PROCEEDINGS B

Research

CrossMark
click for updates

Author for correspondence:
David M. Grossnickle
e-mail: grossnickle@uchicago.edu

THE ROYAL SOCIETY PUBLISHING

Therian mammals experience an ecomorphological radiation during the Late Cretaceous and selective extinction at the K–Pg boundary

David M. Grossnickle[1] and Elis Newham[2]

[1]Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th Street, Chicago, IL 60637, USA
[2]Faculty of Engineering and the Environment, University of Southampton, Southampton, UK

It is often postulated that mammalian diversity was suppressed during the Mesozoic Era and increased rapidly after the Cretaceous–Palaeogene (K–Pg) extinction event. We test this hypothesis by examining macroevolutionary patterns in early therian mammals, the group that gave rise to modern placentals and marsupials. We assess morphological disparity and dietary trends using morphometric analyses of lower molars, and we evaluate generic level taxonomic diversity patterns using techniques that account for sampling biases. In contrast with the suppression hypothesis, our results suggest that an ecomorphological diversification of therians began 10–20 Myr prior to the K–Pg extinction event, led by disparate metatherians and Eurasian faunas. This diversification is concurrent with ecomorphological radiations of multituberculate mammals and flowering plants, suggesting that mammals as a whole benefitted from the ecological rise of angiosperms. In further contrast with the suppression hypothesis, therian disparity decreased immediately after the K–Pg boundary, probably due to selective extinction against ecological specialists and metatherians. However, taxonomic diversity trends appear to have been decoupled from disparity patterns, remaining low in the Cretaceous and substantially increasing immediately after the K–Pg extinction event. The conflicting diversity and disparity patterns suggest that earliest Palaeocene extinction survivors, especially eutherian dietary generalists, underwent rapid taxonomic diversification without considerable morphological diversification.

1. Introduction

Therian mammals (i.e. eutherian-placental and metatherian-marsupial lineages) underwent a major evolutionary radiation that included vast increases in taxonomic, morphological, and ecological diversities. It is often postulated that this radiation accelerated rapidly after the Cretaceous–Palaeogene (K–Pg) extinction event 66.0 Ma [1–6], following a period during which diversity and disparity levels were suppressed by competition with dinosaurs. We title this the Suppression Hypothesis (SH) and conceptualize it in figure 1a. SH is supported by palaeontological evidence suggesting that Cretaceous mammals were taxonomically depauperate, limited to small body sizes, predominantly insectivorous, and likely included few crown eutherian (i.e. placental) lineages [1–6,8–13]. While previous studies have identified taxonomic and ecomorphological diversification events of Mesozoic mammals, these events were largely confined to the Jurassic or involved in non-therian lineages [13–17]. After the K–Pg extinction event, which eliminated non-avian dinosaurs, fossil evidence indicates immediate increases in therian body sizes, body size disparity, taxonomic diversity, and dietary diversity [1–4,6,8,9,11,18], implying that therian mammals adaptively radiated during the earliest Palaeocene [1]. Further, O'Leary *et al.* [5] conclude that placental mammals radiated extremely rapidly in the first 200 000–400 000 years after the K–Pg extinction event. Although this
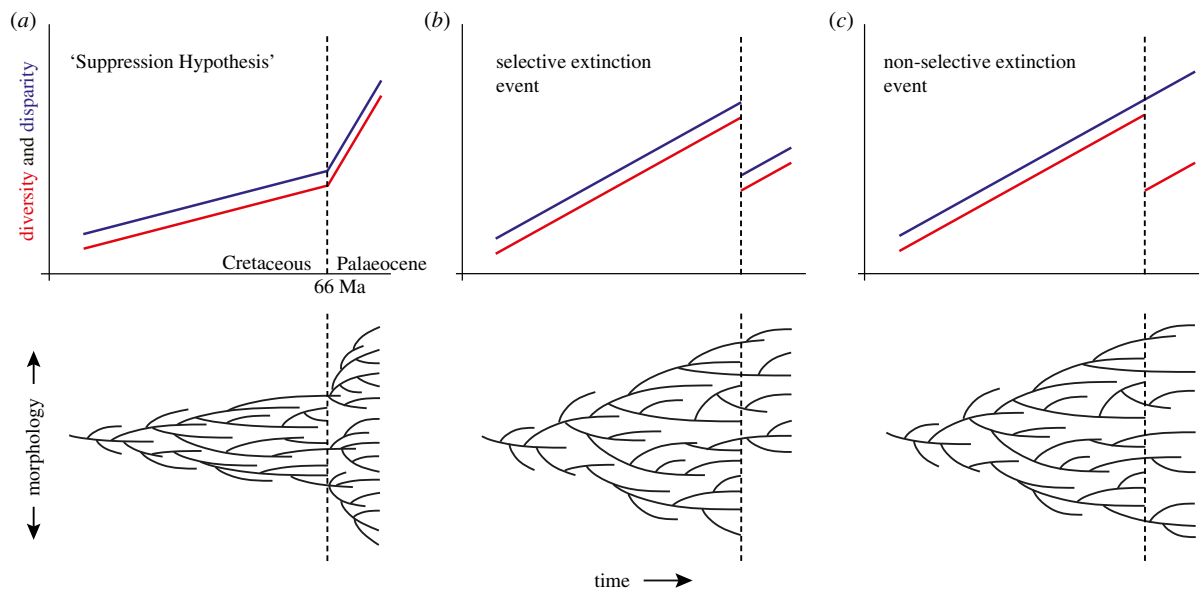
Figure 1. Taxonomic diversity (red) and morphological disparity (blue) patterns for idealized clade histories. (*a*) The hypothesis that mammalian diversity and disparity were suppressed until the earliest Palaeocene. (*b*) A selective extinction event that claimed taxa with specific morphologies, causing a decrease in disparity. (*c*) A non-selective (i.e. random) extinction event. Dashed vertical lines represent a mass extinction event. (*b*,*c*) After Foote [7].

conclusion has been challenged (e.g. [19]), recent phylogenetic studies suggest increased intraordinal diversification of therians, especially placentals, after the K–Pg boundary [10,12,19–21].

