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Changes in morphological disparity in eutherian mammals across the K-Pg boundary and Palaeocene-Eocene Thermal Maximum using discrete morphofunctional characters

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Table 1 Brief summary of changes in disparity metric over the K-Pg and PETM boundaries discusses within this paper. Information on change in metric is gathered from stage level metrics for Sum of Variances (Figure 4), Sum of Ranges (Figure 6), Distance from Centroid (Figure 8) and the Weighted Mean Pairwise Disparity analyses (Figures 11 & 12). Changes are termed 'significant' based on whether the standard deviations for each plot do not overlap, or 'minimal' if standard deviations overlap entirely. _____ 56

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iii. Statement of Originality:

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein has been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

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Changes in morphological disparity in eutherian mammals across the K-Pg boundary and Palaeocene-Eocene Thermal Maximum using discrete morphofunctional characters

iv. Abstract

The mammalian clade Eutheria comprises placental mammals (the dominant group of mammals today, with >6000 living species, ~93% of living diversity) plus their stem relatives. A major event in Earth history that had a profound influence on Eutheria was the Cretaceous–Paleogene (K–Pg) extinction event, ~66 million years ago. Prior to this extinction event, during the Mesozoic, known eutherians were small and apparently predominantly insectivorous, showing relatively limited morphological disparity. After it, during Palaeogene, there was a major increase in eutherian disparity, with a much wider range of body sizes and ecomorphologies (including specialized herbivores and carnivores) appearing in the fossil record, reflecting the availability of new ecological niches. A second key event known to have influenced eutherian evolution is the Palaeocene-Eocene Thermal Maximum (PETM), a period of particularly high global temperatures ~55 million years ago, which coincided with major faunal turnover. However, the extent to which the PETM affected eutherian disparity, and how this compares to the changes seen across the K-Pg boundary, has been less well studied. Previous studies of mammalian disparity using discrete characters have typically used phylogenetic character matrices, which are intended to resolve evolutionary relationships, and so score non-homologous but functionally equivalent structures differently; this may be problematic for estimating changes in disparity. Here, a different approach is used: 61 discrete character traits of the dentition and lower jaw are identified that reflect morphofunctional attributes but that do not take into account specific homologies (e.g. the particular dental locus), and which should more accurately reflect ecomorphological disparity. These characters are scored for 245 eutherian taxa from the Late Cretaceous, Palaeocene and Eocene. The resultant matrix was then used to quantify morphological disparity and changes in morphospace occupancy in eutherians over time using Principal Co-Ordinate Analysis (PCoA) and non-metric multidimensional scaling (NMDS), using both epoch and stage/age time bins, and comparing the global pattern with results for individual landmasses. Disparity changes were then quantified for the PCoA analysis using Sum of Variances (SOV), Sum of Ranges (SOR), Distance from Centroid (DFC) and Weighted Mean Pairwise Disparity analyses. Results confirm a major increase in morphospace occupancy across the K-Pg boundary, with the Late Cretaceous

morphospace entirely within the much larger Palaeocene morphospace. From the Palaeocene to the Eocene, morphospace occupancy again increases to a larger extent, and part of the Palaeocene morphospace is not represented in the Eocene, suggesting that some ecomorphologies were lost across the PETM. Morphological variance disparity increases marginally over the K-Pg, before seeing a much larger increase over the PETM. This study provides a new perspective on trends in eutherian morphological disparity during the late Mesozoic and early Palaeogene, and shows that discrete morphofunctional characters can be used to effectively quantify changes in morphospace occupancy.

v. Keywords:

Eutheria, Mammals, Morphological Disparity, Functional Morphology, K-Pg, PETM.

1. Introduction

1.1 Morphological disparity and its importance in evolutionary biology

Morphological disparity has been defined as the range or variance of morphological form across a variety of species or other taxa, and, as such, is distinct from diversity or taxonomic richness, which refers simply to the number of taxa (Foote 1991; Fortey, Briggs and Wills 1996; Oysten et al 2016). Studies into quantitative disparity analyses were sparked by the 1944 book *Tempo and Mode* by Simpson, in which he describes evolutionary rates and patterns. Quantitative analyses of morphological disparity were originally described as investigating ‘multidimensional morphological dissimilarity at a macroevolutionary scale’ (Runnegar 1987; Gould 1991), and have been a major focus of palaeobiological research over the last 30 years (Hopkins & Gerber 2017; Guillerme et al 2020). These analyses attempt to quantify changes in morphology within and between clades, and so can be used to investigate a wide range of fundamental macroevolutionary questions regarding how clades evolve through time. Disparity analyses through time can look at how clades have evolved on a continuous time scale (Gould 1991) or within discrete time bins (for example, geological epochs or stages/ages, or equally-sized time bins specified by the researcher). Such studies can be used to analyse how disparity changes before, during, and after mass extinction events (Friedman 2010), and how disparity accumulates over a clade’s entire history (Brusatte et al 2008). Changes in the rate of evolution of morphological disparity are important indicators for macroevolutionary change (Lloyd, Wang and Brusatte 2011), and can be linked to adaptive radiations. Adaptive radiation as a concept was conceived by Osborne (1902) and is defined as the ‘evolution of ecological and phenotypic diversity within a rapidly multiplying lineage’ (Gavrilets and Vose 2005). Adaptive radiations are often suggested to be characterised by an “early burst” of evolution, where disparity increases more rapidly in the early diversification of the clade than later in its history (Foote 1996; Wagner 2018). Early peaks in disparity may not always be a signifier of an adaptive radiation, however: if disparity rates are constant but the range of evolutionary outcomes are constrained (either by ecological or developmental factors Foote 1996; Slater 2015), the ‘early peak’ may be more reflective of morphospace saturation.

Many morphological disparity studies have investigated the decoupling of taxonomic diversity (the number of species) and disparity (Wills et al 1994; Bapst et al 2012; Hopkins 2013). Taxonomic diversity and disparity are fundamentally different from one another: for example, a small clade

that contains only a few species that nevertheless differ greatly from each other morphologically will have higher disparity than a larger clade comprising species that are morphologically homogenous (Hughes, Gerber and Wills 2013; Oysten et al 2016). The connection between disparity and ecology has also been studied in detail, as a clade's morphological disparity can be used a proxy for the functional roles its members play within either an ecosystem or a set of ecological niches (Guillerme et al 2020). The relationship between morphology and function (with some morphological traits having multiple functions (Wainwright et al 2005)) has been used to infer competition in the fossil record, for example within communities of brachiopods (Tyler and Leighton 2011), and thus analysis of disparity can be a valuable tool for understanding ecological interactions between extinct species.

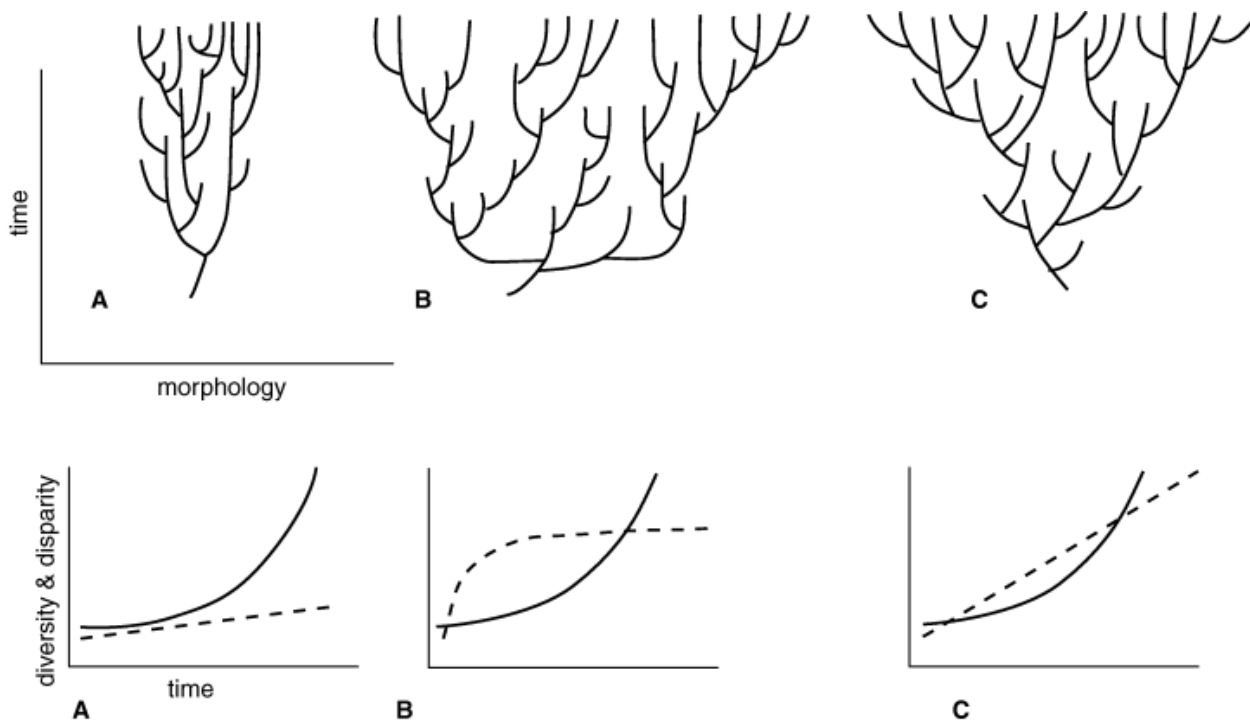


Figure 1. Above: idealized diversity patterns. Below: predicted diversity and disparity curves over time (solid line, taxonomic diversity; dashed line, morphological disparity). A constrained morphological evolution with taxonomic exceeding morphological diversification. B morphological diversification outstrips taxonomic diversification with large morphological steps early in the clade's history; morphological diversity may continue to increase, but steps are smaller. C, morphological diversification is concordant with taxonomic diversification; no constraint on morphological evolution, nor trend in morphological step size (Replicated from Erwin 2007, Fig 1)

1.2. Quantifying morphological disparity

1.2.1 Morphometric methods

Morphological disparity can be measured in different ways. A morphometric approach involves the measurement of continuous variation in shape and/or size of an organism or part of an organism. Morphometric analyses use continuous measurements such as linear, landmark or contour (curved) measurements of anatomical structures (Guillerme et al 2020), which can be obtained from both in person measurements of specimens, or via digital scans/images. Currently, a particularly common approach is the use of geometric morphometrics (GMM). GMM is a specific branch of morphometrics that focuses on shape as defined by its geometric properties, with different shapes compared after first removing differences in position (translation), orientation (position) and size (any scaling). The shape of a structure is specified using sets of two or three dimensional coordinate points that define the geometry of the feature of interest. Each coordinate point reflects a 'landmark', which measures the location of homologous features, or an 'outline', which measures the outer structure of the morphology (von Cramon-Taubadel, Frazier and Lahr, 2007; Hopkins and Gerber 2017, Schaeffer et al 2019). Advantages to using GMM-based methods over other morphometric methods are that they produce clear graphical outputs of the shape changes within a set of taxa (von Cramon-Taubadel, Frazier and Lahr, 2007), but they can also prove more difficult when used within large datasets, as landmark data collected over multiple studies cannot be easily combined for larger scale analyses (Hallgrímsson et al 2009; Davine et al 2020). It also seeks to quantify overall shape, whereas discrete character analysis can be biased by character choice and issues around correlations between characters.

1.2.2 Discrete methods

The other major approach for measuring morphological disparity is via the use of discrete characters. These are typically categorical observations of traits (e.g., the presence or absence of a particular feature), but can also be used as qualitative descriptors of different expressions or states of a present trait (Hopkins, Gerber 2017): for example, the shape or position of particular anatomical structures. They can be a useful in analyses where researchers are unable/choose not to gather primary data from specimens in person, as they can often be gathered from images/scans of specimens that may not include exact measurements, and is the method used in

this study. This method is implemented in this study due to the broad taxonomic sample, which would prove difficult to gather primary data from in person due to the dispersal of taxa specimens globally, and due to the fragmentary nature of the Eutherian taxa selected for within this study.

Direct gathering of data is sometimes not even necessary for discrete disparity analyses: often cladistic/phylogenetic matrices are reused from other analyses, and so a researcher does not need to build a character matrix from scratch. For example, Close et al. (2013) and Halliday and Goswami (2016) carried out morphological disparity analyses of mammals using the phylogenetic matrices of Zhou et al. (2013) and Halliday et al. (2015) respectively. However, phylogenetic matrices may not be the most appropriate choice for analyses of morphological disparity, for several reasons. Phylogenetic character matrices score non-homologous but functionally equivalent structures very differently (Gerber 2018): for example, rodents and lagomorphs have an enlarged anterior lower incisor which is the deciduous i₂, and some plesiadapiforms also have an enlarged lower incisor (Silcox et al 2017), which for them is i₁: these two structures are likely functionally equivalent, but would be scored differently in phylogenetic matrices, in which it is critical to distinguish between homologous and non-homologous structures. Phylogenetic matrices typically also do not include autapomorphies (derived features present in a single taxon) as they are uninformative to phylogenetic relationships, but they do provide information about the morphological distinctiveness of taxa. Phylogenetic character matrices also often use anatomical features that appear to have little to no functional and therefore ecological significance as characters, and these may not be particularly useful for morphological disparity analyses, which (at least implicitly) are often interested in the evolution of morphological adaptations that allow the occupation of novel ecological niches. An alternative approach, which has been less commonly used, is to use discrete characters that have been selected to specifically reflect disparity in functional morphology rather than for resolving phylogeny (Giannini and Garcia-Lopez 2013; Reeves et al 2020). In this approach, functionally similar features are scored as equivalent, even if they are non-homologous. For example, Reeves et al. (2020) analysed disparity in marine tetrapods using nine very broad ecofunctional traits, which included general morphofunctional characters such as the presence and overall type of “armour”, regardless of their specific homology. Focusing specifically on mammals, Giannini and Garcia-Lopez (2013) used this approach to analyse morphological disparity in South American native “ungulates” (Notoungulata), scoring 31 cranial characters that “provided a basic description of shape and an

approximation to sensory and mechanical functions of the skull” (Giannini and Garcia-Lopez, 2013).

Regardless of whether they are recycled phylogenetic character matrices or not, discrete character sets can usually accommodate a broader range of morphologies within a single analysis than can morphometric analyses, meaning that a morphologically more disparate range of taxa can be included (Lehmann et al 2019). They can also incorporate taxa that are known from incomplete specimens, e.g. fossil mammal taxa for which no known specimen preserves a particular tooth or region of the skull, whereas this is more problematic for morphometric studies, as a complete specimen is required to record relevant measurements. This does not mean that discrete character distance matrices are exempt from problems associated with missing data. Simulations show that disparity analyses of discrete character datasets that contain gaps/missing data are still able to function well through the use of distance metrics that aid in ‘filling in’ missing values (Lloyd 2016). Distance metrics are used to determine the distance between all pairs of taxa scored for a set of discrete characters. Missing values/entries in discrete taxon matrices mean that no distance between some species can be calculated due to missing overlapping data (Lehmann et al 2019), so distance metrics like the Gower Coefficient (GC; Gower, 1971) and Maximum Observed Rescaled Distance (MORD) rescale calculable distances based on the number of characters that can be compared between each pair of taxa (Lloyd 2016). MORD is an extension of the GC metric (which divides each distance between points by the number of characters), and is designed to deal with the fact that multistate ordered characters can lead to GC distances of greater than 1. MORD rescales the GC distance by the maximum possible distance that could be observed based on the number of characters codable in each pairwise comparison, meaning all resulting distances are on a zero to one scale (Lloyd 2016). Distance metrics are not always a complete solution for missing data: Lehmann et al (2019) studied the effect of missing data on disparity analyses, and found that using the Generalised Euclidean Distance (GED) metric meant that taxa were more likely to be placed closer to the centroid the more data they were missing, but that MORD (whilst not entirely alleviate the problem of missing data) is more robust to missing data (Lehmann et al 2019). Thus, current evidence favours the use of MORD for disparity analyses of discrete characters. More seriously, if there are no comparable characters between a particular pair of taxa (e.g. if taxon A is only known from upper dentition, and taxon B is only known from lower dentition), a distance cannot be calculated.

1.2.3 Comparison of morphometric and discrete character data for disparity analysis

Morphometric and discrete character scoring differ primarily in the way that they measure morphological variation (continuous variation in shape/size vs discrete observations), but a previous study by Mongiardino Koch et al (2017) found differing results when testing the congruence of both scoring types. In their analysis on the morphological evolution of the scorpion species *Brachistosternus* they found that continuous morphometric characters accelerated the rate of evolution towards the present, suggesting that the acquisition of species-specific adaptations had driven their morphological evolution, whereas discrete characters supported a sharp reduction in evolutionary rate through time, indicative of 'early bursts' seen during adaptive radiations. Other studies into this found differing results, with suggestions that both types of character scoring result in similar disparity analysis (Hetherington et al 2015, Schaeffer et al 2020).

1.2.4 Multidimensional scaling

One method frequently used to quantify similarity or dissimilarity within data (such as in a character-taxon matrix) is Multidimensional Scaling, or MDS. This allows for data to be represented/visualised as points within a lower dimensional space, with the distances between said points reflecting the degree of similarity (or dissimilarity) between the data objects. The overall procedure of representing data in a multidimensional space is known as ordination (MacLeod, 2002). MDS analyses can be separated into two main classes – metric and non-metric.

Metric multidimensional scaling is more commonly known as Principal Coordinate Analysis (PCoA). In disparity analyses, PCoA can be used to take a set of taxa scored for a set of discrete morphological characters and assign those taxa a position within a morphospace (defined as a multidimensional mathematical space that describes and relates the morphology and phenotype of organisms; Mitteroecker & Huttegger 2009), in which the distances between taxa correspond to a pairwise distance metric (e.g. GC or MORD). In PCoA, any distance metric can be used (Jørgensen 1986), whereas in Principal Component Analysis (PCA), the distance metric is always the Euclidean distance; PCA is more often used when the data is continuous rather than discrete. The PCoA morphospace comprises a certain number of axes (typically $n-1$, where n is the total number of taxa in the matrix) that collectively summarise the total variation present in the set of pairwise distances for all the taxa. The axes are ranked according to the amount of variation they explain,

with axis 1 explaining the greatest variation, followed by axis 2, and so on. The morphospace can be partially visualised by plotting two or three axes in a 2D or 3D plot, respectively. Usually only the first two or three axes are plotted, as these explain the greatest amount of variation, but if the percentage of the total variation explained by these is low, then such a plot may not be a particularly accurate representation of the overall morphospace. Nevertheless, such plots can be useful to visualise individual or group differences, and to identify general trends in the data.

Non-metric MDS (NMDS) is similar to PCoA, but converts absolute distances between pairs of taxa into a ranked order, and then creates a morphospace that simply maintains that order rather than the absolute distances. NMDS has been shown to perform well with character-taxon matrices that include gaps (Deline et al 2018), and so is well suited to analysing matrices that contain incomplete fossil specimens, as used here. NMDS uses an iterative approach to generate the morphospace, which attempts to minimise “stress” (the degree to which the ranked distances in the morphospace differ from the original ranked distances); thus, NMDS may return different solutions on re-runs of the same data, whereas PCoA will not. Whereas the number of axes in a PCoA analysis is based on the number of samples (in a morphological disparity analysis, the number of taxa) in the dataset, NMDS analysis allows the user to specify the number of axes. Analogously to PCoA, NMDS axes are ranked according to the amount of stress they reduce. To visualise the NMDS morphospace, these axes can be plotted; again, analogously to PCoA, typically only the first two or three axes (which reduce the greatest amount of stress) are plotted.

Regardless of whether PCoA or NMDS is used, plots of the first two or three axes are commonly used to look at morphospace occupancy of particular groups and how these compare with other groups (if present) in the same morphospace (Friedman 2010; Giannini and Garcia-Lopez 2013; Strickson et al 2016; Reeves et al 2020). They can also be used to analyse changes in morphospace occupancy within and between groups through time (Shelley, Brusatte and Williamson 2021), for example around major periods of change caused by mass extinctions (Friedman 2010; Wilson 2013; Halliday and Goswami 2016; Hopkins and Gerber 2016; Puttick, Guillerme and Wills 2020) or climate change (de Vries et al 2021), or during adaptive radiations (Grossnickle and Polly 2013; Slater 2014; Close et al 2015). They can also be used to infer traits that are hard to measure directly in extinct species, such as diet, by comparing them with extant species (Morales Garcia, 2021).

1.2.5 Disparity Analysis Measures

As discussed above, the first two or three PCoA or NMDS axes may explain only a relatively small percentage of the total variation or reduce only a small proportion of the overall stress respectively; thus, 2D or 3D plots of these axes may not be a particularly accurate representation of the overall morphospace. Thus, for analysis of changes in morphospace occupancy, it is more appropriate to use quantitative approaches that summarise the variation present in the full set of axes, or, alternatively, a subset of axes that have been identified as collectively comprising a sufficient amount of the total variation or stress (for example, as determined by a scree plot). A variety of different indices can be used for this, each with different advantages and disadvantages (Ciampaglio, Kemp & McShea 2001; Korn, Hopkins & Walton 2013), three of the most commonly used being the Sum of Ranges (SOR), the Sum of Variances (SOV) and the Position of the Centroid (POC).

