THE ENIGMATIC EVOLUTIONARY RELATIONSHIPS OF PALEOCENE MAMMALS AND THEIR RELEVANCE FOR THE TERTIARY RADIATION OF PLACENTAL MAMMALS

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I, Thomas John Dixon Halliday, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis

To Charlotte, the best placental mammal

ABSTRACT

Understanding the general pattern of how a clade evolves over time is a central aim of palaeontology and evolutionary biology. The observation that the tree of life is asymmetric in species distribution necessitates that rates of evolution, speciation, and extinction vary through time and across phylogeny. The way this variation is distributed can help to inform on historic events, selection pressures, and relationships. Often, at the origination of a clade, it is supposed that there is an 'early burst' of diversification, before rates of speciation and morphological evolution slow down as the clade ages. One example of a supposed 'early burst' is that of placental mammals, but the internal relationships of the earliest members of this group have prevented further study of macroevolutionary parameters. In this thesis, by building the largest cladistic data matrix to date, I test the relationships of mammals from the earliest Cenozoic, and from the resulting phylogenies, test the hypotheses that the end-Cretaceous mass extinction resulted in an adaptive radiation of placental mammals. I show that Phenacodontidae are most parsimoniously ancestral to Perissodactyla, that a division between Boreoeutheria and Atlantogenata is better supported than one between Xenarthra and Epitheria or Afrotheria and Exafroplacentalia at the root of Placentalia, and that all "condylarths" can be placed, with varying degrees of confidence, as stem members of laurasiatherian orders. I show that there was an increase in rate of morphological evolution immediately after the end-Cretaceous mass extinction, that Placentalia is extremely likely to have originated less than 70 million years ago, and that the rise of Placentalia was associated with an increase in morphospace occupation, and, with a lag, mean pairwise dissimilarity of taxa. These conclusions support the contention that the end-Cretaceous mass extinction was not just an important time in Earth's ecological history, but crucial to the diversification of mammals to the level observed today.

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CHAPTER ONE

INTRODUCTION AND BACKGROUND TO TOPICS

The transition from strata bearing mostly dinosaurian fauna to those with largely mammalian fauna has long been considered a major point of change in the history of life. The early attempts of stratigraphists, broadly dividing periods of time on Earth into Primary, Secondary, Tertiary, and Quaternary (Arduino 1760) gave way to the distinction between ever finer periods of time: the Cretaceous marking the end of the Mesozoic (equivalent to the old Secondary), and the beginning of the Tertiary initially demarcated by the modern mammals of the Eocene – deriving from the Greek meaning “dawn of the recent” (Lyell 1833).

Edward Drinker Cope (1881) discovered in the Puerco beds of North America a fauna that seemed somehow intermediate between the Eocene and Cretaceous faunas, and the Paleocene – a term already referring to the oldest part of the Eocene (Schimper 1874) – was identified as an ecologically distinct period of time. The Paleocene fauna is both intermediate in time between those of the Cretaceous and Eocene faunae, but also, presumably, intermediate in phylogenetic terms. Those mammals which are present in the Paleocene by simple necessity must be descended from Cretaceous forms, and, equally, all modern orders must trace their lineage back through the Paleocene. Paleocene placental mammals have historically, however, been difficult to place taxonomically, as they possess a number of mosaic character states, and appear suddenly in the fossil record as already relatively derived organisms.

The mammals of the Paleocene include the first definitive crown placental taxa, and occur immediately after the last of the mass extinctions at the end of the Cretaceous. As a result of this temporal and probable phylogenetic placement early on in placental mammal evolution, they are critical to the understanding, not only of placental phylogenetics, but of ecological responses of major clades to mass extinction events.

1(a) – *The Paleocene as an important period*

The patterns of diversity and the rules that govern evolution, during different stages of the lifetime of a clade are a constant source of interest among palaeontologists (Simpson 1944; Gould and Eldredge 1977; Cooper and Purvis 2010; Slater 2013). In particular, this is relevant to the understanding of how extinctions play a role in shaping ecological change at the community and global level (Archibald 2011; Jablonski and Raup 1995; Jablonski 2005). Periods of rapid evolution have often been suggested to have occurred during the early part of a clade's life (Simpson 1944), and are frequently attributed to 'adaptive radiation' (Schluter 2000; Foote 1994), defined as the situation where a clade evolves new morphologies very rapidly as adaptations to exploit a variety of newly available ecological niches (Schluter 2000). Suggested examples of this through the fossil record include the multiple evolution of free-swimming animals in the Cambrian (Morris 1989), the radiation of plants on land (Bateman *et al.* 1998), and bivalve molluscs after the end-Permian mass extinction (Stanley 1968). The archetypal example of a supposed adaptive radiation – indeed, the event for which the term was coined by Henry Fairfield Osborn (1902) – is the sudden appearance at the beginning of the Cenozoic of a diverse assemblage of derived (and largely placental) mammals.

However, for an event to qualify as an adaptive radiation, three main requirements must be met (Lieberman 2012) – high lineage origination rates resulting in a large number of new species, high levels of morphological change resulting in highly derived morphologies as adaptations to new niches, and an increase in morphological disparity across the period of the radiation. Without meeting these three criteria, a radiation cannot be considered to be adaptive. Without high lineage origination rates, it cannot be called a radiation; without large amounts of change, which must also be ultimately divergent, it cannot be considered a set of adaptations to novel environments or ecologies.

In general, mass extinctions are often supposed to play a major role in adaptive radiations, because the near-total extinction of large clades (such as the brachiopods at the end-Permian) leaves an ecological niche empty that was previously being exploited (and was therefore a successful and stable life strategy in the pre-extinction ecology). Opportunistic species are then able to adapt to fill the empty niches. Just such a justification has been used in the case of placental mammals. The traditional interpretation of the fossil record has been that the demise of the dominant fauna of the Mesozoic – primarily non-avian dinosaurs, but also other archosaur groups – allowed mammals to evolve to occupy those ecological niches which had been vacated (Novacek 1999). An often-used parameter for estimating ecological niches in extinct taxa is body size, which is a strong correlate of many important ecological and life history traits. Competitive exclusion from certain body sizes has impacted the evolution of many clades. Differing ecologies at different growth stages has been thought to be important in dinosaurian (particularly sauropod) evolution (Codron *et al.* 2012), and the disjunct in typical sizes between birds and pterosaurs has been explained by a competitive exclusion principle (Benson *et al.* 2014b), although patterns of taxonomic diversity through time appear to contradict this (Butler *et al.* 2009). Analysis of the rates of body size evolution strongly favour a model of released constraint in mammals (Slater 2013) at the K-Pg boundary, due to the absence of competition from those taxa previously occupying large body sizes.

The Paleocene began dramatically with the bolide impact which caused the end-Cretaceous mass extinction. The end of the Paleocene was also a period of distinct climatic upheaval – the planet warmed intensely, second only to the present day in rate of temperature increase over time (Cui *et al.* 2011), until there were permanent forests at the poles. The Paleocene-Eocene Thermal Maximum (PETM) has been shown to be a period of radical change in the record of mammalian faunas (Gingerich 2006; Bowen *et al.* 2002; Alroy 2000), with the majority of extant placental mammal orders indisputably represented at this time. Additionally, there was a dramatic size reduction across many placental groups (Clyde and Gingerich 1998; Gingerich 2003) as a response to the higher temperatures. After the PETM, ecosystems recovered to a similar or higher level of complexity (Darroch *et al.* 2014), but the taxa of which the communities were composed were different. Typically, attempts to reconstruct the relationships between extant placental orders have focused on those earliest unambiguous members of the groups, most of which are known only from the Eocene or later. This is problematic, as it is generally supposed that Paleocene taxa represent early forms from which the extant groups must have derived, barring the statistically unlikely possibility that all close relatives of extant clades are unsampled in the fossil record. As a result of this, and as the PETM is a period of transition, using morphologies present at the beginning of the Eocene as an approximation for the earliest morphology of the group may be resulting in inaccurate character polarisation and therefore inaccurate reconstructions of relationships, as well as hindering attempts to reconstruct mammal responses to the end-Cretaceous mass extinction. Indeed, it may be due to this sandwiching of the Paleocene between two periods of climatic and ecological upheaval that the organisms during this 10 million year window are so unusual and have resisted attempts to classify them. This, of course, would only be the case if the climate change and mass extinction events had had some effect on the rate of evolution of these taxa, which, as already discussed, has historically not been clear.

1(b) *The hypothesised effect of the end-Cretaceous on mammal evolution*

The fossil record has tended to favour the view of an adaptive radiation in placental mammals occurring from 66 million years ago throughout the early Palaeogene (Osborn 1902; Alroy 1999; Archibald 2011). The first appearances of large-bodied herbivores, flying, and fully aquatic mammals are in the Paleocene and early Eocene (Simmons *et al.* 2008; Thewissen *et al.* 2007), while prior to the K-Pg, the overwhelming majority of mammals were small, insectivorous and terrestrial to scansorial (Goswami *et al.* 2011), fulfilling a similar ecological niche to the extant tree-shrews, although there are several exceptions among non-eutherians (Meng *et al.* 2015; Luo and Wible 2005; Luo 2007).

However, dating the divergence times between extant mammals using molecular methods has resulted in a completely different view of mammalian evolution. The majority of molecular clock analyses suggest that the divergence of the placental mammal orders occurred long before the K-Pg, often deep within the Cretaceous (Kumar and Hedges 1998; Springer *et al.* 2003; Meredith *et al.* 2011; Bininda-Emonds *et al.* 2007). Such analyses have attracted criticism due to assumptions inherent in the study of molecular clocks (Roger and Hug 2006), although methods have been developed in recent years which overcome some of these shortcomings by allowing for variable rates of evolution of molecular traits (Douzery *et al.* 2004). Molecular approaches such as that of Bininda-Emonds *et al.* (2007) utilised a supertree to show that the K-Pg had no tangible effect on the rate of per-lineage diversification in placental mammals. In other words, that study concluded that those lineages leading to extant mammals did not undergo an increase in speciation rate coincident with the end-Cretaceous mass extinction, but instead underwent a shift much later, in the Eocene. Reconciling this with the presence of highly derived and ecologically novel mammals throughout the Paleocene is difficult, since the paper also concludes that the majority of extant ordinal level clades had already undergone some level of diversification prior to the end-Cretaceous mass extinction.

Diversity and disparity analyses that reconstruct past events from extant taxa generally look at the rate of origin of new lineages on a phylogenetic tree (whether raw, per-lineage, or adjusted for heritability of speciation rate). Without a resolved phylogenetic tree of those organisms which were present before, during and after the period of interest, it is impossible to accurately reconstruct the rate at which diversification of lineages occurred, nor is it possible to study the rate of morphological evolution during that time. A probable reason behind the discrepancy in reconstructed divergence dates is that the supertree takes data only from extant groups, and makes the assumption that there are close to no unambiguous crown placental mammals from the Paleocene (Bininda-Emonds*, et al.* 2007) when building in fossil calibrations. This means that the trees used for certain analyses do not include Paleocene taxa when estimating changes in lineages. Trivially, basing conclusions about a mass extinction on solely extant data does not account for a large amount of data which is available through the fossil record. Excluding those taxa whose descendants happen to have gone extinct in the subsequent 66 million years is to place undue importance on today's biodiversity. Those taxa which were present before, during, and immediately after a historical event of interest must be those for which the event is most relevant, and not obscured by time. Additionally, it highly improbable that accurate reconstructions can be made about diversification events in the past from only studying the present (Tarver and Donoghue 2011; Slater *et al.* 2012; Wood *et al.* 2013), due to the loss of lineages through extinction and an inability to account for varying speciation and extinction rates, although this is disputed by some (Harvey and Rambaut 2000).

As there is such an incongruity between the molecular and morphological dates for mammal evolution, and given that understanding how extinction events affect and alter ecology and evolution is an interesting and important question, it is readily apparent that the Paleocene is a critical period of mammal evolution. However, previous analyses have, for the most part, not sampled the vast diversity of Paleocene mammals when considering the evolution of crown Placentalia. One of the largest analyses of Cretaceous mammals, commonly referred to as the Wible matrix (Wible *et al.* 2007), used a number of crown placental taxa to orient the tree. They concluded that no placental mammal existed significantly earlier than the K-Pg boundary, as all Cretaceous taxa fell outwith the crown. However, as they readily admit, the oldest definitive crown placental was the Middle Paleocene *Mimotona*, a member of Glires (rodents, rabbits, hares, and pikas), and therefore a relatively derived crown placental. Aside from *Mimotona*, there are no other Paleocene taxa in their dataset, and the majority of definitively crown placental mammals are extant. That study was intended to clarify the relationships of specific Cretaceous eutherian taxa (crown group placental mammals and their stem relatives), and, as the largest dataset of its kind at the time of publication provided a strong foundation on which further work was built in understanding the relationships and diversity of Cretaceous eutherians. However, the lack of Paleocene taxa in that analysis demonstrates the general need for analyses that better sample the extremely rich Paleocene fossil record to resolve the relationships within the early radiation of Placentalia.

Despite several scientists hypothesising that rates of evolution at the end-Cretaceous mass extinction, and to a lesser extent the PETM, should increase, the results of such studies have been relatively equivocal. The fact that no phylogenetic tree of Paleocene mammals exists that comprehensively samples a large range of Paleocene mammals is problematic for analysing changing rates of character acquisition along internal branches through this interval. Without such a tree, it is therefore impossible to quantify to what extent the global changes in climate and biota affected placental mammal evolution, once more demonstrating the necessity for analysis of the placental mammals that were present during this crucial period.

1(c) *Measuring morphological rates and disparity*

Rates of evolution can be measured in a number of ways. A traditional method of quantifying evolutionary rate has been using metrics to assess changes in continuous characters over time. The first of these was the darwin, proposed by J.B.S. Haldane (1949). One darwin a change of factor e (the base of the natural logarithm) per million years. The rate of evolution on palaeontological timescales has tended to be measured in terms of millidarwins – Haldane himself said “Rates of one darwin would be exceptional” (Haldane 1949 pg. 55), so small are the apparent shifts in geological time. An alternative metric for measuring change – the haldane, proposed by Philip Gingerich (1993) – is based on the darwin, but includes a component of standard deviation of the samples in order to measure proportional change, and instead of measuring time in millions of years, it is estimated in generations.

The haldane is certainly more philosophically sound than the darwin as a way of measuring evolutionary change. In biology, change is introduced at the beginning of each new generation, so it better reflects the intensity of selective pressure to discuss rates of change as occurring at the per generation level. Moreover, as a species is by definition a collection of individuals, knowing the variance within a population allows a clearer idea of how the population is changing over time. However, it is rarely applicable in the vertebrate fossil record, where the incompleteness of the record is such that species are often represented only by individual specimens, meaning that variance is impossible to quantify. Additionally, errors in dating and lack of sufficient samples mean that generational time can only be assessed either by histological estimation of age of maturity or by inference from some correlating trait, such as body size.

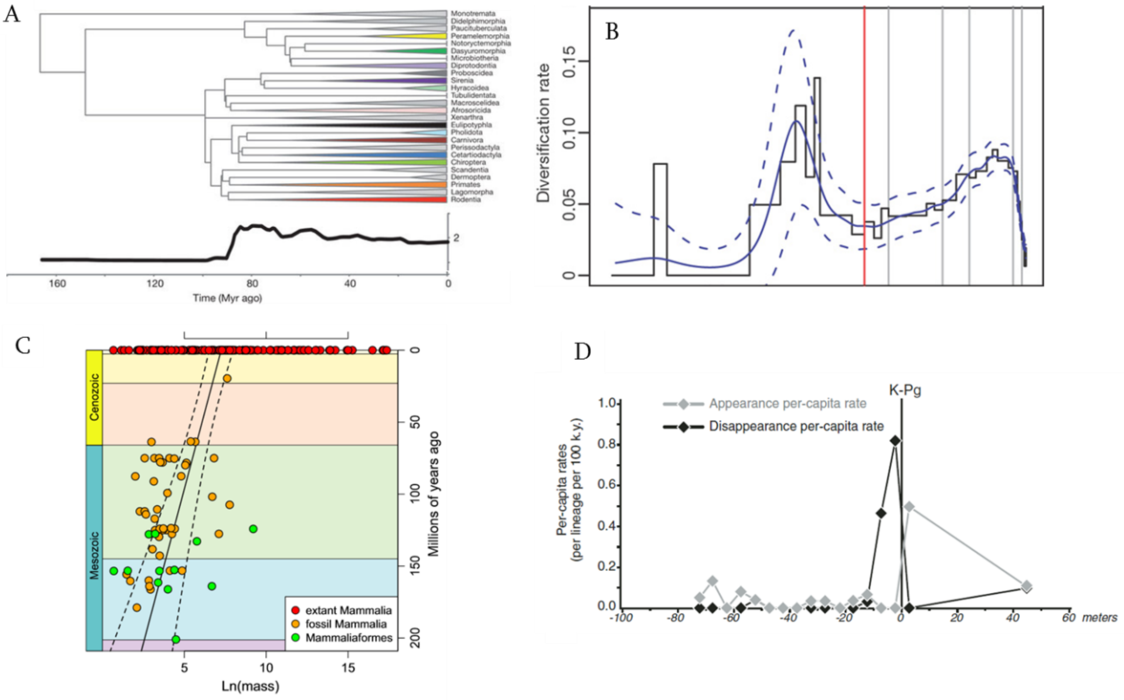


Figure 1.1 – Contrasting results from previous analyses of evolutionary rates of body size (A, C) and lineage accumulation (B, D). With different measures and datasets, different conclusions have been drawn. A – Analysis of rate of body size evolution through time, using body sizes of extant taxa (Venditti *et al.* 2011), finding no effect at the end-Cretaceous mass extinction. B – Rate of lineage accumulation, based on the Bininda-Emonds *et al.* (2007) supertree of extant mammals, which found no increase at the end-Cretaceous mass extinction, marked here by the red line. C – Body size evolution from a dataset of Cretaceous and extant eutherians (Slater 2013), which found a decrease in rate of body size evolution and an ecological release allowing a change in mode. D – Faunal changes across the end-Cretaceous mass extinction in the San Juan Basin (Wilson 2014), with a large increase in per-lineage rates of extinction and origination on either side of the mass extinction event.

Nonetheless, continuous traits are frequently modelled in the fossil record. In particular, body size – an easily measured trait with several important ecological correlates – is a common feature used in the reconstruction of evolutionary rates. Indeed, there are several instances of studies analysing rates of body size evolution across the end-Cretaceous mass extinction. As with analyses of phylogenetic relationships, though, conflicting conclusions have been drawn (Figure 1.1), with some analyses reconstructing no change in body size evolution over the end-Cretaceous mass extinction (Venditti*, et al.* 2011), while others support a decrease in rate of body size evolution but a shift in mode (Slater 2013).

Using continuous characters as proxies for rates of overall evolution is, however, problematic. One could conceive of a situation where body size (for example) remains essentially constant, and yet a great deal of other physiological, developmental or behavioural changes takes place. The use of a single continuous character, then, to assess the change in evolutionary rate as a response to some event is likely to miss important information, and to underestimate absolute amounts of change. In extreme cases, the pattern of reconstructed rates may differ substantially from reality. Additionally, the evolution of body size and shape has been shown to be heavily constrained over evolutionary timescales (Harmon *et al.* 2010), making it difficult to detect adaptive radiations except where the branches are short.

