

Revisiting life history and morphological proxies for early mammaliaform metabolic rates

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Morganucodon and *Kuehneotherium* are two Late Triassic-Early Jurassic stem mammals that are often portrayed as possessing key mammalian characteristics such as multi-cusped molars¹, respiratory turbinates, and Harderian glands (associated with grooming and maintaining insulatory pelage²). Newham et al.³ recently used synchrotron X-ray tomographic imaging of incremental tooth cementum to reconstruct the longevity of large series of *Morganucodon* and *Kuehneotherium*. They conclude that the maximum longevity of these animals was higher than that of similar-sized extant mammals. They infer that these animals must have had low metabolic rates, suggesting ectothermic metabolism, since, they claim, metabolic rates are inversely correlated with longevity. If true, this would mean that mammalian endothermic metabolism evolved tens of millions of years later than currently thought: deep in the Jurassic. We contend that high longevity cannot be taken as a proxy for low metabolic rates. In extant endotherms, the highest metabolic rates characterize birds and bats, two clades that exhibit longer maximum lifespans than terrestrial mammals, which are characterized by lower metabolic rates. Available data likewise suggest that metabolic rates play little role in affecting longevity within and between tetrapod classes once the effects of body size are properly accounted for.

Newham et al.³ found that *Morganucodon* lived up to 14 years and *Kuehneotherium* up to 9 years. These values are high compared to similarly-sized extant mammals. Newham et al. thus concluded that they were characterized by low metabolic rates because “In extant tetrapods, negative correlations exist between maximum lifespan and BMR.” While true (if one divides BMR by mass), this statement ignores the predominant role of body size in affecting both BMR and lifespans. In a recent analysis of the longevity of 4100 tetrapod species, including 1,061 mammals and 1,348 reptiles, Stark et al.⁴ found that ectotherms do not live longer than similar size endotherms. Once body mass was accounted, longevity was independent of basal metabolic rates and of resting metabolic rates in tetrapods in general, and in mammals and reptiles alone (for the subset of data with available metabolic rates; $n = 662$ for BMR). Models with mass alone were superior to models that included both mass and metabolic rates, which

were superior to models with metabolic rates alone⁴. For mammals, this was also true when field metabolic rates were used in lieu of BMR. Likewise, mass explains a larger proportion of the variation in mammalian longevity than does BMR⁵. Newham et al. cite only the work of Hulbert et al.⁴ to state that “In extant tetrapods, negative correlations exist between maximum lifespan and BMR”. Hulbert et al.⁴ use mass-specific metabolic rates as a measure for the “rate of living” but in fact suggest that “there are a number of problems associated with presuming a linkage between rate-of-living and maximum life span potential.”

Newham et al.³ estimated body masses of 10.7–25.0 g for *Morganucodon* and 14.9–32.7 g for *Kuehneotherium*. In data consisting of 587 amniote species weighing 10–33 g⁴, most species (305, including 36 of 105 mammals) have maximum lifespans of 9 years or longer, and 114 (including 20 mammals) have maximum lifespans of 14 years or longer. Thus, the longevity of *Morganucodon* and *Kuehneotherium* are not particularly high. Stark et al.⁴ found no differences in longevity between endothermic and ectothermic tetrapods when size and phylogeny were accounted for. In non-phylogenetic models, mammals had lower size-corrected longevity than reptiles, but birds, with even faster metabolism⁶, had the highest size-corrected longevity. Newham et al.³ recovered a negative relationship between mass-specific metabolic rates and longevity. They also showed that mammals have higher metabolic rates than similar-sized reptiles and higher metabolic rates than reptiles of similar lifespans (their figures 5 C and 6a in ref. 3, respectively). This, however, does not account for the fact that mass-specific metabolic rates, as they acknowledge, decrease with body size. In other words, “size-adjusted metabolic rates” are not independent of size because the relationship is strongly non-isometric (‘Kleiber’s Law’). Hence dividing by size does not remove the effect of mass.

Additional support for the notion of *Morganucodon* as an ectotherm used by Newham et al.³ was the ratio between nutrient foramen area and femur length, which is an index for relative blood flow, Q_i . Q_i was suggested as another proxy for metabolic rate, MMR. Newham et al.³ had 69 data points for Q_i , 11 were collected de novo, and 58 were collected by Seymour et al. 2012⁷ (who measured the foramen area

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directly or from a digital photo of the surface of the bone). They found that *Morganucodon* had a lower Q_i than expected for a mammal (or for ectothermic varanid reptiles) of a similar size¹, and considerably closer to small non-varanid reptiles. Seymour et al.⁷ used mammals from ten orders, including bats, in three mammalian infra-classes. *Morganucodon* Q_i fits well with a linear regression of Q_i on mass in their data. The additional 11 Q_i values of small mammals, added by Newham et al.³, are much higher than expected for mammals of similar sizes from the Seymour et al. dataset⁷. These 11 species form a phylogenetically clustered sample (4 shrews and 7 rodents) and were estimated differently (using a μ CT with a 3D imaging software). We suggest that this may have resulted in *Morganucodon* appearing closer to reptiles.