Sum of Ranges (SOR) is used to describe the total range of morphospace occupation that is represented by the volume of a hypercube that covers all of the taxa within it (Korn, Hopkins & Walton 2013). It does not describe the overall shape of the morphospace but reflects the magnitude of the dissimilarity between the taxa. It is sensitive to outliers with morphologies that differ greatly from those comprising the main body of taxa (Simon, Korn and Koenemann 2010; Guillerme et al 2020), sample size, and axis orientation (Roy and Foote 1997; Hopkins and Gerber 2016). Ciampaglio et al (2001) showed that SOR (as well as range, SOV, PCO volume, average pairwise dissimilarity, and unique pairwise similarity) is sensitive to the number of characters included in a disparity analysis: as the number of characters used increases, there is an increase in disparity as measured by SOR (Ciampaglio, Kemp and McShea 2001 – Fig. 2).

Sum of Variances (SOV) measures the distances between points within a morphospace, and is less affected by taxa sample size (Ciampaglio et al 2001, Villier and Eble 2004, Korn, Hopkins and Walton 2013) making it a good tool for disparity analyses where sample sizes between groups or time bins can vary greatly. However, it can be affected by the immigration of morphologically similar species, which will cause the SOV to decrease (Simon et al 2010, Korn, Hopkins and Walton 2013) as morphological variance is decreasing within the taxa sample. As SOV measures distances between the plot points/taxa within the morphospace, they can also be used to determine whether or not an extinction event was selective or non-selective (Ciampaglio, Kemp & McShea

2001, Simon et al 2010). SOR cannot be used to define this, as it simply measures morphospace occupancy and cannot comment on changes in morphospace shape, which is why SOV is needed to provide a description of morphospace shape changes as a result of changes in variance-based disparity (i.e. extinction events). Selective events will result in the trimming of the morphospace in particular areas, which will often result in a decrease in the SOV value, as opposed to non-selective extinction events that will result in a random trimming of the morphospace and a little change in the SOV (Simon et al 2010), but may result in a minor positional shift of the centroid (the most common taxon morphology in the morphospace). If an event is selective, the position of centroid will change, reflecting the uneven removal of taxa from the morphospace.

The Position of Centroid (POC) measures the average (median, or, more typically, mean) value along each morphospace axis (Korn, Hopkins and Walton 2013), and provides information about the “average”/“typical” morphology within a morphospace. Changes in this can reflect the nature of an extinction event – if there is a large asymmetric/lateral extinction event, the POC will shift towards the area of morphospace not selected against. It can also provide information about the recovery of a morphospace after it has been affected by an extinction event, as the new morphologies arising from either diversification or immigration from surrounding morphospaces may cause a shift in the POC value (Simon et al 2010, Korn, Hopkins and Watson 2013).

1.2.6 Disparity Analysis Tools

Disparity analyses of discrete morphological character matrices are typically done using packages in the R computing environment (R Core Team, 2016). Currently, the two most widely used packages for such analyses, and which will be used in this study, are Claddis (Lloyd, 2016) and DispRity (Guillerme, 2018). Claddis includes functions for performing rate and disparity analyses, and it can also be used to ordinate matrices prior to other forms of analysis (Lloyd 2016).

The DispRity package (Guillerme, 2018) is primarily aimed at discrete morphological disparity analysis, but can also be used for any type of multidimensional data. The package takes multidimensional data (otherwise known as a morphospace in this analysis) – e.g. a character-taxon matrix that has been subjected to ordination via a multivariate method such as Principal Coordinate Analysis (PCoA) or Non Multidimensional Scaling (NMDS) – and calculates one or more disparity metrics from it. A variety of disparity metrics are available in DispRity, including Mean

Pairwise Distance, which is based on distances between points in morphospace (Foote 1993), and Sum of Variances and Sum of Ranges of each axis of the morphospace (Ciampaglio, Kemp and McShea 2001, Wills 2001). Once a disparity metric has been selected, a variety of statistical tests can also be done on this, including nonparametric multivariate analyses of variance (NPMANOVA) and multidimensional permutation tests (Guillerme 2018).

1.3 Previous fossil-based analyses of morphological disparity

The rate at which disparity changes through time is not always constant in a clade's evolutionary history. In a highly influential paper, Gould et al. (1987) discussed three different models for the evolution of disparity rates within a clade, terming them 'bottom heavy' (maximum disparity rates reached early in the clade's history), 'symmetrical' (maximum rates reached roughly at the midpoint of their history) and 'top-heavy' (maximum rates reached near/close to the end of their evolutionary history) (Romano, Brocklehurst and Frobisch, 2017). Gould et al. (1987) found that clades predominantly fall within the 'bottom-heavy' category, with early high levels of disparity that plateau or decrease over time. This was also reflected by a large number of clades (although not all: clades that specifically terminated at one of the major five mass extinction events had a significantly top-heavy centre of gravity) in a study by the Hughes et al. (2013). This overall finding can be explained by clades expanding into a new environment that was either recently vacated by another clade, or by acquiring a new trait/characteristic that lets them successfully dominate the new ecospace uncontested. The expansion into these new morphospaces will prompt rapid diversification to fill the new niche, until a maximum point has been reached and the various niches within the morphospace have been filled. Hyper-specific morphological specialisation that can come about from the need to fill and be successful in a new niche is not always desirable, however: it has previously been linked with extinction susceptibility (Korn, Hopkins and Walton 2013) in species who are only able to survive in very particular niches, as they will often sit at the very edge of a morphospace where they are more at risk of being affected by lateral and marginal extinction events. An example of this can be seen in some hypercarnivorous species being locked into a macroevolutionary 'ratchet', where increasingly specified forms are selected for, resulting in clade extinction (Van Valkenburgh, Wang and Damuth 2004; Balisi and Van Valkenburgh 2020).

Extinction events have the opposite effect on clades' morphological disparity, acting to reduce

disparity within a morphospace. There are three main modes of extinction that are responsible for reductions in morphospace: “marginal extinction”, where the edges of a morphospace are symmetrically trimmed; “lateral extinction”, where one side of the morphospace is eradicated asymmetrically; and “random extinction”, where an unexpected extinction event (e.g., a natural disaster similar to the impact event at the Cretaceous – Palaeocene (K-Pg) boundary) wipes out a random section of the morphospace (Korn, Hopkins and Walton 2013). Lateral extinctions may arise due to selection pressures due to specific environmental/biotic factors, whereas random events are non-selective, with extinction or survival less to do with particular adaptations in morphology. The ‘field of bullets’ (Raup 1981) is an example of a non-selective extinction mode, in which extinction selectivity is unpredictable and not impacted by life history traits. Some studies have found that human activity can lead to this mode of extinction (Duncan and Lockwood 2001). Extinction events (in particular, random extinction events) are often thought to allow for new species to rapidly diversify and refill now empty niches, but that is not always the case: diversity reductions can sometimes cause abandoned niches within morphospaces to disappear permanently (Kirchner and Weil 2000, Lowery and Fraass 2019), suggesting that, although some niches may be independent of their inhabitants, some ecological niches are inseparable from the taxa that created/supported them (Erwin 2007, Lowery and Fraass 2019).

Adaptive radiations and disparity are often closely entwined, as a rapid appearance of new morphologies within a clade will inevitably increase its morphological disparity. Mass extinctions, such as the one found at the K-Pg boundary, are often said to be drivers of adaptive radiation. This is due to the massive increase in available ecospace which has been vacated by now extinct taxa, and which can then be filled by new taxa evolving relevant morphologies (Halliday et al 2016). Other ecological opportunities such as the extinction/absence of competitors and the evolution of a ‘key’ trait that allows taxa to fill a niche (Yoder et al 2010) may also allow for a classical adaptive radiation to occur. The ‘classic’ version of an adaptive radiation involves an early burst of speciation and trait evolution, which then leads to a reduction in diversification rates due to the filling of the ecospace (Simpson 1953; Ingram, Harmon and Shurin, 2012). This does, however, make the assumption that the majority of the branching events occurred in the clade’s early evolutionary history, and that a large proportion of the disparity within its extant members comes about because of said early branching; these may not always be the case, as there can be high

rates of speciation without much change in disparity. For example, diversification within muroid rodents has been accompanied by little increase in morphological disparity (Alhajeri and Stepan 2018).

These early morphological disparity bursts are typically are not very common (with more constant rates of evolution being favoured over early bursts (Slater 2015)), but have been witnessed in clades like mammals (Cooper and Purvis 2010). Identifying classic adaptive radiations from clades that look to have experienced an early disparity burst has proven to be rather difficult, due to a lack of broad-scale comparative datasets. A large proportion of the currently accepted adaptive radiations have come from endemic isolated ocean island/lake island species (Harmon et al 2010). Modern cetaceans are hypothesized to have potentially undergone an early Oligocene adaptive radiation based on extant species, but studies have found little evidence to definitively support this (Slater et al 2010) suggesting that extensive extinctions within the group have masked any sign of a rapid radiation (Rabosky & Lovette 2008). This may be resolved by including fossil species within the analysis (Lloyd and Slater 2021), as they may document stages of the evolutionary process that are not observable when only modern taxa are considered.

Previous studies of adaptive radiations have suggested that low ecological disparity should be expected at the start of a radiation (Mitchell & Makovicky, 2014, Halliday et al 2016) no matter the taxon richness of the group, and that clades tend to saturate morphospace relatively quickly, with much of the major ecomorphological diversity occurring in the early evolutionary history of the clade (Mitchell and Makovicky 2014). After an initial rapid lineage accumulation, diversification rates will typically slow (Ingram, Harmon and Shurin 2012, Harmon et al 2010, Linder and Bouchenak-Khelladi 2009). Within what has been dubbed the Early Burst model by Harmon et al (2010), clades/lineages can enter what Simpson (1944) coined an 'adaptive zone': a space with similar niches that are ecologically viable and empty of competitors for certain lineages/clades to expand into with little resistance from competition (Harmon et al 2010). It has been argued that morphological disparity should increase rapidly until the niche within the zone is filled and then slow, but Harmon et al. (2010) found little support for this, instead finding support for the single stationary peak mode, which predicts that young subclades will capture much of the variation in trait values and be roughly as variable as older clades.

There has been a long history of analysing morphological disparity in the fossil record, and in

particular using this to identify macroevolutionary patterns and trends through time. The ability to quantify change in disparity in “deep time” can give fundamental insights into evolutionary tempo and mode (Simpson 1944). Numerous studies have quantified changes in morphological disparity within a variety of fossil groups through time, including marine tetrapods (Reeves et al 2020), mammals (Goswami, Milne and Wroe 2011; Giannini and Garcia-Lopez, 2013; Close et al 2015; Benevento et al 2019) and dinosaurs (Brusatte et al 2008; Brusatte et al 2012; Schaeffer et al 2020), and some have used morphological disparity analyses to test the relation between changes in morphology in taxa to major events in Earth history, such as end-Cretaceous extinction event (Halliday and Goswami 2016), and the Palaeocene–Eocene Thermal Maximum (PETM; Grossnickle and Polly 2013; de Vries et al 2021). Benevento et al. (2018) used morphometric analyses of lower jaw shape (specifically jaw ratios that relate to mechanical jaw functionality) with mammalian taxa throughout the Mesozoic and Cenozoic periods to determine how jaw morphological disparity has changed through time, and particularly in relation to K-Pg boundary.

Examples of recent mammal- based studies that use discrete characters, meanwhile, are Close et al. (2015), who analysed morphological disparity of stem- and crown-mammals during the Mesozoic , and found support for a mid-Jurassic adaptive radiation, and Halliday and Goswami (2015), who analysed eutherian morphological disparity of eutherian mammals across the K-Pg boundary. As discussed above, both Close et al. (2015) and Halliday and Goswami (2016) used phylogenetic character matrices - those of Zhou et al. (2013) and Halliday et al. (2015), respectively - for their disparity analyses, which may be problematic for reasons already discussed. By contrast, Giannini and Garcia-Lopez (2013) used discrete morphofunctional characters (not intended to resolve phylogenetic relationships, and without specific statements of homology) to create a morphospace of South American native “ungulates (Notoungulata), and found similar, tightly clustered morphologies in earlier time bins (Palaeocene-Eocene), with more distinct and different morphologies appearing in their later time periods (Oligocene and Neogene), showing a divergence into more distinct morphotypes.

1.4 Limitations of morphological disparity analyses

There remain a number of potentially problematic issues known to affect disparity analyses. The use of discrete characters, whilst being a common metric in which to analyse disparity trends

(Hughes 2013; Erwin 2007), can be affected by the choice and number of characters measured, as unconscious bias when choosing said characters can alter perceived patterns and resolution within the analysis (Cartmill, 1982; Worthington, 2017). As morphological disparity analyses measure observable characters in taxa, when working with fossil species, data is necessarily limited to those features that are preserved in the fossil record; thus, soft tissue features, which are very unlikely to be fossilised, typically have to be ignored/excluded in fossil-based disparity analyses, even though they extant taxa demonstrate that such features often show extensive disparity (e.g. pelage colour in mammals; feather morphology in birds). This issue is not unique to disparity analyses, but applies to other studies using discrete characters, most obviously phylogenetic analyses. Even when restricted to characters that are likely to fossilise, a limited fossil record can result in datasets with a high proportion of missing data, especially when one or more taxa are poorly represented for the majority of characters selected in a study; for example, most fossil mammal species are known from dental remains only, and so must be coded as missing for features of the skull and post-cranium. It also proves to be a problem when taxa cannot be scored for any of the set of characters under consideration, and so cannot be included in the analysis. Thus, there will always be some bias when selecting character traits, taxa, or both. Character data can also end up being influenced by sexual dimorphism, where a taxon can be scored for multiple characters, or dimorphism may be missed if the specimens represented are only from one sex. Obviously this is something that would be difficult to confirm/take into account unless another specimen was uncovered, as often fossil taxa are known from a single individual, or only a few specimens. Similarly, if a specimen is a juvenile it may present different morphology to a fully grown individual, but this may not be recognised if there are no obvious indicators of young ontogenetic age (e.g. deciduous dentition, sutures that are not fully formed).

Disparity analyses can also fall foul of more general fossil record biases, notably if entire time periods and/or clades are poorly sampled (Smith 1994, Lane et al 2005). This can potentially lead to misleadingly low estimates of disparity, as the fossil record is only providing an incomplete representation of the true disparity of the clade/time period/location ((Brusatte et al 2011). Obviously, this is very difficult to take into account without major improvements in the fossil record, but the effect can be lessened by using rarefaction techniques to estimate how many species would have been found had the sample size been smaller than it actually was, making it possible to compare estimated diversity at a constant sample size (Raup 1975). The Lagerstätten

effect is in many ways the opposite: Lagerstätten are deposits which yield abundant, exceptionally preserved fossils, (Flannery Sutherland et al 2019), and these sites give a distorted view relative to the 'normal' conditions of the fossil record (Benson et al 2010). An example of this can be seen in the Burgess Shale site, where previous studies have indicated only 10% of the fauna represented there would actually be seen under more 'normal' conditions of fossilisation (Morris and Whittington 1985).

1.5 Overview of eutherian evolutionary history and changes in disparity from the Cretaceous to the early Palaeogene

1.5.1 Origin of crown-clade mammals

Modern mammals comprise three major clades: Placentalia, Marsupialia and Monotremata. Of these, Placentalia is by far the most species rich, comprising >6000 of the ~6500 modern species currently recognised (Mammal Diversity Database, 2021). Placentalia is also much more morphologically disparate than the other two clades, and includes the only fully aquatic mammals (cetaceans and sirenians) and the only mammals capable of powered flight (bats). Placentalia is a crown clade, and is part of the larger (total) clade Eutheria, which comprises Placentalia plus all fossil species more closely related to Placentalia than to its extant sister-clade, Marsupialia.

The oldest members of the clade Mammaliaforms (the common ancestor of crown-clade mammals and *Morganucodon* or *Sinoconodon* and all of its descendants) date to the Late Triassic, whilst the oldest members of the crown clade Mammalia date to either the Late Triassic or Middle Jurassic (Grossnickle, Smith and Wilson 2019; King and Beck, 2020). During the Mesozoic, mammaliaforms were mainly small (<1 kg), terrestrial insectivorous forms (Grossnickle, Smith and Wilson 2019), existing at a time where dinosaurs dominated almost all ecosystems. However, recent discoveries have revealed the existence of a larger range of body masses (with some taxa >5 kg) and greater degree of morphological disparity than previously suspected (e.g., Luo (2007); Krause et al., 2014; 2020; Grossnickle et al 2019). The fossil record of mammaliaforms indicates that various clades underwent radiations at different times, increasing in both taxonomic diversity and morphological disparity (Grossnickle, Smith and Wilson 2019). These radiations include the major Early-Middle Jurassic radiation of mammaliaforms (Luo et al 2007, Close et al 2015), where we see early, predominantly small insectivorous mammaliaforms (comparable to modern

rat/shrew sizes (Simpson, 1929; Lillegraven 1979)) (including the earliest haramiyidans, morganucodontans, docodonts etc) diversify into a range of ecologically diverse lineages, with a wide range of locomotion methods (terrestrial, gliding - Meng et al 2006 - arboreal, semiaquatic - Ji et al 2006 - fossorial and semifossorial - Luo et al 2007, Luo et al 2015), body sizes (Hu et al 2005) and dentition types, suggestive of different dietary niches (Grossnickle, Smith and Wilson, 2019) (Fig 1). Some Mesozoic mammals are known to have reached larger body sizes than previously thought, with the gobiconodontid *Repenomamus giganticus* measuring over a metre in total length (Hu et al 2005), and the gondwanatherians *Adalatherium* and *Vintana* reaching body masses of ~3 kg (Krause et al 2020) and ~9 kg (Krause et al 2014) respectively. *Repenomamus* is also known to have been carnivorous based on its dentition, but, similarly to extant carnivores, it may have included invertebrates and vegetation within its diet (Carbone et al 1999). Another important discovery supports *Repenomamus* carnivory: one individual within the genus (*Repenomamus robustus*) was found with evidence of a juvenile *Psittacosaurus* (an early Cretaceous ceratopsian dinosaur) in its stomach contents (Hu et al 2005), therefore representing direct evidence of mammals inhabiting carnivorous niches, potentially competing with small carnivorous dinosaurs.

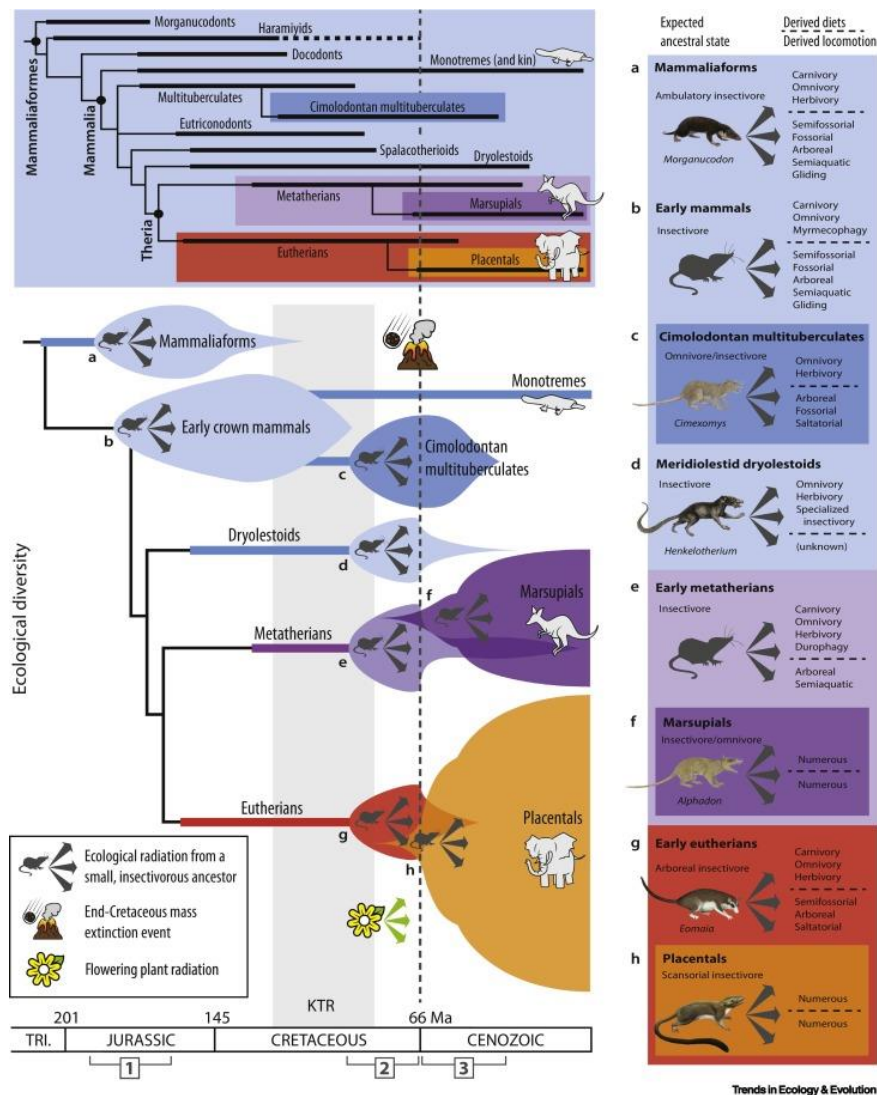


Figure 3. Ecological radiations of early Mammalia (Replicated from Grossnickle, Smith and Wilson 2019, Fig 1.)

