regression of reptilian lifespan against msSMR: log₁₀ msSMR = -0.83(log₁₀ lifespan) – 0.31; 95% CI = 0.25; r² = 0.43, p = 0.01. PGLS regression of mammalian lifespan against growth constant K; log₁₀ K = -0.692(log₁₀ lifespan) – 1.171; 95% CI = 0.101; r² = 0.66, p < 0.01. PGLS regression of reptilian lifespan against growth constant K; log₁₀ K = -0.69(log₁₀ lifespan) – 2.523; 95% CI = 0.339; r² = 0.43, p < 0.01. One-way ANCOVA comparison of OLS regression slopes for Q; against body mass in extant mammals (log₁₀(Q) = 0.513 × log₁₀(body mass) + 6.104) and non-vanriant reptiles (log₁₀(Q) = 0.685 × log₁₀(body mass) – 8.139) show slopes are statistically similar (F = 2.2, p = 0.16) while means are significantly different (F = 87.6, df = 89, partial eta squared effect size = 0.50, p = 7.4E⁻¹⁰)"
16. Shelton, C. D. & Sander, P. M. Long bone histology of \textit{Opisthocoelus} reveals the geologically earliest occurrence of fibrolamellar bone in the mammalian stem lineage. \textit{C. R. Palevol.} 16, 397–424 (2017).
17. Benoit, J., Manger, P. R. & Rubidge, B. S. Palaeoneurological clues to the evolution of defining mammalian soft tissue traits. \textit{Sci. Rep.} 6, 25604 (2016).
18. Hillenius, W. J. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. \textit{Evolution} 48, 207–229 (1994).
19. Bown, C. R., Fernández-V., M. & Rubidge, B. S. Endcranial casts of pre-mammalian therapsids reveal an unexpected neurological diversity at the deep evolutionary root of mammals. \textit{Brain Behav. Evol.} 90, 311–333 (2017).
20. Rowe, T. B.  
21. Rowe, T. B., Macrini, T. E. & Luo, Z. X. Fossil evidence on origin of the Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. \textit{Palaeontology} 53, 627–257 (2016).
22. Luo, Z.-X., Kielan-Jaworowska, Z. & Cifelli, R. L. Evolution of dental replacement in mammals. \textit{Bull. Carnegie Mus. Nat. Hist.} 36, 159–175 (2004).
23. O’Meara, R. N. & Asher, R. J. The evolution of growth patterns in mammalian versus nonmammalian cynodonts. \textit{Paleobiology} 42, 439–464 (2016).
24. Rey, K. et al. Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America). \textit{Paleobiol.} 28, 114–122 (2009).
25. Beinou, J., Fernandez, V., Manger, P. R. & Rubidge, B. S. Palaeoneurological clues to the evolution of defining mammalian soft tissue traits. \textit{Sci. Rep.} 6, 25604 (2016).
26. Rowe, T. B., Macrini, T. E. & Luo, Z. X. Fossil evidence on origin of the Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. \textit{Palaeontology} 53, 627–257 (2016).
27. Hoffman, E. A. & Rowe, T. B. Jurassic stem–mammal perinates and the origin of mammalian reproduction and growth. \textit{Nature} 561, 104–108 (2018).
28. Kielan-Jaworowska, Z. & Hurum, J. H. Limb posture in early mammals: sprawling or parasagittal. \textit{Acta Palaeontol. Pol.} 51, 393–406 (2006).
29. Rey, K. et al. Oxygen isotopes suggest elevated thermometabolism within multiple Permo-Triassic therapsid clades. \textit{eLife} 6, e28589 (2017).
30. Hulbert, A. J., Pamplona, R., Buffenstein, R. & Buttemer, W. A. Life and death: the nasal region of non-mammalian cynodonts and mammaliaforms: speculations on the evolution of mammalian endothermy. \textit{J. Vertebr. Paleontol.} 37, e1269116 (2017).
31. Rodrigues, P. G. et al. Digital cranial endocast of \textit{Biographia guaibensis} (Late Triassic, Brazil) sheds light on the evolution of the brain in non-mammalian cynodonts. \textit{Hist. Biol.} 31, 1195–1212 (2019).
32. Hayes, J. P. & Garland, T. Jr The evolution of endothermy: testing the aerodynamic capacity model. \textit{Evolution} 49, 836–847 (1995).
33. Kohler, M., Marín-Moratalla, N., Jordana, X. & Aanes, R. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. \textit{Nature} 487, 356–362 (2012).
34. Kielan-Jaworowska, Z., Cifelli, R. L. & Luo, Z. X. \textit{Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure} (Columbia University Press, New York, 2004).
35. Hubert, A. J., Pamplona, R., Buffenstein, R. & Buttemer, W. A. Life and death: metabolic rate, membrane composition, and life span of plants. \textit{Physiol. Rev.} 87, 1175–1213 (2007).
36. Magalhães, J. P. D., Costa, J. & Church, G. M. An analysis of the relationship between metabolism, developmental schedules, and lifespan using phylogenetic independent contrasts. \textit{J. Gerontol. A Biol. Sci. Med. Sci.} 62, 149–160 (2007).
37. Werner, J., Skafianakis, N., Rendall, A. D. & Griebel, E. M. Energy intake functions and energy budgets of ectotherms and endotherms derived from their ontogenetic growth in body mass and timing of sexual maturation. \textit{J. Theor. Biol.} 444, 1–25 (2018).
38. Grady, J. M., Enquist, B. J., Dettweiler-Robinson, E., Wright, N. A. & Smith, F. A. Evidence for mesothermy in dinosaurs. \textit{Science} 344, 1268–1272 (2014).
39. Dong, X., Milholland, B. & Viig, J. Evidence for a limit to human lifespan. \textit{Nature} 538, 257–259 (2016).
40. Klevezaal, G. Recording Structures of Mammals (CRC Press, Boca Raton, FL, 1995).
41. Naji, S. et al. Cementochronology, to cut or not to cut? \textit{Int. J. Paleopathol.} 15, 113–119 (2016).
42. Lieberman, D. E. Life history variables preserved in dental cementum. \textit{Science} 312, 137–137 (2006).
43. Stock, S. R. et al. Cementum structure in Beluga whale teeth. \textit{Acta Biomater.} 8, 289–299 (2012).
44. Stutz, A. J. Polarizing microscopy identification of chemical diagenesis in archaeological cementum. \textit{J. Archaeol. Sci.} 29, 1327–1347 (2002).
45. Newham, E. Exploring the Use of \textit{X–ray Tomography for the Quantification of Cementum Growth Patterns Across the Mammalian Phylogeny. PhD} thesis, Univ. Southampton (2018).
46. Le Cabec, A., Tang, N. K., Ruano Rubio, V. & Hillson, S. Nondestructive adult age at death estimation: visualizing cementum annulations in a known age historical human assemblage using synchrotron X-ray microtomography. \textit{Am. J. Phys. Anthropol.} 168, 25–44 (2019).
47. Warr, C. B., Bauchot, J. & Vaupel, J. W. Tooth cementum annulation for age estimation; results from a large known-age validation study. \textit{Am. J. Phys. Anthropol.} 123, 119–129 (2004).
48. Whiteside, D. I., Duffin, C. J., Gill, P. G., Marshall, J. E. & Benton, M. J. The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. \textit{Palaeontology} 49, 397–424 (2017).
49. Shelton, C. D. & Sander, P. M. Long bone histology of \textit{Opisthocoelus} reveals the geologically earliest occurrence of fibrolamellar bone in the mammalian stem lineage. \textit{C. R. Palevol.} 16, 397–424 (2017).
50. Rowe, T. B. Definition, diagnosis, and origin of Mammalia. \textit{J. Vert. Paleontol.} 8, 241–264 (1988).
51. Rowe, T. B., Martini, T. E. & Luo, Z. X. Fossil evidence on origin of the mammalian brain. \textit{Science} 332, 955–957 (2011).
52. Hoffman, E. A. & Rowe, T. B. Jurassic stem–mammal perinates and the origin of mammalian reproduction and growth. \textit{Nature} 561, 104–108 (2018).
53. Benoit, J., Fernandez, V., Manger, P. R. & Rubidge, B. S. Palaeoneurological clues to the evolution of defining mammalian soft tissue traits. \textit{Sci. Rep.} 6, 25604 (2016).
Acknowledgements