Discrete characters have tended not to be used for evolutionary rates analyses – for the very good reason that the change between states of a typical binary character is generally modelled as instantaneous, leading to an all-or-nothing interpretation of rate. However, this is largely a problem for modelling the evolution of single characters. Where it is possible to reconstruct the character states of ancestral nodes for a suite of discrete characters, such as those typically used for cladistic analysis, calculating the amount of character transitions that occur on each branch of a dated phylogenetic analysis presents us with an opportunity to consider rates of change that have manifold advantages over alternative techniques. Firstly, it allows all morphological characters to be included in the calculation of rate, regardless of data type. Secondly, all that is required is a dated phylogeny and a distribution of character states for the tips of that phylogeny. Modelling ancestral states on a tree is independent of the generation of that tree, and as such, the phylogeny can be derived from any source.

In order to establish the truth of the notion that the appearance of numerous derived placental mammals represents a true adaptive radiation, it is also necessary to assess changes in morphological disparity from the late Cretaceous into the

Palaeogene. Disparity is another example of a metric typically only used to assess continuous traits, most often the shape of particular structures (Dyke and Nudds 2009; Davis and Calede 2012). An analysis of eutherian mammal (the clade including Placentalia and all stem relatives) jaw shapes, used as a proxy for dietary niche, during the Cretaceous angiosperm radiation (Grossnickle and Polly 2013) of the 'mid' Cretaceous supports a decrease in morphological disparity at that time. No change was detected in the disparity of lower molars across the end-Cretaceous mass extinction, however, suggesting that the variety of dietary ecology did not fundamentally change in the earliest Paleocene (Grossnickle and Luo 2014). However, a single trait – the shape of the second lower molar – as a proxy for total morphological disparity does not necessarily answer the question of how disparate organisms were when taken on its own. It may be a relatively useful measure for assessing changes in dietary niche specialisation, but many other ecological and life history traits have the potential to be selected for, or non-selectively made extinct, in the course of a mass extinction.

A recently developed method for assessing cladistic disparity using multivariate analysis of discrete characters provides an alternative, robust approach to measuring overall morphological disparity. Cladistic disparity takes a character-taxon matrix of n characters, and plots each taxon in an n-dimensional hyperspace. In unordered characters, differences between all states are considered to have a distance of 1, while in ordered characters, differences between states 0 and 2 would have a distance of 2 along that axis.

Broadly, there are two types of way to measure disparity. The first suite of methods assesses the variance of a sample, by calculating, for example, sums of variance or mean pairwise dissimilarity. This will measure the clustering of a sample, and allows an idea of how evenly spread across a morphospace the group of interest is. The alternative metric methods are range-based, where the total range, including outliers, of a group is assessed. Sums or products may also be used, for example, calculating the volume of the hyperdimensional polyhedron that encompasses all the data points within the group of interest. This lattermost technique has the advantage that all variation within the group is necessarily included, but this might not be informative if there are only a few extreme outliers. Variance-based metrics are generally more robust to sampling, but, as with many types of analysis, a combination of metrics allows a more fine-tuned reconstruction (Brusatte *et al.* 2012).

1(d) – *Biogeographical and climatic context*

Geographically and climatically, the world at 66 million years before the present was very different from today. The Mesozoic breakup of Pangaea had long since been completed – the contacts between the Gondwanan landmasses of Australia, Antarctica, Africa, India, Madagascar and South America having been lost by at least the Albian (Lawver *et al.* in press). Estimates for the degree to which the Atlantic had separated Africa from South America by 40 million years ago are approximately 1500 kilometres (Houle 1998), but in the early Cenozoic, Laurentia had only just begun to separate from Eurasia (Skogseid *et al.* 2000), providing a potential land route through North America connecting Africa and South America. India was completely separate from the rest of Gondwana by the middle of the Cretaceous, and did not collide with Eurasia until the end of the Paleocene (Aitchison *et al.* 2007). Europe was at the time a subtropical archipelago (Csiki-Sava *et al.* 2015), separated from the rest of Central and Eastern Asia by the Turgai Sea, which stretched from the Arctic Ocean to the north-western Tethys Ocean. The mid-west of North America was inundated by another epicontinental sea – the Western Interior Seaway (Boyd and Lillegraven 2011).

Temperatures were higher than the present day, and as a result, so were sea levels. The pattern of dispersal between continents has been suggested to have been more difficult as a result. Indeed, one line of reasoning which has been used in the past in support of an early divergence of Paleocene mammals has been the timing of the breakup of Pangaea, and more specifically Gondwana. As the four clades that comprise Placentalia appear to have evolved (or at least diversified) on separate continents – Xenarthra (sloths, armadillos, anteaters) in South America, Afrotheria (hyraxes, elephants, manatees, aardvarks, tenrecs, golden moles and sengis) in Africa, and Euarchontoglires (primates, tree shrews, flying lemurs) and Laurasiatheria (pangolins, cats, cows, whales, bats, shrews, moles, horses, and allies) in Laurasia – the vicariance of the continents has been suggested as a driver of placental speciation events. As the continents diverged approximately 135 million years ago (Jokat *et al.* 2003), this has led some people to conclude that the date of origin of Placentalia must have been early on in the Cretaceous (Wildman *et al.* 2007; Springer *et al.* 2011).

However, this is a naïve approach; continental breakup is likely to be a relatively minor force in driving biogeographical distributions in deep time (Upchurch *et al.* 2002; Sereno 1999). Long-distance dispersal is known in many clades, in particular from Africa to South America. Known dispersals that occurred well within the Cenozoic include caviomorph rodents (Antoine *et al.* 2012), primates (Poux *et al.* 2006), and even freshwater cichlids (Friedman *et al.* 2013), all of which are South American members of primarily African groups.

Close relatives of several northern crown orders are known from the southern continents, however. The cambaythere *Cambaytherium* from India has recently been suggested to be the closest relative of crown Perissodactyla (Rose *et al.* 2014), while analysis of protein sequences of subfossil material of some South American Native Ungulates (SANUs) have suggested that these enigmatic forms may also be more closely related to perissodactyls than any other extant order (MacPhee *et al.* 2014). With the popular and long-standing hypothesis of perissodactyl origins from the North American "condylarth" group Phenacodontidae (Radinsky 1966; Thewissen and Domning 1991), it appears that the biogeography of the late Cretaceous and Palaeogene was not necessarily a major impediment to dispersal and radiation on evolutionary timescales. Within the Cretaceous, Eutheria is primitively a Laurasian clade, but there is an example of a single genus of eutherian from the Late Cretaceous of India (Goswami*, et al.* 2011), again suggesting that the degree to which dispersal across continents was possible is more likely that the raw distances between continents might suggest.

1(e) – ***Review of placental mammal systematics***

1(e)(i) – *The extant placental tree*

The placental mammal phylogeny has undergone a significant rearrangement in the past two decades (Stanhope *et al.* 1998; Waddell *et al.* 1999b; Springer *et al.* 2004; Hallstrom *et al.* 2007; Hallstrom and Janke 2008; Nishihara *et al.* 2009; dos Reis *et al.* 2012; Hu *et al.* 2012; Morgan *et al.* 2013; Teeling and Hedges 2013; Asher 2007). Although the major patterns of relationships have been known for more than a century, the advent of ever-improving molecular sequencing techniques, as well as improved understanding of morphology (Asher *et al.* 2008), has overturned some of the traditional understanding of interordinal relationships within Placentalia. The majority of changes have occurred within two of the traditional groupings of placental mammals – Insectivora and Ungulata. Insectivora was a group comprising small, insectivorous mammals with generic dentition not far removed morphologically from the ancestral phenotype. It was largely considered to be the most basal of all placental orders, although questions had been raised over its monophyly (MacPhee and Novacek 1993). Molecular analysis confirmed that this group is polyphyletic, and in fact is composed of multiple extant and separate lineages, some of which are highly convergent in their adaptations, albeit to a relatively 'primitive' physiological condition (Madsen *et al.* 2001). Tenrecs, golden moles, and macroscelideans were grouped as Afroinsectivora, while the 'true' shrews, moles, and kin were regrouped as Eulipotyphla.

A similarly large change occurred in the group of 'hoofed' mammals – Ungulata. Superficial similarities had suggested that these largely cursorially adapted mammals were a single clade, but again, molecular evidence split the Paenungulata (elephants, sirenians, and hyraxes) from Perissodactyla (horses, rhinoceroses and tapirs) and Artiodactyla (camels, pigs, whales, deer, cattle, and so on). While it is not yet clear whether Artiodactyla and Perissodactyla represent sister clades in the larger grouping Euungulata, the separation of Paenungulata from these is now certain.

Paenungulata and Afroinsectivora make up the major groupings, along with Tubulidentata – the aardvark – of Afrotheria, a concept entirely novel in mammalian systematics and, until relatively recently (Tabuce *et al.* 2008), generated from genetic data alone. While efforts have been made to propose morphological synapomorphies for this clade (Sanchez-Villagra *et al.* 2007; Werdelin and Nilsonne 1999; Asher and Helgen 2010), it remains best supported by molecular data, which is unequivocal in that support.

The current understanding, then, of the relationships between extant placental mammal orders is known as the 'four clade' model, which posits four large superorders as the major divisions within Placentalia (Springer*, et al.* 2004). The first is the already mentioned Afrotheria, so-called because almost every member of this clade is endemic to Africa, with only the Indian elephant *Elephas maximus*, the manatees *Trichechus manatus* and *T. inunguis*, and the dugong *Dugong dugon* presently found elsewhere, although fossil distributions of proboscideans and hyraxes indicate a slightly more widespread distribution in the past.

The second group of placental mammals, Xenarthra, is today restricted to South America although some members of the clade have been present in North America since the Great American Biotic Interchange 2.5 million years ago (Webb 1991). Xenarthra consists of three orders – sloths, armadillos, and anteaters. Each share a variable number of vertebrae compared with the fixed numbers of the other superorders, each with characteristic xenarthrous processes, which act as additional articulation surfaces, as well as large, powerful forelimbs.

Thirdly, Euarchontoglires is a superorder which originally had support largely from molecular systematics. Prior to this, based on several morphological features, bats had been considered close relatives of primates and tree shrews, but molecular evidence unequivocally supports the exclusion of bats from the group formerly known as Archonta, which became Euarchonta as a result. Today, Euarchontoglires is the pairing of Glires, which contains Rodentia (mice, voles, guinea-pigs, squirrels, etc.) and Lagomorpha (rabbits, hares and pikas), with Euarchonta, which contains Primates (monkeys, lemurs, and apes), Dermoptera (flying lemurs or colugos) and Scandentia (tree shrews). The precise relationships between Scandentia, Dermoptera and Primates is unknown, with a Scandentia-Dermoptera (e.g. Nie *et al.* 2008) or a Dermoptera-Primates hypothesis (e.g. Waddell *et al.* 2001) considered to be the most phylogenetically plausible.

The final and largest grouping of placental mammals is Laurasiatheria, which comprises six diverse orders. Artiodactyla and Perissodactyla, the 'ungulate' grade orders, as well as Carnivora (cats, dogs, bears, seals, weasels etc.) and their probable close relatives Pholidota (pangolins) are four. Chiroptera (bats) are also part of this group, as well as the generically insectivorous clade Eulipotyphla. The topology of the orders within Laurasiatheria is a subject on which no consensus has yet been reached. In fact, from molecular information alone, more than 16 differing hypotheses have been proposed, depending on the dataset used, leading some to propose that the contradictory results from a variety of analyses is down to incomplete lineage sorting in early Laurasiatherian evolution.

The consensus of molecular sequencing of Laurasiatheria is that Eulipotyphla is the most basal clade within the superorder. Evidence supporting a Eulipotyphla-Chiroptera clade as the most basal group comes only from mitochondrial DNA (Nikaido *et al.* 2001), and the suggestion that Perissodactyla (perhaps with Carnivora) is the most basal group has resulted from some molecular analyses, but only very rarely (Madsen*, et al.* 2001; Madsen *et al.* 2002). Euungulata (Artiodactyla and Perissodactyla) is generally recovered as an internal clade within Laurasiatheria by molecular sequences, although evidence from protein sequences (Nishihara *et al.* 2006) support the grouping of the four orders Perissodactyla, Chiroptera, Carnivora and Pholidota as one, which has been called Pegasoferae. This is a rarely obtained topology in molecular systematics and has never been suggested by morphological techniques. The only resolution within the orders of Laurasiatheria that is well supported is the sister relationships of Carnivora to Pholidota to the exclusion of all other Laurasiatherian orders, although it is not clear how closely they are related with respect to putative fossil relatives such as palaeoryctidans, palaeanodonts, or creodonts.

The relationships between the four superorders also remain unclear. Three major hypotheses have predominated. Euarchontoglires and Laurasiatheria are generally agreed to be sister taxa in the grouping Boreoeutheria (Delsuc *et al.* 2002; Asher and Helgen 2010). Which of Boreoeutheria, Afrotheria, and Xenarthra are sister taxa to the exclusion of the other is unknown, as different datasets support different conclusions (Hallstrom*, et al.* 2007; Morgan*, et al.* 2013; Murphy *et al.* 2007; Teeling and Hedges 2013; Romiguier *et al.* 2013). Some have, once again, suggested that the relationships between the four superorders may never be resolved, suggesting that it is also a true hard polytomy (Hallstrom and Janke 2010). However, the nature of the fossil record means that a true hard polytomy is difficult to identify due to non-continuous sampling of populations. Molecular systematics identifies a hard polytomy when divergence appears to be simultaneous, due to the multiple speciation events that must take place to produce four lineages all occurring in a very short period of time, and therefore each preserving a mosaic of characters through incomplete lineage sorting, for instance in cordylid lizards (Stanley *et al.* 2011). Speculation is growing that phylogenetic networks may be a more valid model of organismal evolution and speciation than the traditional bifurcating tree (Bapteste *et al.* 2013), as the bifurcating tree cannot deal with evolutionary mechanisms such as incomplete lineage sorting, but such work is in an infant state at present, and has only been formalised for molecular data: the extent to which morphological data would be appropriate for such analyses remains unclear. Those phylogenetic network analyses which have been conducted on placental mammal origins indicate an exceptionally high level of conflict in the molecular data (Holland *et al.* 2005) suggesting that early placental mammal evolution was highly complex, and possibly also indicative of a sudden and rapid burst of speciation. Whether this pattern of speciation is typical of a response to a mass extinction, or of adaptive radiations in general, is not known.

The subsequent changes that occurred later in the tree are also obscured by the fact that, after the origin of the crown orders, the earliest definitive crown members of each superorder are already nested within extant orders. The earliest xenarthran, for example, is the highly derived armadillo *Riostegotherium*, known only from osteoderms (Figure 1.2) meaning that there is no clear definition of what a basal xenarthran would have looked like.

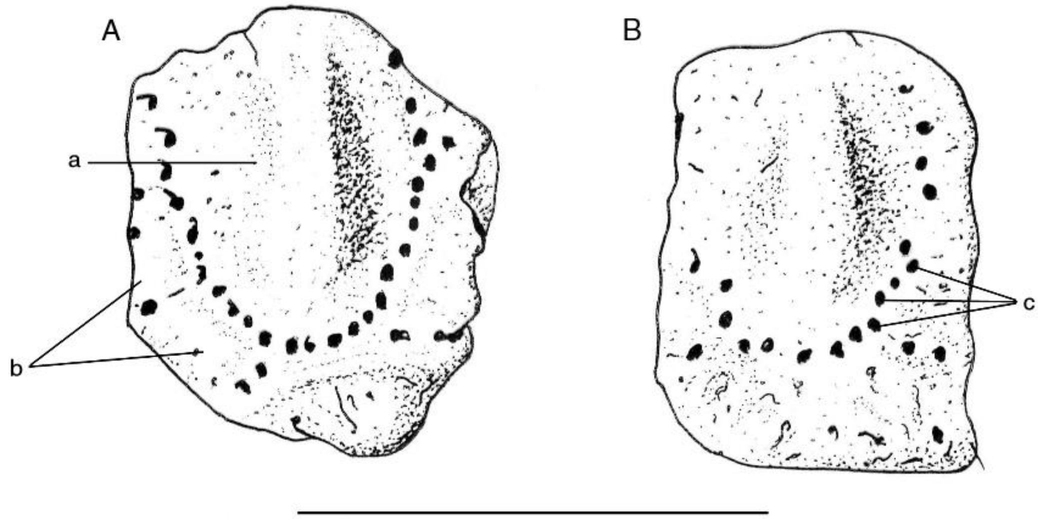


Figure 1.2 - The earliest known xenarthran, *Riostegotherium yanei*, an already derived dasypodid from the Late Paleocene, known from buckler (A, B), movable, and caudal osteoderms, with morphologies characteristic of Dasypodidae. Labelled above are the main figure of the osteoderms (a), peripheral figures (b) and a large number of pits (c). The last common ancestor of xenarthrans would not be expected to possess synapomorphies of dasypodids, and as a result, there is a gap in our understanding of the placental fossil record, and of character evolution in this superorder. Figure from Bergqvist *et al.* (2004), originally from Oliveira and Bergqvist (1998). Scale bar = 1cm.

Resolving the early evolution of placentals is precisely where information from Paleocene taxa is needed. While the majority of methods reconstruct the origins of the placental superorders as being in the Cretaceous, observing the patterns of features in the organisms of the Paleocene will potentially allow us to identify a lineage as being stem-Euarchontoglires, for example, which would provide a foundation for understanding the events and selection pressures that were in force during the last few million years of the Mesozoic and first few of the Paleocene. Moreover, if the origin of crown Placentalia was truly in the Paleocene, the earliest “condylarths” would represent the earliest known definitive placentals, and it would be possible to ascertain the early patterns of morphological evolution, given a knowledge of their phylogenetic relationships with earlier and later taxa. However, these relationships are far from clear.

1(e)(ii) – *Paleocene clades and grades*

By far the largest component of the mammalian biota in the Paleocene is the collection of 'archaic ungulates' known as 'condylarths'. While this grouping is almost certainly an anachronistic grade of largely terrestrial, bunodont, herbivorous to omnivorous mammals, there are several well-defined families which fall within "Condylarthra".

Arctocyonidae

Supposed relationships

The arctocyonids are a primarily European group (Russell 1964) which has variously been considered ancestral to Carnivora (Van Valen 1969), to specifically miacid carnivorans (see Van Valen 1978), to artiodactyls (Rose 1996), and as part of the ancestral ungulate group (Kondrashov and Lucas 2004; De Bast and Smith 2013). Arctocyonidae was one of the two groups (the other being Oxyclaenidae) that was assigned to the most primitive groupings of 'archaic ungulate' – the Procreodi – by Matthew (1915). Simpson (1937) preferred to amalgamate Oxyclaenidae and Arctocyonidae, the latter taking precedence as the name for the whole group. McKenna and Bell (1997), however, placed Arctocyonidae within Procreodi once more, and divided the family into three main subgroups – the Arctocyoninae, Loxolophinae, and Oxyclaeninae. Some debate has concerned whether the particularly primitive but ungulate grade organism *Protungulatum*, excluded from Arctocyonidae by Prothero, Manning and Fischer (1988), should be included within the family.

Composition

The Arctocyonidae includes some of the best known of the 'archaic ungulates', such as the type species *Arctocyon primaevus*, discovered in 1841 (de Blainville 1841), and the arboreal mammal *Chriacus*. Other genera include *Mentoclaenodon*, *Lambertocyon*, *Thryptacodon*, *Anacodon*, and *Claenodon*. It has been disputed whether *Claenodon* is considered a separate genus in its own right (Rose 1981), a synonym of *Arctocyon* (Rigby Jr. 1980), or a synonym of *Arctocyonides* (Van Valen 1978). Some recent studies (Williamson and Carr 2007; De Bast and Smith 2013) have hinted that the subfamilies of Arctocyonidae may be polyphyletic, with the Oxyclaeninae occurring at the base of crown placentals (although all taxa sampled in those analyses are certain or probable laurasiatheres), Arctocyoninae as a sister group to the Mesonychia and Triisodontidae, and Loxolophinae closest to a broader clade comprising ancestors of Artiodactyla and Perissodactyla. According to De Bast and Smith (2013), arctocyonids have "been used as a wastebasket for basal condylarths"; making arctocyonids particularly enigmatic, as the general consensus is that "Condylarthra" is itself a wastebasket taxon (Archibald 1998).