However, some lines of evidence are inconsistent with SH. For instance, recent studies demonstrate that end-Cretaceous therians achieved greater ecomorphological diversity than previously realized [22–26], and mammals began a trend of increasing average body size 10–20 Myr before the K–Pg boundary [13,15,27]. Multituberculates, a diverse clade of extinct non-therian mammals, experienced a Late Cretaceous radiation that included increases in dietary, morphological, and taxonomic diversities [13,15]. Further, Wilson [26] reports a decrease in mammalian disparity immediately across the K–Pg boundary in Montana, suggesting a selective extinction event followed by a recovery period [7] (figure 1*b*) rather than a rapid morphological radiation. Finally, diverse archaic ungulates from the earliest Palaeocene of North America have been interpreted as immigrants [8,26,28], suggesting that these taxa diversified elsewhere, prior to the K–Pg boundary.

These conflicting lines of evidence suggest that our understanding of the timing and dynamics of the start of the therian radiation is incomplete. SH predicts that mammals adaptively radiated in the earliest Palaeocene, and Schluter [29] defines an adaptive radiation as including increases in taxonomic, morphological, and ecological diversities. However, previous studies on the early therian radiation have been limited in their ability to examine all three types of diversity. For instance, body mass patterns have been used to test for a mammalian radiation in the earliest Palaeocene [3,4,11], but body sizes alone may be a poor metric for ecomorphological diversity [30]. Further, the timing of the early therian radiation has been assessed in a phylogenetic context by examining the timing of originations of crown mammalian clades [5,21]. However, for taxa in deep time, taxonomic and ecomorphological diversities cannot adequately be assessed with phylogenetic data of modern taxa [31,32], especially as many

radiating clades may not have living representatives. Halliday *et al.* [6] use palaeontological data to test for an adaptive radiation of early Palaeocene eutherians, but their analyses are limited to eutherian disparity patterns.

Here, we assess SH using fossil data from the mid-Early Cretaceous to the mid-Palaeocene (i.e. 130.8–61.6 Ma). We calculate taxonomic diversity using two recently developed techniques that account for sampling biases: shareholder quorum subsampling [33] and modelling-based residual analyses [34]. We examine morphological disparity using morphometric analyses of molar shape. The tribosphenic molar morphology of early therians provides a structure with homologous landmarks among diverse taxa separated by considerable temporal spans. In addition, molar morphology reflects diet, meaning that the diversity of morphologies can be indicative of ecological diversity (e.g. [15]). Thus, our methods allow for a more complete examination of the tempo of the early therian radiation by examining taxonomic, morphological, and ecological diversities.

2. Material and methods

(a) Morphometric analyses

Occlusal surfaces of tribosphenidan (i.e. boreosphenidan) penultimate lower molars were photographed at the Field Museum of Natural History, New Mexico Museum of Natural History and Science, Sam Noble Oklahoma Museum of Natural History, University of California Museum of Paleontology (UCMP), and Burke Museum of Natural History and Culture. This collection was supplemented with images from the primary literature (e.g. [10,35]). For the geometric morphometrics (GM) analysis, one specimen was chosen to represent each genus, and this choice was based primarily on quality of preservation and accurate centring of cusps in the photograph. Tribosphenida consists of eutherians, metatherians, and taxa with true tribosphenic molars that could not be classified into Eutheria or Metatheria. Penultimate molars of most early eutherians and
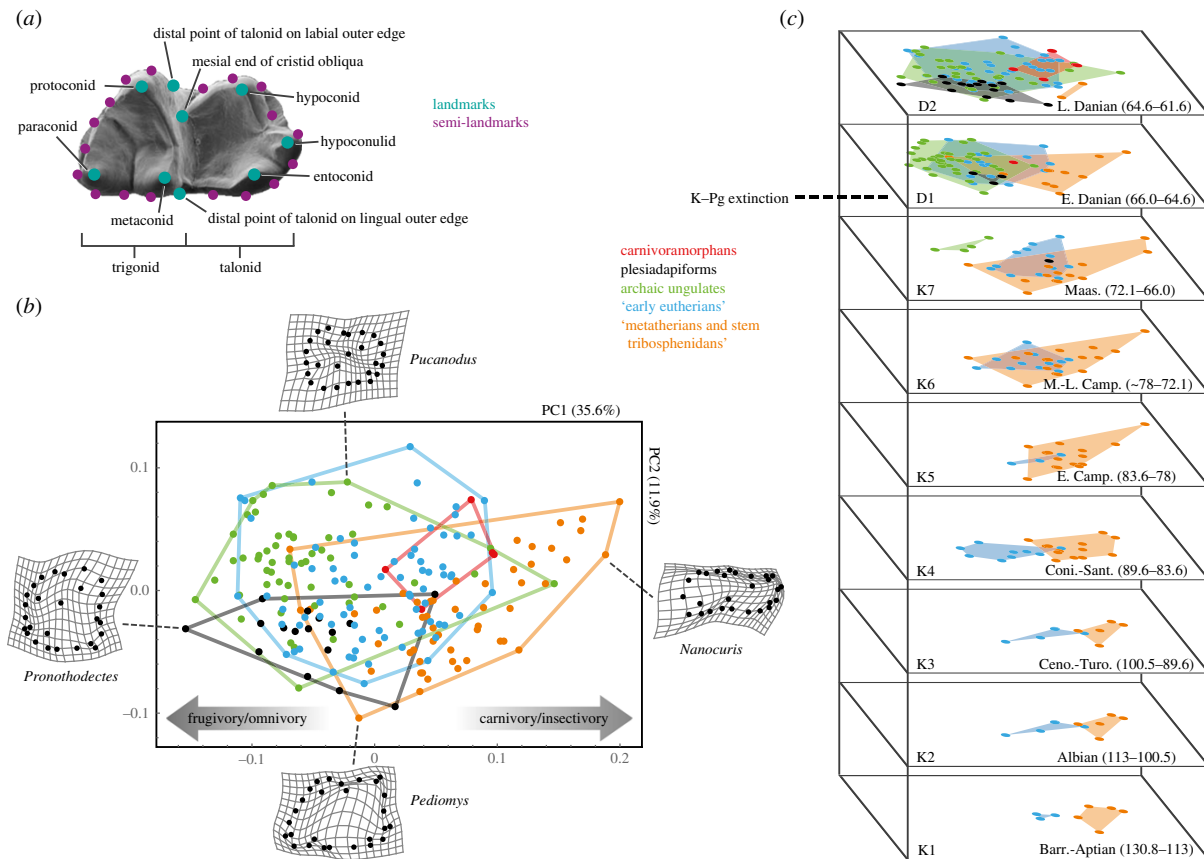
Figure 2. (a) Occlusal surface of a lower tribosphenic molar [35] with labelled landmarks and equally spaced semi-landmarks around the talonid and trigonid. (b) PC1 and PC2 results for 203 tribosphenidan genera, with thin plate splines of outlying taxa. Arrows indicate the interpreted dietary spectrum, with increased frugivory/omnivory to the left and increased carnivory/insectivory to the right. (c) Morphospace occupation through time with ages (Ma) of each time bin. See electronic supplementary material for abbreviations and figures with labelled genera. Polygons in (b) and (c) represent morphospace regions of the five mammalian groups listed in the figure. A majority of 'early eutherians' are stem eutherians and taxa previously considered members of 'Insectivora'.