We acknowledge the European Synchrotron Radiation Facility, Grenoble, France for provision of synchrotron radiation facilities on beamlines ID19 and ID16A (project ES152) and thank Peter Cloetens for assistance in using beamline ID16A. We also acknowledge the Paul Scherrer Institut, Villigen, Switzerland for provision of synchrotron radiation beamtime at beamline TOMCAT of the Swiss Light Source (project 20141278). The research leading to these results has received funding from the European Community’s Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 312284 (for CALIPSO). We thank Keijo Hamalainen for his help in the initial stages of the synchrotron imaging. This project was part-funded by a Natural Environmental Research Council studentship and an Engineering and Physical Sciences Research Council studentship, awarded to E.N. and P.S. (Grant number NE/R009783/1), and we also thank the Academy of Finland for part-funding the project. Thank you to the Natural History Museum London for contributing to travel for P.B. via the Departmental Investment Fund for Earth Sciences. We thank Ginko Investments Ltd. for funding for materials and travel and the University of Bristol Bob Savage memorial fund for travel for E.N. Many thanks to the Natural History Museum London for supporting and supervising E.N. and I.J.C. and supporting the project. We also thank the University of Southampton for part-funding the project. Thank you to the Finnish Museum of Natural History, Helsinki, Finland for loans of specimens. Facilitated by Martha Richter, Rob Asher, Matt Lowe and Martti Hildén. For assistance with laboratory work and materials, we thank Tom Davies, Wendy Dirks, Dani Schmidt, Remmert Schouten, Pedro Viegas, John Cunningham & Duncan Murdoch. Discussions: Roger Benson, Chris Dean, Wendy Dirks, Jim Hopson, Fabien Lafuma, Thomas Martin, Rachel O’Meara, Stephen Naji, Tanya Smith and Emily Rayfield.