Ecology

The species *Arctocyon primaevus* was originally described as being aquatic (de Blainville 1841), and has been hypothesised as being variously terrestrial (Russell 1964), fossorial (Kondrashov 2009), and scansorial-arboreal (Argot 2013) by subsequent authors. More consistent in interpretation, *Chriacus* is considered to be arboreal (Rose 1987) on the basis of features of its tarsal bones, among others. The climbing of *Chriacus* is largely inferred from various skeletal features of the almost complete postcranial specimen USGS 2353, which includes all but portions of the femur and a number of vertebrae (Rose 1987). The shape of the acromion process in *Chriacus*, combined with the extensive deltopectoral ridge of the humerus is indicative of powerful forelimb musculature, and the presence of large forefeet with curved claws suggests either climbing or burrowing ability. Comparisons may be made between the humerus of *Chriacus* and that of various arboreal carnivorans such as the coati, civets and red pandas (Rose 1987). There is a great diversity of locomotor styles within Procreodi/Arctocyonidae; it has been suggested that some members of the group – *Arctocyon mumak* and *Anacodon* – may be semifossorial, based on morphological features of the astragalus (Gould and Rose 2014). In general, the arctocyonids possess teeth adapted for some degree of carnivory, even if it is not as extensive as that displayed by the creodonts and true carnivorans, lacking as they do any specialised shearing carnassials. Often present are large canines, and the premolars are relatively sharp, but the molars are bunodont, suggesting a largely omnivorous dietary niche.

Periptychidae

Periptychid condylarths are characterised by highly bunodont, square molars which are of roughly equal size along the tooth row. They are represented by several North American genera, such as *Periptychus*, *Anisonchus*, *Ectoconus*, and others, and, in the case of *Periptychus*, among the earliest of known crown placental mammals (Lofgren *et al.* 2004; Prothero 1998). They first appear in the San Juan Basin as immigrants (Clemens 2010; Wilson 2014) at approximately 500,000 years after the end-Cretaceous mass extinction event, and are, as a result, usually thought to be basal among "condylarths" (Prothero 1994).

Composition

Periptychidae is composed of the subfamilies Periptychinae, Anisonchinae, and Conacodontinae (Archibald *et al.* 1983), the latter of which comprises *Conacodon* and *Oxyacodon*. According to Archibald and colleagues (Archibald*, et al.* 1983), the most "primitive" periptychid is *Mimatuta*, although Van Valen (1978) recognised five lineages of periptychids and suggested that they all descended directly from *Protungulatum*, the Cretaceous-Palaeogene proto-ungulate grade eutherian.

Hyopsodontidae

Hyopsodontid condylarths are one of the most widespread groups of archaic ungulate. They are found from the Middle Paleocene, with the earliest representatives found across North and South America. Eocene representatives are known from Europe and Asia, and they are a remarkably cosmopolitan group until they disappear during the Eocene (Hooker and Dashzeveg 2003). That such a globally distributed group to be lost in the absence of clear global climatic change (for instance, they survive the PETM very well), has led to suggestions that they are perhaps ancestral to a modern group.

Depending on interpretation, Hyopsodontidae is synonymous with Mioclaenidae (Williamson and Weil 2011); other authors prefer Mioclaenidae to be an entirely separate group, an interpretation backed up with some cladistic evidence (Ladevèze *et al.* 2010), although both groups were represented by only a single genus, and the sample size of the entire analysis was not sufficient to draw an informed judgement on the relative positions of the "condylarth" lineages.

Ecology

The type genus, *Hyopsodus* is primarily Eocene, and is found across all Laurasian land masses. Analysis of the braincase of *Hyopsodus lepidus* has indicated that possessed strong abilities to accurately detect the positions of acoustic stimuli, due to an enlarged inferior colliculus. This has been interpreted as implying an ability to echolocate in a similar way to some burrowing and nocturnal shrews and tenrecs (Orliac *et al.* 2012a). However, because the postcranium of *Hyopsodus* is not strongly adapted for digging, and as the genus is more usually reconstructed as a scansorial herbivore (Williamson and Lucas 1992), the more likely interpretation is of at least a nocturnal habit, although some digging ability – as well as the possibility of living in vacated burrows – cannot be discounted.

Supposed relationships to extant taxa

Hyopsodontids are typical of the archaic ungulate families in that they have been considered ancestral to many different groups of ungulate grade mammal.

Traditionally, they were considered to be early ancestors of artiodactyls (Simpson 1937; Schaeffer 1947), but later hypotheses have placed them with either afrotheres – whether hyracoids (Godinot *et al.* 1996) or macroscelideans (Tabuce *et al.* 2001), as well as the enigmatic South American ungulates (Cifelli 1983; de Muizon and Cifelli 2000). The characters that have linked hyopsodontids to these large variety of clades are mostly dental, although in the case of the macroscelidean relationships, this depends on the assumption that apheliscid "condylarths" fall within Hyopsodontidae, and is supported for the most part by the morphology of the tarsals. Since both teeth and tarsals have morphologies that are highly tied to their ecology (diet and locomotor ability respectively), the conflicting evidence suggests that hyopsodontids are convergent in one or both of these regions. This is problematic when there is little in the way of postcranial remains of hyopsodontid "condylarths".

Pleuraspidotheriidae

Pleuraspidotheriidae is a small group sometimes placed within Meniscotheriidae, Hyopsodontidae or Phenacodontidae, and recently affined to the early arctocyonids. It is exclusively found in Europe, mainly in northern France and Belgium, and consists of three genera – *Pleuraspidotherium*, *Orthaspidotherium* and the enigmatic Turkish fossil *Hilalia*. Their basicranial morphology is similar to that of the early artiodactyls such as *Gobiohyus*, their teeth resemble the previously mentioned "condylarth" groups, and their tarsal morphology is basal in appearance, with little in the way of unambiguous synapomorphies. Preservation of the two better known genera is very good, with an almost complete skeleton known for *Pleuraspidotherium*, and a complete skull with assorted postcranial material known for *Orthaspidotherium*. Ladevèze *et al.* (2010) hypothesised that Pleuraspidotheriidae are closest relatives to arctocyonids such as *Chriacus*, in a group also including the basal artiodactyls, but the taxonomic sampling was very low, and only very few representatives of each supposed group were present.

The pseudohypocone that characterised the square molars of the Pleuraspidotheriidae mark the difference between this morphology and the superficially similar molars of perissodactyls (Ladevèze*, et al.* 2010).

Since the majority of the "condylarth" material has been collected from North America, or are parts of families that are present in North America with representatives elsewhere, the phylogenetic position of a clade from another continent is of interest when considering biogeographic questions regarding the origin of the modern orders.

Phenacodontidae

Phenacodontids are superficially similar to the modern groups of ungulate mammals, with a herbivorous diet, and generalised, often slightly cursorial limbs, especially in more derived forms (Thewissen 1990). The forelimbs of *Tetraclaenodon* has been described as having features associated with both terrestriality and climbing, although these attributes are weakly developed, and it has been suggested that *Tetraclaenodon* behaved in such a way that it was facultatively terrestrial, but able to scale trees for food or safety (Kondrashov and Lucas 2012). This hypothesis is borne out by the morphology of the hind limb, which is far more specialised for terrestriality, though not cursoriality (Kondrashov and Lucas 2012).

Like the apheliscid "condylarths", phenacodontids have been suggested to be closely related to afrotherian and laurasiatherian orders. In particular, Phenacodontidae was resolved by Tabuce *et al* (2001) as being part of a clade comprised of Paenungulata, Phenacodontidae and Perissodactyla. While Perissodactyla is certainly not related to

Paenungulata, being consistently resolved as being in a totally different superorder by modern molecular methods, Phenacodontidae represent the phenotype that was previously thought to link the two groups ancestrally. It is not clear whether support for the affinity was driven largely by one order or another, but it is difficult to extract the true signal from a set of largely convergent characters related to similar dietary adaptations.

Morphology

Phenacodontids share a number of identifying synapomorphies of the dentition and postcranium. The third trochanter on the femur is a cursorial adaptation, as is the weakening of the deltopectoral crest of the humerus. Upper molars are bunodont and square, with the presence of a hypocone being relatively derived. Lower molars, however, are reduced in the number of cusps, with the paraconid having been lost.

Mioclaenidae

Mioclaenidae are a little known group of archaic ungulates considered by some to be a subgroup or synonym of Hyopsodontidae (Williamson and Weil 2011). Originally erected as a monospecific family (Osborn and Earle 1895), it includes several taxa from across North America and Europe, as well as a few in South America. Those that subscribe to this viewpoint place all the mioclaenid genera in the subfamily Mioclaeninae (e.g. Zack *et al.* 2005b). Regardless of phylogenetic topology, then, the mioclaenids are considered by all to be a clade. The most recent summary of Mioclaenidae was a reanalysis of two genera – *Bomburia* and *Ellipsodon* – by Williamson and Carr (2007), where the family was rediagnosed as "Ungulate with P4 metacone absent, upper molar postcingulum continuous with metastyle, lower molar metaconid nearly lingual to protoconid, ratio of m3 Length/m2 Length between 0.9 and 1.1". Lack of a metacone aside, these traits are relatively primitive for a large number of groups of "archaic ungulates" (see Prothero*, et al.* 1988).

Other non-ungulates

Outwith the condylarths, there are several other controversial and enigmatic mammal groups represented by Paleocene and Cretaceous fossils. These include two groups, Leptictida and Cimolestidae, variously considered to be stem to the placental lineage, or ancestral to an extant order or group of orders. Both show relatively basal general morphology, but are specialised in ways that have led researchers to debate whether they are part of another group.

Leptictida

The leptictids are one of the few orders of mammals to definitively cross the K-Pg boundary. A few representatives from the Cretaceous, such as *Gypsonictops*, hint at an early branching from the placental mammal tree, although some analyses have preferred to place them within the crown (Meehan and Martin 2010; Kielan-Jaworowska *et al.* 2004). Leptictida, then, are one of the key groups for understanding the timescale of placental evolution. Their presence on both sides of the K-Pg boundary means that, were they to fall well within the placental radiation, it would provide conclusive proof of the early rise of placental mammals. Conversely, a basal position would hint at, but not prove, that the interordinal radiation of placental mammals occurred after the K-Pg mass extinction event.

Leptictida are a specialised Laurasian group, occurring throughout northern North America from the Cretaceous to the Oligocene, with four isolated examples – the Mongolian *Praolestes*, French *Pseudorhynchocyon*, German *Leptictidium*, and a Spanish *Leptictis* – from the Eocene of Europe and Paleocene of Asia. Of these four genera, only *Leptictis* is found elsewhere. They are characterised by their long hind limbs, superficially resembling jerboas and sengis, although this is probably entirely convergent.

The order Leptictida consists of three families – Gypsonictopidae, a monogeneric family containing only *Gypsonictops*; Leptictidae, consisting of several North American genera, and Pseudorhynchocyonidae.

Supposed relationships

The initial discovery of *Leptictis haydeni* was in outcrops of the White River Formation in Dakota, identified along with *Ictops dakotensis* (now known as *Leptictis dakotensis*) as two genera of "insectivorous mammals, which appear to be peculiar, but related to the hedge-hogs" by Joseph Leidy (1868). Leidy placed them within the order Insectivora, and they were first identified as a separate family with the name Leptictidae by Gill (1872).

Leptictida was first identified as a valid order in its own right by McKenna (1975), in which it was proposed to be a clade of crown-group placental mammals with unclear affinities, whose closest relatives were the Kennalestidae. In McKenna and Bell (1997), Leptictida is a diverse assemblage of mammals including as members several suborders of Cretaceous mammals, with genera such as *Zhelestes*, *Gypsonictops*, *Lainodon* and *Gallolestes*, as well as the kennalestids themselves, previously excluded as a sister taxon. There was also included the traditional leptictid forms such as *Prodiacodon* and *Leptictis*, as well as the first appearance of the European Pseudorhynchocyonidae. This large assemblage of ecologically diverse mammals would be a group seemingly little affected by the K-Pg mass extinction; in terms of raw count of genera, the number either side of the boundary is roughly equal.

However, in revision the membership of the Leptictida, and in further refining our understandings of the relationships between the Cretaceous mammals, further study in the 21st century has defined Leptictida as a more restricted group. Archibald *et al.* (2001) provided some evidence that *Gypsonictops* was part of a separate group from

Zhelestes and its kin, implying that the concept of Leptictida as it then stood was not a biologically realistic one. In that study, both clades were found to be crown placental mammals, with *Gypsonictops* closer to Glires, and *Zhelestes* to Ungulata (represented in this case solely by *Protungulatum*, whose placement as a crown ungulate is questionable). Kielan-Jaworowska *et al.* (2004) maintained the presence of Gypsonictopidae in Leptictida, but considered that Leptictida was, as had originally been suggested, within Insectivora, as a sister group to Lipotyphla. Gypsonictopidae also was rendered smaller, removing *Zhelestes*, as well as other forms previously allied to Leptictida such as *Lainodon* into the new and separate Zhelestidae, which here was a subgroup of Ungulatomorpha, well within the crown of placental mammals.

Wible *et al.* (2007; 2009) further modified the position of Leptictida. Here, rather than being a crown-group placental mammal, *Leptictis* and *Gypsonictops* were placed at the crownward end of the placental stem, more derived than Zalambdalestidae but less than *Protungulatum*. Meehan and Martin (2010), however, favoured inclusion of Leptictida in 'Insectivora', which is largely an abandoned clade thanks to evidence from molecular data. They noted that the morphology of leptictidans was highly convergent to that of extant macroscelideans, due to similar ecological specialisations to insectivory, digging, and salutatory locomotion.

Recently, the subgroup of Leptictida *sensu* McKenna and Bell (1997), the European Eocene-Miocene Pseudorhynchocyonidae, has been found to be a separate lineage from Leptictida entirely, the latter being closer to Palaeanodonta and Pantodonta (Hooker 2013). However, the presence of *Gypsonictops* as an outgroup means that this topology, if left unrooted, is entirely consistent with a monophyletic Leptictida to the exclusion of the latter two clades, rather than making the *a priori* assumption that *Gypsonictops* was not a member of Leptictida, contrary to general findings.

The membership of Leptictida, therefore, has been largely settled on, but the precise position of their relationships to extant orders of mammals remains under question, and they occupy a crucial position in the temporal story of eutherian mammal evolution.

Cimolestidae

The cimolestids are a second group whose phylogenetic placement should inform strongly on the date of origin of the major clades of placental mammals, since they too are hypothesised to occupy a variety of phylogenetic positions, as well as crossing the K-Pg boundary. It is a bone of contention whether the Pantodonta are part of this clade (see differences between McKenna and Bell 1997; Wible*, et al.* 2007), but even excluding the pantodonts, the cimolestids are a highly diverse and probably monophyletic lineage (Archibald 2011).

Five species of *Cimolestes* (*C. magnus, C. cerberoides, C. incisus, C. stirtoni,* and *C. propalaeoryctes*), as well as *Batodon tenuis* and *Maelestes gobiensis* are found in the Cretaceous – the former two in North America, and the latter in Mongolia, spanning the Judithian and Lancian North American faunal stages (83.3–65.5 Ma). Of these, *Cimolestes* is unusual in that it is a genus spanning the K-Pg boundary, and is found in the Puercan of North America, equivalent aged rocks in Bolivia, and the Thanetian of Morocco. Nonetheless, it must be pointed out that the monophyly of *Cimolestes* has at times been questioned, such that the Paleocene and Cretaceous forms of *Cimolestes* may not be monophyletic, with some concluding that Carnivora and Creodonta were derived from different species of *Cimolestes* (McKenna 1975; Lillegraven 1969). For the purposes of this study, and lacking any conclusive evidence as regards the monophyly or otherwise of *Cimolestes*, all species assigned to this genus have been considered to truly represent *Cimolestes*, and are coded into the same terminal.

By the earliest Paleocene, the group has diversified to include the South American *Alcidedorbignya*, and the Laurasian *Puercolestes*. Some also include the Paleocene taxon *Procerberus* in the cimolestid lineage, although *Procerberus* is also considered to be a very basal eutherian by many, and still others favour a relationship with Carnivora and close relatives.

Considering *Procerberus* as a stem eutherian mammal need not necessarily remove *Procerberus* from the cimolestids, however, as evidence has suggested that cimolestids might be a group of stem placental mammals as well, although others have likened them to the hypothesised ancestors of modern carnivorans and creodonts. Since Carnivora is a group nested well within crown Eutheria, the placement of Cimolestidae is one which impinges strongly on the timescale of placental diversification. If Cimolestidae are indeed closer to Carnivora than to many other Laurasiatherian groups, this would prove that the diversification of the placental mammal lineages occurred at least before the earliest cimolestid material, which is from the Middle Campanian Foremost Formation (approximately 80Ma), probably significantly earlier. If, however, Cimolestidae are shown to be basal to crown Eutheria, along with the other clades that originate in the Cretaceous, it would be strongly suggestive of a Paleocene diversification event within placental mammals.

Anatomical features consistent with a basal position include the presence of an unusual morphological trait – the prootic canal – found only in Asioryctitheria, Zhelestidae and Cimolestidae. Since both Asioryctitheria are uncontroversially Cretaceous stem placental mammals, it is not unreasonable to suppose that Cimolestidae are also close to the base of placental mammals. Within Eutheria, only *Solenodon* possesses a prootic canal, which appears to be a result of convergence (Wible*, et al.* 2009).

Ecology

Cimolestids have in general been considered to have incipiently carnassial teeth (Rana and Wilson 2003), and as such have been inferred to be faunivorous, if not carnivorous. Indeed, it is the dental similarities that have led to the attribution of this group to the stem of Carnivora. The presence of steep shearing wear marks on the molars of cimolestids (Butler 1972) illustrates that their teeth were capable of slicing actions, and thus adapted for this diet, but this would be convergent with Carnivora if they are resolved as members of the placental stem.

Cimolestids are relatively primitive in their postcrania, and, like the majority of Cretaceous mammals, their ankle bones reveal that they were adapted for a scansorial existence (Szalay and Decker 1974).

Pantodonta

The pantodonts, for the purposes of this introduction, are considered separately from the Cimolestidae, although they are considered a suborder in McKenna and Bell (1997). Superficially, pantodonts are distinct from the majority of the rest of the supposed cimolestids, being large, ground-dwelling and herbivorous, as opposed to small, scansorial, and carnivorous or insectivorous. Additionally, this classification is a departure from the more traditional interpretations of being related to either an assortment of unusual South American ungulates or being related to Paenungulata – the Afrotherian lineage including proboscideans, sirenians and hyracoids. They appear in the Early Paleocene, with a largely global distribution, and survive to the Middle to Late Eocene, whereupon they become extinct approximately 33 Ma.

Pantodonts include some of the largest terrestrial mammals of the period – the coryphodontids – enormous rhinoceros-like herbivores which lived from the Arctic to the southern edge of North America (Dawson 2012), as well as in the Palaeogene of eastern Asia (Ting *et al.* 2003). They are extremely common components of North

American Eocene faunas, being common enough to be a stratigraphic indicator for several North American Land Mammal Ages (NALMAs), and have smaller representation throughout the Paleocene.