metatherians (m2 and m3, respectively) are likely homologous [5], although carnivoramorphan molars are an exception. To maximize sample sizes of depauperate Cretaceous time bins, m1 of eutherians and m2 of metatherians were used for Cretaceous taxa if penultimate molars were unavailable. Genera were assigned to time bins [36] based on their temporal ranges, determined by first and last appearances of fossils. Time bins include the Barremian–Aptian (K1; 130.8–113 Ma), Albian (K2; 113–100.5 Ma), Cenomanian–Turonian (K3; 100.5–89.6 Ma), Coniacian–Santonian (K4; 89.6–83.6 Ma), Early Campanian (K5; 83.6–78 Ma), Middle-Late Campanian (K6; ~78–72.1 Ma), Maastrichtian (K7; 72.1–66 Ma), Early Danian (D1; 66–64.6 Ma), and Late Danian (D2; 64.6–61.6 Ma).

A GM analysis [37] was performed using two-dimensional landmarks, including seven landmarks that designate cusps, two landmarks at the junctions between the trigonid and talonid, nine equally spaced semi-landmarks around the trigonid, and nine equally spaced semi-landmarks around the talonid (figure 2a). Using the *Geomorph* package [38], landmark data were subjected to a Procrustes analysis that 'slides' semi-landmarks along their tangent directions to minimize Procrustes distances. Geometric morphometrics for Mathematica v. 12.0 [39] was used to perform a principal components analysis and produce thin plate splines. Disparity was calculated independently for each time bin or rock formation as the variance of the Procrustes distances from the Procrustes mean of the bin. To evaluate the amount of variance associated with the subjective nature of photographing occlusal molar surfaces and identifying landmarks, we performed an error test by repeatedly

photographing molars and implementing GM procedures. Resulting variance per molar suggests that these sources of error do not substantially affect broad disparity trends (electronic supplementary material, table S4). Cusp heights-to-molar length ratios were calculated from lateral molar images by summing the maximum talonid and trigonid elevations above the talonid basin and dividing by molar length.

See the electronic supplementary material for more detailed discussion of the methodologies of the morphometric analyses.

(b) Taxonomic diversity analyses

Counts of unique occurrences of genera were generated for each time bin as a taxonomic diversity estimate (TDE), calculated using fossil occurrence data of Tribosphenida downloaded from the Paleobiology Database on 19 November 2015. Ichnofossils were removed from the dataset, occurrence information was vetted and all unique fossil occurrences were assigned to time bins. The resulting dataset contains 1 180 unique occurrences of 280 genera. To account for potential geographical heterogeneity, a second dataset of only North American occurrences was created for comparison with the global dataset (electronic supplementary material).