1.5.2 Origin of eutherian mammals

Recent molecular clock divergence estimates place the divergence between Theria (= Metatheria + Eutheria) and Monotremata at ~190 – 220MYA (Meredith 2011; dos Reis et al 2012), and the divergence between Metatheria (the total clade that comprises Marsupialia and all taxa more closely related to Marsupialia than to Placentalia) and Eutheria at around 170-190MYA (Eizirik 2016). In terms of fossil evidence, *Juramaia sinensis* from the Middle Jurassic (~160 MYA) of modern-day China (Luo et al 2011) appears to be the earliest known eutherian. However, some studies have argued its morphology is unexpectedly advanced for its reported age (Sullivan et al 2014), as it is very similar to eutherians such as *Ambolestes*, *Eomaia* and *Sinodelphys* that are

125MYA, ~40 million years younger than *Juramaia* (Meng 2014; Bi et al 2018). King and Beck (2020) used tip dating phylogenetic methods to test whether the morphology of *Juramaia* was congruent with its reported Middle Jurassic age, and found that in fact it was predicted to be Middle Cretaceous in age when its age was allowed to vary, whereas other Middle Jurassic mammaliaforms did not show the same behaviour. Based on this evidence, Eldridge et al (2018) suggested that it is appropriate to assume a minimum age for the metatherian-eutherian divergence of ~125 MYA .

Around the mid-Cretaceous there was a period of considerable turnover in terrestrial faunas, including in mammal faunas, known as the Cretaceous Terrestrial Revolution (KTR). The KTR (roughly 125-80 MYA) was marked by a rise in angiosperm species, at the expense of ferns and gymnosperms (Dilcher, 2000, Lloyd et al 2008; Condamine et al 2020), which appears to have led to a greater range of dietary niches for herbivorous mammal species, as well as for insectivorous mammal species due to the coevolution of pollinating insects alongside angiosperm plants (Grossnickle and Polly, 2013). Increased numbers, size and diversity of fruit and seeds in angiosperms has been seen to correlate directly with increased body size within omnivorous species, and may also have had some effect on locomotion methods (Eriksson, Friis and Lofgren 2000; Tiffney 2004): arboreal omnivorous species with grasping hands and feet would have benefited from being able to access a wider range of fruits, seeds, tree gums and flowers, as well as insect pollinator species (Szalay 1968; Chester et al 2015; Hughes et al 2021). In early mammalian history (Triassic – Early Cretaceous) there appears to have been little adaptation to herbivory as the major dietary mode (although some taxa may have had predominantly herbivorous diets, like the haramiyidans), but the acquisition of the tribosphenic tooth in the ancestor of therians probably allowed for a greater range in diet due to its shearing and grinding capabilities (Luo 2007; Grossnickle and Newham 2016). The KTR saw a small decrease in mammaliaform diversity, with some groups going entirely extinct (Luo 2007), and an overall decrease in abundance in groups such as the docodonts, eupantotherians, symmetrodontans and the triconodonts (Grossnickle and Polly 2013). Eutherians appear to have begun radiating widely after the KTR, from the middle-late Campanian onwards (Grossnickle and Newham, 2016; Grossnickle et al., 2019).

1.5.3 Eutherian disparity during the Late Cretaceous and placental origins

Based on their known morphology and estimated body sizes, Mesozoic eutherians (similarly to most Mesozoic mammaliaforms in general) appear to have been small, insectivorous or insectivory-dominated omnivorous species (Ji et al 2002; Luo et al 2011; Grossnickle and Polly 2013; Sweetman, Smith and Martill 2017); however there are exceptions to this, most notably the probable taeniodont *Schowalteria* from the Late Cretaceous of Canada, which appears to have been predominantly herbivorous (Fox and Naylor, 2003), as well as adaptations to frugivory/omnivory in groups like the zhelestids (Grossnickle and Newman 2016). The morphology of Mesozoic eutherians suggest a variety of different locomotory modes, with more arboreal climbing adaptations seen in the early eutherians *Juramaia* and *Eomaia* (Ji et al 2002, Luo et al 2011, Karantanis et al 2018), whereas zalambdalestids appear to have been more cursorially adapted (Kielan-Jaworowska 1978).

The timing of origin of the eutherian crown-clade, Placentalia, remains controversial, with different analyses pointing to different emergence dates. Molecular studies place the origin of Placentalia within the late Cretaceous (Meredith et al 2011, Springer 2003), with some even suggesting an early Cretaceous origin (Bininda-Emonds 2007). These suggestions are primarily proposed by molecular clock analyses, which appear to be in conflict with the fossil record. Despite both molecular data predicting that there should be some fossil evidence of placental mammals within Late Cretaceous fossil deposits (dos Reis, Donoghue and Yang 2014; Halliday, Upchurch and Goswami 2016, Halliday et al 2019), no Cretaceous eutherian has been unambiguously resolved within the Placentalia (Halliday 2016, Goswami et al 2011, Wible et al 2009). The oldest record of the “condylarth” genus *Protungulatum* (Sloan and Van Valen 1965) is from the very Late Cretaceous (Archibald et al., 2011), and *Protungulatum* has been recovered in some studies as a placental, specifically a member of the laurasiatherian clade Euungulata (O’Leary et al 2013; Halliday et al 2019), but others have placed it as a stem eutherian outside Placentalia (Wible et al 2007; Wible et al 2009; Halliday, Upchurch and Goswami 2015). The lack of definitive placentals in the Late Cretaceous record, despite molecular clock studies suggesting that Placentalia predates the K-Pg boundary, has led to some questioning of the origin location of placental mammals. Eutherian fossils are more common in Laurasia, and it is more commonly argued that Placentalia originated in Laurasia rather than Gondwana; however the lack of placentals in the Late Cretaceous Laurasian fossil record has led some authors to suggest a

Gondwanan origin for Placentalia (Maas and Krause 1994; Smith, De Bast and Sige 2010), although this has been rejected by others (Hunter and Janis 2006; Wible et al 2007; Goswami et al 2011).

Throughout the Palaeocene, stem taxa of the major orders began to appear, including groups like plesiadapiforms (stem primates, e.g. *Purgatorius*; Van-Valen and Sloan, 1965; Fox and Scott 2011) carnivoramorphans (e.g. *Pristinictis*, *Ravenictis*; Fox and Youzwshyn, 1994), and stem Proboscidea (*Eritherium*; Gheerbrant, 2009). The crown members of modern placental orders began to primarily appear during the Eocene, a period which also saw the origin of major new morphotypes, including the first fully aquatic stem whales (e.g., *Rodhocetus*, order Cetacea) (Gingerich et al 1994), and the first stem bats (Smith et al., 2012). Within Placentalia, molecular studies consistently identify four superordinal clades (Asher, Bennett and Lehmann 2009; Teeling and Hedges 2013): Laurasiatheria (e.g. artiodactyls, perissodactyls, carnivorans), Euarchontoglires (e.g. primates, rodents, rabbits), Xenarthra (e.g. armadillos, anteaters and sloths) and Afrotheria (e.g. elephants, tenrecs and manatees) (Asher 2007, Foley et al 2016), with Euarchontoglires and Laurasiatheria consistently found to form a clade that has been named Boreoeutheria (Springer & de Jong 2001, Murphy et al 2007, Springer et al 2003, Meredith et al 2011, Romiguier et al 2013, Tarver et al 2016). Xenarthra and Afrotheria are also frequently found to form a clade, that has been named Atlantogenata (Hallstrom et al 2007, Meredith et al 2011, Morgan et al 2013, Liu et al 2017), but some molecular studies have not supported this relationship (McCormack et al 2012).

1.5.4 Impact of K-Pg mass extinction on eutherian disparity

The end Cretaceous (K-Pg) mass extinction event marks one of the largest ecological shifts in the history of life, and is the second largest mass extinction event after the end Permian (Vajda and McLoughlin 2007). Some 75% of terrestrial species perished during the K-Pg extinction event (Halliday et al 2017, Jablonski & Chaloner 1994), which also saw extreme changes to marine productivity and ocean chemistry (D'Hondt 2005). A range of factors have been proposed to have contributed causes to the K-Pg mass extinction event (including an already variable climate during the late Cretaceous - Renne et al 2013), but the general consensus is that the major cause was an extra-terrestrial impact event that occurred ~66MYA (Schulte et al 2010; Renne et al 2013; Canudo et al 2016). Before this, dinosaurs were the dominant large-bodied vertebrates in most terrestrial ecosystems, with their rise beginning in the Late Triassic/Early Jurassic (Brusatte et al 2008). The

most accepted cause of mass dinosaur extinction is the impact event at the K-Pg boundary, but recent studies suggest that dinosaur diversity may have been declining before this, primarily due to global climate cooling, and a drop in herbivorous diversity (Condamine et al 2021), however there has also been doubts about the methods used within this analysis (Černý et al 2021). As already discussed, during the Mesozoic, eutherians and other mammaliaforms occupied a relatively limited set of ecological niches and body sizes compared to the Cenozoic (Kielan-Jaworowska et al., 2004; Grossnickle et al., 2019). It is generally accepted that the removal of non-avian dinosaurs from terrestrial ecosystem allowed mammals to radiate and increase in both diversity and disparity, leading to the Cenozoic sometimes being dubbed the 'Age of the Mammals' (Rose 2006).

The Cretaceous-Paleogene (K-Pg event) 66 MYA has long been considered a key event in the evolutionary history of eutherians in particular (Wilson 2013). Fossil evidence suggests that over the K-Pg there were immediate changes in morphology within both Mammaliaforms as a whole and Eutheria in particular, with increases in overall body mass and other measures of morphological disparity (Alroy 1999, Slater 2013; Halliday and Goswami 2015; Benevento et al 2019). Alroy (1999) found that there was an abrupt shift in the mean body mass around the K-Pg (65-64 MYA), resulting from a combination of the evolution of towards larger body sizes and the extinction of many small/medium sized mammals (i.e. comparable to the size of a modern elephant shrew), with a steady expansion in the overall body mass post K-Pg into the Cenozoic. Previous studies indicated that the increase in eutherian body size was very rapid after the K-Pg extinction event, happening within a few hundred thousand years of the extinction event (Wible et al 2009; O'Leary et al 2013; Halliday, Upchurch and Goswami 2015). The K-Pg event also appears to have been ecologically selective: eutherians that were more generalized in their diets were found to be more likely to survive than more specialised ones (Wilson 2013), with the same pattern also found for metatherians (Grossnickle and Newman 2016; Pires et al 2018). The fossil record also indicates a significant taxonomic diversification post-KPg for eutherians: as already discussed, many stem taxa of current extant placental orders first appear in the fossil record in the earliest Palaeocene, such as the stem-primate *Purgatorius* (Chester et al 2015), stem carnivorans *Pristinictis* and *Ravenictis* (Fox and Youzwyshyn 1994), and stem proboscidean *Eritherium* (Gheerbrant, 2009). Evidence from molecular data has been used to instead propose that crown-group Placentalia underwent a continuous radiation across the K-Pg, beginning in the Late

Cretaceous (~75.2MYA) and ending in the early Eocene (~55.3MYA - Lui et al, 2017); however, a recent paper by Upham et al (2021) suggests that phylogenetic studies with no fossil species may not be entirely accurate when considering events deeper in time like the K-Pg/PETM, as they found evidence that there was a diversification event at the K-Pg boundary, but that this is only detectable after including evidence from the fossil record.

Numerous studies have analysed how disparity in eutherians changed across the K-Pg boundary. Halliday and Goswami (2016) used a set of discrete morphological characters, originally developed to resolve eutherian phylogeny (Halliday, Upchurch and Goswami 2015), to look at changes in eutherian disparity over the K-Pg and surrounding epochs. They found increases in the morphospace occupancy of eutherians over the boundary using SOR analyses; however, they found no significant increases in variance-based disparity when analysed with MPD and SOV methods, suggesting that the K-Pg had a selective effect on eutherian extinction. This may have been due to the decline or extinction of some eutherian clades prior to the K-Pg boundary (such as zhelestids and zalambdalestids), whilst others underwent a radiation (progenitors to the placental crown clade, as no definitive placentals are known pre-K-Pg). A morphometric study of lower jaw shape from the late Triassic to the Eocene by Benevento et al. (2019) agreed, supporting an increase in therian jaw functional disparity during the Palaeocene and Eocene, and over the K-Pg boundary, which was almost entirely driven by the eutherians in their taxon sample.

Wilson (2013) found a decrease in disparity of dental shape and body size in the immediate stages either side of the K-Pg over a much smaller times (Lancian (~69-66MYA) – Puercan (66-63.8MYA), showing an active selection against larger bodied taxon and against dietary specialists – in particular carnivorous species (e.g. *Cimolestes magnus*) and species whose diet is largely herbivorous. However, this is a very narrow timescale for comparison, focused immediately either side of the K-Pg boundary, and so does not take into account earlier or later events (e.g. potential declines in eutherian disparity Campanian/Maastrichtian found by Halliday and Goswami (2016), and subsequent radiation throughout the Danian and Selandian).

1.5.5 Eutherian disparity during Palaeocene

The Palaeocene saw an increase in morphological disparity seen within eutherians, with many distinct morphologies appearing for the first time in the fossil record. More species adapted for

carnivory began to appear, like the stem carnivorans (Carnivoramorpha) in the Early Palaeocene, including genera like *Pristinictis* and *Ravenictis* (Fox and Youzwshyn 1994). Some of the important herbivorous eutherian groups also make their first appearance in the early Palaeocene (Danian), including Pantodonta (Dawson 2012). The earliest pantodonts were represented by small, omnivorous species like *Alcidedorbignya* (Muizon and Marshall 1987) from the Tiupampa of South America, known from exceptionally well-preserved specimens detailed by de Muizon et al. (2015). Despite being roughly one third of the size (de Muizon et al (2015) estimating a mean body mass of 483.63g for *A.inopinata*), *Alcideorbignya* shares many morphological similarities with its relative *Pantolambda*, but was thought to be relatively scansorial as opposed to *Pantolambda* and other more terrestrial, less omnivorous, and larger species like *Titanoides* and *Barylambda*, from the Palaeocene of North America. The development into more herbivorous diets also came with morphological adaptations to suit a lifestyle for suited to browsing – *Barylambda*, unlike most other pantodont species, had a large and heavy tail that allowed for some weight bearing, as well as a graviportal pelvis and massive hindlimbs that enabled bipedal herbivorous browsing (Janis et al 1998).

1.5.6 Impact of PETM on eutherian disparity

Around the Palaeocene/Eocene boundary (~55.5MYA) there was an abrupt global warming event (Palaeocene-Eocene Thermal Maximum, or PETM), leading to much higher global temperatures than previously seen in the Palaeocene (Wing, Alroy and Hickey 1995, MacFadden 2000; Secord et al 2012). The PETM saw a spike in global temperatures over a relatively short period of time, with global temperatures increasing by ~5°C over 100,000-200,000 years (Gingerich 2006), which is recognised in the fossil record by an abrupt carbon isotope excursion in marine and continental records (Secord et al 2012). This temperature spike resulted in an abrupt warming of the Northern hemisphere, coinciding with a strong mammalian immigration to the North American continent (Woodburne, Gunnell and Stucky 2008). These immigrant mammal species include some of the earliest crown members of modern orders, such as primates, artiodactyls and perissodactyls (termed 'APP taxa'; Gingerich, 2010; Clyde and Gingerich, 1998), and saw a distinct increase in the diversity of browsing herbivores, such as phenacodontid "condylarths" (e.g. *Ectocion*) and perissodactyls (e.g. *Hyracotherium*; Gingerich, 2010, Secord et al., 2012). *Ectocion* and

Hyracotherium underwent dwarfing within the Wasatchian (North American Land Mammal Age, spanning 55.8 – 50 MYA, Rose 2006), as did several primarily insectivorous eutherians such as *Macrocranion*, *Leptacodon*, and *Wyonycteris* - Strait, 2004; D'Ambrosia et al 2017), which has been attributed to climate modification (Woodburne, Gunnell and Stucky 2008). This is congruent with the ecogeographic pattern called Bergmann's Rule, which states that populations or closely related species of endotherms typically have a larger body size in colder climates as a result of thermoregulation (Rodríguez, Olalla-Tarraga and Hawkins 2008; Salewski and Watt 2016; Fan et al 2019). Secord et al. (2012) looked specifically at equid perissodactyl *Sifrhippus sandrae* and found a clear decrease in body size over 130,000 years of warming, followed by a distinct increase during the recovery phase of the PETM: body mass went from 5.6kg pre-PETM, down to 3.9kg at its lowest point during the PETM, and then increased significantly to an average of 7.0kg during the recovery period. These changes post-PETM were not isolated to herbivorous species like perissodactyls, however carnivoramorphans like *Uintacyon* also saw a PETM decrease in body size and a post-PETM increase in body mass, likely in response to increasing and decreasing prey sizes (Chester et al 2010) as well as a direct response to temperature. The PETM also marked distinct changes in therian morphology and locomotion – species showed more terrestrial morphologies as opposed to semiarboreal/arboreal, and major groups represented in the Palaeocene were replaced by new groups (e.g. phenacodontid condylarths and plesiadapids were the major herbivores in the Palaeocene, but the Eocene saw more herbivorous/frugivorous taxon like hyopsodontid condylarths and perissodactyls - Woodburne, Gunnell and Stucky 2009). Fully aquatic (e.g. the stem cetacean *Rodhocetus*; Gingerich et al.,1994) and volant taxa (e.g. the stem-bat *Icaronycteris*; Jepsen, 1966) also made their first appearances post-PETM.

The K-Pg extinction event and its impact on eutherian disparity has been the major focus in previous studies, with less focus on the PETM. However, Halliday and Goswami (2016) did find an increase in variance-based disparity over the PETM boundary as opposed to a lack of increase in variance-based disparity over the K-Pg. In addition, Benevento et al. (2019) found that the functional disparity of therian mammals increased over the PETM, and that it exceeded any Mesozoic levels during the Eocene, at a similar rate to that seen over the K-Pg. Benevento et al. (2019) also noted disparity continuing to increase in disparity throughout the rest of the Eocene, with eutherians being responsible for further spread into areas of function space not previously occupied by Mesozoic mammals. However, there is clear scope for further studies to

quantitatively test the relative impact of the K-Pg mass extinction event and the PETM on eutherian disparity, to determine whether one had a greater effect than the other, or whether their impacts were of similar magnitude; this forms the rationale of the current study.

1.6 Aims of current study

The goals of this study are to use discrete morphofunctional characters to quantify changes in the disparity of eutherian mammals during the Late Cretaceous and early Palaeogene, focusing specifically on changes across the K-Pg boundary and PETM. The K-Pg and the PETM are of importance as they represent periods of particularly profound environmental change that have long been identified as having a major impact on mammalian evolution: the K-Pg boundary marks the beginning of what some call the 'Age of the Mammals' (Rose 2006), and coincides with major increases in diversity and disparity in eutherians (Wilson 2013; Halliday and Goswami 2015; Benevento, et al 2019).

Previous attempts to quantify changes in eutherian disparity during this timeframe have either used morphometric approaches (e.g., using geometric morphometrics of molar shape – Wilson, 2013 - or ratios of measurements of lower jaws – Benevento et al., 2019), or sets of discrete characters that were originally intended to resolve phylogenetic relationships (Halliday and Goswami 2016). Datasets comprising discrete characters that have been specifically developed to describe morphofunctional differences (which presumably have ecological significance) may be preferable to phylogenetic characters when attempting to analyse changes in disparity through time, however are yet to be applied to analyse trends in eutherian disparity during the Late Cretaceous and early Palaeogene, despite the potential insight such an analysis might provide into this key period in mammal evolution.

Here, I present novel dataset of 61 discrete morphofunctional characters of the dentition and lower jaw, and score this for 235 eutherian taxa (28 Late Cretaceous, 132 Palaeocene, 75 Eocene) based on published literature and available images. I then analyse the resultant dataset using a range of multivariate techniques to quantify changes in disparity through time, focusing on changes across the K-Pg boundary and across the PETM.

I conclude that this morphofunctional dataset is a powerful method for investigating trends in eutherian disparity through time that provides a different perspective from that offered by morphometric methods, and one that is potentially more appropriate than methods based on phylogenetic character sets. The dataset and methods used here could be expanded to include characters from the rest of the skeleton, and/or other mammalian clades besides Eutheria (e.g., Metatheria, Multituberculata).

2. Materials and Methods

2.1 Matrix preparation

In order to analyse changes in disparity within Eutheria across the K-Pg boundary and Palaeocene-Eocene Thermal Maximum (PETM), a novel dataset of 61 discrete morphofunctional characters of the dentition and lower jaw was created. Morphofunctional characters are considered here to be characters that refer to structures of the dentition (e.g., overall size, shape and orientation of teeth, presence or absence of diastemata) and lower jaw (e.g., size, shape and orientation of particular processes, such as the angular and coronoid processes, and the dental condyle) that are likely to have functional importance due to their role in food processing, attachment of jaw muscles etc. Although such characters can be, and indeed are, used in phylogenetic analyses of mammals (e.g., that of Halliday et al., 2015), the morphofunctional character matrix used here is distinct from a phylogenetic character matrix in two main ways: firstly, no attempt has been made to distinguish between non-homologous structures that appear to be functionally equivalent (e.g., the anterior most lower incisor has been treated as the same morphofunctional structure for all taxa, even though the precise dental locus it represents varies between taxa, for example between members of Glires and members of Plesiadapiforms, and so may be non-homologous; Lockett, 1985), whereas this is of critical importance in phylogenetic analyses; secondly, minor variations in morphology that are often used as phylogenetic characters but that seem likely to be of little functional significance (e.g., small differences in the relative heights and orientations of molar cusps and crests) have not been included. As a result of the second issue, the number of morphofunctional characters used here (61) is markedly smaller than the 269 craniodental and lower jaw characters used by Halliday et al. (2015) in their phylogenetic analysis of Eutheria. Nevertheless, because the characters used here have been specifically selected to reflect morphofunctional features, they may be more suited for analyses of disparity than are phylogenetic character matrices, which are intended for a different purpose (Gerber, 2019; Smith et al., 2021).