Arctostylopidae

Little is known of the enigmatic North American and East Asian group Arctostylopidae. The most recent review of their systematic relationships was in 1989 (Cifelli *et al.* 1989), with little progress since then. At that time, they were considered to be possible relatives of lagomorphs. All genera but *Arctostylops* itself are Asian. Cifelli and Schaaff (Cifelli and Schaff 1998) summarised the ecology of the group as being small herbivores – the taxon is known for lophodont dentition with reduced cones and conids, but prominent stylar cusps and lophs.

Creodonta

Composition and relationships

The status of Creodonta has long been considered controversial, and the precise composition of the group has changed radically across the history of the literature. Originally described as a group within "Insectivora" (Cope 1884c), Creodonta has been through several iterations, including being related to mesonychians, arctocyonids, carnivorans, palaeoryctids, and even briefly being abandoned as a group completely (for a summary, see Gunnell and Gingerich 1991). While there has been considerable confusion over what defines a creodont (Polly 1994; Morlo *et al.* 2009), the consensus today is that Creodonta is likely a close relative of, although not ancestral to, Carnivora .

Whether the two major groups within Creodonta – Oxyaenidae and Hyaenodontidae – are sister taxa to one another (in other words, whether Creodonta can be considered monophyletic) is not clear (Zack 2011; Morlo*, et al.* 2009). Indeed, their affinity with Carnivora has been suggested to be an artefact of convergent evolution – the superficially similarly shaped carnassial teeth are, developmentally, different teeth (Van Valkenburgh 1999), suggesting that Carnivora could not have evolved directly from a creodont without significant rearrangement of the developmental programmes.

Ecology

Prior to the origin of Carnivora, creodonts are the most well adapted placental mammals to carnivory, with some members of the group achieving a hypercarnivorous state (Stucky and Hardy 2007). Members of Creodonta can be considered analogues of several carnivoran clades, with examples of dog-like, civet-like, and cat-like forms (Van Valkenburgh 1999). The ecological niches exploited by Creodonta are similar enough to Carnivora that hypotheses of competitive exclusion have been invoked to explain the eventual replacement in ecosystems of the one by the other (Wesley-Hunt 2005).

Mesonychia

An enigmatic group of "archaic ungulate", often considered separate from the "condylarths" are mesonychians. The giant mammal *Andrewsarchus*, the largest terrestrial carnivorous mammal of all time, has historically been considered to be a mesonychian. However, a competing hypothesis that *Andrewsarchus* may in fact be an entelodont artiodactyl is gaining traction.

Mesonychians were considered, on the basis of shared simplification of the dentition, to be related to whales, but this hypothesis was overturned by the discovery of early whale postcrania (Thewissen *et al.* 2001), cementing the position of Cetacea within Artiodactyla, separate from mesonychians.

Apart from a few mesonychians such as *Hapalodectes*, which lack specialised running features of the humerus (O'Leary 1998), mesonychians have been described as having an ecological niche similar to wolves – that of a cursorially adapted predator (O'Leary and Rose 1995).

South American Native Ungulates (SANUs)

The placental fauna of South America, with the exception of the native Xenarthrans and later invasions of African and North American groups, include three to five orders of ‘ungulate’. These orders – Xenungulata, Notoungulata, Litopterna, and, if they are considered separate, Pyrotheria and Astrapotheria – are highly enigmatic with respect to their relationships with extant placental orders. They first appear in South America during the Paleocene, and were extant until only a few thousand years ago.

Although some hypotheses have suggested that SANUs are more closely related to Afrotheria (Agnolin and Chimento 2011), or descended from “condylarths” (de Muizon and Cifelli 2000), recent analysis of protein sequences from subfossil material (Welker *et al.* 2015) has indicated that the closest extant relatives of both Notoungulata (represented by *Toxodon*) and Litopterna (represented by *Macrauchaenia*) are Perissodactyla. As morphological analyses have been inconsistent in terms of the relationships of these unusual taxa, this particular topology opens many biogeographical questions.

Ecologically, the SANUs are remarkably diverse, with analogues of several artiodactyl and perissodactyl clades, most clearly emphasised in the similarity between litopterns, artiodactyl camelids, and perissodactyl equids (Bond *et al.* 2006). It is their especially derived morphology and geographical isolation that presents problems when determining their closest relatives, despite a relatively good fossil record from the Late Paleocene onwards.

1(e)(iii) – Earliest members of extant placental clades

Afrotheria (elephants, hyraxes, aardvarks, manatees, tenrecs, sengis, golden moles)

The earliest afrotherians to be known from the fossil record are found in the Middle Paleocene. The species *Ocepeia daouiensis* is known from the Selandian (61.6-59.2 Ma) of Morocco, and appears to show a mosaic of characters which suggests that it is close to the divergence of Paenungulata and Afroinsectiphilia (Gheerbrant *et al.* 2014). Its presence in Africa during this time suggests that Afrotheria arose, or at least initially diverged, in Africa, in contrast to some hypotheses which have suggested that at least some afrotherian groups arose in North America (Zack *et al.* 2005a).

Xenarthra (sloths, anteaters, armadillos)

The location and phylogenetic affinities of the earliest xenarthran is disputed. The earliest members of the crown group that is not disputed are *Riostegotherium* and some xenarthran remains of unknown affinity from the Late Paleocene Itaborai Formation of Brazil (Bergqvist*, et al.* 2004). More controversial is the inclusion of the Asian Paleocene genus *Ernanodon* (Ding 1987), supposedly part of the suborder Ernanodonta (McKenna and Bell 1997). This is in part because it is in a completely different continent from the rest of the superorder, with the exception of the other Guangdong putative xenarthran, *Asiabradypus*, which was considered by Rose and colleagues (Rose *et al.* 2005) to be an animal of unknown affinity, "irrelevant to xenarthran origins". Aside from the biogeographical oddity, xenarthrans have historically been grouped together on the basis of simplistic characters such as a lack of teeth, rather than on a large number of positive characters, with the exception of the additional articulations of the vertebrae which characterise them as xenarthrous, and a variable vertebral number. No clear affinity with typical xenarthran characters has been definitively shown for *Ernanodon*, and Gaudin (1999) suggested that the articulations of the vertebrae of *Ernanodon* “only vaguely resembles that characteristic of most true xenarthrans”.

Euarchontoglires (rodents, rabbits, primates, tree shrews, flying lemurs)

Rodentia

The earliest definitive rodents are known from the Paleocene of North America, with *Tribosphenomys* as a close outgroup to Rodentia (Meng and Wyss 2001) and *Paramys*. If anagalids are considered rodents, *Heomys* is of equivalent age, but in East Asia (Li 1977). Both are known entirely from tooth fragments, but contain crucial synapomorphies that allow identification to their respective positions. Both have the definitive rodent pattern of a single pair of continuously growing incisors with enamel only on the anterior edge.

Primates

While there are no definitive crown primates in the Paleocene, there is strong evidence of the presence of plesiadapiforms. These are considered by most to be ancestral to primates, and are arboreal specialists, consistent with the interpretation of many primate features as adaptations for an arboreal lifestyle – grasping hands, good depth of vision, and so on. Among more definite plesiadapiforms, one controversial genus is *Purgatorius*. This is considered to be plesiadapiform based on teeth, and recently, tarsal material. However, its relationships to modern forms has also been controversial, with some analyses reconstructing *Purgatorius* outwith crown eutheria, as a stem placental. If the Cretaceous Indian genus *Deccanolestes* is, as some have suggested, closely related to nyctitheres (Hooker 2001), and if nyctitheres are euarchontan (Hooker 2014), then *Deccanolestes* would represent a Cretaceous example of a euarchontan. However, *Deccanolestes* has been shown to be more closely related to asioryctitheres (Goswami*, et al.* 2011), and nyctitheres appear to be closer to eulipotyphlans (Manz *et al.* 2015).

Laurasiatheria (cats, pangolins, shrews, moles, bats, horses, cattle, deer)

Carnivora (cats, dogs, bears, otters, badgers, mongooses)

The earliest major groups of carnivorans – the families Miacidae and Viverravidae – are both known from the Paleocene. Earlier than these, though, are the genera *Ravenictis* and *Pristinictis*, which are from the earliest Paleocene (Fox and Youzwyshyn 1994). These earliest forms have relatively unspecialised molars, suggesting a generalised omnivorous diet with only limited specialisation to true carnivory, though *Pristinictis* has been considered a primitive member of the near-crown group Viverravidae.

Diversification into the major two groups of extant carnivorans – caniforms and feliforms – occurred in the Eocene, but the precise timing is dependent on the phylogenetic position of some enigmatic members of the miacid carnivorans (Tomiya 2011).

Pholidota (pangolins)

Pholidotans are known from the middle Eocene of Europe, being represented by the two genera *Eomanis* and *Eurotamandua* (although the latter was originally considered to be a xenarthran) from the Messel Pits of Germany (Rose*, et al.* 2005; Storch 1978). Already relatively derived, a relationship with the Paleocene palaeanodonts has been proposed (Gaudin *et al.* 2009; Rose 1999a).

Eulipotyphla (shrews, moles, hedgehogs, Solenodon)

Eulipotyphla are the remnants of what once was “Insectivora”, the basalmost clade of placental mammals from which all others were supposed to have derived. Now recognised as a derived group, if morphologically plesiomorphic, the split between Eulipotyphla and Scrotifera (non-eulipotyphlan laurasiatheres, including bats, cats, horses, whales, and pangolins) is generally considered to be the basalmost division within Laurasiatheria (Zhou *et al.* 2012; Nishihara*, et al.* 2006; Waddell *et al.*

1999a), although some earlier molecular analyses support a sister relationship between Eulipotyphla and Chiroptera (Onuma *et al.* 2000). Combined morphological and molecular analyses have been consistently able to distinguish the 'true' insectivores – which comprise moles, shrews, hedgehogs and kin – from the African insectivores – elephant shrews and tenrecs , now known to be members of Afrotheria.

If nyctitheres are eulipotyphlans, as appears to be the case (Manz*, et al.* 2015), the earliest eulipotyphlans in the fossil record are earliest Paleocene nyctitheres such as *Leptacodon* (Van Valen and Sloan 1965), with putative but controversial members of the group in the latest Cretaceous (Antunes *et al.* 1986). Other than nyctitheres, the first eulipotyphlans known from the fossil record are from the Late Paleocene, by which time some division into the erinaceids and soricids had taken place (Rose 1981).

Chiroptera (bats)

The first bat fossils are of already relatively derived bats from the Green River Formation of the Early Eocene of Wyoming – *Onychonycteris finneyi* (Simmons*, et al.* 2008) and *Icaronycteris index* (Jepsen 1966). Morphologically, they were capable of true flight, but unable to echolocate (Simmons*, et al.* 2008). Other dissimilarities with modern bats include a relatively large tail, and, in the case of *Onychonycteris*, the presence of claws on all forelimb digits. No earlier fossil material is attributable to either the crown or stem of bats, making their origins difficult to determine.

Perissodactyla (horses, rhinoceroses, tapirs)

The earliest perissodactyls are also known from the early Eocene. Of the five main clades of Perissodactyla – Equidae (horses), Tapiridae (tapirs), Rhinocerotidae (rhinoceroses), Brontotheriidae, and Chalicotheriidae – all are known in the earliest Eocene with superficially similar, small, browsing forest-dwelling (Eberle *et al.*

2014) forms. The earliest equid, *Hyracotherium*, underwent a dramatic taxonomic revision (Froehlich 2002)(Froehlich 2002)(Froehlich 2002)(Froehlich 2002)(Froehlich 2002)(Froehlich 2002)(Froehlich 2002), with the separation of the genus once more into a multitude of new (and resurrected) genera. Tapirs and rhinoceroses, which are monophyletic to the exclusion of equids (Froehlich 1999), are also present in the earliest Eocene, represented by *Heptodon* (Radinsky 1965) and *Hyrachyus* respectively. *Heptodon* is known primarily from the earliest Eocene of North America, which is where the majority of perissodactyl evolution occurred, although there are reports of the genus from China (Chow and Li 1965). *Hyrachyus* is known from the earliest Eocene of Europe and Asia, but has also been reported from the Caribbean (Domning *et al.* 1997). Along with all these members of the perissodactyl families are early members linking the lineages, such as *Mesolambdolophus setoni*, which appears to be close to the base of the tapiromorphs (Holbrook and Lapergola 2011).

No perissodactyls are known from the Paleocene or earlier, with some group of “archaic ungulate”, probably phenacodontid “condylarths”, generally supposed to be close relatives.

Artiodactyla (cattle, sheep, deer, giraffes, antelopes)

Artiodactyls are another of the extant orders whose first members appear at the base of the Eocene (Rose 1996), with the basal group Dichobunidae, a speciose northern hemisphere group whose best known member is the genus *Diacodexis*, which is represented by near complete specimens (Orliac *et al.* 2012b; Rose 1982b). *Diacodexis* is known from layers immediately above the Paleocene-Eocene boundary (Smith *et al.* 1996), and was a cursorial animal capable of high speeds and agile turns, as evidenced by the morphology of the semicircular canals (Orliac*, et al.* 2012b) and postcranium (Rose 1982b).

1(f) – Aims and objectives of the thesis

The story of the evolution of the modern orders of placental mammals is currently unknown. Several hypotheses of relationships between the ancient and modern orders have been proposed, but none has been without significant debate.

Breaking the polyphyly that is currently the state of Paleocene mammal phylogenetics is a crucial task, as it will enable future studies to be conducted on a wide variety of macroevolutionary topics, such as biogeography, patterns and rates of character evolution, and so on.

This thesis comprises four analyses that reconstruct the relationships and early evolution of placental mammals, in order to answer several questions.

1) What are the relationships among Cretaceous eutherians, Paleocene eutherians, and modern placental clades? I conducted the largest phylogenetic analysis of Cretaceous and Palaeogene placental mammals to date, including members of all major "condylarth" groups, other archaic ungulates such as mesonychians and pantodonts, and members of the enigmatic Cretaceous and Paleocene groups Cimolestidae and Leptictida. The sampling concentrated on Laurasiatheria, as the majority of the hypotheses of relationships for archaic ungulates and archaic insectivores concern extant laurasiatheres, but in order to accommodate all proposed hypotheses of Paleocene placental mammal affinities, members of all four extant superorders were included.

2) Were rates of morphological evolution significantly affected by the end-Cretaceous mass extinction, or by the origin of Placentalia? Following on directly from the phylogenetic analysis, the second portion of the thesis is a

pair of macroevolutionary studies assessing the effect of the end-Cretaceous mass extinction on the rate of discrete character evolution and lineage origination. To accomplish this, the phylogenies generated from the cladistic analysis were dated using newly-described maximum likelihood methods (Bapst 2013), and character state transitions optimised across the dated phylogenies. This allowed for robust testing of the null hypotheses that there are no significant differences in evolutionary rate through the Cretaceous to early Palaeogene interval. Further, I tested for differences in evolutionary rate across the eutherian mammal phylogeny, to assess if the origin of Placentalia was coincident with an increase in rate of morphological evolution. This analysis aimed to provide evidence for or against the hypothesis that the Paleocene was a special period in macroevolutionary terms for placental mammals, and more specifically whether the end-Cretaceous mass extinction preceded a period of unusually high rates of evolution, as would be expected in the case of an adaptive radiation.

3) Did morphological disparity in mammals increase after the K-Pg mass extinction? Disparity is a useful metric that allows morphological variability of a group of organisms to be calculated (Foote 1992). Disparity metrics calculated from cladistic matrices are associated with measures of ecological or functional variability (Anderson and Friedman 2012). Character states for all characters were reconstructed across all extant and hypothetical ancestral nodes. In conjunction with the dated phylogenies, this allowed the calculation of morphological disparity through time. By time-slicing the dated phylogeny that was generated in the second chapter, and including the morphologies that are implied by the presence of ghost lineages, a truer picture of morphological disparity through time can be assessed than if solely the tree tips were used. Principal Coordinates Analysis was used to assess morphospace occupation, and relative disparity was quantified for time bins,

particularly those near the end-Cretaceous mass extinction. As a result, the level of changing disparity through time was calculated for multiple most parsimonious trees, and a general picture of the changing ecological disparity of eutherian mammals through the Cretaceous and Palaeogene was built.

4) Did similar developmental constraints shape the evolution of early and extant mammals? The evolution of distinct morphologies through deep time, whether through ordinary speciation processes or during an adaptive radiation, are constrained by the developmental models that underpin the origin of the morphology. Indeed, modification of developmental pathways is an important source of variation in biology. Here, an assessment of the degree to which one particular developmental model – the Inhibitory Cascade model for lower molar development of Kavanagh *et al.* (Kavanagh *et al.* 2007) – is consistently present was explored across Placentalia, and Mammalia in general. Dental, and in particular molar, characters were used as the major source of phylogenetic information in morphological analyses of mammals. The diversity within mammal teeth makes them an interesting example of constraint and adaptation to diverse feeding ecologies, most of which are first present at the beginning of the Paleocene. Understanding how shared developmental patterns result in the restriction of available morphologies, and therefore constrain the paths along which evolution can select, is important in the context of evolutionary radiations. Here, I asked whether the new ecological roles exploited by Cenozoic mammals are the result of the origination of an entirely distinct and novel developmental mode, or a variation within pre-existing developmental constraints.

   By taking the product of the length and width of the sequence of lower molars as a proxy for area, I assessed the degree to which the predictions of the Inhibitory Cascade Model are fulfilled across Mammalia. I tested whether different taxonomic divisions and dietary categories can be said to explore different regions of the dental morphospace, and asked whether the apparent radiation of mammals at the beginning of the Cenozoic coincides with a distinct exploration of new regions of dental morphospace.

Combined, these four chapters provide a means of testing the contention that the end-Cretaceous mass extinction represents a real adaptive radiation, and that the extinction event itself provided the opportunity for mammals to diversify. Moreover, it results in better support for the affinities of a number of placental mammal groups, thereby providing the foundation for further studies of the macroevolutionary parameters and biogeography that were in existence during the earliest part of the Cenozoic. By establishing the phylogenetic position of the earliest clades of placental mammals, it can be tested whether the requirements for an adaptive radiation are met. High evolutionary rates, high rates of lineage accumulation, and a rapid filling of novel morphospace would indicate that placental mammals, during this time, underwent selection for novel adaptations and novel niches. It provides an essential source of data for future studies, and throws light on the ecological and evolutionary aftermath of the last great mass extinction.

CHAPTER TWO

PHYLOGENETIC RELATIONSHIPS AMONG PALAEOGENE AND CRETACEOUS MAMMALS

2(a) – *Abstract*

The 'Age of Mammals' began in the Paleocene epoch, the 10 million year interval immediately following the Cretaceous-Palaeogene mass extinction. The apparently rapid shift in mammalian ecomorphs from small, largely insectivorous forms to many small-to-large-bodied, diverse taxa has led to the hypothesis that the end-Cretaceous heralded an adaptive radiation in placental mammal evolution. However, the affinities of most Paleocene mammals have remained unresolved, despite significant advances in understanding of the relationships of the extant orders, hindering efforts to robustly reconstruct the origin and early evolution of placental mammals. Here I present the largest cladistic analysis of Paleocene placentals to date, from a data matrix including 177 taxa (130 of which are Palaeogene) and 680 morphological characters. I improve the resolution of the relationships of several enigmatic Paleocene clades, including families of "condylarths". *Protungulatum* is resolved as a stem eutherian, meaning that no crown placental mammal unambiguously predates the Cretaceous-Palaeogene boundary. Our results support a split between Atlantogenata (Afrotheria + Xenarthra) and Boreoeutheria at the root of crown Placentalia, the paraphyly of Phenacodontidae with respect to Perissodactyla, Euungulata, and the placement of Arctocyonidae close to Carnivora. Periptychidae and Pantodonta are resolved as sister taxa, Leptictida and Cimolestidae are found to be stem eutherians, and Hyopsodontidae is highly polyphyletic. The inclusion of Paleocene taxa in a placental phylogeny alters interpretations of relationships and key events in mammalian evolutionary history. Paleocene mammals are an essential source of data for fully understanding the biotic dynamics associated with the end Cretaceous mass extinction, and the relationships

presented here mark a critical first step towards accurate reconstruction of this important interval in the evolution of the modern fauna.