To confidently analyse taxonomic diversity, we assessed the dataset for potential biases that have been shown to distort observed diversity patterns in the fossil record [40,41]. Modelling-based residual analyses were performed to attempt to correct for the effects of several aspects of fossil sampling that may affect the proportions of observed occurrences. Residual
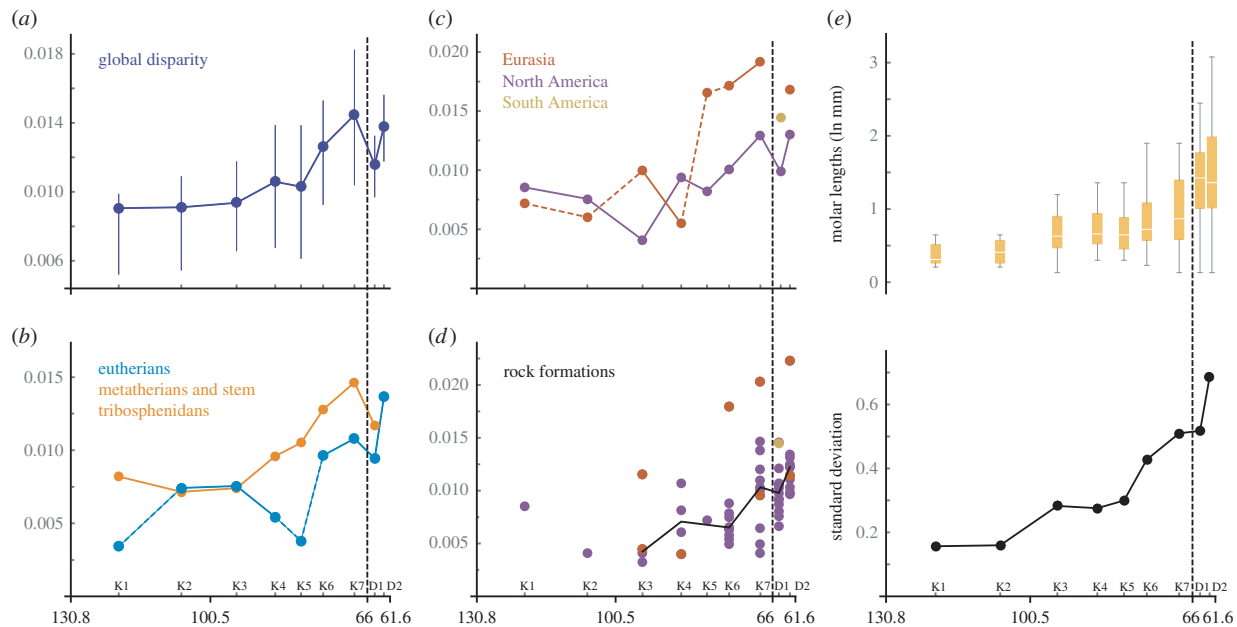
Figure 3. (*a,d*) Disparity levels through time based on the molar GM analysis for the global sample (*a*), major clades (*b*), continents (*c*), and rock formation faunas (*d*). Ages are Ma, and time bin age ranges are given in the material and methods section. Disparity is calculated independently for each time bin (or formation) as variance from the Procrustes mean. Error bars are ±1 s.d. generated from 1 000 bootstrap replicates. Disparity was not calculated for metatherians in D2 or Eurasian taxa in D1, because sample sizes were less than three genera. Dashed lines connect time bins for Eurasian faunas (K1, K2, and K5) and eutherian faunas (K1 and K5) in which variance is based on three or four genera. All other bins include at least five genera. In (*d*), the point colours correspond to the continents of (*c*), and the black trend line represents the median formation values for bins with four or more formations. Several formations are represented in multiple bins if they contain significant faunas from more than one bin (electronic supplementary material, table S5). (*e*) Therian molar lengths (natural log mm) and standard deviation from the mean length.

analyses model theoretic diversity patterns that would be expected to occur if completely controlled by a specific bias, often modelled using a proxy (e.g. [16,41]). Here, counts of unique therian-bearing formations (TBFs; $n = 95$) for each time bin were used as a proxy for taphonomic bias, and counts of unique fossil collections containing therians (TBCs; $n = 378$) were used as a proxy for anthropogenic sampling bias. All TDE counts were $\log_{10}$ transformed and ranked. A modelled diversity estimate (MDE) for each interval was then generated for each sampling proxy by applying linear ordinary least-squares regression between ranked proxy and TDE data [41]. Subtracting the MDE from the TDE of each interval left a residual diversity estimate unexplained by variation in the proxy under scrutiny (i.e. high residual values for a bin indicate 'genuine' diversification). Modelling followed the refinements of Lloyd [34], allowing us to determine via Akaike information criterion scores that a linear model best fits the relationship between global TDE and the proxies in question.

In addition, shareholder quorum subsampling (SQS) was employed to help correct for unevenness in the proportion of fossil observations sampled between intervals, by generating a standardized subsample of observations within each interval [33]. Unlike other subsampling techniques such as rarefaction, SQS allows the intensity of sampling to change between intervals based on the frequency of observations of particular taxa within the interval in question. Taxa observed within an interval are treated as 'shareholders' whose frequencies of observations form their 'share'. Good's *u* coverage estimate [42] is used to estimate the relative proportions of 'true' diversity represented in each interval. Fossil occurrences within an interval are then randomly drawn until taxa that have been sampled at least once have summed a total number of frequencies ('shares') to meet a predetermined quorum. We use a range of increasingly stringent quorums from 0.2 to 0.8.

See the electronic supplementary material and Newham *et al.* [16] for more detailed discussion of the taxonomic diversity analysis methodologies.

3. Results and discussion

(a) Morphospace occupation and diet

The GM analysis of early therian molars results in a dietary spectrum along the first principal component (PC1) axis (figure 2*b*; electronic supplementary material, figure S3): frugivorous/omnivorous taxa (e.g. most archaic ungulates, plesiadapiforms, and taeniodonts) are on the left, and carnivorous/insectivorous taxa (e.g. cimolestids, carnivoramorphans, mesonychids, and deltatheroidans) are largely on the right. This dietary interpretation is supported by the thin plate splines in figure 2*a*, which demonstrate broader molars to the left and thinner, more blade-like molars to the right. In addition to PC1, the PC2 axis may also capture morphological variance associated with diet, but the trend is not as distinct as PC1 (electronic supplementary material). We use 'frugivore' broadly (*sensu* [9]) and consider it to include strict frugivores, granivores, and non-high-fibre herbivores/omnivores. High-fibre herbivorous therians do not appear in the fossil record during the temporal range of this study [9,43]. We use dietary 'generalists' to refer to inferred omnivores. Hunter [18] concluded that many archaic ungulates were generalists based on quantitative comparisons to modern mammal molars.

(b) Ecomorphological diversification during the Late Cretaceous

Morphological disparity results contradict SH and demonstrate a steady rise of functional diversity through the Late Cretaceous (figure 3). The increase is maintained when genera are separated by major clade (figure 3*b*) and continent (figure 3*c*). Increases during the early Late Cretaceous

(i.e. time bins K3 and K4) were likely triggered by the appearance of zhelestid eutherians, which inhabit the frugivore/omnivore region of morphospace. Disparity continues to increase during the late Late Cretaceous (K6 and K7) with the appearance of taxa with molars indicating plant-dominated diets (e.g. [22]) and carnivory (e.g. [23]). This increase is most notable in metatherians (figure 3b) and Eurasian faunas (figure 3c). Results support previous studies that have noted elevated levels of ecological and taxonomic diversity of Late Cretaceous metatherians (e.g. [44]). Congruent with the pattern seen in therians, late Late Cretaceous multituberculates also experience an increase in disparity [13,15], suggesting that mammals as a whole were diversifying ecomorphologically during this period.