Only features of the dentition and lower jaw were considered, for three reasons: most fossil mammals (including most eutherians) are known from isolated dental and lower jaw remains only (Kielan-Jaworoska et al., 2004; Rose, 2006), and so including features of the rest of the skull and skeleton would either result in a very large proportion of missing data (which can be problematic

for analyses of disparity; Gerber, 2019), or require use of a very restricted set of taxa for which more complete remains are known; the morphology of the dentition and lower jaw strongly reflects diet and feeding, which are one of the most fundamental aspects of mammalian ecology; and finally time constraints. Characters were identified based on examination of (predominantly phylogenetic) character lists from previous studies (e.g., Halliday et al. 2015) and personal observations. Characters representing putative morphoclines/transformation series (e.g., progressive changes in the size or orientation of teeth) were specified as ordered, as ordered characters can be used in disparity analyses using Claddis via use of Maximum Observable Rescaled Distances (MORD – see below; Lloyd 2016). The full list of 61 morphofunctional characters is given in Appendix A.

Initial selection of taxa followed Halliday and Goswami (2016), who used the phylogenetic character matrix of Halliday et al. (2015) to analyse changes in morphological disparity in Eutheria, focusing on the K-Pg boundary. Given that the specific focus of the current study is changes in eutherian disparity across the K-Pg boundary and PETM, non-eutherian outgroup taxa were removed, and only those eutherian taxa occurring in the Upper Cretaceous (Campanian and Maastrichtian), Palaeocene and Eocene were retained, with older and younger taxa also removed. This initial taxon set was further modified by replacing a few taxa with congeners that were better described and/or illustrated in available sources, and the addition of nine further taxa not included by Halliday et al. (2015) or Halliday and Goswami (2016). Taxa included by Halliday et al. (2015) and Halliday and Goswami (2016) but for which adequate descriptions and illustrations could not be obtained were also removed. To maintain comparability, taxa were generally scored under the same names that were used in the Halliday et al. (2015) matrix, even if these names are not the ones currently preferred, but for some specimens the name recorded by Halliday et al. (2015) in their taxon list differed entirely from the name associated with the specific specimen used for scoring purposes (e.g. *Onychodectes acolytus* was changed to *Promioclænus acolytus*, the correct name for the specimen scored), so were changed to reflect the specimen scored. This resulted in a total of 235 individual taxa used for initial scoring (28 Late Cretaceous, 132 Palaeocene, 75 Eocene); a full list of these taxa is given in Appendix B.

The morphofunctional character matrix was initially created using Morphobank (O’Leary and Kaufman 2012). Scoring of taxa for the set of characters was based on figures and descriptions from the literature, and from digital images available in online repositories (Smithsonian Natural History Museum (<https://collections.nmnh.si.edu/search/paleo/>), Yale Peabody Museum (<https://collections.peabody.yale.edu/search/>), Berkeley Natural History Museum (<https://calphotos.berkeley.edu/>), Museum of Paleontology – University of Michigan (<https://umorf.ummp.lsa.umich.edu/wp/>); no specimens were examined first-hand. The sources used to score each taxon are given in Appendix C.

For some genera, multiple species were scored, and then merged to form a single genus-level taxon (e.g. *Viverravus sicarius*, *V. gracilis* and *V. browni* were merged into a single *Viverravus* spp. taxon) using the ‘Merge Taxon’ function in Mesquite (Maddison and Maddison, 2021) prior to the disparity analyses. This merging procedure sometimes resulted in a genus being scored as polymorphic for a particular character; in such cases, the scorings of the individual species that were merged were checked and revised if necessary. The number of taxa remaining after merging was 144, of which 20 first appear in the Late Cretaceous, 75 in the Palaeocene and 49 in the Eocene. The final morphofunctional matrix was converted into a NEXUS formatted-file using Mesquite, which was used for the disparity analyses.

2.2 Disparity analyses

Quantitative analyses of morphological disparity using the final morphofunctional matrix were carried out with a range of packages in the R statistical computing environment (R Core Team, 2021), primarily Claddis (Lloyd 2016) and dispRity (Guillerme 2018). Ordination of the matrix and calculation of morphological distances was carried out in Claddis using the Maximum Observable Rescaled Distance (MORD) of Lloyd (2016), which is a modification of the Gower Coefficient (Gower, 1971). The Gower Coefficient (GC) is the raw Euclidean distance between a pair of taxa rescaled by the number of characters that can be coded for both taxa, and so corrects for missing data. However, if multi-state ordered characters are used (as is the case here), then GC can be greater than 1; MORD rescales GC by the “maximum possible distance that could be observed based on the number of characters codable in each pairwise comparison” (Lloyd 2016), and so

MORD values will always be between 0 and 1. MORD is the default distance metric for ordination and calculation of morphological distances in Claddis.

Principal Coordinate Analysis (PCoA) was applied to the ordinated matrix of pairwise MORD distances. The first two PCoA axes were plotted to create a visual representation of the morphospace, with taxa grouped according to either three time bins corresponding to epochs (Upper Cretaceous, Palaeocene, Eocene), that span the two major boundaries investigated here, namely the K-Pg boundary (between the Upper Cretaceous and Palaeocene, or Maastrichtian and Danian) and the PETM (between the Palaeocene and Eocene, or Thanetian and Ypresian). Taxa were assigned to time bins based on their first appearance date (FAD), as indicated by the Paleobiology Database (PBDB) (www.paleobiodb.org), and stratigraphic ages were sourced from the most recent version of the International Chronostratigraphic Chart (ICS; Cohen et al 2013). Convex hulls were added help visualise morphospace occupancy during each time bin.

Sum of Ranges (SOR), Sum of Variances (SOV) and Distance from Centroid (DFC) were calculated from the PCoA analysis, using the time bins discussed above. Using all three metrics is useful, as they represent different aspects of disparity (Halliday and Goswami 2015). SOR describes the total range of morphospace occupation by showing the overall spread of species within a morphospace, whereas SOV represents the distances between the taxa points in the constructed morphospace (Korn, Hopkins and Walton 2013). DFC captures where a group/taxon lies within trait space in relation to the centroid point of the morphospace plot – the further away from the centroid, the greater the disparity the metric will show. All three disparity analyses were plotted as box plots in both wide (Late Cretaceous, Palaeocene, Eocene) and Narrow (Cenomanian – Priabonian) timebin versions to show stage and epoch changes in disparity, with both types including 95% confidence intervals and standard deviations. Confidence intervals were created by bootstrapping the data using DispRity (Guillerme 2018) as to replicate Halliday and Goswami (2016) and the overlapping of said intervals was used as a measure of significance in place of specific statistical significance tests.

In addition to Principal Coordinate Analysis, Non-Metric Multidimensional Scaling (NMDS) analysis was applied to the ordinated matrix to visualise morphospace, using the metaMDS function in the R Package Vegan (Oksanen et al 2016). The general approach of Reeves et al. (2020) was followed, except that the number of stress plots was decreased from 10,000 to 1000 to reduce

computational burden. Taxa were grouped into the same time bins as for the PCoA analysis, and convex hulls were again created for each time bin. NMDS provides a good alternative to PCoA analyses as they have the ability to handle large amounts of missing data (Deline et al 2018), which in a PCoA analysis can cause low overall percentages of variation to be represented by the axes on the visual plot.

As a third method for calculating disparity, pairwise MORD distances were used to calculate Weighted Mean Pairwise Disparity (WMPD; Close et al., 2015), again following a similar approach to the paper by Reeves et al (2020). WMPD measures how similar a given number of taxa are (i.e., how closely packed they are in a morphospace), giving more weight to pairwise distances based on more comparable characters (Nordén et al 2018), and is a good alternative to methods that require ordination (PCoA, NMDS) as taxa lacking any comparable characters need not be deleted. For this analysis, taxa were assigned the same time bins – either epoch level (Late Cretaceous– Palaeocene - Eocene), or stage level bins (Campanian– Lutetian) as in the PCoA and NMDS analyses.

3. Results

3.1 Principal Coordinate Analysis (PCoA)

After ordination of the 61 character 144 taxon morphofunctional character dataset with Maximum Observable Rescaled Distances (MORD; Lloyd, 2016), the resultant ordinated matrix was subjected to Principal Coordinate Analysis (PCoA). The results of this analysis were then visualised by plotting the first two Principal Coordinate axes (PCO1 and PCO2), and Sum of Ranges (SOR), Sum of Variance (SOV), and Distance From Centroid (DFC) were calculated across all axes, in order to quantify changes in morphological disparity through time.

3.1.1 Plot of PCO1 and PCO2

Figure 3 shows a plot of PCO1 (x-axis) and PCO2 (y-axis) of the ordinated matrix, which has been created to visualise morphospace occupancy. Taxa are colour-coded by time bin (Late Cretaceous, Palaeocene and Eocene), and time bins delimited by convex hulls to allow qualitative identification of trends in morphospace occupancy through time. In terms of overall distribution of taxa, the x-axis (PCO1), which represents 2.13% of the overall variation, appears to segregate taxa according to their likely diet, with probable herbivorous taxa (such as the Eocene perissodactyls *Homogalax* and *Eohippus* and the Eocene artiodactyl *Elomeryx*) showing the most negative values, most probable insectivorous taxa (such as Late Cretaceous zhelestids like *Aspanlestes* and *Lainodon*) clustering towards the centre of the morphospace, and several carnivorous taxa (*Miacis*, *Viverravus*, *Didymictis*) showing the most positive values. The y-axis (PCO2), which represents 1.57% of the overall variation, does not appear to show a clear morphological trend, although several taxa with hypselodont lower anterior incisors (e.g., *Tribosphenomys*, *Rhombomylus*) are characterised by strongly positive values.

Looking at trends through time, the Late Cretaceous taxa occupy the smallest amount of morphospace of the three time bins, with most taxa clustered close together in the morphospace (e.g. *Kennalestes*, *Maelestes*, *Cimolestes*). However, there are outliers, namely *Daulestes*, who has a markedly more positive y-axis value than any other Late Cretaceous taxon, which causes it to sit close to the outermost Palaeocene convex hull, outside of the Eocene hull, which otherwise encompasses all Late Cretaceous species. *Daulestes* likely sits in this location due to the presence of its premolariform, carnassial-like lower posterior premolars, as well as its large lower canine.

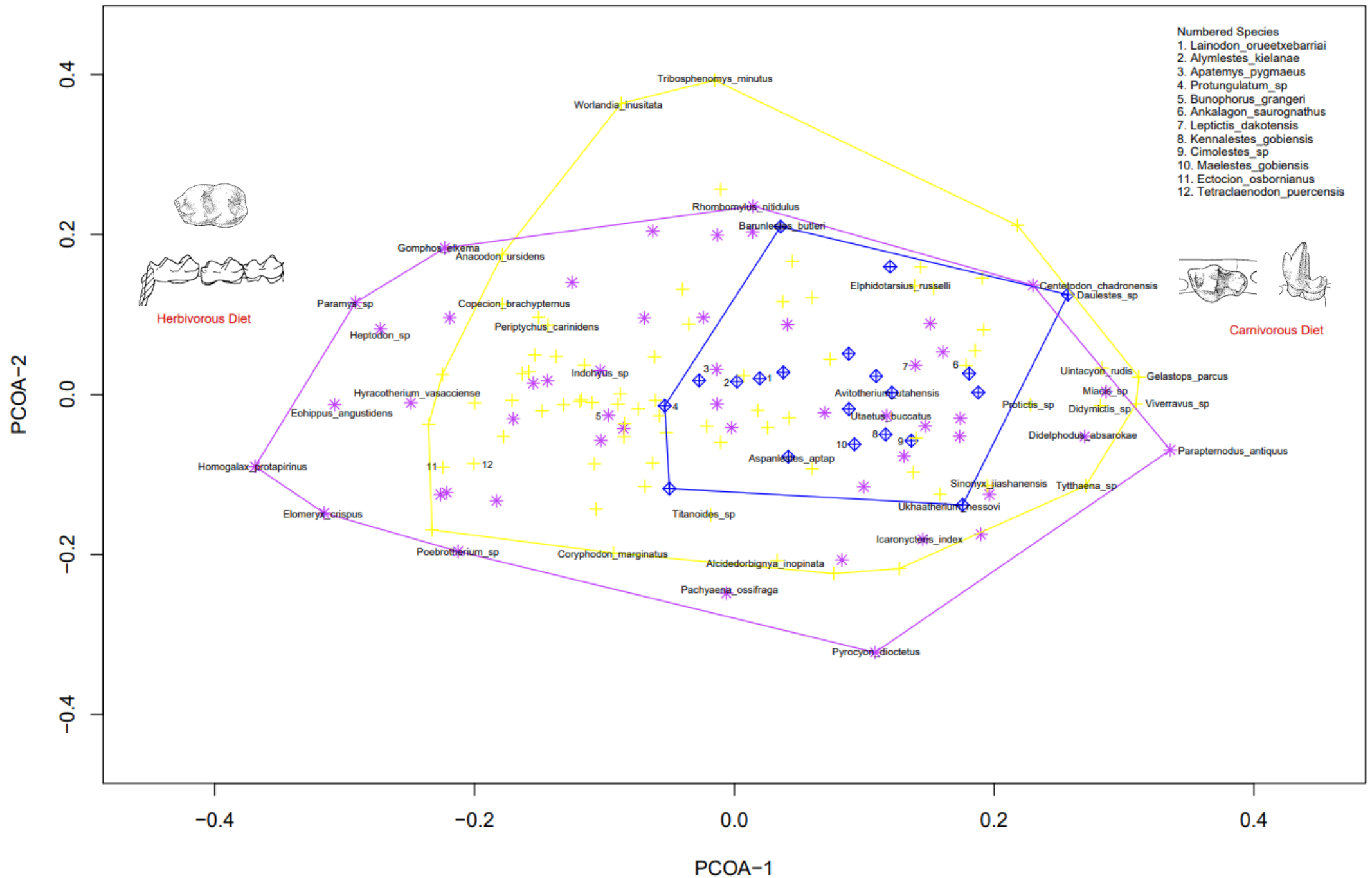


Figure 3. Principle Coordinate Analysis (PCoA) of the first two axis plots for the morphofunctional discrete taxon-character matrix. Data points are named with the taxon they represent, and are coloured and marked by relating symbols for each time bin. Only taxon discussed by name are labelled and for ease of reading overlapping taxon are labelled by number and noted on graph. Convex hulls were added to allow for easier visual comparison of morpho space occupancy and expansion. Taxon with a FAD in the Late Cretaceous taxon are marked in blue, Palaeocene taxon marked in yellow, and Eocene taxon marked in Purple. General diet trends noted on extremes of graph, along with visual representation. Dentition images directly reproduced from sources, included as visual examples of general dentition type at extremes of morphotype. Left – *Homogalax protapirinus* (m1 – m3, m3 – Gingerich, 1991) Right – *Viverravus boweni* (m1; Gingerich and Winkler, 1985)

Morphospace occupancy increases from the Late Cretaceous to the Palaeocene; most obviously, there is expansion into more positive values along PCO1 and more positive values along PCO2. Palaeocene taxa with the most positive PCO1 values include the carnivoramorphans *Viverravus*, *Uintacyon* and *Didymictis*, as well as the cimolestid *Gelastops*, whom were all likely to be adapted for a more carnivorous diet. Palaeocene taxa with the most positive PCO2 values are *Tribosphenomys* and *Worlandia*, both of which have hypselodont, procumbent lower incisors, but a relatively plesiomorphic/generalised tribosphenic dentition. *Tribosphenomys* does not plot closely to the other members of Glires included in this analysis (namely *Paramys* and *Gomphos*), probably reflecting the former's more plesiomorphic molar dentition, i.e. less derived tribosphenic morphology (Meng and Wyss, 2001). However, most Palaeocene taxa overlap with the Late Cretaceous taxa within the centre of the morphospace, presumably reflecting their overall unspecialised dental morphology. From the Palaeocene to the Eocene, there is an expansion in morphospace at both extremes along PCO1, and at the negative end of PCO2, but a contraction at the positive end of PCO2. Expansion at the negative end of PCO1 is due to the perissodactyls *Eohippus*, *Homogalax* and *Hyracotherium*, and the artiodactyl *Elomeryx*, all of which were probably specialised herbivores (Rose 2006). Expansion at the positive end of PCO1 is due to the cimolestid *Didelphodus*, carnivoramorphans *Miacis* and the eulipotyphlan *Parapternodus*. Both *Didelphodus* and *Miacis* show carnivorous adaptations, and therefore sit closely with the other Palaeocene carnivorous taxa. *Parapternodus*' presence in this region of morphospace is more surprising, as eulipotyphlans are generally not recognised as having carnivorous adaptations; it is likely placed here due to its similar lack of talonid basin (and therefore lack of pestle and mortar structure with the upper molar protocone), and narrow talonid structure. Contraction at the positive end of PCO2 is because no Eocene taxa plot near the Palaeocene *Worlandia* or *Tribosphenomys*. The expansion at negative end of PCO2 is due to the hyaenodontid creodont *Pyrocyon* and the mesonychid *Pachyaena*. Both show some adaptation for carnivory with large lower canines (upper canines are not preserved in known specimens of either taxon) and carnassially-adapted lower premolars in *Pyrocyon*.

In agreement with the overall trend along PCO1 already discussed, Palaeocene taxa with carnivorous adaptations group to the right of the plot, with strongly positive PCO1 values. These include carnivoramorphans such as taxon, *Viverravus* and *Protictis*, as well as the cimolestan *Gelastops* and the mesonychid condylarth *Sinonyx*. Most taxa interpreted as herbivorous are

grouped to the left of the plot (more negative PCO1 values), including the phenacodontid condylarths *Copecion*, *Ectocion* and *Tetraclaenodon*. However, *Titanoides*, which is one of the largest herbivorous species of the Palaeocene (Gingerich 1996), sits more centrally within the plot, close to another large herbivore *Coryphodon* (McGee 2002). There seems to be little correlation between position in morphospace and body size: *Titanoides* and *Coryphodon*, whilst being close together in the morphospace, also sit near *Alcidedorbignya*, known to be <1kg.

Eocene taxa typically fall into agreement with overall trends, similar to Palaeocene taxa: Eocene taxa with carnivorous adaptations group to the right of the plot with strongly positive PCO1 values, including the cimolestid *Didelphodus* and carnivoramorphan *Miacis*. *Parapternodus* also groups within the carnivorously-adapted taxa, however this is likely due to its reduced talonid basins (a shared trait with carnivorous species). The majority of the herbivorous taxa all group to the left of the plot, with strongly negative PCOA-1 values, including perissodactyls *Eohippus*, *Heptodon* and *Homogalax*, and artiodactyls *Poebrotherium* and *Elomeryx*. However, there are a number of artiodactyls and perissodactyls that are less herbivorously specialised, and that group closer to the centroid, including the artiodactyls *Bunophorus* and *Indohyus*. The most positive end of the PCO1 region also includes Glires taxa *Paramys* and *Gomphos*, likely due to their hypsodont molar morphology.

3.1.2 Sum of Variances (SOV)

The Sum of Variances metric is the sum of variances along the morphospace axes and represents a measure of the distances between points in a morphospace plot. Figures 4 and 5 show boxplots of Sum of Variances (SOV) calculated from all axes of the PCoA analysis, with taxa binned either by Epoch (Figure 4) or Stage/Age (Figure 5). Strikingly, SOV showed very little change in disparity across the K-Pg boundary. The mean variance shows a slight increase at the epoch level (Fig 4); however, the standard deviation and 95% confidence intervals overlap, showing no substantial increase in variance-based disparity. Looking at SOV in narrower stage level time bins (Fig 5), there is a clear increase in disparity between the Campanian and the Maastrichtian during the Late Cretaceous, but it is not significant enough for the standard deviation to move beyond overlapping. At the stage level (Fig 5), the Early Late Cretaceous (Cenomanian - Coniacian) began with mid-level SOV values and showed no change in SOV over the first two timebins (Cenomanian, Turonian) but the latter half of the epoch each stage saw subsequential slight increases in variance-based disparity. Over the K-Pg boundary at the stage level the SOV drops, indicating a drop in disparity, and only sees an increase to greater than the Maastrichtian level by the Ypresian. This is indicative of a slow recovery of eutherian variance levels post-K-Pg that lasts until the Thanetian. At the stage level, variance-based disparity rises gradually through the Palaeocene, seeing its highest point in the Thanetian. Comparing the first and last Palaeocene stages, there is a clear increase between the standard deviations and mean variance, with the Thanetian being much higher in comparison for both. The Palaeocene–Eocene changes show a different pattern: there is a large leap in variance-based disparity over the PETM (Thanetian – Lutetian), suggesting that taxon variance within the morphospace increased substantially, with the Lutetian seeing the highest SOV value for the entire analysis. This is likely indicative of the variation of new morphologies that appeared during this time – for example, there was a greater representation of herbivorous species seen to arise during the Eocene in comparison to other epochs (e.g., the artiodactyl *Elomeryx*, perissodactyls including *Eohippus* and *Hyracotherium*).