2(b) - ***Introduction***

2(b)(i) – *The Effect of the end-Cretaceous Mass Extinction*

The Cretaceous-Palaeogene (hereafter K-Pg) mass extinction represents one of the largest global ecological turnovers in the history of life. Occurring 66 million years ago, it was the second largest mass extinction of all time, during which some 75% of terrestrial species were extinguished (Jablonski and Chaloner 1994), dramatically altering both terrestrial and marine ecosystems (Sessa *et al.* 2012; Vajda *et al.* 2001). Palaeontologists usually reconstruct this point as the beginning of the so-called 'Age of Mammals'; prior to the K-Pg, mammals were mainly small, terrestrial to arboreal insectivores with low ecological disparity (Goswami*, et al.* 2011; Grossnickle and Polly 2013), albeit with a few notable exceptions (Luo 2007). In contrast, Palaeogene mammals include the first large-bodied herbivores, specialised carnivores, and later, radiations of gliding, flying, and fully aquatic organisms, with a corresponding increase in diversity (Darroch*, et al.* 2014).

This apparently sudden increase in ecospace occupation has been interpreted as an adaptive radiation, particularly in placental mammals (Alroy 1999; Raia *et al.* 2013). However, macroevolutionary studies of placental mammals in this period are limited by the lack of a comprehensive phylogeny for Paleocene placentals. With the exception of Primates (Russell 1964), Rodentia (Jepsen 1937), and Carnivora (Fox *et al.* 2010), no extant order of placental mammal has an unambiguous representative during the Paleocene, minimally leaving a ten million year gap between the K-Pg mass extinction and the origin of most extant orders. Pertinent to the question of when placental mammals diversified are the currently unresolved phylogenetic relationships of the majority of Paleocene mammals, as they occur during the period of rapid ecological diversification for placental mammals, but predate the definitive first appearances of most of the extant orders.

Many previous studies have assessed the timing of the origin of placental mammals (Bininda-Emonds*, et al.* 2007; O'Leary *et al.* 2013), or examined changes in rates of evolution of body size or diversification across the K-Pg boundary (Springer*, et al.* 2003; Slater 2013; Venditti*, et al.* 2011), but all have used datasets that mostly or entirely excluded Paleocene taxa, thereby ignoring the important period during which an adaptive radiation would seem, from superficial observation of the fossil record, to have occurred. These analyses, using a diverse array of datasets and dating techniques, have tended to favour a 'mid' to Late Cretaceous origin of placental orders and superorders, including phylogenetic, (Springer*, et al.* 2003) phylogenomic (dos Reis*, et al.* 2012), and supertree (Bininda-Emonds*, et al.* 2007) methods. Since the earliest definitive members of crown orders are mostly known from the Late Paleocene or Eocene, this requires the existence of ghost lineages. Estimates for the age of the last common ancestor of crown Placentalia have progressively decreased from 130 Ma when dating under a strict clock model (Kumar and Hedges 1998; Springer 1997) to about 90 Ma when allowing rate heterogeneity and incorporating more data (Hallstrom and Janke 2010; dos Reis*, et al.* 2012), or 85 Ma when accounting for convergent molecular evolution (Kitazoe *et al.* 2007). These lower dates are nonetheless 33% older than the end-Cretaceous mass extinction – if true, it would mean that no placental mammal is known from 25% of the existence of the clade. It has been suggested that a particular problem with clocklike models suffer from artefacts resulting from historical changes in evolutionary rate (Beck and Lee 2014), meaning that interpretation of the date of origin of placental mammals is highly contingent on method and dataset.

Inclusion of fossil members of lineages in such analyses can critically alter the interpretation of results in a wide range of macroevolutionary scenarios (e.g. Slater*, et al.* 2012; Pyron and Burbrink 2012; Raj Pant *et al.* 2014; Tarver and Donoghue 2011; Wood*, et al.* 2013), but is only possible where the phylogenetic relationships of those fossil forms is understood. Identifying the phylogenetic position of the enigmatic Palaeogene taxa with respect to extant orders and Cretaceous groups is therefore essential to understand the timing of divergence of extant orders. The earliest Paleocene taxa first appear within a million years of the K-Pg boundary, and if they are crown placental mammals, this would imply that speciation between extant orders most likely occurred cryptically during the Cretaceous. Establishing how many mammalian lineages span the Cretaceous-Paleocene boundary also allows for greater accuracy in assessing the role of mass extinctions in evolutionary dynamics more generally.

Further, ascertaining the phylogenetic relationships of fossil forms allows for robust, inclusive studies of character evolution that directly sample taxa from the relevant intervals and better represent true clade diversity. Ultimately, a phylogeny of Paleocene mammals is sorely needed, but has not been forthcoming, despite a great deal of energy directed towards study of the end-Cretaceous mass extinction and its aftermath.

2(b)(ii) – *Hypothesised relationships among Paleocene placental mammals*

The phylogenetic relationships among extant placental mammals have a long history of study with morphological data, with some stability in tree topology for several decades. This traditional topology accommodated many of the Paleocene mammal clades in a relatively straightforward manner, such as "condylarths" being identified as stem ungulates (Figure 2.1A). However, towards the latter half of the 20th century, questions were raised about some of these groupings, such as the traditional clades of "Insectivora" (insectivorous mammals) and "Ungulata" (hoofed mammals) (see Asher*, et al.* 2008). Indeed, the distinction between the Afrotherian golden mole *Chrysochloris* and European moles was suggested as early as the 19th century (Cope 1884c). The advent of molecular sequencing and its application to mammalian phylogenetics confirmed the suggestions that Insectivora and Ungulata were polyphyletic (Stanhope*, et al.* 1998). With the division of Insectivora into Eulipotyphla and Afroinsectivora, and Ungulata into Perissodactyla, Artiodactyla, and Paenungulata, the several fossil taxa were left without a well-supported position in the placental tree of life. In particular, “Condylarthra”, historically thought to be ancestral to “Ungulata”, was reduced to the status of ‘wastebasket taxon’, into which any generically bunodont, hoofed mammal from the Palaeogene has been consigned (Archibald 1998). Patently, these taxa must have ancestors, and extant orders likely

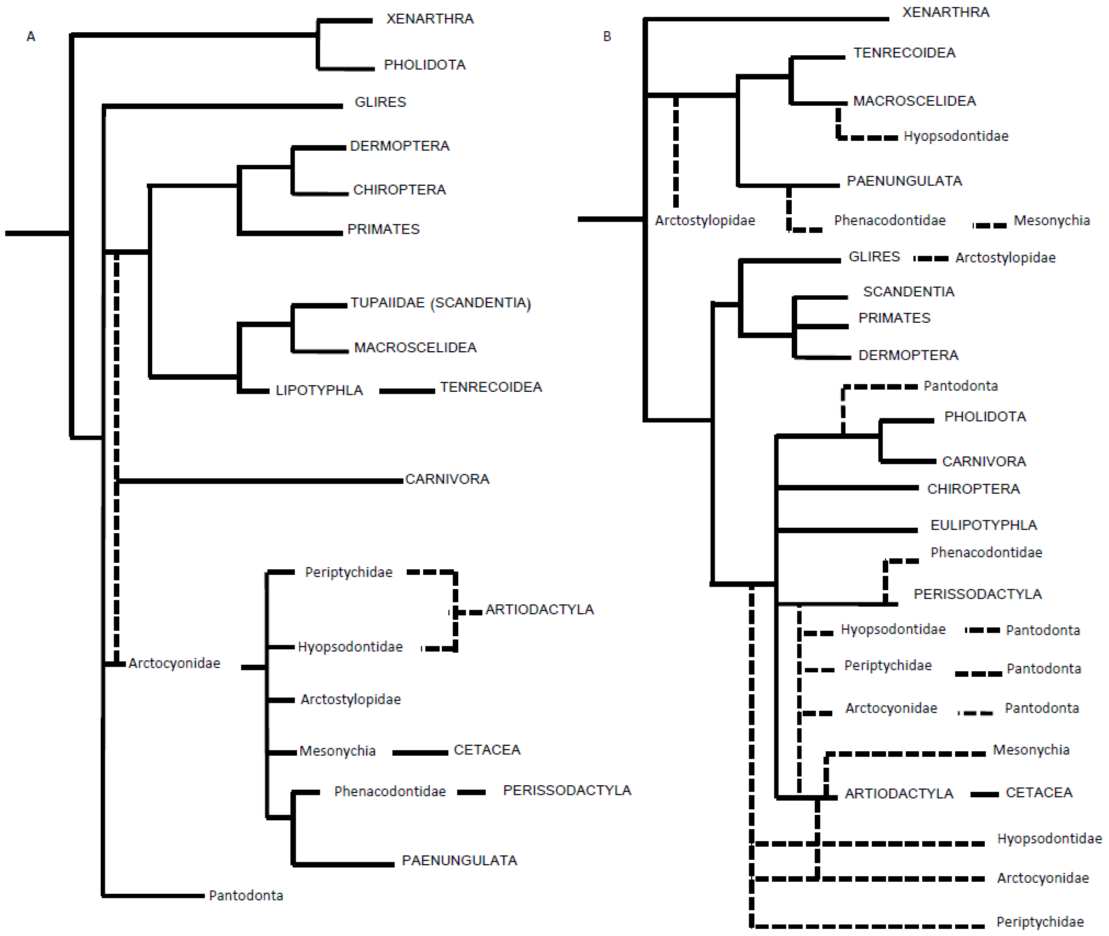


Figure 2.1 – A depiction, in broad terms, of the changes in the understanding of the relationships of placental mammals over the last twenty years. (A) The scientific consensus of placental mammal relationships prior to the advent of molecular data. “Condylarth” families were considered basal to Ungulata, a number of plesiomorphic taxa were grouped together as Insectivora, whales were considered a separate order, and pangolins were joined with xenarthrans in Edentata. (B) The current consensus on placental mammal phylogeny. While the relationships of extant groups are clear – Cetacea is a subgroup of Artiodactyla, Carnivora and Pholidota are sister taxa, Ungulata and Insectivora are polyphyletic – the relationships of Paleocene taxa have become far more uncertain. In both, dotted lines represent uncertainty.

evolved from some of the ambiguous Paleocene taxa, but the nature of their relationships remains perplexing. Indeed, every "condylarth" family-level clade has been suggested to be related to one or more extant clade, with several hypotheses existing for each (Figure 2.1B). For the most part, these "condylarth" clades themselves are considered monophyletic, but the relationships among them, and between the several "condylarth" clades and extant orders are unknown.

2(b)(iii) – *Objectives*

Here, I present the results of the largest cladistic analysis of Palaeogene mammals to date, with the aim of resolving the relationships of some of the aforementioned enigmatic groups. Inclusion of key representative taxa from this important period in placental evolution in a wide-reaching study such as this is a crucial requirement for future analysis of the early evolution of this clade.

This analysis represents a significant methodological improvement over all previous analyses that have sought to understand the affinities of enigmatic Paleocene groups. The only study to approach similar numbers of Palaeogene taxa (130 in this analysis) is the unpublished PhD thesis of Shawn Zack (2009). However, several of the terminals in that analysis are composites of many genera, which therefore may not represent the character distributions of any actual organism, and may result in topologies supported by none of the data from each constituent taxon (Malia *et al.* 2003). While a few Palaeogene genera are suspected to be wastebaskets themselves, and therefore not as appropriate to be coded as single taxa, this is likely to be less of a problem regarding character distributions than condensing an entire family into a single terminal. However, in this analysis, certain genera which have been considered both as separate and synonymous (for example, *Arctocyon* and *Claenodon*, and *Hyracotherium* and *Eohippus*), are treated separately to minimise this potential issue. Further, the Zack analyses present trees derived primarily from dental and postcranial material. While cranial material, a rich source of data, is included in a single analysis, this is unconstrained to a backbone of known relationships, and as a result contains highly improbable topologies that contradict the body of scientific work to date. Excluding cranial data in all other analyses effectively ignores a rich source of phylogenetic information which may be more reliable than dental data in phylogenetic analyses (Sansom 2014) due to atomisation of characters and strong functional correlations among occluding teeth. Otherwise, all other studies of mammal phylogenetics have included few, if any, Paleocene taxa; those that do have focussed on individual family-level clades (e.g. Chester and Bloch 2013; Missiaen *et al.* 2012). While adequate for understanding relationships within groups, these smaller analyses are unable to test all competing hypotheses of placental interrelationships. For instance, by studying apheliscid and louisinid "condylarths", but only including single members of Macroscelidea, Amphelimuridae, Adapisoriculidae, and outgroups (as in Hooker and Russell 2012), it is possible to study the interrelationships of apheliscids and louisinids, but not possible to robustly test alternative hypotheses of the relationships between these taxa and the rest of the placental tree. Here, inclusion of 177 taxa from across Eutheria allows analysis of multiple hypotheses of higher-level relationships.

2(c) – ***Methods***

2(c)(i) – *Choice of Taxa and Characters*

A wide sample of taxa was selected in order to test hypotheses of relationships across Placentalia. For both extant orders and extinct groups of unknown affinity, taxa were selected based on several criteria, generally selecting the most basal members of each lineage. For groups with a limited fossil record, such as all xenarthran groups, dermopterans, and scandentians, and groups where the early relationships and character polarities are not clear, such as in Eulipotyphla, extant taxa were used to supplement fossil material. The reason for preferring fossil taxa over extant forms is the length of time and amount of evolutionary change that has occurred over the last 66 million years. By taking the basalmost and/or earliest members of an order, the chances that key synapomorphies of that group have been obscured through convergence or reversal are far lower. Completeness and quality of fossil material was also taken into account, preferring taxa with a higher proportion of codable characters, and, with the exception of the problematic South American meridiungulate groups of Notoungulata and Litopterna, each group was represented by multiple taxa, to avoid apomorphies being taken as plesiomorphic for a higher clade. In total, 865 specimens and casts were examined in international museum and university collections, supplemented by character data from the published literature, including character state data matrices, scans, and photographs (Appendix 2.1, electronic supplementary information). In total, 680 morphological characters – 48 of which are continuous – were coded for 177 taxa, 18 of which are extant, resulting in two matrices, one traditionally discrete (Appendix 2.2, electronic supplementary information), and one with continuous characters treated as such (Appendix 2.3, electronic supplementary information).

Characters were derived from four major sources – the PhD thesis of Shawn Zack (Zack 2009), which studied postcranial and dental morphology of largely Paleocene mammals, but excluded cranial characters from the supplied data matrix and included several terminals that were composites of multiple genera; a matrix from Williamson and colleagues focusing on the Cretaceous-Palaeogene group Cimolestidae (Williamson *et al.* 2011), which ultimately descends from the Wible matrix for Cretaceous eutherians (Wible*, et al.* 2007; Wible*, et al.* 2009); a matrix used for establishing the relationships of the Palaeogene 'ungulate' mesonychians (Geisler and McKenna 2007); and a matrix containing several 'archaic ungulate' characters, with particular focus on the enigmatic Pleuraspidotheriidae (Ladevèze*, et al.* 2010). Characters were modified such that they were consistently applicable, easily interpreted, and divisions between character states were better and more consistently defined. This resulted in a final list of 680 morphological characters, consisting of 235 dental, 264 cranial, and 181 postcranial characters (Appendix 2.4, electronic supplementary information). TNT by default treats missing data as uncertainty, and gaps (evidence of absence of a feature) as an additional state.

Where a trait is polymorphic (for example between states 1 and 2 in a 3 state character), that condition is treated as an uncertainty between those two states.

2(c)(ii) – *Use of continuous characters*

There is much debate over the benefits of using continuous traits in morphological phylogenetic analysis (Rae 1998; Goloboff *et al.* 2006; Wiens 2001). While more objective than the traditional division of character states in discretized continuous traits, issues arise when determining the relative weighting of a continuous trait. Here, I weight the continuous characters such that the difference between the maximum and minimum values for the trait is equivalent to a single step. This treats the character as effectively equivalent to a binary discrete trait, with the variation in between represented by decimal places within that range. As a result of this treatment of the characters, the steps that take place along the branches of the phylogeny are necessarily on average shorter than when the trait is discretized, which means that the trees are also concomitantly shorter. As a result, it is not possible to directly compare the accuracy of the topology by tree length alone when comparing datasets with and without continuous traits. However, to make sure that the difference in length was exclusively due to the alternate methods of coding particular characters, the discretised continuous characters were also weighted such that the entire range represented a single step. For binary characters, this requires no weighting, but a three-state character would be weighted at 0.5 the value of a binary character, since it takes two changes to get from one endpoint to another. I modified the weights of continuous and discretized characters using TNT (Goloboff *et al.* 2008; Goloboff*, et al.* 2006).