Author contributions

I.J.C. and P.G.G. conceived and designed the project. E.N., P.G.G., P.B., K.R. and I.J.C. selected, prepared and curated specimens. E.N., P.G.G., P.B., V.F., D.H., T.K., A.K., A.P., P.S., H.S., P.T., B.Z.-P. and I.J.C. performed the synchrotron experiments. E.N., A.K. and I.J.C. performed the micro-CT experiments. E.N. processed and E.N., C.N. and K.W. analysed the synchrotron data. E.N. and I.J.C. analysed the micro-CT data. E.N., P.G.G. and I.J.C. discussed the interpretations. E.N. wrote the first draft and created all figures; E.N., P.G.G. and I.J.C. wrote the manuscript; all authors provided a critical review of the manuscript and approved the final draft. Authors M.J.B., V.F., N.J.G., D.H., J.J., T.K., A.K., C.N., A.P., K.R., K.R.B., P.S., H.S., P.T., K.W. and B.Z.-P. contributed equally to this work and are listed in alphabetical order. This article originated as a Master’s thesis (University of Bristol), then a PhD thesis (University of Southampton), performed by E.N. and supported and supervised by P.G.G., P.S., N.J.G., J.J., K.R.B., M.J.B. and I.J.C.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41467-020-18898-4.

Correspondence and requests for materials should be addressed to E.N., P.G.G. or I.J.C.

Peer review information Nature Communications thanks Zhe-Xi Luo and the other anonymous reviewer for their contribution to the peer review of this work. Peer reviewer reports are available.

Reprints and permission information is available at http://www.nature.com/reprints

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s) 2020