Disparity was calculated for therian faunas of individual rock formations to help account for sampling biases that may result from differences in the number of fossil-bearing formations between time bins (figure 3d). Results support the conclusion that therian disparity was increasing prior to the K–Pg boundary. Disparity levels for rock formations in the Middle-Late Campanian (K6) remain relatively low (figure 3d) even as global disparity increases (figure 3a). This suggests that Middle-Late Campanian faunas possessed greater β-diversity/disparity (i.e. proportionally more endemic taxa), whereas Maastrichtian (K7) faunas experienced greater α-diversity/disparity (i.e. increased local diversity and proportionally more cosmopolitan taxa). This is congruent with results for dinosaurs [45] and local ecosystems [46].

The ecological diversification of flowering plants in the late Late Cretaceous [47–50] has been suggested as a plausible trigger for the ecomorphological radiation of multituberculates [13,15], and this may also apply to therians. Angiosperms invaded an increasing number of environments [49] and may have triggered greater overall biodiversity in ecosystems [50]. Besides directly benefitting therian omnivores/frugivores by providing novel dietary options, angiosperms could have indirectly aided therian insectivores by prompting co-evolutionary diversifications in insects (e.g. [51]), although a close association between insect and angiosperm diversities is not supported by fossil evidence [52].

(c) Selective extinction

The observed number of unique molar morphologies increased during the earliest Palaeocene (D1) time bin (figure 2c). However, contrary to the prediction of SH (figure 1a) and the non-selective extinction model (figure 1c), molar disparity (i.e. variance of morphologies) appears to have decreased in response to the K–Pg extinction event. On smaller temporal and geographical scales, Wilson [26] also shows a decrease in molar disparity across the K–Pg boundary. The decrease is maintained when disparity is calculated as variance at global (figure 3a), subclade (figure 3b), continental (figure 3c), and formation/regional (figure 3d) levels, and when global disparity is calculated as the rarefied sum of ranges (i.e. area occupied in morphospace) (electronic supplementary material, figure S4). To ensure that the relatively short duration time of the D1 bin (i.e. Early Danian) is not distorting results, disparity was calculated for a combined D1 and D2 bin and results remain lower than the K7 value. Cusp heights-to-molar length ratios were measured to help assess shape variance not fully captured by two-dimensional GM, and the standard deviation of these ratios also decreases after the K–Pg boundary (electronic

supplementary material, figure S6). Standard deviation of molar lengths is the only disparity metric that does not show a decrease across the K–Pg boundary (figure 3e). See the electronic supplementary material for additional discussion.

The decrease in disparity across the K–Pg boundary supports previous conclusions that the accompanying extinction event was selective among mammals, likely targeting ecological specialists [8,26,44]. A selective mass extinction is more likely to cause a decrease in disparity than a non-selective (i.e. random) mass extinction, because it will have enhanced effects on a particular clade or ecological niche [7] (figure 1). As discussed by Wilson [26], much of the decrease in disparity may be due to the loss of metatherian specialists, such as carnivorous deltatheroidans (e.g. *Nanocuris*). Two metatherian outliers from the Late Cretaceous, *Pediomys* and *Nanocuris*, are labelled in figure 2b. By contrast, eutherian generalists such as archaic ungulates appear to have preferentially survived and taxonomically diversified after the extinction event. The targeting of specialists is consistent with the broad hypothesis that specialists have a higher risk of extinction than generalists (e.g. [53]), especially during periods of significant variability in resources. In D2, the appearance of eutherian morphological outliers and specialists, such as some plesiadapiforms (e.g. *Picrodus*) and mesonychids (e.g. *Ankalagon*), helped instigate a rebound in disparity.

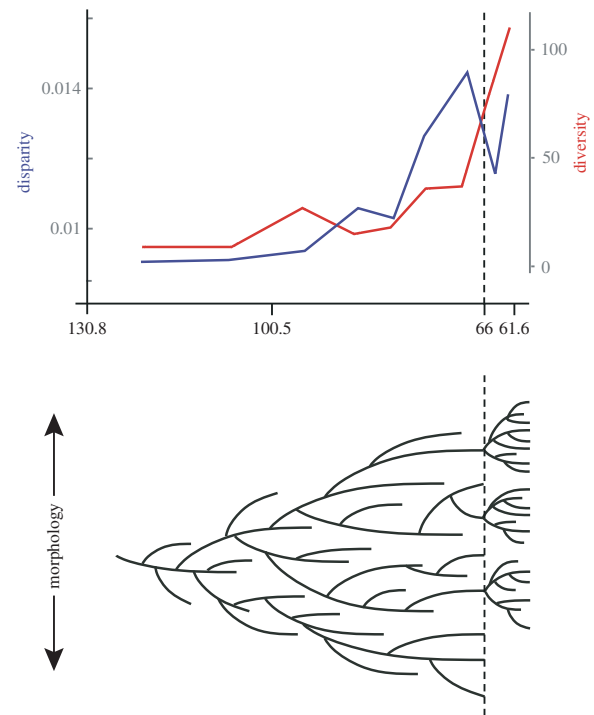## (d) Evolutionary dynamics across the K–Pg boundary

Unlike disparity, taxonomic diversity patterns support SH, showing a rapid generic level diversification immediately following the K–Pg boundary (figure 4). This is likely driven by eutherians that include early placentals [3,5,10,12,44]. The pattern remains after data are corrected for sampling biases using SQS (figure 4b) and residual analyses for TBFs (figure 4c). This pattern is also shown in residual analyses for TBCs, although it is less pronounced (electronic supplementary material, figure S7). The rapid taxonomic diversification in the earliest Palaeocene is especially striking considering the substantial loss of mammalian genera during the extinction event [44]. Alroy [3] documents elevated extinction and origination rates in the earliest Palaeocene of North America, suggesting rapid taxonomic turnover as ecosystems were re-established. The Danian (D1 and D2) bins are dominated (more than 90%) by North American occurrences, suggesting a potential geographical sampling bias for global patterns. Further, immigration of mammals into North America in D1 may be artificially inflating taxonomic diversity levels [8,26,28,44]. However, both bias correction methods indicate that taxonomic diversity during D1 was considerably greater than during K7, which represents a more geographically diverse assemblage. Thus, we posit that a single geographical region showing substantially higher diversity than a more 'global' preceding stage indicates a significant increase in global taxonomic diversity during D1. This inference is supported by occurrences in a third Palaeocene (Selandian) time bin, which contains a more cosmopolitan geographical range in occurrences and a similarly high taxonomic diversity (electronic supplementary material, figure S7).