2(c)(iii) – *Constraining relationships*

Within Placentalia, convergent adaptive radiations in different groups have led to occupation of similar niches in their respective ecosystems (Madsen*, et al.* 2001), with concomitant morphological similarities. As a result, relationships derived from solely morphological data have often resulted in a situation where homoplasy has overridden the true phylogenetic signal at higher phylogenetic levels (Lee and Camens 2009). Indeed, the base of Placentalia shows much higher character conflict (ie homoplasy) than later divergences (Holland*, et al.* 2005). Within a fossil-based analysis, where morphology is by necessity the only data type available for use, this is potentially problematic. While morphological traits are extremely useful for distinguishing between species of a genus, or between genera of a family, the larger length of time since higher level divergences means that convergence, and therefore loss of signal, is a potential issue with using morphological analysis to distinguish between groups that are temporally far removed from their divergence events, as is the case for the extant placental orders. The most obvious problem with morphological phylogenetic analyses of Placentalia is the common failure to reconstruct the major placental "superorders" – Afrotheria, Xenarthra, Euarchontoglires, and Laurasiatheria, each of which are very well supported in most molecular studies. In order to incorporate the uncontentious aspects of topology for living placentals provided by molecular data – unavailable for the fossil taxa with which this analysis is concerned – I constrained the relationships among extant clades with a molecular scaffold that is consistent with the vast majority of molecular analyses of placental mammals. I accounted for areas of uncertainty such as the topology of the Laurasiatherian orders (Hu*, et al.* 2012) and the relationships between Boreoeutheria, Atlantogenata and Xenarthra (Murphy*, et al.* 2007; Nishihara*, et al.* 2009) by treating them as unresolved polytomies within the scaffold. Two levels of constraint were implemented; one imposed a 'minimum' constraint, including single members of each crown group as far as possible. For example, while both *Pakicetus* and *Rodhocetus* are undoubtedly closest relatives in this dataset, both being stem cetaceans, only *Pakicetus* was included in the constraint. This minimises the degree to which constraints are allowed to affect the data, and is a test that known relationships can still be recovered from the data with

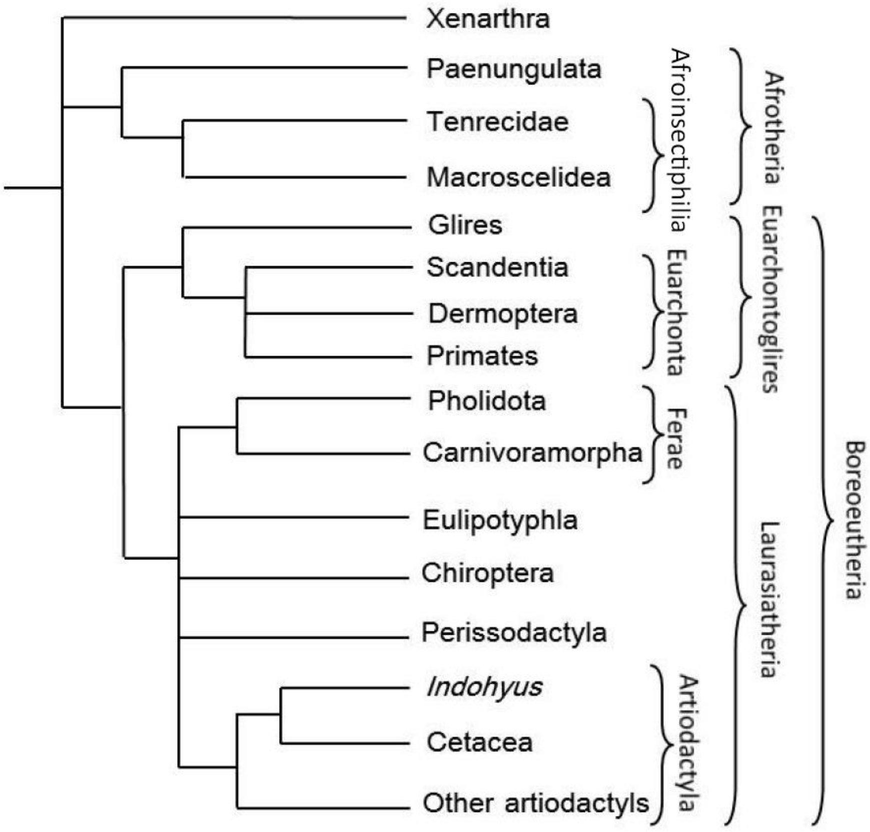


Figure 2.2 – The constraint applied to all analyses, derived from the molecular understanding of the relationships of extant placental mammal groups. In CE and DE analyses, Xenarthra was composed of *Chaetophractus*, *Bradypus*, and *Tamandua*; Paenungulata: *Eritherium* and *Procavia*; Tenrecidae: *Potamogale*; Macroscelidea: *Chambius* and *Rhynchocyon*. Glires was composed of *Tribosphenomys*, *Paramys* and *Gomphos*; Scandentia: *Tupaia* and *Ptilocercus*; Dermoptera: *Cynocephalus*; Primates: *Saxonella, Cantius,* and *Adapis*. Pholidota was composed of *Eomanis* and *Eurotamandua*, Carnivoramorpha by *Miacis* and *Viverravus*. Eulipotyphla was represented by *Domnina*, *Oreotalpa*, *Blarina*, *Solenodon*, and *Echinosorex*. Chiroptera was represented by *Pteropus*, Perissodactyla by *Eohippus* and *Hyracotherium*, Cetacea by *Rodhocetus*, and artiodactyls by *Gobiohyus*, *Poebrotherium*, *Leptomeryx* and *Elomeryx*. In the CF and DF analyses, additional taxa were, for Xenarthra, *Utaetus*; *Dilambdogale* was added in a polytomy with Macroscelidea and Tenrecidae within Afroinsectiphilia; for Glires, *Rhombomylus*; for Dermoptera *Elpidophorus*, *Worlandia* and *Plagiomene*; for Primates, *Elphidotarsius*, *Plesiadapis* and *Notharctus*; for Carnivoramorpha, *Didymictis*, *Vulpavus*, *Protictis* and *Uintacyon*; for Eulipotyphla, *Litocherus*, *Uropsilus*, and *Centetodon*; for Chiroptera, *Onychonycteris* and *Icaronycteris*; for Perissodactyla, *Heptodon*, *Homogalax*, *Litolophus* and *Lambdotherium*; and for Cetacea, *Pakicetus*. In the CP and DP analyses, *Purgatorius* was further constrained within Primates.

a minimal constraint. The second constrained all taxa which were unequivocally accepted as stem members of the extant orders (Figure 2.2), in order to ensure that well-established and evidenced relationships were recovered.

Further, there remains particular doubt as to the status of the enigmatic genus *Purgatorius*. This early Paleocene genus has been allied by many to the plesiadapiforms (Clemens 2004; Fox and Scott 2011), with the implication that it represents an early stem primate. Alternative topologies have placed *Purgatorius* on the stem of Placentalia, due to the conservativeness of its morphology (Wible*, et al.* 2009; Rook and Hunter 2014), although counterarguments suggest that this more basal position is due to inadequate sampling of plesiadapiforms and early Primates, which could also potentially affect its positioning in this analysis. In order to accommodate these alternative hypotheses, which are both substantially supported on the basis of tarsal and dental similarities respectively, *Purgatorius* was constrained along with Primates and their kin in a further analysis, and left unconstrained in the others.

When constraining, all taxa involved in the constraint were set as 'non-floaters' in TNT, while all others were set as 'floaters', meaning that they are able to invade an otherwise constrained topology. *Peramus*, *Deltatheridium*, and *Bobolestes* were set as sequential outgroup taxa in the constraint, as all are unambiguous stem eutherians (McKenna and Bell 1997), in order to ensure that trees were rooted appropriately.

In total, I used three different constraints with two types of data, as well as running an unconstrained analysis with both data matrices, resulting in eight separate sets of most parsimonious trees that, when discussing results, will be abbreviated as follows. CU and DU represent the continuous and discretised unconstrained analyses. CE and DE the minimum constraints; CF and DF the full constraints in which all unambiguously placed fossil taxa are included, and CP and DP the constraints equivalent to CF and DF, but with *Purgatorius* constrained with the Primates.

Constraining relationships based on molecular evidence for use with morphological data is not an ideal solution, as both molecular and morphological data are prone to convergence and error. Many phylogenetic analyses have used a total evidence approach to explore the relationships of groups, incorporating both molecular and morphological data. While it is true that this would be possible for these fossil groups, the aim of this thesis has been to elucidate the relationships among the placental mammals of the Paleocene and their affinities with extant orders. Total evidence analyses have, as yet, not consistently resolved the relationships of the laurasiatherian orders, in part thanks to the lack of clear fossil calibration points for internal nodes of the orders. Identifying the relationships of the extinct mammals of the Paleocene on the basis of their morphology (the only available data), will allow future work to be better informed as to the likely position of useful calibration points when simultaneously reconstructing topologies and dates.

2(c)(iv) – *Phylogenetic analysis*

Maximum parsimony phylogenetic analysis was carried out in the freeware program TNT (Goloboff*, et al.* 2008), using the New Technology Search algorithms. The consensus was stabilized twice with factor 75, employing sectorial searches (RSS and XSS), drift (rejection factor 50) and tree fusing, dumping fused trees for computational ease due to the size of the dataset. This was followed by a round of traditional TBR searching, using the MPTs from the New Technology Search as starting trees for the TBR analyses, following Mannion et al. (2013). Analyses each took approximately 350 to 500 hours of computing time. Multistate characters were treated as ordered where meristic or where they represented a morphological sequence in which one or more states represent discrete intermediates between end-member states (Wilkinson 1992). For example, the character describing the position of the palatine foramen has the ordered states ‘within palatine’, ‘between palatine and maxilla’ and ‘within maxilla’. Due to the precision of continuous and weighted discrete analyses of multiple decimal places, near-optimal trees which were less than a step longer than the most parsimonious trees were also recovered. As a result, I performed 16 different analyses in total (Table 2.1).

Table 2.1 – Abbreviations for sets of trees deriving from the analyses in this chapter, and throughout the thesis. Each cell states the abbreviation given for the analysis represented by a different combination of continuous/discrete characters, level of constraint, and whether the sets of trees discussed are most parsimonious trees or those within a single step in length. Where larger subsets of trees are mentioned in the text, shorter combinations are used. For example, “DU” refers to both the “DUO” and “DUS” sets of trees.

Abbreviations for sets	Discrete		Continuous	
of trees and analyses	MPT	Within One Step	MPT	Within One Step
Unconstrained	DUO	DUS	CUO	CUS
Reduced Constraint	DEO	DES	CEO	CES
Full Constraint	DFO	DFS	CFO	CFS
Purgatorius Constraint	DPO	DPS	CPO	CPS

2(c)(v) – *Templeton’s Tests*

Templeton’s Tests (Templeton 1983) allow several alternative, suboptimal topologies to be tested in order to ascertain whether the additional length is considered significantly longer, and therefore able to be rejected as unsupported by the data, than the optimal topology. Where two competing hypotheses for the phylogenetic placement of a taxon exist, Templeton’s tests are therefore a useful way to determine whether a dataset supports one hypothesis strongly over another.

As each analysis resulted in a slightly different topology, the length of each topology was calculated using both discrete and continuous datasets, with Templeton's tests being performed on each suboptimal tree for that dataset (in other words, relative to the least constrained trees). Tests were carried out using Microsoft Excel.

2(c)(vi) – *Relative Bremer Support*

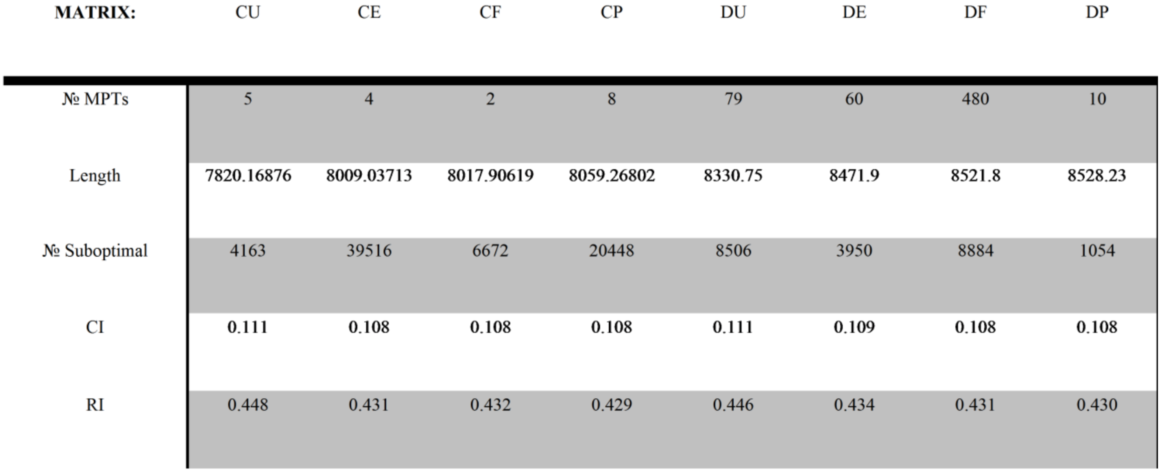
Relative Bremer supports were calculated by searching for suboptimal trees at increasing levels of suboptimality until the storage limit of 99,999 trees was reached in TNT, calculating relative support, and subsequently pruning out those taxa that were causing local reduction in support due to their instability. Relative Bremer supports measure the degree to which topologies supporting a clade outnumber those invalidating a clade within a set of trees, and give a corresponding value between -100 and 100, where -100 represents topologies that are never supported, and 100 clades that are always present. Values of 0 or below result in the node being collapsed.

2(d) – Results

2(d)(i) – *Phylogenetic topology*

The topology of the unconstrained tree contained many of the groupings that are generally supported by previous morphological analyses, and failed to recover Eulipotyphla as a monophyletic group to the exclusion of other laurasiatherians. Afrotheria was polyphyletic and Chiroptera allied with a reduced Euarchontoglires (Figure 2.3). This topology is consistent with the pre-molecular understanding of mammalian phylogenetic relationships, and demonstrates the need for constraining relationships among extant clades to topologies recovered primarily from molecular

Table 2.2 – Numbers of most parsimonious trees, their lengths, the number of trees within a single step, and consistency and retention indices. Across all analyses, homoplasy is extremely high. Lengths of trees that are not whole numbers are due to the presence and weighting of continuous characters or discretised and reweighted continuous characters.



MATRIX:	CU	CE	CF	CP	DU	DE	DF	DP
№ MPTs	5	4	2	8	79	60	480	10
Length	7820.16876	8009.03713	8017.90619	8059.26802	8330.75	8471.9	8521.8	8528.23
№ Suboptimal	4163	39516	6672	20448	8506	3950	8884	1054
CI	0.111	0.108	0.108	0.108	0.111	0.109	0.108	0.108
RI	0.448	0.431	0.432	0.429	0.446	0.434	0.431	0.430

data. When constrained at the various levels described above, the topology agreed with the consensus for the relationships among the extant orders of placental mammals, although the precise topology varied where there was uncertainty, for example in the relationships among the laurasiatherian orders (Figure 2.4-2.9). Numbers of most parsimonious trees, number of suboptimal trees within a single step of the most parsimonious trees, and tree metrics are summarised in Table 2.2. Despite the major differences between the unconstrained and constrained analyses, topological relationships of the clades of interest were generally consistent among all constrained analyses. The retention and consistency indices were, for all practical purposes, the same, whether constrained or not, indicating that the level of homoplasy in the unconstrained tree was almost as high as when constrained.

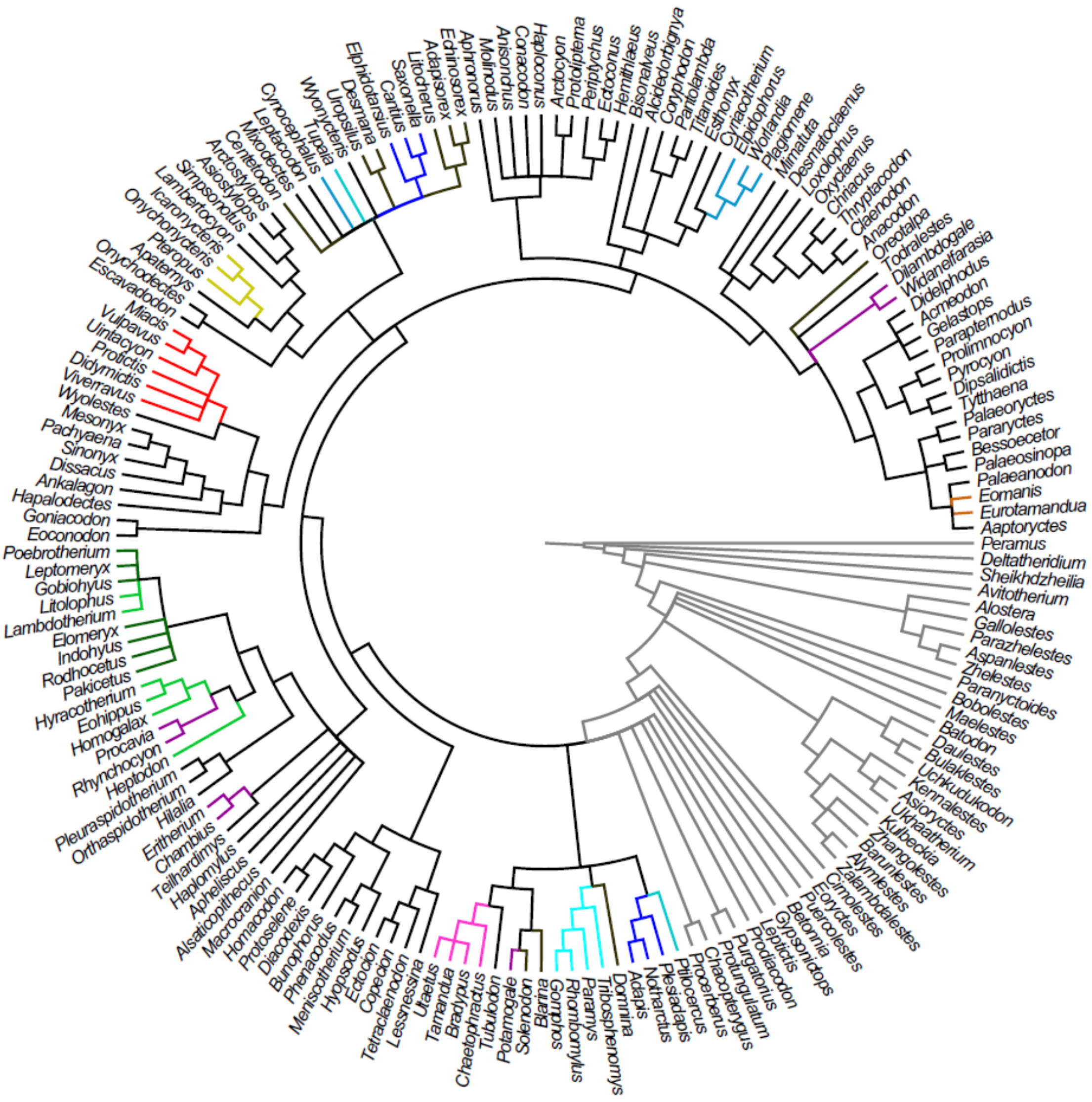


Figure 2.3 – Strict consensus of 8506 discrete, unconstrained trees within one step of the most parsimonious trees, which were of length 8330.75. Colours represent members of extant orders as follows: Pink – Xenarthra, Purple – Afrotheria, Sky blue – Glires, Light blue – Scandentia, Mid-blue – Dermoptera, Royal blue – Primates, Brown – Eulipotyphla, Dark green – Artiodactyla, Light green – Perissodactyla, Yellow – Chiroptera, Orange – Pholidota, Red – Carnivora.