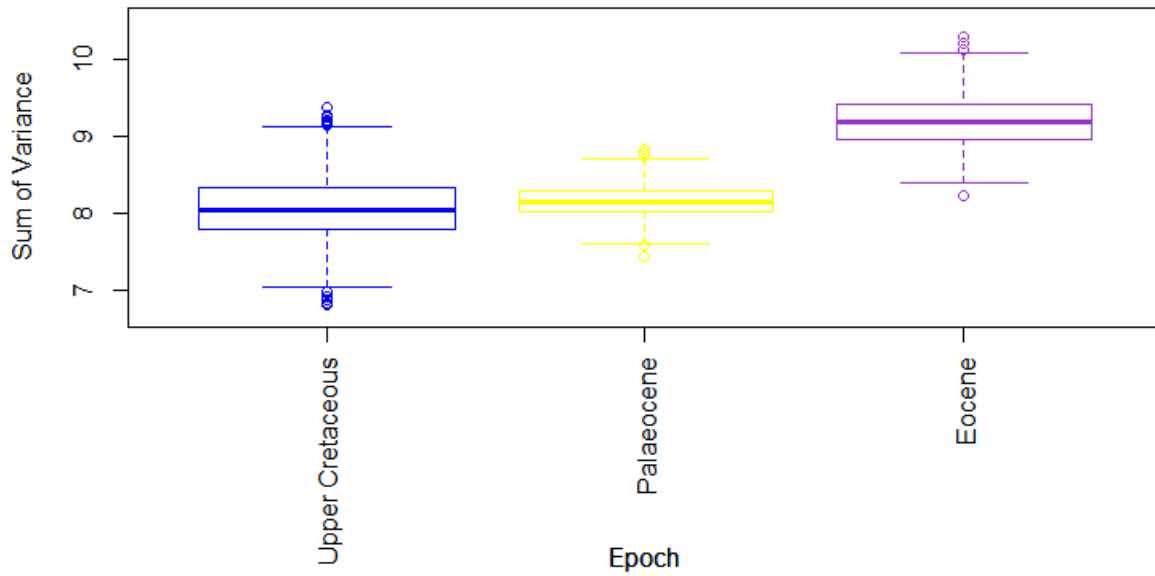


Figure 4. Sum of Variances box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in wide, epoch level timebins. Thick line in centre of boxplot representing the mean variance, and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

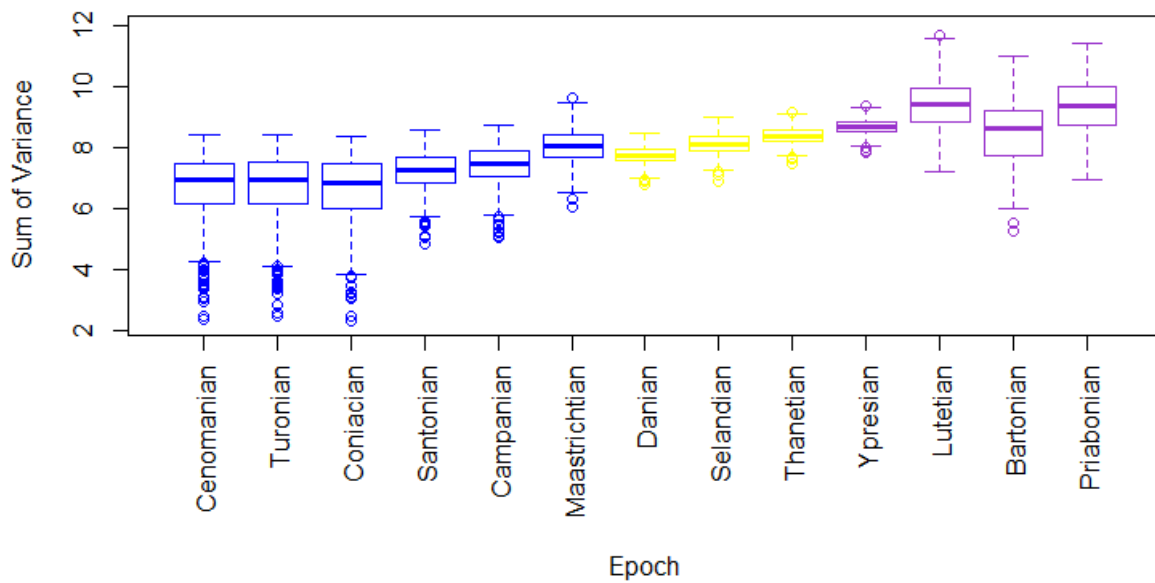


Figure 5. Sum of Variances box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in narrow, stage level timebins. Thick line in centre of boxplot representing the mean variance, and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

3.1.3 Sum of Ranges (SOR)

The SOR metric is a description of the total range of morphospace occupation, and shows the size of dissimilarity within a morphospace. As it cannot relay any information about changes in shape of the morphospace, SOV measures are often useful for quantifying changes in morphospace shape (e.g. noting whether large reductions are based on selective/non-selective extinctions, whether a diversification was random or non-random). Similarly to SOV, Figures 6 and 7 show Sum of Ranges (SOR) calculated from all axes of the PCoA analysis, with taxa again binned either by epoch (Figure 6) or stage/age (Figure 7). In direct contrast to the SOV analyses that saw very minimal increase, there is a major change in SOR over the K-Pg Boundary, between the Late Cretaceous and Palaeocene (Fig 6). Mean SOR shows very large increases, with both the standard deviation and the 95% confidence intervals increasing to show no overlap between the two epochs. A significant increase in SOR combined with a non-significant change in SOV is suggestive of a random distribution of newly introduced taxa, with no particular expansions in any region, which is supported by the morphospace expansion in all directions in Figure 3. The substantial increase from the Late Cretaceous to the Palaeocene may be indicative of the SOR's response to outliers – it is much more heavily influenced by outliers than the SOV or DFC metrics. The Palaeocene sees two notable outliers in the PCoA (Fig 3) morphospace visualisation, *Tribosphenomys* and *Worlandia*, which likely have some effect on this large increase. At the stage level (Fig 7), the Early Late Cretaceous (Cenomanian - Coniacian) began with low SOR values and showed no change in SOR over the first two timebins (Cenomanian, Turonian) similarly to the SOV and DFC metrics, but over the latter half of the epoch each stage saw substantial increases in SOR. The large increase from Late Cretaceous to Palaeocene suggests a substantial increase in morphospace occupancy. This large increase in morphospace occupancy is also reflected by the increased overall occupancy shown within both PCoA (Fig 3) and NMDS plots (Fig 10). The standard deviation also reduced considerably in comparison to the Late Cretaceous plot over the epoch level result.

Over the Palaeocene SOR overall remained high, but did experience a dip within the Selandian stage, where the mean range and standard deviation dropped considerably. By the Thanetian however, it had risen again to slightly above the levels seen within the Danian stage – a very large increase. Over the PETM, there was again an increase in SOR, but not to a lesser extent than over the K-Pg boundary. Mean range and standard deviation rose high enough to no longer overlap the

Palaeocene range, but the confidence intervals still saw some overlap. The Eocene saw the highest levels of SOR over the entire three epochs, suggesting morphospace occupancy was highest at this point, which can be confirmed by the PCoA and NMDS visual morphospace representations. The increase over the PETM was not as great as the increase in SOR over the K-Pg, however, with the confidence intervals for the two epochs overlapping. At the stage level, the Ypresian experienced the highest range of morphospace occupancy within the entirety of the study, but after the Ypresian, there are large fluctuations, with a large drop in SOR through the Lutetian and Bartonian to pre-K-Pg levels, followed by a rise in the Priabonian.

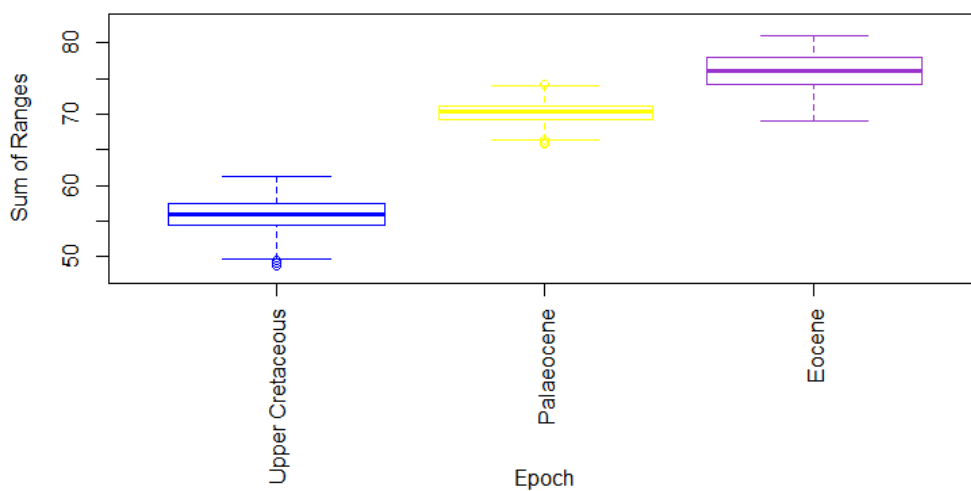


Figure 6. Sum of Ranges box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in wide, epoch level timebins. Thick line in centre of boxplot representing the mean range and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

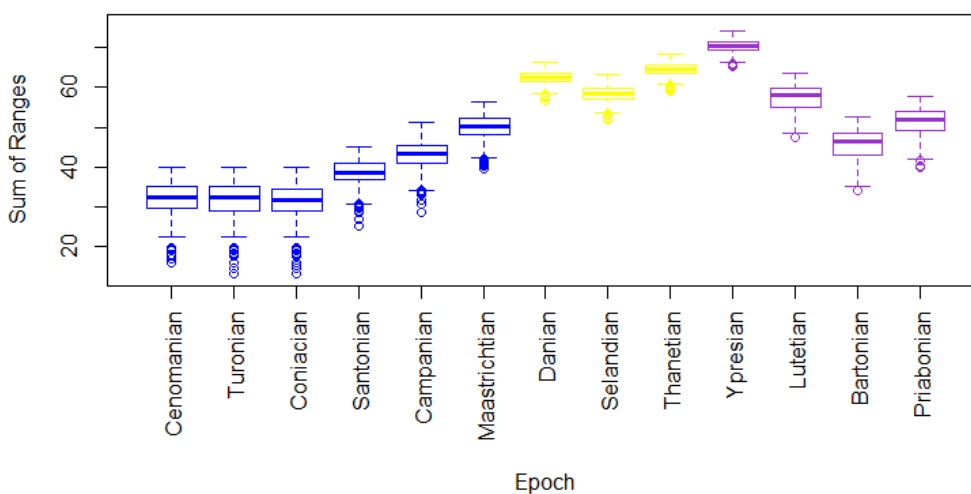


Figure 7. Sum of Ranges box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in narrow, stage level timebins. Thick line in centre of boxplot representing the mean range, and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

3.1.4 Distance from Centroid (DFC)

Finally, in addition to SOV and SOR, Distance from Centroid (DFC) was calculated from all PCoA axes, with taxa again binned either by epoch (Figure 8) or stage/age (Figure 9). DFC is an indicator of the distance each point is from the centroid within the morphospace, so is useful to quantify how disparate taxa are from the most common morphology (i.e., the centroid) within the morphospace. Overall, DFC suggests a steady increase in disparity over both the stage (Fig 8) and epoch levels (Fig 9), with no major increases over either K-Pg or PETM boundary, unlike those seen in the SOR analysis. The Late Cretaceous shows mid-level (neither low nor considerably high) levels of DFC, and (as seen in both the SOR and SOV measures) sees no change over the first two Late Cretaceous stages (Cenomanian and Turonian). There is little change over the first half of the Late Cretaceous (Cenomanian – Coniacian), but the start of a slow increase over the latter half, suggesting little expansion in DFC, and therefore few new, distinct morphologies. The confidence intervals are much larger in the Late Cretaceous than in the SOV and SOR however. There is a clear increase in mean DFC over the K-Pg boundary at the epoch level, rising to above the standard deviation levels for the Late Cretaceous plot, which suggests the introduction of new morphologies into the morphospace that sit further away from the centroid: this is reflected in the expansion from the centroid seen in both PCoA (Fig 3) and NMDS analyses (Fig 10) with the appearance of new, more carnivorous species (*Viverravus*, *Tytthaena*, *Uintacyon*). Looking at the stage level, there is minimal increase across all three stages, with considerable overlap of means and standard deviations. The standard deviations and confidence intervals in these plots are much narrower than those seen throughout the Late Cretaceous or Eocene however. The increase in DFC is greater over the PETM than that seen over the K-Pg, suggesting the taxa that originated during the Eocene were more disparate in their distance from centroid to those originating within the Palaeocene. This is again reflected in the expansion from the centroid seen in the PCoA and NMDS analyses (Fig 3 and 10): the taxa introduced in the Eocene expand the morphospace in almost every direction. Over the epoch level, there is some fluctuation, with the highest overall distance from centroid measure within the Ypresian/Lutetian, followed by a distinct drop in the Bartonian, rising again finally for the final Priabonian stage.

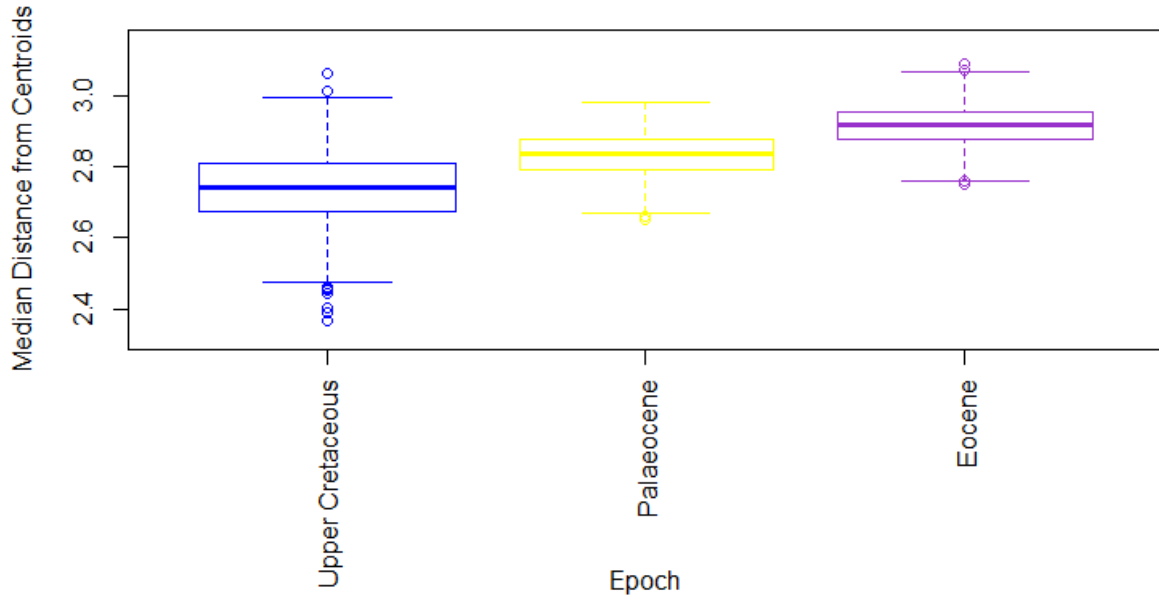


Figure 8. Distance from Centroid box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in wide, epoch level timebins. Thick line in centre of boxplot representing the mean distance from centroid and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

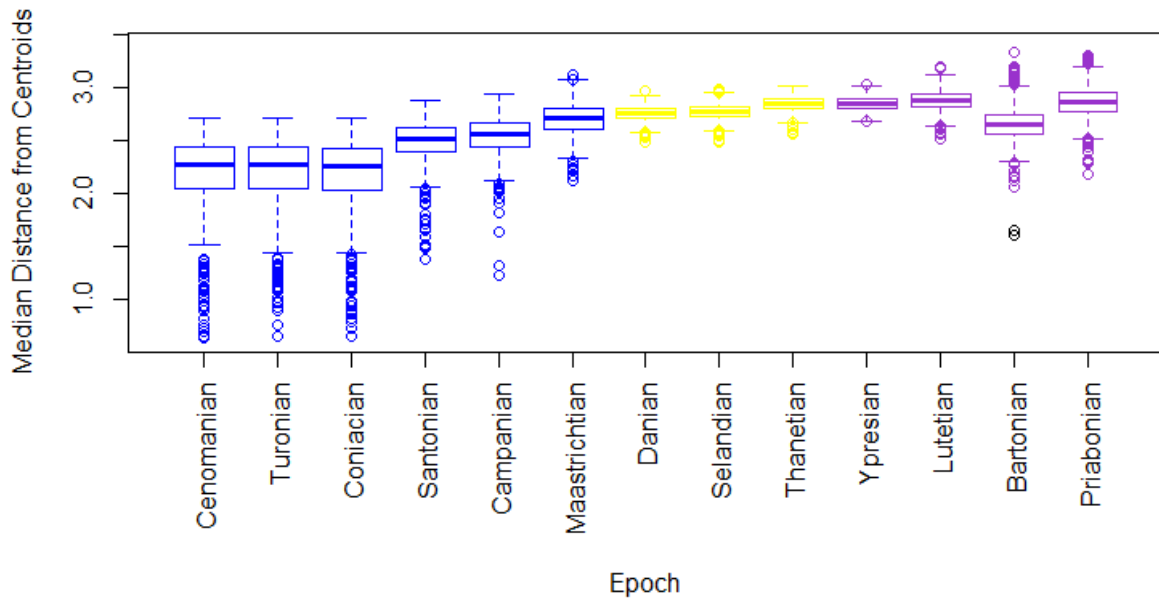


Figure 9. Distance from Centroid box and whisker plots for the PCoA scores from the taxon-character morphofunctional matrix in narrow, stage level timebins. Thick line in centre of boxplot representing the mean distance from centroid, and the box outline representing the standard deviation from the mean. Confidence intervals are set at 95%, and outliers are plotted as circles at the end of confidence intervals. Colours match those previously used in PCoA plots.

3.2 Non-Metric Multidimensional Scaling (NMDS)

NMDS and PCoA analyses are similar in that they both ordinate a character-taxon matrix, but NMDS provides an alternate visualisation of the morphospace which can be less affected by missing data in the character-taxon matrix. The first two axes of a NMDS analysis of the ordinated matrix were plotted, again to visualise morphospace, and to act as a non-metric comparison to the PCoA analysis, as shown in Figure 10; taxa are coloured in the same way as the for the PCoA analysis (Figure 3) to aid comparisons, and with convex hulls again used to allow for easy analysis of trends within the morphospace. The PCoA and NMDS analysis shows similar overall trends: NMDS1 (x-axis) separates taxa by supposed diet, but whilst the PCoA places likely herbivorous taxa (*Elomeryx*, *Poebrotherium*) at the negative end of the axis, NMDS shows them to have the most positive values. Probable insectivorous taxa are grouped in the towards the centre of the morphospace (*Alymlestes*, *Apatemys*), and a range of carnivorous taxa (*Uintacyon*, *Didephodus*) group at the negative values. NMDS-2 (y-axis) shows a large expansion towards to the positive value by the presence of *Utaetus*, a homodont member of Cingulata that is the only non-heterodont taxa within the analysis, which explains its large differences from the remaining taxa, and the negative value shows gathering of taxa with enlarged (*Elphidotarsius*) or hypselodont upper or lower incisors (*Worlandia*, *Tribosphenomys*, *Barunlestes*).

Difference between the PCoA and NMDS analyses can also be found in the trends of morphospace occupancy through time. The NMDS analysis sees the multiple taxa from the Late Cretaceous not fully enclosed within morphologies found in the other two time bins: *Ukhaatherium* and *Barunlestes* both sit outside of the Eocene convex hull, whilst the PCoA analysis places them within both Palaeocene and Eocene hulls. The NMDS analysis also resolves the primate *Elphidotarsius* in an entirely different region in the Palaeocene, placing it as an outer taxon point outside of both Late Cretaceous and Eocene convex hulls at the negative end of the NMDS-2 whereas the PCoA analysis places it fully within all the convex hulls and closer to the centroid on both axes. It does share some similarities with the taxa grouped at the negative end of the plot, including enlarged upper incisors, but its blade-like/plagiulacoid premolars are likely a factor that causes its slightly isolated placement within the plot. *Centetodon* and *Parapternodus* are grouped at the negative end of the plot and share some similarities with the carnivorous species, which share narrow talonid basins, tall trigonid cusps and premolariform posterior premolars. The majority of the expansion throughout time occurs to the positive ends of both NMDS-1 and

NMDS-2; however, the large expansion in the Eocene of the NMDS-2 axis is due to the presence of *Utaetus* alone. The Late Cretaceous sees taxa primarily clustered towards the negative values of both NMDS-1 and 2, with notable exceptions being *Ukhaatherium* which skews towards the positive NMDS-1 axis. The Palaeocene sees a large overall expansion, but particularly towards the positive end of the NMDS-1 and NMDS-2 axes. Taxa with the most positive NMDS-1 values include *Tetraclaenodon*, *Anacodon* and *Copecion*, all North American “condylarth” species, which were all likely adapted for herbivory, with deep mandibular bodies and large talonid basins. Palaeocene taxa with the most positive NMDS-2 values are *Alcidedorbignya* and *Coryphodon*, which both score for similar dental morphologies, including reduced incisors, large upper and lower canines and molariform premolars. A large proportion of Palaeocene taxa sit around the centre of the morphospace, similarly to the results of the PCoA analysis, likely reflecting a lack of specialisation. From the Palaeocene to the Eocene there is another expansion to the positive ends of NMDS-1 and NMDS-2 (discussed previously as being heavily caused by the presence of *Utaetus*), and a slight expansion to the negative end of NMDS-2. The positive expansion of NMDS-1 relates to the appearance of more specialised herbivores, similar to that seen in the PCoA analysis (*Eohippus*, *Hyracotherium*, *Elomeryx*), with the expansion to the negative end of NMDS-1 due to the presence of *Parapternodus*, again, likely to be for similar reasons seen in the PCoA analysis (lack of talonid basin, narrow talonid structure) that causes it to sit near to carnivory-adapted species.