The predominant therian diet shifts from insectivory to frugivory at the K–Pg boundary [9] (figure 2c). This is due to an influx of taxa with inferred frugivorous or omnivorous diets, including archaic ungulates (55% of unique Palaeocene occurrences), taeniodonts, and polydolopimorphian metatherians.
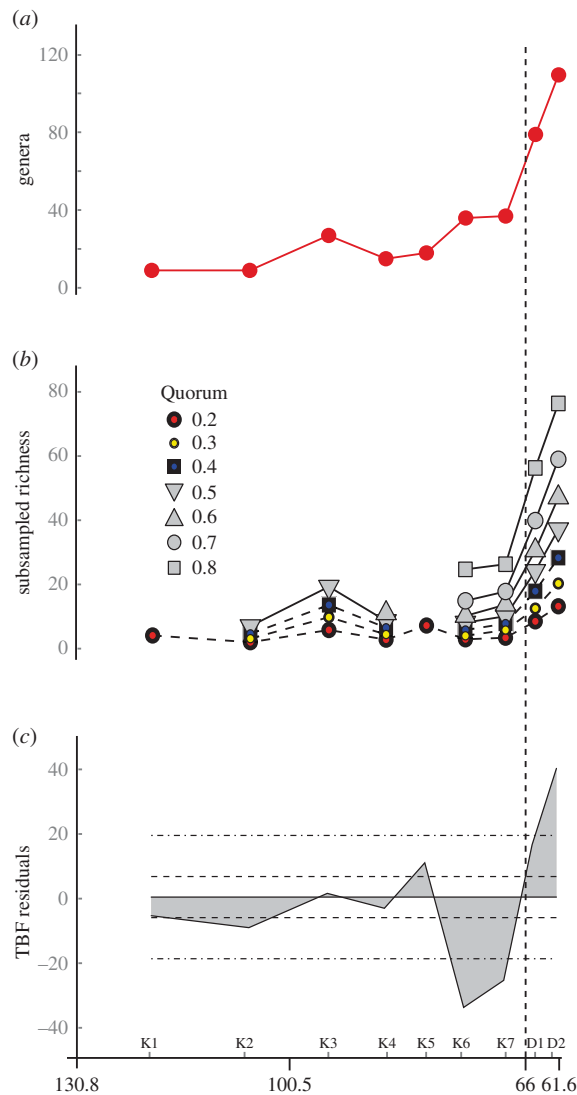
Figure 4. (*a*) Observed (uncorrected) taxonomic diversity through time, calculated as raw counts of unique genera per time bin (TDE, taxonomic diversity estimate). (*b*) Global generic level richness after employing SQS. (*c*) Global residual diversity patterns based on therian-bearing rock formations (TBF). Shaded regions represent divergence from diversity levels that would be predicted by the TBFs alone. Dashed lines mark standard error 95% CIs. Dashed-dotted lines mark standard deviation 95% CIs. Ages are Ma, and time bin age ranges are given in the material and methods section.

Figure 5. (*a*) Observed generic level diversity (red; figure 4*a*) and morphological disparity (blue; figure 3*a*), highlighting the reversal of patterns at the K–Pg boundary. (*b*) Idealized clade history of early therians that displays the increase in Cretaceous disparity, selective extinction event, and taxonomic diversification after the K–Pg boundary.

The abrupt increase in taxonomic diversity of relatively large archaic ungulates and taeniodonts instigated the sudden increase in average body size (figure 3*e*). In D2, plesiadapiforms and pantodonts further fill the frugivore/omnivore morphospace region. In addition to therians, many multituberculates demonstrate frugivorous/omnivorous diets [15], and multituberculates reach their peak dietary and body size diversities in the earliest Palaeocene [15,54]. Therian and multituberculates with plant-dominated diets may have profited from increases in average angiosperm seed size and a greater role as seed dispersers [55]. Further, it has been hypothesized that the loss of large, herbivorous dinosaurs permitted the expansion of dense, closed canopy forests in the Palaeocene [47]. This may help explain the diversification of frugivorous/omnivorous mammals and lack of larger, high-fibre herbivores that may require open habitats [43,47].

Our results indicate that the therian response to the K–Pg extinction event was a decrease in morphological disparity and a rapid increase in taxonomic diversity. To help reconcile these conflicting patterns, we posit that extinction survivors, especially generalists, radiated taxonomically without considerable morphological diversification, filling morphospace regions with similar taxa. This resulted in proportionally fewer morphological outliers and disparity levels that remained low even as the number of taxa increased rapidly. This hypothesis is conceptualized in figure 5, and it is consistent with previous conclusions that generalists such as archaic ungulates dominated the early Palaeocene radiation [6,8,18,56]. Interestingly, the therian response to the K–Pg extinction event is inconsistent with the observation that morphological diversification in clades tends to outpace taxonomic diversification after a mass extinction event (e.g. [57]). Thus, we posit that the response of a clade to a mass extinction event is largely dependent on ecological factors, and the 'disparity-first' model might only be favoured in situations in which ecological opportunities favour specialists over generalists.

4. Conclusion

Our data refute the hypothesis that the ecomorphological diversity of therian mammals was suppressed during the Cretaceous and dramatically increased following the K–Pg extinction event. Instead, we suggest that therian disparity and dietary diversity were increasing through the Late Cretaceous, similarly to the pattern observed in multituberculates [15]. This suggests that mammals as a whole began to diversify

ecomorphologically 10–20 Myr prior to the K–Pg extinction event, during a period marked by the ecological radiation of angiosperms. Further, a decrease in morphological disparity immediately after the K–Pg boundary suggests that an adaptive radiation of therians did not begin in the earliest Palaeocene, although the extinction event may have been a catalyst for a taxonomic diversification of frugivores/omnivores (e.g. archaic ungulates). The K–Pg extinction event was likely selective against ecological specialists and metatherians, and the ecomorphological diversification of mammals, especially placentals, likely resumed in the mid-Palaeocene after the filling of generalist niches.