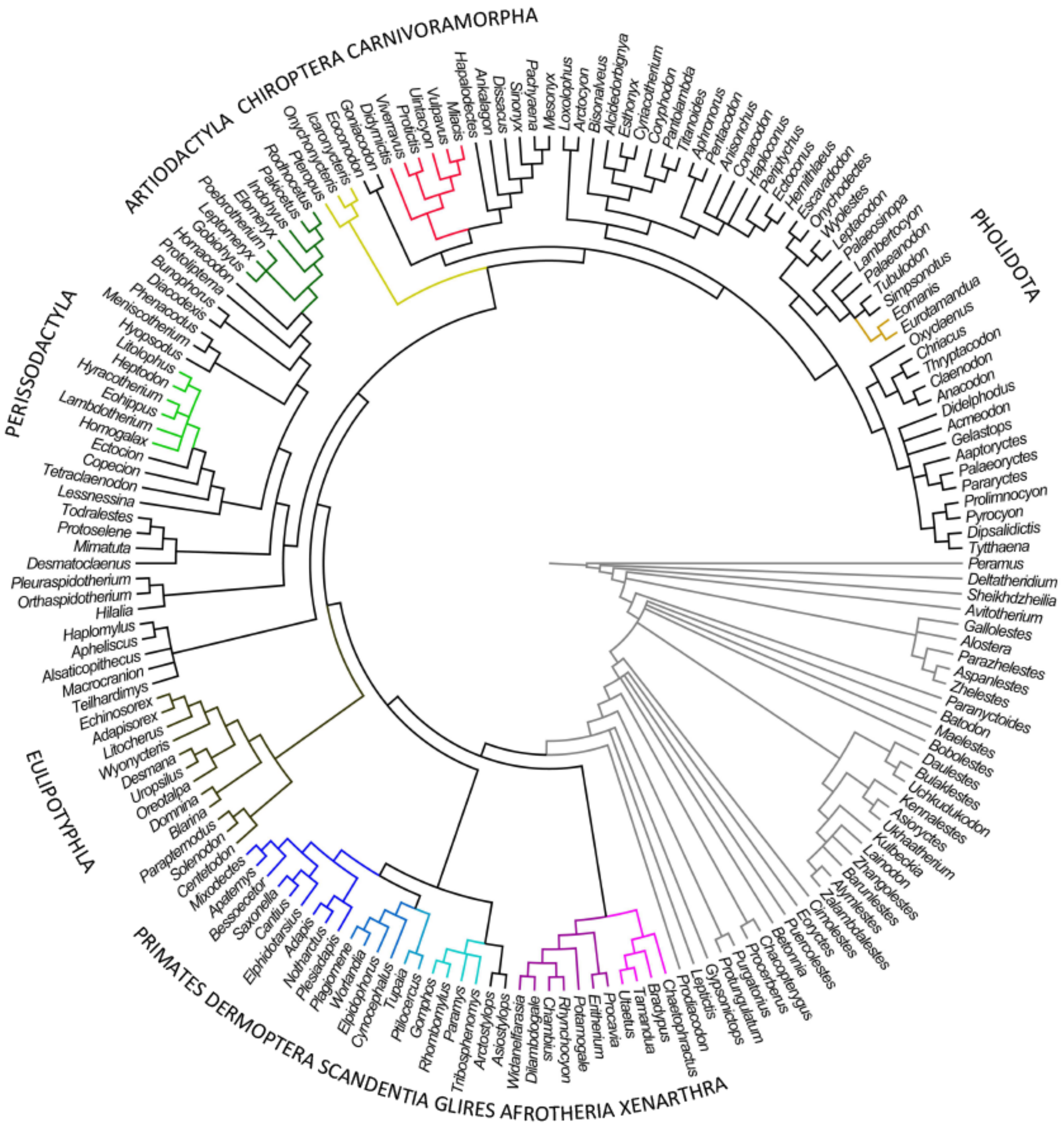


Figure 2.4 – Strict consensus of 8884 trees derived from the discrete dataset with the ‘full’ constraint applied, within one full step of the most parsimonious trees of length 8521.8. Colours are as those seen in Figure 2.3.

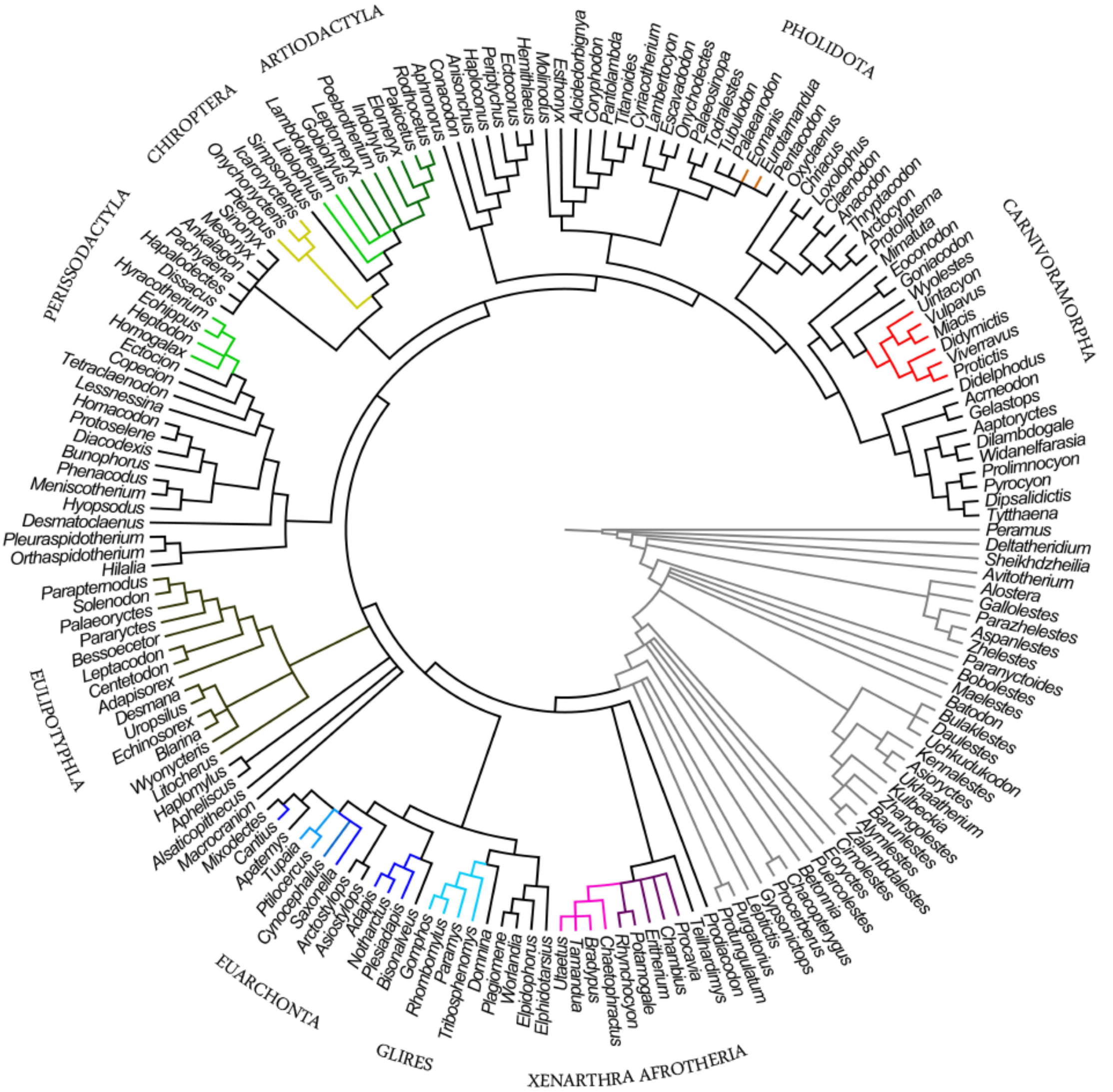


Figure 2.5 – Strict consensus of 3950 trees derived from the discrete dataset with the reduced constraint applied within one full step of the most parsimonious trees of length 8471.9. Colours are as seen in Figure 2.3.

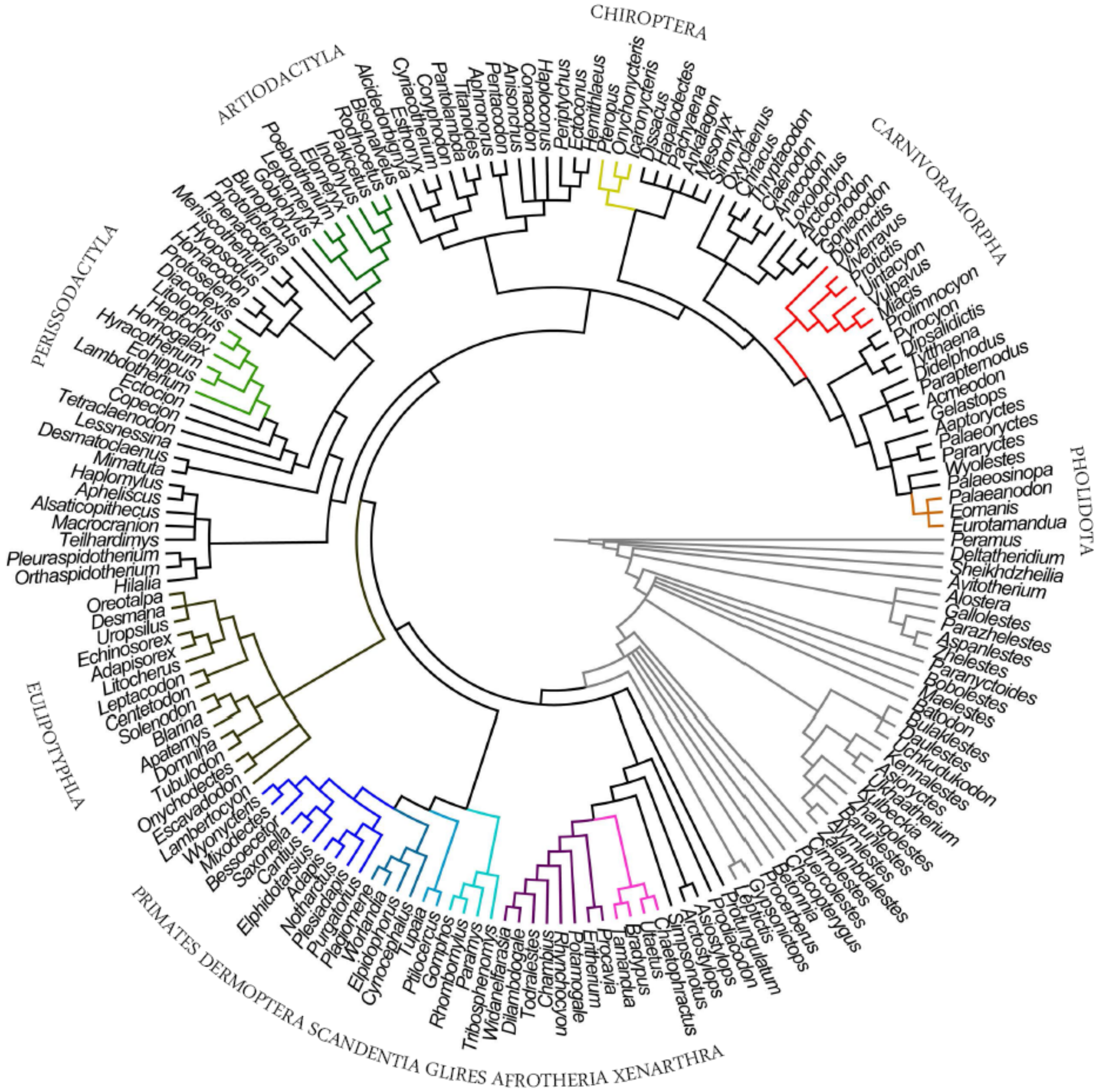


Figure 2.6 – Strict consensus of 1054 trees from the discrete dataset with *Purgatorius* constrained as a stem primate within one full step of the most parsimonious trees of length 8528.23. Colours of extant clades are as those in Figure 2.3.

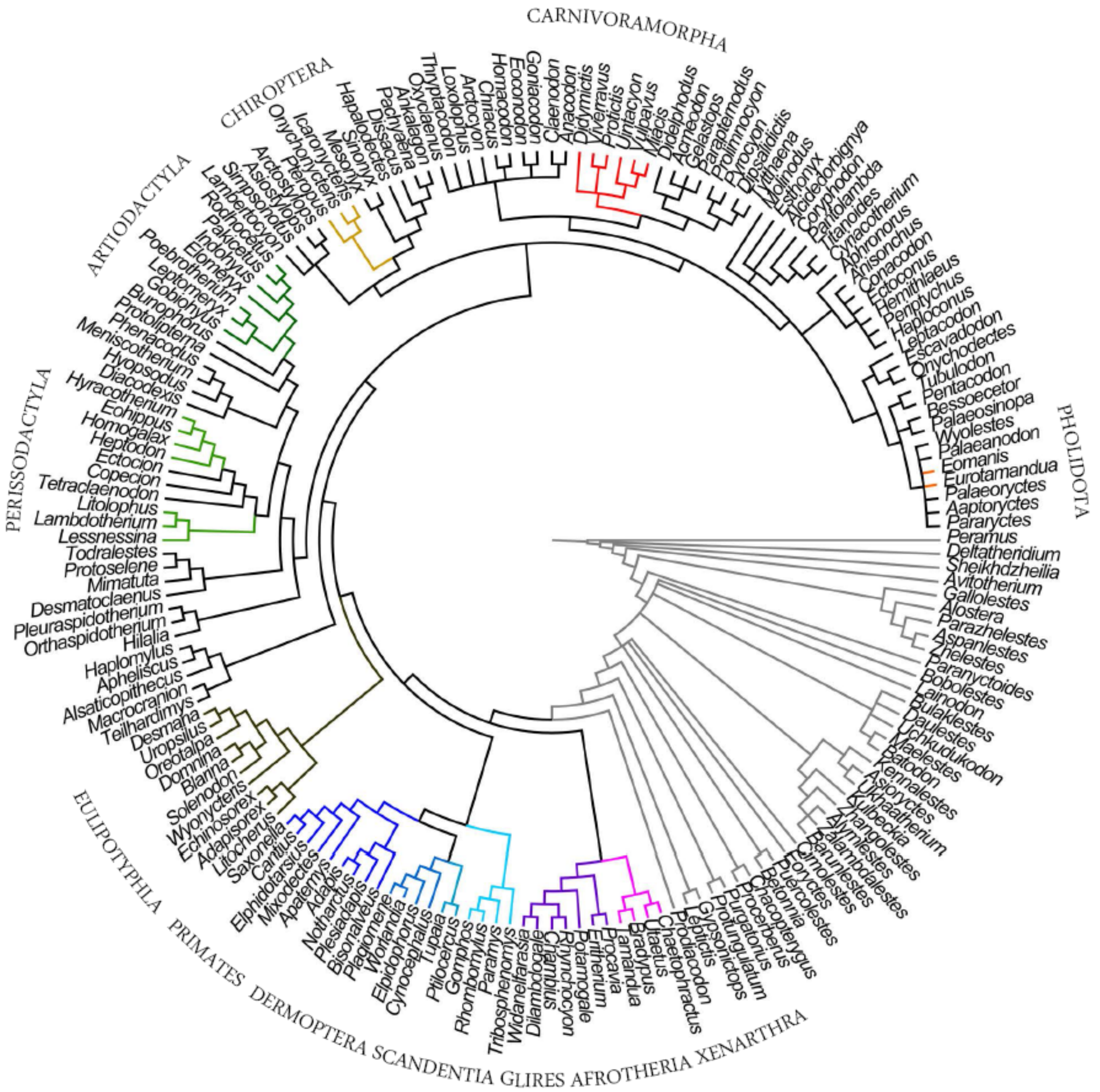


Figure 2.7 – Strict consensus of 6672 trees derived from the continuous dataset with a 'full' constraint within one full step of the most parsimonious trees of length 8017.90619. Colours are as those in Figure 2.3.

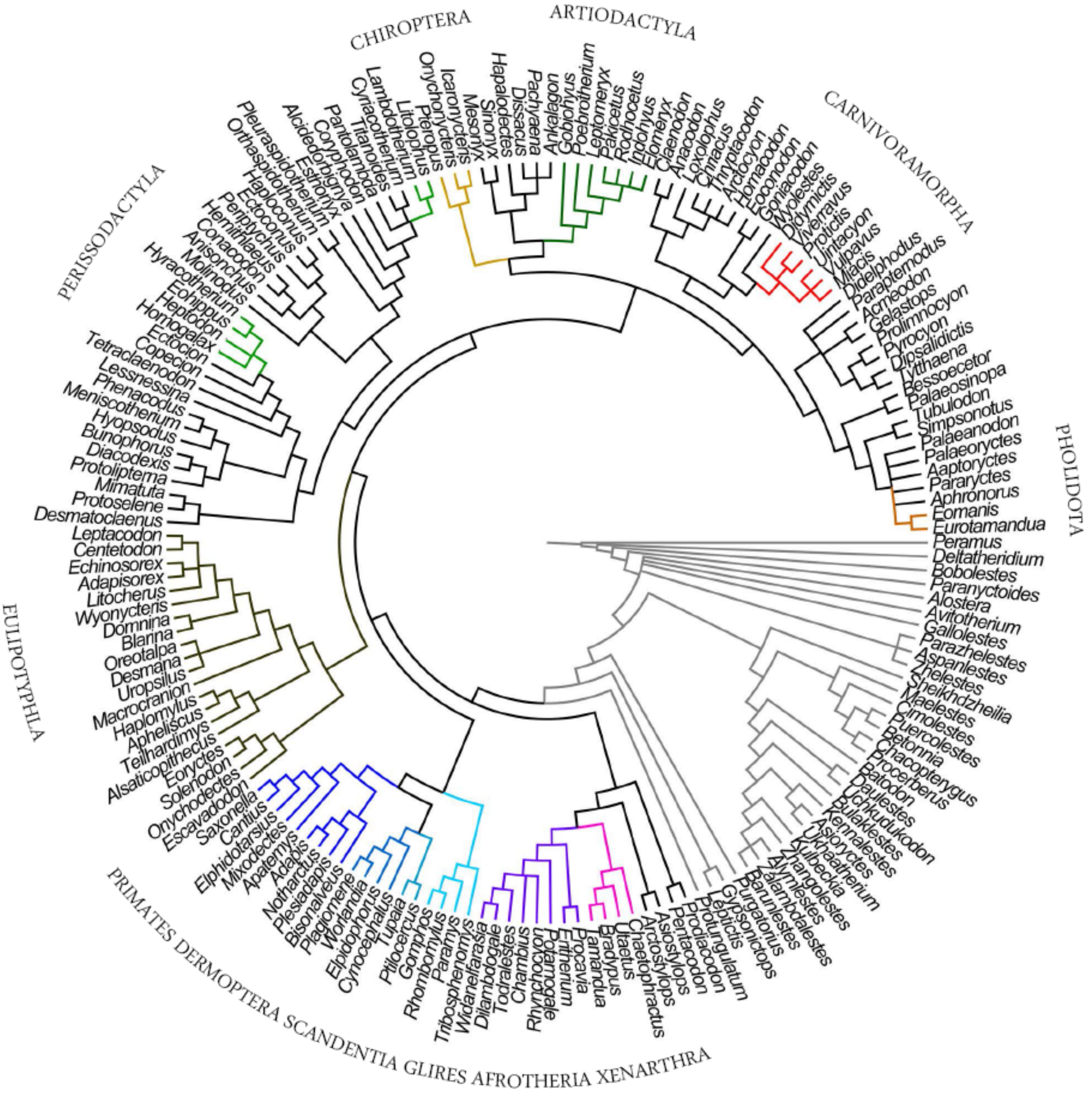


Figure 2.8 – Strict consensus of 39516 trees from the continuous dataset with the reduced constraint applied within one full step of the most parsimonious trees of length 8009.03719. Colours are as those in Figure 2.3.