There are however some notable similarities between the two analyses – both PCoA-1 and NMDS-1 axis shows very clear groupings of herbivorous and carnivorous taxa at opposite ends of the axis, but there are a large range of species that do not fall into these categories grouping at the positive-most and negative-most values - *Centetodon* and *Daulestes* are at the negative value of NMDS-1 and positive value of PCoA-1 with the carnivory adapted species, and *Gomphos* and *Paramys* at the positive value of NMDS-1, and the negative of PCoA-1. Similar dental features that show an adaptation for herbivorous lifestyle seem to be causing the grouping of *Gomphos* and *Paramys* with the herbivorous species: deep mandibular bodies (*Gomphos*, *Paramys*, *Homogalax*, *Hyracotherium*), and square molars with similar trigonid and talonid cups heights (*Elomeryx*, *Gomphos*, *Paramys*, *Hyracotherium*) are all shared as common morphologies. Similarly, *Centetodon* and *Daulestes* both share common morphologies with the carnivorous species they are grouped with. namely premolariform posterior premolars, tall trigonid cusps and narrow talonid basins.

3.3 Weighted Mean Pairwise Distance (WMPD)

In addition to the PCoA and NMDS analyses of the ordinated matrix, Weighted Mean Pairwise Distance (WMPD) analysis of the original matrix was carried out and used to plot disparity through time (Figures 11 and 12). WMPD analyses measure how similar taxa are, giving more weight to pairwise distances based on more comparable characters (Nordén et al 2018), and are a way of quantifying changes in disparity through time. For the entirety of the Late Cretaceous – Eocene, changes in WMPD are fairly steady throughout the first few epochs (including the Cenomanian and Turonian), but saw an increase in disparity during the Coniacian and Santonian. This may be due to the lack of first appearance ages in the Turonian for the taxa selected within this analysis, meaning no change in disparity, which is also reflected in the same bins in the SOV, SOR and DFC analyses. There is a sharp increase throughout the latter half of the Coniacian, leading to a mild spike of disparity in the Santonian, before steadily decreasing throughout the Maastrichtian. The Campanian sees a very slight continuation of this decline in ecological disparity, before beginning to rise again from the Campanian through the K-Pg boundary to the Danian. There is no obvious, immediate dip or change in ecological disparity, however a few million years into the Palaeocene we see a dramatic, rapid increase over a very short period of time (Danian – Selandian, potentially ~4-5 MY). From here the increase in ecological disparity continues to rise, but less rapidly throughout the remaining Palaeocene, through the PETM boundary and to the Priabonian. From the Priabonian, there begins a decline through the start of the Oligocene, but as the number of taxa present in the Oligocene in this analysis is very low, and the main stages of interest are the Late Cretaceous, Palaeocene and Eocene they were not considered within this analysis. Standard deviations change over the plot, seeing their widest points within the Late Cretaceous, but narrowing considerably through the Palaeocene.

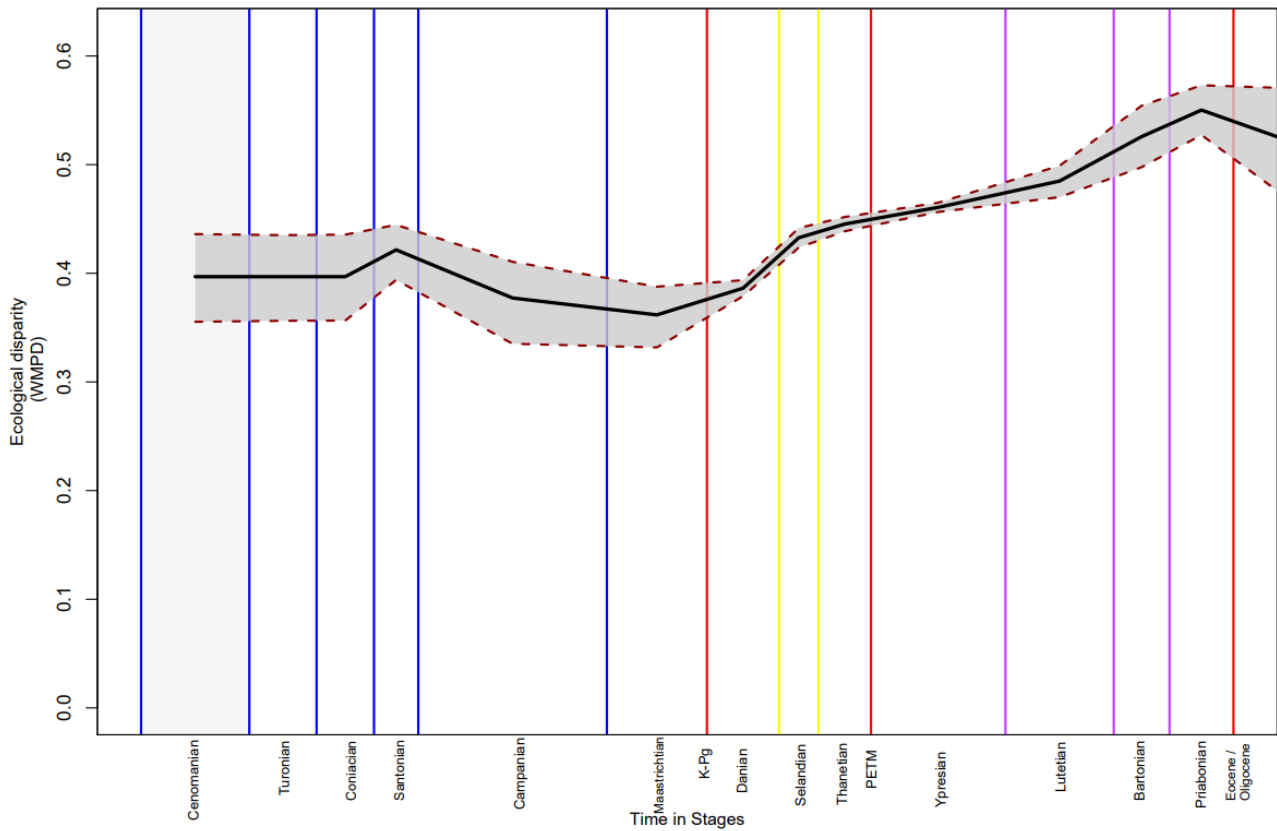


Figure 11. Weighted Mean Pairwise Distance analysis histogram of the taxon-character morphofunctional matrix. Each alternating grey and white box represents a timebin at the stage level, with data plots beginning from the left in the Cenomanian and ending in the Priabonian on the right. Red lines represent epoch boundaries and are labelled. Thick black line indicates the mean pairwise distance between taxa, with the grey surrounding shadowing representing the standard deviation.

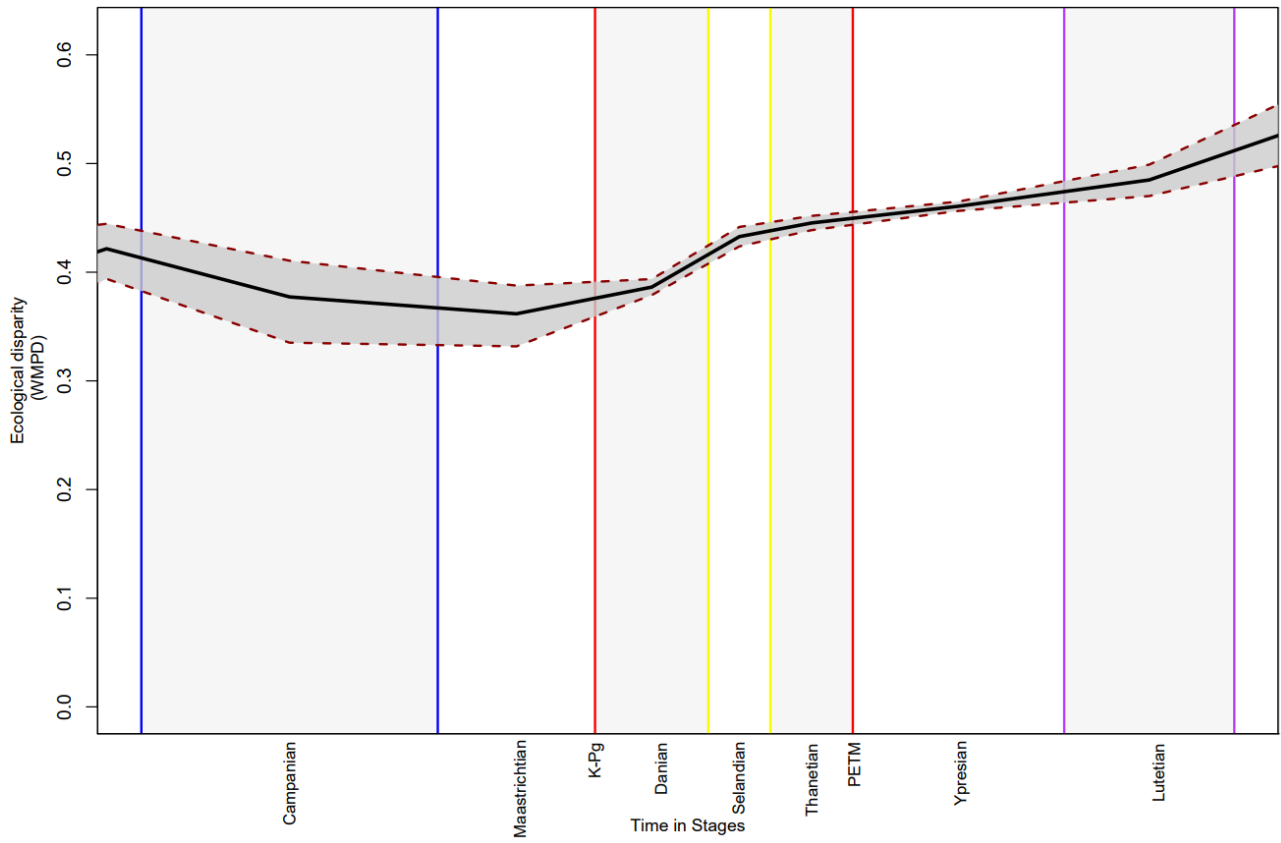


Figure 12 Weighted Mean Pairwise Distance analysis histogram of the taxon-character morphofunctional matrix. Each alternating grey and white box represent a timebin at the stage level, and are labelled with stage names. Red lines represent epoch boundaries and are labelled. Thick black line indicates the mean pairwise distance between taxa, with the grey surrounding shadowing representing the standard deviations.

4. Discussion

4.1 Changes in disparity across the K-Pg boundary

The results presented here by the PCoA (Fig 3), NMDS (Fig 10) and Sum of Ranges (Fig 6 and 7) show clear evidence of expansion in morphospace occupancy in Eutheria across the K-Pg boundary. Both the Sum of Variance (Fig 4) and the WMPD (Fig 11 and 12) also agree and show an increase in disparity over the boundary, with changes in SOV (Fig 4) being much more minimal (Table 1). However, the greatest changes in disparity occur primarily from the early to the middle Palaeocene, post K-Pg, suggesting a lag between eutherian radiation in the Late Cretaceous and their major disparity changes.

Table 1. Brief summary of changes in disparity metric over the K-Pg and PETM boundaries discussed within this thesis. Information on change in metric is gathered from stage level metrics for Sum of Variances (Figure 4), Sum of Ranges (Figure 6), Distance from Centroid (Figure 8) and the Weighted Mean Pairwise Disparity analyses (Figures 11 & 12). Changes are termed 'significant' based on whether the standard deviations for each plot do not overlap, or 'minimal' if standard deviations overlap entirely.

| Disparity Metric | Stage Boundary | |
|--|----------------------|----------------------|
| | K-Pg | PETM |
| Sum of Variances (SOV) | Minimal increase | Substantial Increase |
| Sum of Ranges (SOR) | Substantial Increase | Increase |
| Distance from Centroid (DFC) | Increase | Increase |
| Weighted Mean Pairwise Distance (WMPD) | Increase | Increase |

Disparity seen within the Late Cretaceous is low, as expected given that known Late Cretaceous eutherians were almost all small (<1kg), generalised insectivorous forms (Kielan-Jaworowska et al., 2004; Halliday and Goswami, 2016). The Cenomanian and Santonian eutherian taxa all belong to four clades – Zalambdalestidae, Zhelestidae, Cimolesta or Asioryctitheria - which are small, predominantly insectivorous forms (Wible, Novacek and Rougier 2004; Archibald and Averianov 2006; Wible et al 2009), and so, unsurprisingly, there is little change in disparity from the Cenomanian to the Santonian (Fig 5, 7, 9 and 11). The origination of a wider range of eutherian taxa that might have been more frugivorous/omnivorous (such as *Protungulatum* and *Avitotherium*) in the Late Cretaceous coincides with angiosperm ecological diversification (wide global diversifications of angiosperm seed size/fleshy fruits began ~80MYA, but the presence fleshy fruits in the record was noted from the Early Cretaceous of Europe, (Eriksson et al 2000; Eriksson 2016)), meaning they would have directly benefitted from novel dietary niches (Grossnickle and Newham 2016). There is a decrease in WMPD (Fig 11 and 12) disparity levels

prior to the K-Pg (Campanian/Maastrichtian) - this may be in response to the global climate instability that began during the end of the Late Cretaceous, including abrupt shifts in North American continental temperature within ~1 MY of the boundary (the largest of these shifts being a drop of 6-8°C in modern North Dakota; Wilf, Johnson and Huber 2003), which aligns with notable mammal turnover in the Hell Creek area (Wilson 2005; Renne 2013). As the majority of taxa included within this analysis are North American (103/144 taxa), it is likely that any North American specific biotic changes that had an effect on eutherian populations would have a direct effect on disparity measures.

The rapid increase in Sum of Ranges (SOR; Fig 6) disparity between the Late Cretaceous and Palaeocene suggests an increase in morphospace occupancy over the K-Pg boundary, which is supported by findings of the PCoA analysis (Fig 3). The SOR (Fig 6) may have been influenced by an increase in number of species from the Late Cretaceous (20 taxa) to the Palaeocene (74 taxa), as this metric is affected by sample size in smaller samples (<100 species; Simon et al 2010), as is the case here. The SOR is also notably more sensitive to outliers than other analyses like SOV and Distance from Centroid (DFC) (Guillerme et al 2020), which can cause inaccurate changes in range-based disparity results – there are a few taxa that may be considered outliers within the Palaeocene, notably *Tribosphenomys* and *Worlandia*, which together expand occupancy within the PCoA (Fig 3) towards the positive end of the PCOA-2 axis.

However, there is a the much smaller increase in Sum of Variances (SOV; Fig 4) disparity across the boundary. This may suggest that the K-Pg constrained increases in variance-based disparity, as in the stages prior to the boundary (Maastrichtian and Campanian), there was a trend at the stage level (Fig 5) for increasing SOV value. This lack of change between the Late Cretaceous and the Palaeocene likely reflects a 'recovery' period for eutherian SOV disparity, as SOV values do not reach the same levels until the final stage of the Palaeocene (Thanetian - Fig 5).

Previous analyses have found a decrease in variance-based disparity over the K-Pg along with a substantial increase in range-based disparity (Wilson, 2013; Halliday and Goswami 2015). This may be suggestive of a selective extinction event, where particular areas of the morphospace are reduced (Korn, Hopkins and Walton 2013; Halliday and Goswami 2015). Whilst little change is seen in SOV over the K-Pg at the epoch level in this analysis (Fig 4), it does not decrease, therefore no support is found for a selective extinction based on this metric, instead suggesting that the taxa

appearing in the Palaeocene were relatively randomly distributed in morphospace. The lack of increase in SOV immediately (in the Danian) post-K-Pg suggests that the increase in eutherian body size theorised to have occurred a few hundred thousand years post boundary (Wible et al 2009; O'Leary et al 2013; Halliday, Upchurch and Goswami 2013) is not supported by an increase in character-based morphologies.

Variance-based disparity and WMPD do begin to rise throughout the Palaeocene post K-Pg, which is unsurprising: eutherian mammals began to radiate rapidly post K-Pg into new ecological niches, and so the appearance of new morphologies that represent functional adaptations to those niches should be expected. The results of the WMPD (Fig 11 and 12) suggest a delay in disparity increase, with disparity rates beginning their Palaeocene spike during the Danian and reaching it in the Selandian: this is likely due to the existence of a period of "recovery time" post-K-Pg, congruent with the results of other studies (Wilson 2013, Grossnickle and Newham 2016); full recovery from an extinction event can take up to 10 MY (Benevento et al 2018). Biotic recovery times encompass ecosystem re-diversification and reconstruction following an extinction event that caused major ecosystem disruption and biodiversity losses (Droser et al 1977), but also can involve expansion of ecospace into new regions (Erwin 2008). Recovery from large biotic losses at an extinction event like the K-Pg might transition into an evolutionary radiation, where clade expansion is accompanied by increases in ecomorphological diversity and taxonomic diversity (Wilson 2013) - increases in the SOV (Fig 5) and WMPD analysis (Fig 11 and 12) support this idea of an increase in ecomorphological disparity post K-Pg recovery phase. Whilst taxonomic diversity has not been quantified within this analysis and therefore cannot be commented on for this analysis, previous studies have found an increase in taxonomic diversification post K-Pg in Eutherians, finding large increases in the rate of species diversification throughout the Palaeocene (Grossnickle and Newham 2016; Phillips and Fruciano 2018).

Morphological disparity rates then steadily increase throughout the remainder of the Palaeocene and PETM, likely implying that new taxa being introduced are less functionally disparate. The slowing increase of mean pairwise difference (MPD) has been previously noted for Eutheria post-PETM by Halliday and Goswami (2016), with their suggestion that extinction events aside, rates of evolution naturally decline over time; this is partially similar to Simpson's (1944) early burst model of adaptive radiations in the rate of evolution, but with a reverse of the high morphological

disparity and low taxonomic diversity suggested by Simpson (1944) in this analysis, which is similar to the pattern reported by Halliday and Goswami (2016).

Throughout the Palaeocene, eutherian morphological disparity sees a distinct increase, with the appearance of taxa functionally adapted for more carnivorous lifestyles (*Viverravus*, *Protictis*), potentially due to the removal of other carnivores from the ecosystem, including carnivorous non-avian dinosaurs and large (~5.2kg) durophagous metatherians like *Didelphodon* (Wilson et al 2016). The appearance of taxa with more plant-dominated diets (*Ectocion*, *Copecion*, *Peritychus*) during this period may also be linked to increases in angiosperm seed size (Grossnickle and Newham 2016), which would have increased available niches for frugivorous species (Eriksson 2016). There has also been speculation around the loss of large herbivorous dinosaurs allowing dense, canopied forests to expand (Wing and Tiffney 1987) during the Palaeocene, allowing for greater diversification in therian and multituberculate mammals (Grossnickle and Newham 2016).

Few taxa included within this analysis were seen to cross the K-Pg boundary and be found in both Late Cretaceous and Palaeocene sites; one of the few is the arctocyonid “condylarth” *Protungulatum*, which has relatively unspecialised dentition that might have aided its survival through a selective extinction event. Whilst a single taxon cannot definitively confirm that certain morphologies aided in survival over the K-Pg boundary, and locomotion has not been considered in this study, *Protungulatum*'s terrestrial locomotory mode (Chester et al 2015) and its presence in both Late Cretaceous and Palaeocene lends support to the hypothesis that nonarboreal/semi-arboreal locomotory modes may also have aided K-Pg survivorship (Hughes et al 2021).

4.2 Changes over the PETM

The Palaeocene-Eocene Thermal Maximum also sees increases in morphospace occupancy and functional disparity within Eutherians, with all three disparity metrics identifying an obvious expansion from the Palaeocene to the Eocene. SOR (Fig 6), SOV (Fig 4) and DFC (Fig 8) all experience an increase from the Palaeocene to the Eocene, in particular the SOR. Increases in both the SOR and SOV are suggestive of an expansion in the morphospace with higher numbers of taxa at its margins (Simon, Korn and Koenemann 2010), which is also reflected in the PCoA and NMDS plots (Fig 3 & 10). Increases in the SOR seem to be driven by the introduction of more morphologically more specialised herbivorous taxa along the positive end of the PCO1 axis in Figure 3 (*Eohippus*, *Homogalax*), both of which are terrestrial perissodactyls, the presence of which in the record has previously been noted to peak post PETM (Gingerich, 2010; Secord 2012).