7

rspb.royalsocietypublishing.org   Proc. R. Soc. B 283: 20160256

References

1. Osborn HF. 1902 The law of adaptive radiation. Am. Nat. 36, 353–363. (doi:10.1086/278137)

2. Patzkowsky ME. 1995 A hierarchical branching model of evolutionary radiations. Paleobiology 21, 440–460. (doi:10.1017/S0094837300013476)

3. Alroy J. 1999 The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. Syst. Biol. 48, 107–118. (doi:10.1080/106351599260472)

4. Smith FA et al. 2010 The evolution of maximum body size of terrestrial mammals. Science 330, 1216–1219. (doi:10.1126/science.1194830)

5. O'Leary MA et al. 2013 The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339, 662–667. (doi:10.1126/science.1229237)

6. Halliday TJD, Goswami A. 2015 Eutherian morphological disparity across the end-Cretaceous mass extinction. Biol. J. Linn. Soc. Lond. 118, 152–168. (doi:10.1111/bij.12731)

7. Foote M. 1993 Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19, 185–204.

8. Simpson GG. 1937 The beginning of the age of mammals. Biol. Rev. Camb. Philos. Soc. 12, 1–46. (doi:10.1111/j.1469-185X.1937.tb01220.x)

9. Collinson ME, Hooker JJ, Skelton PW, Moore PD, Ollerton J, Alexander RMcN. 1991 Fossil evidence of interactions between plants and plant-eating Mammals. Phil. Trans. R. Soc. Lond. B 333, 197–208. (doi:10.1098/rstb.1991.0068)

10. Wible JR, Rougier GW, Novacek MJ, Asher RJ. 2009 The eutherian mammal Maelestes gobiensis from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. Bull. Am. Mus. Nat. Hist. 327, 1–123. (doi:10.1206/623.1)

11. Slater GJ. 2013 Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Paleogene boundary. Methods Ecol. Evol. 4, 734–744. (doi:10.1111/2041-210X.12084)

12. Halliday TJ, Upchurch P, Goswami A. 2015 Resolving the relationships of Paleocene placental mammals. Biol. Rev. Camb. Philos. Soc. (doi:10.1111/brv.12242)

13. Grossnickle DM, Polly PD. 2013 Mammal disparity decreases during the Cretaceous angiosperm radiation. Proc. R. Soc. B 280, 20132110. (doi:10.1098/rspb.2013.2110)

14. Luo Z-X. 2007 Transformation and diversification in early mammal evolution. Nature 450, 1011–1019. (doi:10.1038/nature06277)

15. Wilson GP, Evans AR, Corfe IJ, Smits PD, Fortelius M, Jernvall J. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483, 457–460. (doi:10.1038/nature10880)

16. Newham E, Benson R, Upchurch P, Goswami A. 2014 Mesozoic mammaliaform diversity: the effect of sampling corrections on reconstructions of evolutionary dynamics. Palaeogeogr. Palaeoclimatol. Palaeoecol. 412, 32–44. (doi:10.1016/j.palaeo.2014.07.017)

17. Close RA, Friedman M, Lloyd GT, Benson RB. 2015 Evidence for a mid-Jurassic adaptive radiation in mammals. Curr. Biol. 25, 2137–2142. (doi:10.1016/j.cub.2015.06.047)

18. Hunter JP. 1997 Adaptive radiation of early Paleocene ungulates. PhD dissertation, State University of New York, Stony Brook, NY, USA.

19. dos Reis M, Donoghue PCJ, Yang Z. 2014 Neither phylogenomic nor palaeontological data support a Palaeogene origin of placental mammals. Biol. Lett. 10, 20131003. (doi:10.1098/rsbl.2013.1003)

20. Meredith RW, Westerman M, Case JA, Springer MS. 2008 A phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. J. Mamm. Evol. 15, 1–36. (doi:10.1007/s10914-007-9062-6)

21. Meredith RW et al. 2011 Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334, 521–524. (doi:10.1126/science.1211028)

22. Fox RC, Naylor BG. 2003 A Late Cretaceous taeniodont (Eutheria, Mammalia) from Alberta, Canada. N. Jb. Geol. Paläont. Abh. 229, 393–320.

23. Fox RC, Scott CS, Bryant HN. 2007 A new, unusual therian mammal from the Upper Cretaceous of Saskatchewan, Canada. Cretaceous Res. 28, 821–829. (doi:10.1016/j.cretres.2006.12.005)

24. Archibald JD, Zhang Y, Harper T, Cifelli RL. 2011 Protungulatum, confirmed Cretaceous occurrence of an otherwise Paleocene eutherian (placental?) mammal. J. Mamm. Evol. 18, 153–161. (doi:10.1007/s10914-011-9162-1)

25. Prasad GVR, Verma O, Sahni A, Parmar V, Khosla A. 2007 A Cretaceous hoofed mammal from India. Science 318, 937–937. (doi:10.1126/science.1149267)

26. Wilson GP. 2013 Mammals across the K/Pg boundary in northeastern Montana, USA: dental morphology and body-size patterns reveal extinction selectivity and immigrant-fueled ecospace filling. Paleobiology 39, 429–469. (doi:10.1666/12041)

27. Clauset A, Redner S. 2009 Evolutionary model of species body mass diversification. Phys. Rev. Lett. 102, 038103. (doi:10.1103/PhysRevLett.102.038103)

28. Clemens WA. 2002 Evolution of the mammalian fauna across the Cretaceous-Tertiary boundary in northeastern Montana and other areas of the Western Interior. Geol. Soc. Spec. Pap. 361, 217–245. (doi:10.1130/0-8137-2361-2.217)