Morganucodon and *Kuehneotherium* led long lives for mammals their size. Small mammals at the higher end of the longevity spectrum are mostly bats, which Newham et al.³ omitted from their datasets. Small birds are likewise characterized by longer lives than other small tetrapods^{4,8}. Flight probably enhances longevity by reducing extrinsic mortality rates (i.e., predation rates). We think this is not a reason to omit flying organisms from the discussion, because extrinsic mortality rates for small mammaliaforms in the Late Triassic and early Jurassic are unknown and could have been substantially lower than modern rates (e.g., no avian, mammalian, or ophidian predators have evolved by then, and carnivorous dinosaurs were probably too large to care). Bats and birds share some of the highest metabolic rates in the animal kingdom, at rest and in the field, and yet live longer than similar-sized terrestrial mammals and reptiles^{4,8}. Longevity data are therefore inadequate or at least insufficient for inferring metabolic rates with a reasonable degree of confidence.

Newham et al.³ cited evidence for increased metabolic rates in the metabolic scope of mammaliaforms preceding the evolution of *Morganucodon* and *Kuehneotherium* – by nearly 50 million years (i.e., 270–250MA^{9–12}), as well as works that are equivocal or suggest later dates^{13–16}. Interestingly, one of these¹⁶ supports the role of turbinates as heat exchange surfaces in *Morganucodon*, as they do in extant (endothermic) mammals. While far from conclusive, these data are better proxies for metabolic rates than maximum longevity (see also¹⁷). Based on the admittedly limited paleontological evidence we think it is at least as likely that early mammaliaforms such as *Morganucodon* and *Kuehneotherium* were endotherms rather than ectotherms, and the recent findings regarding their maximum longevity do little to alter this view.

References

- Conith, A. J., Imburgia, M. J., Crosby, A. J. & Dumont, E. R. The functional significance of morphological changes in the dentitions of early mammals. *J. Roy. Soc. Int.* **13**, 20160713 (2016).
- Ruben, J. A. & Jones, T. D. Selective factors associated with the origin of fur and feathers. *Am. Zool.* **40**, 585–596 (2000).
- Newham, E. et al. Reptile-like physiology in Early Jurassic stem-mammals. *Nat. Commun.* **11**, 5121 (2020).
- Stark, G., Pincheira-Donoso, D. & Meiri, S. No evidence for the “rate-of-living” theory across the tetrapod tree of life. *Glob. Ecol. Biogeog.* **29**, 857–884 (2020).
- Hulbert, A. J., Pamplona, R., Buffenstein, R. & Buttemer, W. A. Life and death: metabolic rate, membrane composition, and life span of animals. *Phys. Rev.* **87**, 1175–1213 (2007).
- Guigueno, M. F., Shoji, A., Elliott, K. H. & Aris-Brosou, S. Flight costs in volant vertebrates: A phylogenetically-controlled meta-analysis of birds and bats. *Comp. Biochem. Physiol. A.* **235**, 193–201 (2019).
- Seymour, R. S., Smith, S. L., White, C. R., Henderson, D. M. & Schwarz-Wings, D. Blood flow to long bones indicates activity metabolism in mammals, reptiles and dinosaurs. *Proc. R. Soc. B* **279**, 451–456 (2011).
- Munshi-South, J. & Wilkinson, G. S. Bats and birds: exceptional longevity despite high metabolic rates. *Age. Res. Rev.* **9**, 12–19 (2010).
- Benoit, J., Manger, P. R. & Rubidge, B. S. Palaeoneurological clues to the evolution of defining mammalian soft tissue traits. *Sci. Rep.* **6**, 25604 (2016).
- Huttenlocker, A. K. & Farmer, C. G. Bone microvasculature tracks red blood cell size diminution in Triassic mammal and dinosaur forerunners. *Curr. Biol.* **27**, 48–54 (2017).
- Olivier, C., Houssaye, A., Jalil, N. E. & Cubo, J. First palaeohistological inference of resting metabolic rate in an extinct synapsid, *Moghreberia nmachouensis* (Therapsida: Anomodontia). *Biol. J. Linn. Soc.* **121**, 409–419 (2017).
- Rey, K. et al. Oxygen isotopes suggest elevated thermometabolism within multiple Permo-Triassic therapsid clades. *eLife* **6**, e28589 (2017).
- Hayes, J. P. & Garland, T. Jr. The evolution of endothermy: testing the aerobic capacity model. *Evolution* **49**, 836–847 (1995).
- Köhler, M., Marín-Moratalla, N., Jordana, X. & Aanes, R. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. *Nature* **487**, 358–361 (2012).
- Rodrigues, P. G. et al. Digital cranial endocast of *Riograndia guai-bensis* (Late Triassic, Brazil) sheds light on the evolution of the brain in non-mammalian cynodonts. *Hist. Biol.* **31**, 1195–1212 (2019).
- Crompton, A. W., Owerkowicz, T., Bhullar, B. A. & Musinsky, C. Structure of the nasal region of non-mammalian cynodonts and mammaliaforms: speculations on the evolution of mammalian endothermy. *J. Vertebrate Paleontol.* **37**, e1269116 (2017).
- Araújo R. et al. Inner ear biomechanics reveals a Late Triassic origin for mammalian endothermy. *Nature* **607**, 726–731 <https://doi.org/10.1038/s41586-022-04963-z> (2022).

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Author contributions

S.M. and E.L. conceived and planned the work. S.M. examined longevity data, E.L. examined Q_i data. S.M. wrote the first draft. Both authors contributed to further drafts and refinements.

Competing interests

The authors declare no competing interests.

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