The PETM saw a short period of time (170,000 KY) where the Northern Hemisphere experienced an abrupt warming (~5°C) (Jaramillo et al 2010), which is thought to provoke a strong pulse of mammalian immigration to modern day North America (Woodburne, Gunnell and Stucky 2009) from South America and Europe (Hooker 2015). Obviously, the eutherian record is represented globally and is not just isolated to North America, but the North American fossil record is the richest and most well-studied of any continent over all three epochs included within this analysis (Alroy 1999). Out of 144 taxa included in the disparity analyses, 103 are from North American locations (Appendix B), so it can be assumed that they likely reflect the effects of any North American-specific biotic changes such as a post-PETM the immigration event. Wing et al (2005) found that over the PETM terrestrial flora underwent rapid (~10KY) individualistic range changes (both inter and intracontinental) as a response to PETM global warming, which may have prompted further herbivorous specialisation by eutherians during the early Eocene. SOR is known to be affected by morphological outliers to a greater degree than are other measures of disparity (Simon, Korn and Koenemann 2010; Guillerme et al 2020), and whilst the herbivorous taxa *Eohippus* and *Homogalax* are not as distinct as the outliers seen in the Palaeocene (*Tribosphenomys* and *Worlandia*), they do sit in a relatively unoccupied new region of the morphospace. The SOV (Fig 5) and DFC (Fig 9) metrics also reach their highest points within the early Eocene and combined with the expansion in SOR may lend support to the immigration of new taxa into North America over the PETM, causing expansions in both morphospace occupancy and variance-based disparity in this analysis. The increase in DFC (Fig 8), (whilst not showing the

same large increase SOV and SOR do for the Eocene at the epoch level) suggests that Eocene taxa were more disparate in their morphologies, with less clustering around the centroid. This is reflected by the PCoA and NMDS visualisations (Fig 3 and 10): a large proportion of the new taxa introduced in the Eocene overlap heavily with Late Cretaceous and Palaeocene morphologies (e.g. *Ankalagon*, *Leptictis*), but these are less clustered around the centroid in comparison to the Palaeocene, showing greater disparity.

At the stage level, both SOV and SOR (Fig 5 & 7) disparity measures follow the same pattern as the epoch stage bins in the stages directly before and after the PETM. There is no change in the DFC (Fig 9) however (as opposed to at the epoch level where it sees an overall increase; Fig 8), which should suggest that although the new morphologies introduced during the Ypresian were random, they were mainly grouped around the centroid and did not represent greatly disparate taxa. However, this is not the case: the Ypresian saw the FAD's of a multitude of taxa that sit in a variety of regions in the PCoA and NMDS (Fig 3 and 10) morphospace, including the stem carnivoramorph *Miacis* and the eulipotyphlan *Parapternodus* at the positive end of the PCOA-1 axis, and the perissodactyl *Homogalax* at the negative end of the PCOA-1 axis, all of which sit at some of the furthest points from the centroid.

The Eocene shows considerable change in the SOV and SOR at the stage level (Fig 5 and 7). The Ypresian shows the highest SOR disparity within the entire study, accompanied by a moderate increase in SOV, suggesting that the Ypresian saw an inflation of the morphospace with a high number of species at its margins. This is reflected in the large number of species in this analysis that have their FAD in the Ypresian: out of 50 Eocene taxa, 35 of them originate directly after the PETM (Appendix B). This may be indicative of stem taxa of modern placental orders beginning to specialise, including individuals like *Icaronycteris*, which is one of the earliest known chiropterans (Gunnell and Simmons 2005; Smith, Habersetzer and Gunnell 2012). There is a distinct, rapid decrease in SOR beginning in the Lutetian, suggesting that occupied morphospace decreases. This is accompanied by a significant increase in SOV to the highest point in the analysis, which may be an indication of an extinction that affects the centre of the morphospace (Simon, Korn and Koenemann 2010). The taxa placed centrally within the morphospace within this analysis are largely represented by insectivorously-adapted taxa, which have previously been suggested to decrease throughout the Eocene (Hooker 2000), particularly after the Early Eocene Climatic Optimum (EECO - ~53-50 MYA; Hooker 2000; Woodburne, Gunnell and Stucky 2009). This does fall

prior to the Lutetian, which may suggest that if the insectivoran taxa within this analysis were affected by this decrease, it may have been a few million years post EECO. The EECO reflects a time where highest mean ocean temperature of the Cenozoic was recorded (Zachos et al 2008; Woodburne et al 2014).

The WMPD results (Fig 11 and 12) sees very similar patterns of disparity change over the PETM and K-Pg: WMPD is higher during the PETM, but the magnitude of increase over the two events is very similar, suggesting that (in this metric) disparity changes occur at the same rate over both boundaries. WMPD agrees more with the pattern of disparity changes reflected by the SOR (Fig 6), as this also sees significant increases over both the K-Pg and PETM, whereas the SOV (Fig 4) shows largely different increases over both boundaries: a very minimal increase for the K-Pg, and a significant increase over the PETM. Results of the WMPD disparity analysis of the Eocene do show increasing levels of dissimilarity within taxa throughout the Eocene, which is reflected by the PCoA (Fig 3) morphospace visualisation: there is a definite increase in morphospace occupation over the entire stage, and new morphologies do appear (as previously mentioned in describing the SOV). However, many of the new taxa introduced sit within a very similar morphospace location to the Late Cretaceous and Palaeocene taxa. As WMPD is robust to sample size variation (Ciampaglio et al 2001) and does not require taxa with no comparable characters to be removed (Butler et al 2011; Benson and Druckenmiller 2013), it has been argued to be superior to methods that involve ordination of the character-taxon matrix and calculate multivariate variance (Close et al 2015) meaning that it likely reflects a more accurate portrayal of the disparity changes seen within the eutherians in this analysis over the K-Pg and PETM.

The fact that eutherians saw the greatest change in morphological disparity during the Eocene suggests that for this analysis, they fit the top-heavy model of evolution suggested by Gould (1987), where clades experience highest points of evolutionary disparity late in their evolutionary history. This may not be the case for the entirety of eutherian history, as this analysis only considers taxa from the Late Cretaceous to the Eocene, and so does not consider changes in disparity seen from the Oligocene onwards (which includes the radiation of many ordinal and subordinal level crown-clades), or the very early stages of eutherian evolution during the Early Cretaceous (potentially the Upper Jurassic, if the divergence dates associated with *Juramaia* (Luo et al 2011) are accurate and it is the earliest Eutherian mammal)).

4.3 Comparison with previous studies

Visualisation of the PCoA (Fig 3) and analysis of SOR (Fig 6 and 7) in this analysis are congruent with Benevento et al.'s (2018) results: I found that eutherian morphospace occupancy increases throughout the Late Cretaceous up to the K-Pg boundary but find disagreement when considering SOV (Fig 4 and 5), which does not see a notable increase. This suggests that the large increase seen in SOR may be due to the appearance of a few outlier taxa with unusual morphologies, as SOR is known to be more affected by outliers than is SOV (Guillerme 2020). In particular, *Tribosphenomys* and *Worlandia* appear as striking Palaeocene outliers (Fig 3) and may be driving this SOR result. The lack of major change in the SOV within the taxa including in this study may be linked to the different morphologies measured – the Benevento et al (2019) study used morphometric measurements of certain aspects of lower jaws only, whereas this study used discrete measurements of both dental and mandible characters. This could suggest that when combined, less changes in morphofunctional disparity are seen, which may indicate that eutherian dentition changes less over the K-Pg than the lower jaw does. Benevento et al (2019) found that jaw functional disparity of therian mammals increased over the K-Pg boundary, whereas disparity for mammals as a whole did not increase. Benevento et al. (2019) also found that the majority of the change in therian disparity was driven by eutherians, and that eutherians increased their functional morphospace occupancy in every time bin analysed during the Mesozoic era.

Halliday and Goswami's (2016) analysis agrees with this study in finding an increase in SOR across the K-Pg boundary, but also observed a decrease in the SOV and Mean Pairwise Distance (MPD) in the Campanian and Maastrichtian prior to the K-Pg boundary, and suggested that they found higher clustering of similar morphologies within an increasing morphospace over the K-Pg. WMPD and MPD analyses both measure the similarity of taxa within a timebin, (Norden et al 2018) but where MPD doesn't give any extra weight to comparable characters, WMPD does, meaning that characters that can be scored for multiple taxa are comparable and are therefore given more weight, meaning that they will affect changes in disparity more. WMPD analysis in this study (Fig 11 and 12) and MPD from Halliday and Goswami (2016) both agree with a decrease in disparity prior to the boundary, which differs to the changes in disparity suggested by the SOV (Fig 5) in this paper: variance-based disparity shows a consistent increase throughout the latest stages (Santonian, Campanian, Maastrichtian) of the Cretaceous, analogous to an overall steady increase in morphological disparity among the taxa present in these stages. This is comparable with the rise

in disparity seen in eutherians within the Grossnickle and Newham (2016) paper prior to the K-Pg, which suggests that increases in eutherian disparity in the latter stages of the Late Cretaceous coincided with the rise of angiosperms - likely due to the increased dietary options that became available.

The difference between the results of the SOV analysis and that of Halliday and Goswami (2016) is likely due to differences in the sets of discrete characters used - Halliday and Goswami (2016) used a phylogenetic character matrix, whereas here I used a novel set of discrete characters that were specifically selected because they seem to be of obvious morphofunctional relevance. The difference found here may be because functionally important characters might be expected to be more likely to evolve in direct response to environmental or biotic change (e.g., mass extinctions opening up new ecological niches, appearance of new dietary options such as the fruits of angiosperms; Grossnickle and Newham (2016) than characters that are likely to be of less functional relevance (e.g., minor differences in molar cusp and crest morphology). If so, use of morphofunctional characters may be preferable for use in disparity analyses, rather than recycling existing phylogenetic character matrices, as the former are more likely to reflect the occupation of new ecological niches, which has been a key focus of macroevolutionary studies since Simpson's (1944) pioneering work; furthermore, it would imply that conclusions regarding eutherian disparity that are based on analyses of phylogenetic character matrices (e.g. Halliday and Goswami, 2016) should be treated with caution.

Both Benevento et al. (2019) and Halliday and Goswami (2016) observed increases in disparity over the K-Pg boundary for eutherians, in agreement with the results found within this thesis. When considering Mammalia jaw functional disparity as a whole, Benevento et al (2019) found no increase over the K-Pg, although mandibular functional disparity of therians did increase. Benevento et al. (2019) suggested that this increase in therian disparity but the apparent stasis in overall jaw disparity of mammals during the Palaeocene may have been due to therian mammals moving into niches ones occupied by non-therian or stem therian lineages that became extinct at the end of the Cretaceous, tentatively suggesting that therians benefitted from the K-Pg in the opening of niches during the recovery phase of the extinction event. This increase in functional disparity was accompanied by an increase in morphospace occupation for eutherians - the Principal Components Analysis of Benevento et al. (2019) found that after the K-Pg boundary eutherians expanded into new regions of morphospace, which finds general agreement in the

overall morphospace occupancy increases/expansions seen in the PCoA (Fig 3) and NMDS (Fig 10) analyses of occupation in this paper for both the K-Pg and PETM boundaries, but as this study specifically considers eutherians and not Mesozoic mammals in general, a true comparison between the two results cannot be commented on.

The increase in SOV disparity immediately after the K-Pg found in this analysis is mirrored by that found by Halliday and Goswami (2016) - they observed an overall increase in SOV disparity, and similarly reported large increases in range-based SOR disparity in the immediate stages post K-Pg. They also report the K-Pg as having a selective effect on eutherian extinction across the boundary by finding decreases in variance-based disparity in the Palaeocene. I did not find a decrease in SOV over the K-Pg, instead finding little change in mean variance from the Late Cretaceous to the Palaeocene. Loss of phylogenetic diversity is also likely to be reflected in Halliday and Goswami's (2016) SOV results due to their use of phylogenetic characters, whereas changes in phylogenetic diversity will not have any effect on the functional disparity measured with discrete functional characters in this analysis (Fig 6 & 7). This suggests that variation within eutherians over the boundary experienced little functional change, while seeing some expansion in morphospace occupation – as previously mentioned, the large change in SOR is likely the result of Palaeocene outliers inflating the SOR disparity, so may be more likely to experience a similar increase to that noted by Halliday and Goswami (2016).

Over the PETM, Benevento et al. (2019) found that there was another significant increase in therian functional disparity, primarily driven by eutherians. They found eutherians were responsible for changes in morphospace occupancy to previously not occupied regions, with “ungulates” occupying a large range of their morphospace. I find agreement in this: “condylarths” and representatives of some modern “ungulate” orders (Perissodactyla and Artiodactyla) also make up a considerable proportion of the Eocene taxa within this analysis (17 of the 50 taxa present with FAD's in the Eocene are condylarths, artiodactyls and perissodactyls (Appendix B). Halliday and Goswami (2016) also found that the variance-based disparity within Eutheria increased across the PETM, reaching higher levels than that seen in the Mesozoic. The current study finds similar results: the highest levels of eutherian SOV disparity found here is during the Lutetian in the middle Eocene (Fig 5).

Halliday and Goswami's (2016) MPD findings differ from the WMPD results (Fig 11 and 12) found in this study, however: Halliday and Goswami (2016) find a large decrease in the Campanian-Maastrichtian of the Late Cretaceous, followed by a decelerating increase throughout the Cenozoic. This study finds an increased rate in WMPD increase towards the late Eocene, punctuated by a rapid decrease in the Priabonian across the Eocene-Oligocene boundary, which is likely due to minimal inclusion of Oligocene taxon in this analysis. As WMPD gives more weight to comparable characters in the disparity analysis, it is likely to be a better representative of disparity changes in discrete characters than MPD, which will not distinguish between comparable and non-comparable characters. MPD has also been suggested to show increased levels of disparity when the amount of missing data is increased (Ciampaglio, Kemp and McShea 2001), which may inaccurately inflate disparity measures when analysing matrices with large amounts of missing data.

4.4 Conclusion

The novel set of 61 morphofunctional characters used here represents a new approach for analysing changes in morphological disparity in eutherians, and one that may be superior to phylogenetic character matrices because they are more likely to reflect the occupation of new ecological niches, and are more likely to evolve in direct response to environmental or biotic change. Previous studies, including the Giannini and Garcia-Lopez (2016) and Reeves et al (2020) papers, have also made use of discrete morphofunctional characters, finding agreement in their superiority to non-functional characters to better reflect ecological niche occupancy. The major findings of this study are that overall, eutherian functional disparity increased from the Late Cretaceous to the Eocene. In the immediate stage following the K-Pg boundary, eutherian disparity as measured by these morphofunctional characters decreased, presumably as a result of the mass extinction, but then saw an overall rise through the Palaeocene and Eocene including through the PETM. Morphospace occupancy saw consistent increases throughout all three epochs, reaching its highest peak in the Eocene (Fig 3 and 10). These results are broadly congruent with previous analyses of eutherian disparity: I find agreement with the studies of Benevento et al. (2019) and Halliday and Goswami (2016), who also found that eutherians consistently increased their morphospace occupation from the Late Cretaceous to Eocene, and that mean variance saw increases across the PETM boundary. However, I find differing results in the patterns of disparity measured by SOV found by Halliday and Goswami (2016) paper: they observed a decrease in the SOV, and also Mean Pairwise Distance (MPD), in the Campanian and Maastrichtian prior to the K-Pg boundary, suggesting greater clustering of similar morphologies within an increasing morphospace at this time. This differs to the results of the SOV in this thesis: variance-based disparity shows a consistent increase throughout the end stages (Santonian, Campanian, Maastrichtian; Fig 5) of the Late Cretaceous, analogous to an overall steady increase in morphological disparity within taxa present at this time. This SOV result does however find agreement with Grossnickle and Newman (2016), who also observed an increase in eutherian disparity prior to the K-Pg in the latter stages of the Late Cretaceous. This study represents a promising novel approach for analysing changes in eutherian disparity through time, by using characters that are specifically intended to reflect functionally significant changes in morphology. This study could be extended by the inclusion of morphofunctional characters from the skull and post-cranial skeleton; in this respect, Halliday and Goswami's (2016) study is perhaps superior, in

that it includes characters from all parts of the skeleton. Of course, an improved fossil record would help reduce the amount of missing data present in the matrix used here, although this applies to any palaeobiological study that relies on incomplete fossil taxa. Additional explorations of rarefaction may also prove useful in accounting for differences in sampling between bins, and the inclusion of more eutherian species, as well as other mammalian groups like Metatheria and Multituberculata would allow greater understanding of the changes in disparity experienced by eutherians and other mammals during their long, remarkable and fascinating evolutionary history.

5. References

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6. Appendices

6.1 Appendix A – Character List

1. Functional Dentition: Absent (0); Present (1).
2. Tooth differentiation: Simple, Peg-like (0); Heterodont (1).
3. Enamel Absent: (0); Present (1).
Based on overall presence of the enamel on entire dentition.
4. Post-canine molar enamel: Non-crenulated (0); Crenulated (1).
Based on whether enamel shows crenulations post-canine.
5. Molar size gradient: Molars increase in size posteriorly (0); Molars similar in size across toothrow (1); Molars decrease in size posteriorly (2).
Based on the size difference between anterior-most molar to second molar – can be scored on upper or lower molars if uppers not preserved. If uppers preserved – score there.
6. Anterior upper incisor procumbency: Non-procumbent (0); Procumbent (1).
Based on level of procumbency – if tooth is obviously angled anteriorly, score as (1).
7. Anterior upper incisor size: Non-enlarged (0); Enlarged but not open rooted/hypselodont (1); Enlarged and open rooted/hypselodont (2).
If the tooth is obviously enlarged (i.e., larger than the canine, or obviously enlarged but not expanded)
8. Relative Size of Upper Incisors: First upper incisor larger than following incisors (0); All upper incisors similar in size (1); Middle incisors larger than anterior/posterior incisors (2); Posterior-most incisor larger than others (3).
Based on upper incisor overall size – if not present and no alveoli present score as (?)
9. Upper Incisor Arcade Shape: Narrow V shape (0); Broad V or U shape (1); Transverse row (2).
Based on the incisor arcade curvature (how curved the incisor row is). Transverse scoring would be effectively a straight line/minimal curvature.
10. Hunter-Schreger bands: Absent (0); Present (1).
Based on limited HS Band imaging/scans
11. Upper incisor accessory cusps: Absent (0); Present (1).
Score as inapplicable for individuals with ever-growing teeth
12. Diastema between posterior incisor and canine (if present): Absent (0); Present, small (1); Present, large (2).
Small – narrower than the incisor/alveoli for incisor if incisor not present
Large – Wider than incisor/alveoli for incisor
13. Upper canine morphology: Canine absent (0); Present and small (1); Present and large (2).
Based on overall size, and comparison to other surrounding teeth
14. Presence of enamel on upper canine: Absent (0); Present (1).
15. Upper canine hypselodonty: Absent (0); Present but small (1); Present but large (2); Present, large & ever-growing/hypselodont (3).
Hypselodonty determined by enamel presence/open root presence, so scorable without tooth present
16. Canine cusp morphology: Main cusp blunt (0); Main cusp sharp (1).
Based on cusp morphology without wear – score as (?) if not able to tell because of wear.
17. Canine Venom Groove: Absent (0); Present (1).
18. Canine - post canine diastema: Absent (0); Present, Small (1); Present, Large (2).
Based on where the premaxilla-maxilla suture is if absent, based on size of canine/alveolus if present (If smaller than alveolus/tooth width – small)

19. Upper premolars: No premolars (0); One premolar or one large premolar & remaining premolars small (1); 2+ premolars present (2).
Tooth has to be considerably larger to be considered for (1)
20. Upper posterior-most premolar: Unicuspid and single rooted (0); Premolariform (1); Carnassial (2); Blade-like/Plagiaulacoid (3); Molariform (4).
If posterior most tooth has evidence of an obvious protocone structure, then score as molariform.
21. Upper anterior premolar morphology: Unicuspid & Single Rooted (0); Premolariform (1); Carnassial (2); Blade-like/Plagiaulacoid (3); Molariform (4).
22. Molar morphology: Brachydont (0); Hypsodont (1); Hypselodont (2).
Based on the tooth cusp height/if ever-growing or not (based on the tooth cervix)
23. Molar crest morphology: Absent (0); Trigonid/Talonid cusps similar in height (1); Trigonid cusps taller than talonid cusps (2).
Scored on unworn molars – if completely worn down, score as inapplicable
24. Upper molar protocone pestle & mortar arrangement: Absent (0); Present (1).
Can only be scored if lower dentition is present to confirm presence of mortar structure. Needs to have a definite protocone-talonid structure.
25. Upper molar ectoloph arrangement: W shaped ectoloph arrangement (0); Non W-shaped ectoloph arrangement (1).
26. Upper anterior molar general shape: Triangular with three major cusps (0); Square with four major cusps (1); Rectangular with 4+ major cusps (2).
Only counting major cusps, not supernumerary cusps and must be elongated antero-posteriorly
27. Posterior Molar Size: Posterior molar decreases in size (0); Posterior molar similar in size to preceding molar (1); Posterior molar increases in size (2).
Based on posterior most molar and molar anterior to it (typically M2-3). Can be scored in upper or lower - if upper present, score there.
28. Lophodonty: Absent (0); Present (1).
29. Selenodonty: Absent (0); Present (1).
Can only be scored in taxa who have square upper molars with four well developed cusps with W shaped crests linking both the lingual and labial cusps. Only present in taxa that score for presence of W shaped ectoloph.
30. Lamellae Absent: (0); Present (1).
31. Upper Carnassial Shear: Absent (0); Present (1).
32. Upper Carnassial Shear: Location Posterior-most Premolar (0); Anterior-most Molar (1); Posterior-most Molar (2).
33. Lower anterior incisor size: Non-enlarged (0); Enlarged and non open-rooted/hypselodont (1); Enlarged and open rooted/hypselodont (2).
34. Anterior lower incisor procumbency: Non-procumbent (0); Procumbent (1).
35. Diastema between lower incisors and canines: Absent (0); Present (1).
36. Lower canine procumbency: Absent (0); Present (1).
37. Lower canine morphology: Absent (0); Present and small (1); Present and large (2); Present, large and open rooted (3).
38. Lower canine accessory cusps: Absent (0); Present (1).
39. Enamel presence on lower canine: Absent (0); Present (1).
40. Diastema present between canine and post canine teeth: Absent (0); Present, small (1); Present, large (2).
41. Lower premolars: Absent (0); One lower premolar, or one large lower premolar and remaining premolars small (1); 2+ premolars present (2).