29. Schluter D. 2000 The ecology of adaptive radiation. Oxford, UK: Oxford University Press.

30. Slater GJ. 2015 Iterative adaptive radiations of fossil canids show no evidence for diversity-dependent trait evolution. Proc. Natl Acad. Sci. USA 112, 4897–4902. (doi:10.1073/pnas.1403666111)

31. Mitchell JS. 2015 Extant-only comparative methods fail to recover the disparity preserved in the bird

fossil record. *Evolution* **69**, 2414–2424. (doi:10.1111/evo.12738)

32. Tarver JE, Donoghue PC. 2011 The trouble with topology: phylogenies without fossils provide a revisionist perspective of evolutionary history in topological analyses of diversity. *Syst. Biol.* **60**, 700–712. (doi:10.1093/sysbio/syr018)

33. Alroy J. 2010 Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* **53**, 1211–1235. (doi:10.1111/j.1475-4983.2010.01011.x)

34. Lloyd GT. 2012 A refined modelling approach to assess the influence of sampling on palaeobiodiversity curves: new support for declining Cretaceous dinosaur richness. *Biol. Lett.* **8**, 123–126. (doi:10.1098/rsbl.2011.0210)

35. Davis BM. 2007 A revision of 'pediomyid' marsupials from the Late Cretaceous of North America. *Acta Palaeontol. Pol.* **52**, 217.

36. Gradstein FM, Ogg JG, Schmitz M, Ogg G. 2012 *The geologic time scale 2012*. Amsterdam, The Netherlands: Elsevier.

37. Rohlf FJ, Marcus LF. 1993 A revolution in morphometrics. *Trends Ecol. Evol.* **8**, 129–132. (doi:10.1016/0169-5347(93)90024-J)

38. Adams DC, Otarola-Castillo E. 2013 Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* **4**, 393–399. (doi:10.1111/2041-210X.12035)

39. Polly PD. 2015 *Geometric morphometrics for Mathematica Version 11.4*. Bloomington, IN: Department of Geological Sciences, Indiana University.

40. Smith AB, McGowan AJ. 2007 The shape of the Phanerozoic marine palaeodiversity curve: how much can be predicted from the sedimentary rock record of Western Europe? *Palaeontology* **50**, 765–774. (doi:10.1111/j.1475-4983.2007.00693.x)

41. Crampton JS, Beu AG, Cooper RA, Jones CM, Marshall B, Maxwell PA. 2003 Estimating the rock volume bias in paleobiodiversity studies. *Science* **301**, 358–360. (doi:10.1126/science.1085075)

42. Good IJ. 1953 The population frequencies of species and the estimation of population parameters. *Biometrika* **40**, 237–264. (doi:10.1093/biomet/40.3-4.237)

43. Janis CM. 2000 Patterns in the evolution of herbivory in large terrestrial mammals: the Paleogene of North America. In *Evolution of herbivory in terrestrial vertebrates* (ed. H-D Sues), pp. 168–222. Cambridge, UK: Cambridge University Press.

44. Wilson GP. 2014 Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary in northeastern Montana, USA. *Geol. Soc. Spec. Pap.* **503**, 365–392. (doi:10.1130/2014.2503(15))

45. Vavrek MJ, Larsson HC. 2010 Low beta diversity of Maastrichtian dinosaurs of North America. *Proc. Natl Acad. Sci. USA* **107**, 8265–8268. (doi:10.1073/pnas.0913645107)

46. Mitchell JS, Roopnarine PD, Angielczyk KD. 2012 Late Cretaceous restructuring of terrestrial communities facilitated the end-Cretaceous mass extinction sin North America. *Proc. Natl Acad. Sci. USA* **109**, 18 857–18 861. (doi:10.1073/pnas.1202196109)

47. Wing SL, Tiffney BH. 1987 The reciprocal interaction of angiosperm evolution and tetrapod herbivory. *Rev. Palaeobot. Palynol.* **50**, 179–210. (doi:10.1016/0034-6667(87)90045-5)

48. Feild TS et al. 2011 Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proc. Natl Acad. Sci. USA* **108**, 8363–8366. (doi:10.1073/pnas.1014456108)

49. Coiffard C, Gomez B, Daviero-Gomez V, Dilcher DL. 2012 Rise to dominance of angiosperm pioneers in European Cretaceous environments. *Proc. Natl Acad. Sci. USA* **109**, 20 955–20 959. (doi:10.1073/pnas.1218633110)

50. Boyce CK, Brodribb TJ, Feild TS, Zwieniecki MA. 2009 Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proc. R. Soc. B* **276**, 1771–1776. (doi:10.1098/rspb.2008.1919)

51. McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD. 2009 Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl Acad. Sci. USA* **106**, 7083–7088. (doi:10.1073/pnas.0810618106)

52. Labandeira CC, Sepkoski JJ. 1993 Insect diversity in the fossil record. *Science* **261**, 310–315. (doi:10.1126/science.11536548)

53. Smits PD. 2015 Expected time-invariant effects of biological traits on mammal species duration. *Proc. Natl Acad. Sci. USA* **112**, 13 015–13 020. (doi:10.1073/pnas.1510482112)

54. Williamson TE, Brusatte SL, Secord R, Shelley S. 2015 A new taeniolabidoid multituberculate (Mammalia) from the middle Puercan of the Nacimiento Formation, New Mexico, and a revision of taeniolabidoid systematics and phylogeny. *Zool. J. Linn. Soc.* **177**, 183–208. (doi:10.1111/zoj.12336)

55. Eriksson O. 2014 Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. *Biol. Rev. Camb. Philos. Soc.* **91**, 168–186. (doi:10.1111/brv.12164)

56. Archibald JD. 2011 *Extinction and radiation: how the fall of dinosaurs led to the rise of mammals*. Baltimore, MA: The Johns Hopkins University Press.

57. Benton MJ. 2015 Exploring macroevolution using modern and fossil data. *Proc. R. Soc. B* **282**, 20150569. (doi:10.1098/rspb.2015.0569)