42. Anterior lower premolar: Unicuspid (0); Premolariform (1); Molariform (2); Blade-like/Plagiaulacoid (3).
43. Posterior-most lower premolar: Unicuspid (0); Premolariform (1); Molariform (2); Blade-like/Plagiaulacoid (3).
44. Lower Carnassial Shear: Absent (0); Present (1).
45. Location of Lower Carnassial Shear: Lower anterior molar (0); Lower second most posterior molar (1); Lower posterior-most premolar (2).
46. Talonid Morphology: Absent (0); Small (considerably narrower than the trigonid) (1); Large (as wide as the trigonid) (2).
47. Coronoid Process Shape: Absent (0); Reduced (1); Present (2).
48. Angle of Coronoid Process: Vertical/close to vertical angle of coronoid anterior margin (0); 45 degree angle of coronoid anterior margin (1); More than 45 degrees (2).
49. Dental Condyle Position Relative to Tooth Row: Below the tooth level (0); At tooth level (1); Above tooth level (2).
50. Angular Process Size Absent: (0); Small (1); Large (2).
51. Angular Process: Hooked (0); Non-hooked (1).
52. Angular Process in relation to the condyle process: Posterior to the condyle process (0); Level with the condyle process (1); Anterior to the condyle process (2).
53. Angular Process: Orientation Non-medially inflected (0); Medially inflected (1).
54. Mandibular Symphysis: Size Does not extend to the post-canines (0); Extends to/beyond the post-canines (1).
55. Depth of Mandibular Body: Narrower than molar height from alveolus (0); Same width as molar height from alveolus (1); 1.5x width of molar height from alveolus (2); Double or greater than width of molar height from alveolus (3).
56. Mandibular Symphysis: Unfused (0); Fused (1).
57. Relationship between ultimate molar and coronoid process: Distinct gap between ultimate molar and anterior margin of coronoid process (0); Ultimate molar in line with anterior margin of coronoid process (1); Anterior margin of coronoid process overlaps molar row (2).
58. Lower incisor-canine: diastema length Absent (0); Present, Small (1); Present, Large (2).
59. Canine-Premolar diastema length: Absent (0); Small (1); Large (2).
60. Condyle Shape: Rounded (0); Antero-posteriorly elongated (1); Mediolaterally elongated (2).
61. Condylar Process: Vertically directed (0); Posteriorly directed (1); Posteriovertically directed (2).
62. Number of Mental Foramina: One (0); More than one (1).

Appendix B – Taxon Information

| Species | Matrix | Earliest | Latest | Earliest_Age | Latest_Age | FAD | LAD | Location | Family | Order |
|---------------------------|-----------------------------|-----------------|-----------------|--------------|---------------|--------|------|---------------|--------------------|----------------|
| Aptoryctes_iyvi | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.2 | 55.8 | North America | Palaeoryctidae | Cimolesta |
| Adapisorex_abundans | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 61.7 | 58.7 | Europe | Adapisoricidae | Macroscelidea |
| Alcidedorbignya_inopinata | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 65.118 | 59.2 | South America | Alcidedorbignyidae | Pantodonta |
| Alsaticopithecus_leemanni | Halliday and Goswami (2016) | Eocene | Eocene | Lutetian | Lutetian | 47.8 | 41.2 | Europe | Amphilemuridae | Macroscelidea |
| Alymlestes_kielanae | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Afro-Arabia | Zalambdalestidae | incertae_sedis |
| Amelotabes_simpsoni | Addition | Palaeocene | Palaeocene | Danian | Thanetian | 61.7 | 56.8 | North America | Epoicotheriidae | Palaeanodonta |
| Anacodon_ursidens | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 59.4 | 53 | North America | Arctocyonidae | Condylarthra |
| Anisonchus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 63.6 | 63.6 | North America | Periptychidae | Condylarthra |
| Ankalagon_saurognathus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 63.3 | 61.7 | North America | Mesonychidae | Condylarthra |
| Apatemys_pygmaeus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 50.3 | North America | Apatemyidae | Apatotheria |
| Apheliscus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.4 | 53.3 | North America | Apheliscidae | Macroscelidea |
| Aphronorus_orieli | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Selandian | Selandian | 60.5 | 60.4 | North America | Pentacodontidae | Cimolesta |
| Arctocyon_corrugatus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Selandian | Thanetian | 61.7 | 58 | North America | Arctocyonidae | Condylarthra |
| Arctostylops_steini | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Thanetian | Thanetian | 57.7 | 56.4 | North America | Arctostylopidae | Arctostylopida |
| Asioryctes_nemegetensis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Asia | Palaeoryctidae | Cimolesta |
| Asiostylops_spanios | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | Asia | Arctostylopidae | Arctostylopida |
| Aspanlestes_aptap | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Coniacian | 94.3 | 89.3 | Asia | Zhelestidae | incertae_sedis |
| Avitotherium_utahensis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Campanian | Campanian | 83.4 | 83.2 | North America | Zhelestidae | incertae_sedis |
| Barunlestes_butleri | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Campanian | 84.9 | 70.6 | Africa | Zalambdalestidae | incertae_sedis |

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|-----------------------------|-----------------------------|-----------------|-----------------|---------------|---------------|------|------|---------------|------------------|-----------------|
| Batodon_tenuis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Maastrichtian | Maastrichtian | 69 | 67.5 | North America | Cimolestidae | Cimolesta |
| Bessoecetor_septentrionalis | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 63.3 | 58.1 | North America | Pantolestidae | Cimolesta |
| Betonnaia_tosia | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64.1 | 63.8 | North America | Cimolestidae | Cimolesta |
| Bisonalveus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Selandian | Thanetian | 60.4 | 58.3 | North America | Pentacodontidae | Cimolesta |
| Bulaklestes_kezbe | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Coniacian | 94.3 | 89.3 | Asia | incertae_sedis | Asioryctitheria |
| Bunophorus_grangeri | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 54.5 | 52.8 | North America | Diacodexidae | Artiodactyla |
| Cantius_trigonodus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 48.6 | North America | Notharctidae | Primates |
| Centetodon_chadronensis | Halliday and Goswami (2016) | Eocene | Oligocene | Priabonian | Rupelian | 37.3 | 33.3 | North America | Geolabidae | Eulipotyphla |
| Chacopterygus_minutus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 63.8 | 63.8 | North America | Cimolestidae | Cimolesta |
| Chambius_kasserinensis | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Bartonian | 55.8 | 40.4 | Africa | Macroscelididae | Macroscelidea |
| Chriacus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 63.5 | 58 | North America | Arctocyonidae | Condylarthra |
| Cimolestes_sp | Halliday and Goswami (2016) | Late Cretaceous | Palaeocene | Campanian | Thanetian | 72.1 | 55.8 | North America | Cimolestidae | Cimolesta |
| Claenodon_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 63.3 | 59.9 | North America | Arctocyonidae | Condylarthra |
| Conacodon_matthewi | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64.9 | 64.9 | North America | Periptychidae | Condylarthra |
| Copecion_brachypternus | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 59.8 | 52.8 | North America | Phenacodontidae | Condylarthra |
| Coryphodon_marginatus | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 56 | 47.8 | Europe | Coryphodontidae | incertae_sedis |
| Cyriacotherium_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58 | 55.8 | North America | Cyriacotheriidae | incertae_sedis |
| Daulestes_sp | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Coniacian | 94.3 | 89.3 | Asia | incertae_sedis | Asioryctitheria |
| Desmatoclaenus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 66 | 63.3 | North America | Arctocyonidae | Condylarthra |
| Diacodexis_metsiacus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.7 | 52.8 | North America | Diacodexidae | Artiodactyla |
| Didelphodus_absarokae | Halliday and Goswami (2016) | Eocene | Oligocene | Lutetian | Rupelian | 55.7 | 52 | North America | Hyaenodontidae | Creodonta |

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|-------------------------------|-----------------------------|-----------------|-----------------|---------------|---------------|--------|-------|---------------|-------------------|-----------------|
| Didymictis_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Priabonian | 55.7 | 46.3 | North America | Viverravidae | Carnivoramorpha |
| Dilambdogale_gheerbranti | Halliday and Goswami (2016) | Eocene | Eocene | Bartonian | Priabonian | 37.2 | 33.9 | Africa | incertae_sedis | Afrosoricida |
| Dipsalidictis_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 61.7 | 54.6 | North America | Oxyaenidae | Creodonta |
| Domnina_sp | Halliday and Goswami (2016) | Eocene | Oligocene | Lutetian | Rupelian | 42.2 | 32.1 | North America | Soricidae | Eulipotyphla |
| Ectocion_osbornianus | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Bartonian | 58.1 | 54.2 | North America | Phenacodontidae | Condylarthra |
| Ectoconus_majusculus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 65.722 | 63.6 | North America | Periptychidae | Condylarthra |
| Elomeryx_crispus | Halliday and Goswami (2016) | Eocene | Oligocene | Bartonian | Chattian | 37.2 | 23.03 | Europe | Anthracotheriidae | Artiodactyla |
| Elphidotarsius_russelli | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 61.7 | 56.8 | North America | Carpolestidae | Primates |
| Elpidophorus_elegans | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Selandian | Thanetian | 63.3 | 58.3 | North America | Plagiomenidae | incertae_sedis |
| EOconodon_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 65.2 | 63.7 | North America | Triisodontidae | Condylarthra |
| Eohippus_angustidens | Halliday and Goswami (2016) | Eocene | Eocene | Lutetian | Lutetian | 53.7 | 52.8 | North America | Equidae | Perissodactyla |
| Eoryctes_melanus | Halliday and Goswami (2016) | Eocene | Eocene | Lutetian | Lutetian | 55 | 55 | North America | Palaeoryctidae | Cimolesta |
| Eritherium_azzouorum | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Thanetian | Thanetian | 58.7 | 55.8 | Africa | incertae_sedis | Proboscidea |
| Escavadodon_zygus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Selandian | Selandian | 63.3 | 61.7 | North America | Escavadodontidae | Palaeanodonta |
| Esthonyx_spatularius | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 54.3 | North America | Esthonychidae | Trogontia |
| Gallolestes_pachymandibularis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Campanian | Campanian | 72.3 | 72.1 | North America | Zhelestidae | incertae_sedis |
| Gelastops_parcus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 63.3 | 60.7 | North America | Cimolestidae | Cimolesta |
| Gobiohyus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Priabonian | 48.6 | 37.2 | Asia | Helohyidae | Artiodactyla |
| Gomphos_elkema | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 48.6 | Asia | Mimotonidae | Glires |
| Goniacodon_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 66 | 61.7 | North America | Triisodontidae | Condylarthra |
| Gypsonictops_hypoconus | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Maastrichtian | Maastrichtian | 69 | 66.7 | North America | Gypsonictopidae | Leptictida |

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|----------------------------|-----------------------------|-----------------|-----------------|------------|---------------|------|------|---------------|----------------------|-----------------|
| Hapalodectes_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 48.6 | North America | Hapalodectidae | Condylarthra |
| Haploconus_angustus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 65.3 | 61.7 | North America | Periptychidae | Condylarthra |
| Haplomylus_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 50.3 | North America | Apheliscidae | Macroscelidea |
| Hemithlaeus_kowalevskianus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64.1 | 63.7 | North America | Periptychidae | Condylarthra |
| Heptodon_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 53.8 | 46.2 | North America | Helaletidae | Perissodactyla |
| Hilalia_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Priabonian | 48.6 | 37.2 | Afro-Arabia | Pleuraspidotheriidae | Condylarthra |
| Homogalax_protapirinus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 52.9 | North America | Isectolophidae | Perissodactyla |
| Hyopsodus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Bartonian | 55.2 | 40.7 | North America | Hyopsodontidae | Condylarthra |
| Hyracotherium_vasacciense | Addition | Eocene | Eocene | Ypresian | Lutetian | 53.7 | 46.2 | North America | Equidae | Perissodactyla |
| Icaronycteris_index | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 50.3 | North America | Archaeonycteridae | Chiroptera |
| Indohyus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Priabonian | 55.8 | 37.2 | Asia | Choeropotamidae | Artiodactyla |
| Kennalestes_gobiensis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Afro-Arabia | incertae_sedis | Asioryctitheria |
| Kulbeckia_kulbecke | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Santonian | 94.3 | 84.9 | Afro-Arabia | Zalambdalestidae | incertae_sedis |
| Labidolemur_kayi | Addition | Palaeocene | Eocene | Thanetian | Ypresian | 59 | 52.8 | North America | Apatemyidae | Apatotheria |
| Lainodon_orueetxebarriai | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Europe | Zhelestidae | incertae_sedis |
| Lambdotherium_popoagicum | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 53.7 | 46.2 | North America | Brontotheriidae | Perissodactyla |
| Lambertocyon_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.4 | 55.8 | North America | Arctocyonidae | Condylarthra |
| Leptacodon_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Danian | Ypresian | 63.3 | 48.6 | North America | Nyctitheriidae | Eulipotyphla |
| Leptictis_dakotensis | Halliday and Goswami (2016) | Eocene | Oligocene | Priabonian | Rupelian | 35.5 | 33.1 | North America | Leptictidae | Leptictida |
| Lessnessina_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 48.6 | Europe | Hyopsodontidae | Condylarthra |
| Litocherus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 63.3 | 57.9 | North America | Apheliscidae | Macroscelidea |
| Litolophus_gobiensis | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 48.6 | Asia | Eomoropidae | Perissodactyla |

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|----------------------------|-----------------------------|-----------------|-----------------|------------|---------------|--------|--------|---------------|----------------------|----------------|
| Loxolophus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64.7 | 62.2 | North America | Arctocyonidae | Condylarthra |
| Macrocranion_nitens | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 52.1 | Europe | Amphilemuridae | Macroscelidea |
| Maelestes_gobiensis | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Asia | Cimolestidae | Cimolesta |
| Metacheiromys_dasyypus | Addition | Eocene | Eocene | Lutetian | Lutetian | 46.5 | 46.4 | North America | Metacheiromyidae | Palaeonodonta |
| Miacis_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Priabonian | 55.7 | 37.2 | North America | Miacidae | Carnivoramorph |
| Mimatuta_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 65.3 | 64 | North America | Periptychidae | Condylarthra |
| Mixodectes_pungens | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 62.517 | 62.221 | North America | Mixodectidae | incertae_sedis |
| Molinodus_suarezi | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 65.118 | 59.2 | South America | Hyopsodontidae | Condylarthra |
| Notharctus_tenebrosus | Addition | Eocene | Eocene | Ypresian | Bartonian | 50.3 | 40.4 | North America | Notharctidae | Primates |
| Onychodectes_tisonensis | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64.3 | 63.8 | North America | Conoryctidae | Taeniodonta |
| Onychonycteris_finneyi | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 50.3 | North America | Onychonycteridae | Chiroptera |
| Oreotalpa_florissantensis | Halliday and Goswami (2016) | Eocene | Eocene | Priabonian | Priabonian | 37.2 | 33.9 | North America | Talpidae | Lipotyphla |
| Orthaspidotherium_edwardsi | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | Europe | Pleuraspidotheriidae | Condylarthra |
| Oxyclaenus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 66 | 61.7 | North America | Oxyclaenidae | Condylarthra |
| Pachyaena_ossifraga | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.5 | 53.1 | North America | Mesonychidae | Condylarthra |
| Pakicetus_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Lutetian | 56 | 41.3 | Afro-Arabia | Pakicetidae | Artiodactyla |
| Palaeoryctes_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 60.4 | 50.3 | North America | Palaeoryctidae | Cimolesta |
| Palaeosinopa_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 50.3 | North America | Pantolestidae | Cimolesta |
| Pantolambda_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 63.3 | 60.5 | North America | Pantolambdidae | Cimolesta |
| Paramys_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Priabonian | 55.6 | 33.9 | North America | Ischyromyidae | Rodentia |
| Paranyctoides_quadrans | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Coniacian | 94.3 | 89.3 | Afro-Arabia | incertae_sedis | incertae_sedis |
| Parapternodus_antiquus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.3 | 55 | North America | Parapternodontidae | Eulipotyphla |

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|-------------------------------|-----------------------------|-----------------|------------|---------------|-----------|------|------|---------------|----------------------|----------------|
| Pentacodon_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 63.3 | 61.7 | North America | Pantolestidae | Cimolesta |
| Periptychus_carinidens | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 62.1 | 59.7 | North America | Periptychidae | Condylarthra |
| Phenacodus_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.1 | 48.6 | North America | Phenacodontidae | Condylarthra |
| Plagioctenodon_sp | Addition | Palaeocene | Palaeocene | Thanetian | Thanetian | 56.8 | 56.3 | North America | Nyctitheriidae | Eulipotyphla |
| Plagiomene_multicuspis | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 54 | North America | incertae_sedis | Dermoptera |
| Pleuraspidothierium_aumonieri | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | Europe | Pleuraspidothieridae | Condylarthra |
| Poebrotherium_sp | Halliday and Goswami (2016) | Eocene | Oligocene | Priabonian | Rupelian | 35.8 | 33.3 | North America | Camelidae | Artiodactyla |
| Procerberus_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 65.2 | 64.9 | North America | Cimolestidae | Cimolesta |
| Prodiacodon_tauricinerei | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 57.7 | 53 | North America | Leptictidae | Leptictida |
| Prolimnocyon_elisabethae | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 53 | 46.2 | North America | Hyaenodontidae | Creodonta |
| Promioclaenus_acolytus | Addition | Palaeocene | Palaeocene | Danian | Selandian | 63.3 | 59.8 | North America | Hyopsodontidae | Condylarthra |
| Protictis_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Thanetian | 63.3 | 58.8 | North America | Viverravidae | Carnivoramorph |
| Protoselene_opisthacus | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 63.3 | 59.7 | North America | Hyopsodontidae | Condylarthra |
| Protungulatum_sp | Halliday and Goswami (2016) | Late Cretaceous | Palaeocene | Maastrichtian | Danian | 70.6 | 63.5 | North America | Arctocyonidae | Condylarthra |
| Puercolestes_simpsoni | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Danian | 64 | 63.3 | North America | Cimolestidae | Cimolesta |
| Pyrocyon_dioctetus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 54.5 | 54.4 | North America | Hyaenodontidae | Creodonta |
| Rhombomylus_nitidulus | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.8 | 48.6 | Asia | Eurymylidae | Glires |
| Rodhocetus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Lutetian | Lutetian | 47.8 | 41.3 | Afro-Arabia | Protocetidae | Artiodactyla |
| Saxonella_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 61.6 | 59.2 | North America | Saxonellidae | Primates |
| Sinonyx_jiashanensis | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | Asia | Mesonychidae | Condylarthra |
| Teilhardimys_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 58.7 | 48.6 | Europe | Louisinidae | Condylarthra |
| Tetraclaenodon_puercensis | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Danian | Selandian | 61.7 | 59.5 | North America | Phenacodontidae | Condylarthra |

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|------------------------|-----------------------------|-----------------|-----------------|------------|---------------|------|------|---------------|------------------|-----------------|
| Thryptacodon_australis | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 59.9 | 55.8 | North America | Arctocyonidae | Condylarthra |
| Titanoides_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Selandian | Ypresian | 59.7 | 55.8 | North America | Titanoideidae | Cimolesta |
| Todralestes_variabilis | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | Africa | Todralestidae | Cimolesta |
| Tribosphenomys_minutus | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 58.7 | 55.8 | North America | Alagomyidae | Rodentia |
| Tubulodon_taylori | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 50.3 | 46.2 | North America | Epoicotheriidae | Palaeanodonta |
| Tytthaena_sp | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Thanetian | Thanetian | 58.3 | 56.7 | North America | Oxyaenidae | Creodonta |
| Uchkudukodon_nessovi | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Cenomanian | Coniacian | 94.3 | 89.3 | Afro-Arabia | incertae_sedis | Asioryctitheria |
| Uintacyon_rudis | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 56.8 | 53.3 | North America | Miacidae | Carnivoramorpha |
| Ukhaatherium_nessovi | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Asia | incertae_sedis | Asioryctitheria |
| Utaetus_buccatus | Halliday and Goswami (2016) | Eocene | Eocene | Bartonian | Priabonian | 40.4 | 37.2 | South America | Dasypodidae | Cingulata |
| Viverravus_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Danian | Bartonian | 55.1 | 40.4 | North America | Viverravidae | Carnivoramorpha |
| Vulpavus_sp | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Lutetian | 55.3 | 46.2 | North America | Miacidae | Carnivoramorpha |
| Widanelfarasia_sp | Halliday and Goswami (2016) | Eocene | Oligocene | Priabonian | Rupelian | 33.9 | 28.4 | Africa | incertae_sedis | Afrosoricida |
| Worlandia_inusitata | Halliday and Goswami (2016) | Palaeocene | Palaeocene | Thanetian | Thanetian | 57.2 | 56.3 | North America | Plagiomenidae | incertae_sedis |
| Wyolestes_apehes | Halliday and Goswami (2016) | Eocene | Eocene | Ypresian | Ypresian | 55.3 | 54.9 | North America | Didymoconidae | incertae_sedis |
| Wyonycteris_sp | Halliday and Goswami (2016) | Palaeocene | Eocene | Thanetian | Ypresian | 56.7 | 50.3 | North America | Nyctitheriidae | Eulipotyphla |
| Zalambdalestes_sp | Halliday and Goswami (2016) | Late Cretaceous | Late Cretaceous | Santonian | Maastrichtian | 84.9 | 70.6 | Asia | Zalambdalestidae | incertae_sedis |

6.3 Appendix C – Taxa References

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