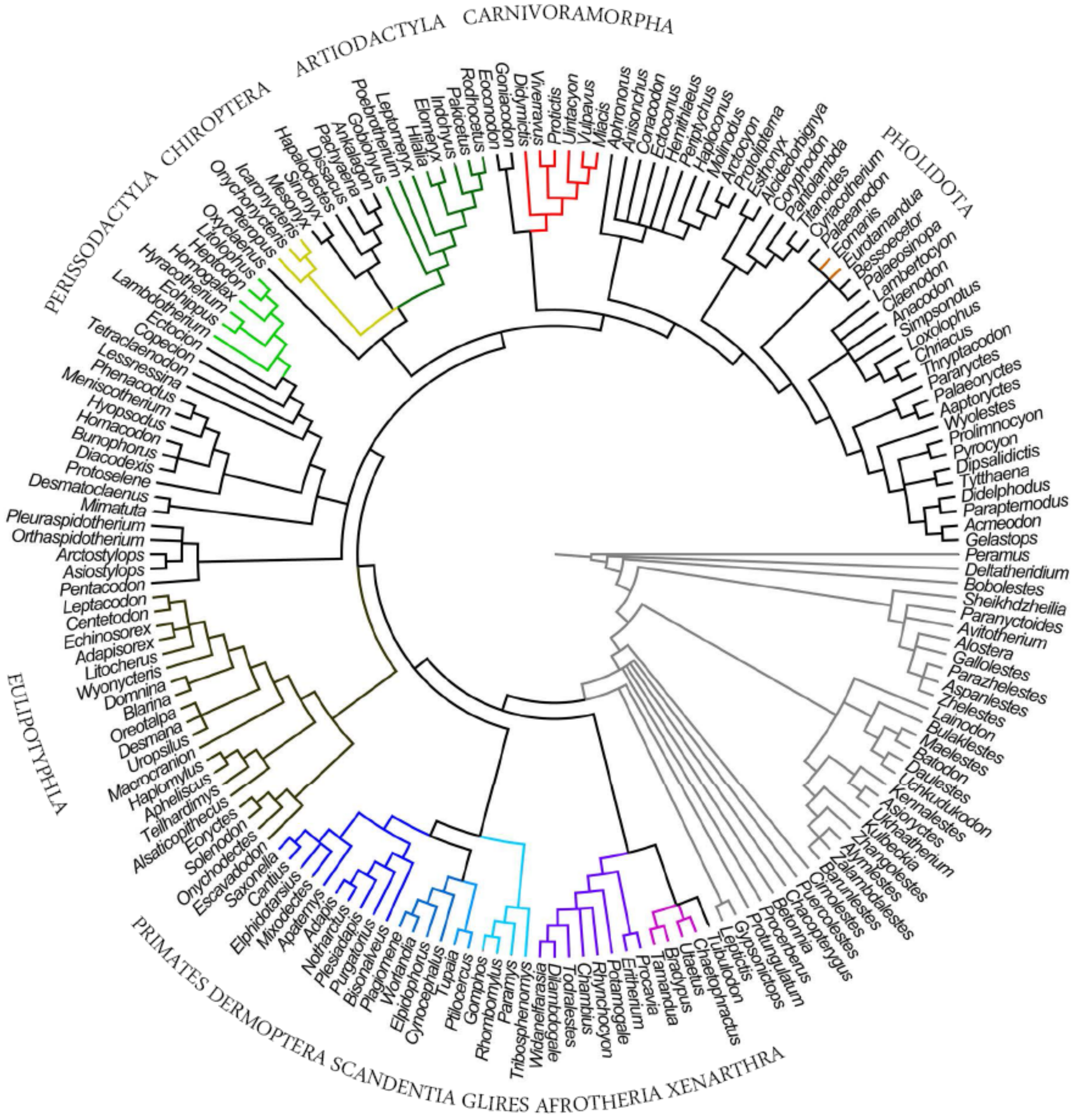


Figure 2.9 – Strict consensus of 20448 trees from the continuous dataset with *Purgatorius* constrained as a stem primate within one full step of the most parsimonious trees of length 8059.26802. Colours are as those in Figure 2.3.

Summaries of synapomorphies for consistently resolved clades of interest are included in the text below, with full lists for important relationships found in Appendix 2.5 (electronic supplementary information). The details of the common similarities and differences within the six constrained analyses are detailed below.

Stem placentals

In all analyses, *Protungulatum* was most parsimoniously reconstructed as a non-placental eutherian, contrary to previous suggestions that it represented the earliest crown placental, or that it was an arctocyonid "condylarth". Where *Purgatorius* was left unconstrained, it was found consistently as sister taxon to *Protungulatum*, as in Wible *et al.* (2007) with both taxa either immediately crownward, or immediately stemward, to a paraphyletic Leptictida. Zhelestidae, in line with most recent analyses of eutherian mammals, was found very basally on the stem as opposed to being a stem member of an 'ungulate' clade within the crown. Zalambdalestidae, too, was recovered as a monophyletic group of stem placentals in all analyses, agreeing with the majority of studies, and was supported by several unambiguous synapomorphies, including the development of an enlarged, procumbent lower first incisor with an extensive root, a more anterior position of the posteriormost mental foramen (below p3 rather than p4), the lack of an ectoflexus on any upper molar, an uneven distribution of enamel on the incisors, and the presence of a separate metaconid on the fourth lower premolar.

The Placental Root and Higher-Level Relationships

Molecular and morphological analyses have been equivocal in support for the three prevailing hypotheses for the placental root topology (e.g. Churakov *et al.* 2009). Here, in all analyses, a split between Atlantogenata and Boreoeutheria was favoured as the root of placental mammals, rather than either Xenarthra or Afrotheria being most basal among placental superorders, as has previously been hypothesised (Gaudin *et al.* 1996; Waddell, *et al.* 2001). This is consistent with many recent genetic and genomic analyses of placental mammals (Murphy, *et al.* 2007; Hallstrom, *et al.* 2007; Kuntner *et al.* 2011). Morphological synapomorphies for Atlantogenata were inconsistent depending on constraint, due to the shifting relationships of other taxa. Those which remain across the majority of analyses are dental, which poses problems for identifying these traits in edentulous taxa such as the majority of Xenarthra. Nonetheless, simplification of the upper molars by loss of the pre- and postcingula was here reconstructed as synapomorphic to Atlantogenata, as well as a vertical lingual face of the protocone, and the presence of a hypoconid on the second lower molar. In the DF and CF analyses, 26 and 25 synapomorphies respectively supported Atlantogenata, of which 21 were common to both (Appendix 2.5, electronic supplementary information). Examples of these are postcranial characters including an increase in the number of thoracic vertebrate, a rounded rather than ovoid radial head, and a shortened astragalar neck, as well as many additional losses in cheek tooth complexity. However, no taxon was consistently resolved on the stem of either Atlantogenata or Boreoeutheria. The North American and East Asian clade of Palaeogene herbivores Arctostylopidae was found on the Atlantogenatan stem in the DP and CE analyses, but in all other analyses, no taxon was found on the Atlantogenatan stem.

Although Laurasiatheria and Euarchontoglires were constrained to form monophyletic clades in all analyses, each was nonetheless supported by a number of unambiguous synapomorphies. Character transitions which consistently occurred at the base of Laurasiatheria include the movement of the foramen ovale to a medial position relative to the glenoid fossa, the opening of the cavum epiptericum, the loss of the hypotympanic sinus, and, where present, more distal re-entrant grooves on the molars. Euarchontoglires was supported unambiguously by an extended ectopterygoid process of the alisphenoid, an anteriorly expanded tegmen tympani, a small and shallow stapedius fossa, and a reduction to three sacral vertebrae from four.

Eulipotyphla was supported as the most basal extant order within Laurasiatheria in all constrained analyses, but the relationships among other laurasiatherian orders was more variable. The four remaining clades – Artiodactyla, Perissodactyla, Ferae (throughout this thesis taken to mean the smallest clade including Carnivora and Pholidota (Asher and Helgen 2010)) and Chiroptera – were reconstructed differently depending on the constraint applied. For example, in the DP, CP, DF, and CF analyses, Euungulata (Artiodactyla and Perissodactyla) was recovered, with Chiroptera closer to Ferae. Characters supporting Euungulata include a flattened ulnar facet on the radial head, the lack of a paraconid or preparacristid on the lower molars, and an elongate calcaneal tuber, while the Chiroptera-Ferae clade is supported by a loss of a postpalatine torus, a laterally exposed mastoid region, three sacral vertebrae, and an inferior petrosal sinus that is housed between the petrosal, basisphenoid and the basicranium. Conversely, in the DE and CE analyses, Perissodactyla was the next most basal clade to Eulipotyphla, and Chiroptera was closest to Artiodactyla, this latter relationship supported by the presence of a supraorbital process, an expanded tegmen tympani, and a keel on the posteroventral portion of the axis. The topology of Laurasiatheria had only little impact on the interpretation of several extinct groups, but the lack of resolution only perpetuates the current lack of understanding over higher-level Laurasiatherian interrelationships.

Cimolestidae

The cimolestids included in this analysis were found to be diphyletic in all eight analyses. One group, consisting of *Cimolestes*, *Procerberus*, *Chacopterygus*, *Betonnia*, and *Puercolestes*, was consistently placed in a relatively basal position on the eutherian stem. However, the cimolestid *Gelastops* was reconstructed as part of the broadly carnivorous radiation of mammals including palaeoryctidans, creodonts, and Ferae, falling out specifically with the palaeoryctidan *Acmeodon* and the mesonychid *Wyolestes*. While the position of *Gelastops* was consistent across analyses, the stem eutherian group of cimolestids was found to be paraphyletic with respect to more crownward taxa in five of the six analyses, and to be a monophyletic sister clade to zalambdalestids in the CE analysis.

Leptictida

The three leptictidans were not recovered as monophyletic in any analysis, but *Gypsonictops* and *Leptictis* were found to be sister taxa in all analyses, with synapomorphies including prominent premolar conules, a developed cristid obliqua, and the presence of a hypoconule on upper molars. This pairing was positioned as the sister taxon to crown Placentalia in both CF and DF analyses, and sister to a Placentalia-*Protungulatum* clade in other constrained analyses. *Prodiacodon* was variously found as a stem Atlantogenatan or also as a stem eutherian, rendering Leptictida either diphyletic (in the former case) or paraphyletic (in the latter).

"Condylarths"

Despite use of disparate constraints, there were several points of consistency across all or most analyses in the positions of the various "condylarth" clades. All major "archaic ungulate" groups were resolved within Laurasiatheria, with a division between broadly herbivorous taxa on the one hand and carnivorous-insectivorous ones on the other. Most of Phenacodontidae (*Tetraclaenodon*, *Copecion*, and *Ectocion*) was consistently resolved as paraphyletic with respect to Perissodactyla; this was one of the best supported relationships, even being recovered in unconstrained analyses. However, *Phenacodus* was itself placed among hyopsodontids in all analyses, and with the exception of the presence of a mesostyle, there was no single synapomorphy that is unambiguously associated with this node across all six constrained analyses. Nonetheless, several character states, such as a strong metalophid, highly molarised premolars and the loss of upper molar conular cristae are synapomorphies in a majority of analyses. Pleuraspidotheriidae was also consistently included towards the base of an ungulate group including Perissodactyla, and, sometimes, Artiodactyla.

Contrary to suggestions that Apheliscidae is related to Macroscelidea, apheliscids were here recovered in a basal position within Laurasiatheria, either sister to Eulipotyphla (CE), to Scrotifera (the clade comprised of all laurasiatherian orders except Eulipotyphla – CF, CP, DE, DF), or to Euungulata (DP). Hyopsodontids were, in CE and DE, found as sister to the Phenacodontidae-Perissodactyla clade. In CF, DF, CP, and DP, they were sister taxa to Artiodactyla. Periptychidae and Pantodonta were consistently found to be sister taxa, and were found in all analyses to be more closely related to Ferae and Chiroptera than to other Laurasiatherian orders, with the exception of CE, in which they formed a polytomy with the perissodactyl stem and with the remainder of Laurasiatheria.

Arctocyonidae was found to be diphyletic in DE, with triisodontids found to be stem carnivorans, and the remaining arctocyonids sister to the larger Carnivora-Creodonta clade. In DP it was resolved as the monophyletic sister taxon to Ferae, and in DF it was polyphyletic, with *Arctocyon* and *Loxolophus* sister to the Pantodonta-Periptychidae clade, *Goniacodon* and *Eoconodon* sister to a Carnivora-Mesonychia clade, and the remaining genera allied with creodonts and palaeoryctidans. In all analyses, the closest living relative was Carnivora, and sometimes also Pholidota.

Other Paleocene taxa

The close relationship between Creodonta and Carnivora was very consistently recovered, with other pseudocarnivorous genera such as *Gelastops*, *Acmeodon*, *Wyolestes* and *Didelphodus*, as well as Palaeoryctidae, also placed as close relatives to this grouping. Moreover, all analyses consistently favoured one or more palaeanodonts as sister taxa to Pholidota (represented here by *Eomanis* and *Eurotamandua*).

The enigmatic South American meridiungulates were represented in this study by the henricosbornid notoungulate *Simpsonotus* and the early litoptern *Protolipterna*. *Protolipterna* was resolved alongside archaic dichobunid artiodactyls in the DF, DP, CE, CF and CP analyses, and near chriacid arctocyonids in DE. *Simpsonotus*, however, had a less consistent position, being found next to Palaeanodonta in DF, CE and CP, but on the atlantogenatan stem with Arctostylopidae in DP, on the chiropteran stem with Arctostylopidae in CF, and close to Artiodactyla in DE. As the sampling in this study did not adequately capture the diversity of meridiungulates, which include at least five distinct and unusual clades, further work focusing on this group is certainly required to clarify their affinities. The relationships presented here provide a starting point from which a more detailed analysis of this group can proceed, by including these potential close relatives of the South American ungulates.

The relationships of Arctostylopidae are extremely poorly understood (Zack 2004), but they have been thought to be related to Glires or Notoungulata (Cifelli*, et al.* 1989), both of which were supported here – the former by DF, and the latter by CF and DP – and Artiodactyla (McKenna and Bell 1997), which was not supported in any of the analyses presented here. The characters that supported a sister taxon relationship with *Simpsonotus* or an Atlantogenata-*Simpsonotus* clade were related to simplification of the dentition, with reduced metacone, protocone, less distinct canines, reduction of the protocristid, and a more even-sized tooth row, while affiliation with Glires was supported by mandibular and postcranial characters such as a single mental foramen, a space between m3 and the coronoid process, and a rotated sustentacular facet of the astragalus. A more focused study of this enigmatic and rare family is required to resolve the character conflict here.

2(d)(ii) – *Templeton's Tests*

Templeton's Tests were used to compare the alternative topologies described above. The lengths of all constrained topologies were found to be significantly longer than those of unconstrained trees, with the latter bearing no relationship to the known topologies of placental mammal phylogenies derived from either molecular data, or indeed hypotheses deriving from comparative anatomy and morphological cladistic analyses at lower taxonomic levels. Morphological traits vary substantially in the degree to which they are evolutionarily plastic – some traits will be synapomorphic at ordinal level, and some at familial level. Maximum parsimony analysis treats each trait as identical, with no *a priori* hypothesis for the taxonomic level at which each trait is likely to be most informative. In the case of a large dataset such as this, which includes a broad ranging sample of a diverse clade, secondary loss or convergent evolution is more likely to be captured by the sampled taxa. Where this homoplasy occurs to a great extent, as is suggested here by the consistency indices of all sets of trees (Table 2.2), constraints can be implemented. These constraints to provide extrinsic information to help polarise the more homoplasious characters and ensure that character polarities reflect well-supported higher relationships. Morphological data contain highly phylogenetically informative information that allows the distinguishing of high-level clades through unambiguous synapomorphies, such as the presence of xenarthrous vertebrae in Xenarthra, but also includes characters which are more variable within high-level clades, such as the repeated evolution of hypercarnivory in carnivorans (Van Valkenburgh 1991). Given that a significant proportion of the characters are homoplastic (Table 2.2), a scaffold is useful for ensuring that established relationships are recovered. The constraints in these analyses were based upon well-established relationships that are consistently retrieved from molecular, lower taxonomic level morphological, and combined morphological-molecular analyses.

Table 2.3 – Results of Templeton's tests, comparing each set of topologies under both discrete and continuous datasets. Of all constrained topologies, the only comparison that was considered to be significantly different is that between the discrete and continuous reduced constraints under the discrete dataset.

DATASET	TOPOLOGY 1	TOPOLOGY 2	W	n	Z	P-VALUE (TWO-TAILED)
Continuous	CF	CP	1184	294	0.41	0.6816
Continuous	CF	CE	1071	327	0.31	0.7566
Continuous	CF	DF	1838	313	0.57	0.5687
Continuous	CF	DP	2207	305	0.72	0.4715
Continuous	CF	DE	2009	329	0.58	0.5619
Continuous	CP	CE	1451	345	0.39	0.6965
Continuous	CP	DF	370	201	0.22	0.8259
Continuous	CP	DP	1842	305	0.6	0.5485
Continuous	CP	DE	999	358	0.25	0.8026
Continuous	CE	DF	342	353	0.09	0.9283
Continuous	CE	DP	2856	353	0.74	0.4593
Continuous	CE	DE	2733	327	0.8	0.4237
Continuous	DF	DP	161	301	0.05	0.9601
Continuous	DF	DE	2389	360	0.6	0.5485
Continuous	DP	DE	5259	380	1.23	0.2187
Discrete	DF	DP	1049	296	0.36	0.7188
Discrete	DF	DE	4359	348	1.16	0.246
Discrete	DF	CF	439	306	0.14	0.8887
Discrete	DF	CP	1751	194	1.12	0.2627
Discrete	DF	CE	3334	339	0.92	0.3576
Discrete	DP	DE	5911	370	1.44	0.1499
Discrete	DP	CF	1397	302	0.46	0.6455
Discrete	DP	CP	2756	302	0.91	0.3628
Discrete	DP	CE	1865	346	0.5	0.6171
Discrete	DE	CF	5980	324	1.77	0.0767
Discrete	DE	CP	5623	348	1.5	0.1336
Discrete	DE	CE	7540	321	2.27	**0.0232**
Discrete	CF	CP	1613	284	0.58	0.5619
Discrete	CF	CE	2282	316	0.7	0.4839
Discrete	CP	CE	1274	334	0.36	0.7188

Among the constrained topologies, no significant differences were found in either discrete or continuous character optimisations using the same constraints (Table 2.3). For each dataset, no particular constraint resulted in significantly longer trees than any other constraint. Given the constraint, neither did treating continuous characters as continuous or discrete. Therefore, given that some constraint was necessary to enforce the relationships known from molecular and total evidence phylogenies, and the precise nature of the constraint does not alter the length of the most parsimonious trees significantly, additional constraints such as the presence of *Purgatorius* as a primate relative cannot be rejected as inappropriate. When different constraints and data types were compared in concert, significant differences were found between DE and CF, and between DE and CP under the discrete dataset, with the continuous topologies being significantly longer in each case. All other differences in length between combinations of dataset and constraint were not significant.

2(d)(iii) – *Relative Bremer Supports*

When the storage limit in TNT of 99,999 trees had been reached, the relative Bremer supports suggested that several of the nodes are relatively poorly supported across all trees. Relative Bremer support trees are viewable as supplementary files (Appendix 2.6, electronic supplementary information), as they contain too much detail to be conveniently displayed here. However, this lack of support in large part due to a few very unstable taxa, as identified by the "Pruned trees" option, which identifies taxa that, when removed, result in the resolution of polytomies. The taxa that were pruned for each analysis were as follows: CES – *Hilalia*, *Lainodon*, *Oxyclaenus*, *Lambertocyon*; CPS – *Prodiacodon*; CFS – *Centetodon*; DES – *Lainodon*, *Oreotalpa*; DPS – *Lainodon*, *Eoryctes*, *Molinodus*; DFS – *Molinodus*; DUS – *Lainodon*, *Pentacodon*. When relative Bremer supports were calculated after pruning these unstable taxa from the set of suboptimal topologies, the level of support increased markedly. In the CF analysis, many higher-level relationships are strongly supported, being found in all suboptimal topologies to the limit. This includes the placement of all "condylarths" within Laurasiatheria, the monophyly of Euungulata, the affinity of Phenacodontidae with Perissodactyla, and the affinity of Hyopsodontidae with Artiodactyla. Additionally, the placement of triisodontids with Arctocyonidae as a sister clade to Carnivora and Creodonta is very strongly supported. When *Eoryctes* is excluded, Atlantogenata is supported 100% of the time, as is the paraphyletic relationship of Leptictida with respect to crown Placentalia.

In the CE analysis, node support was in general weaker, although monophyly of many Paleocene clades was conserved. Phenacodontidae were, however, still strongly supported as stem perissodactyls. After excluding unstable taxa (*Lainodon* and *Hilalia*) from the CE analysis, Atlantogenata was well supported, but Laurasiatherian clades received very poor support compared with other analyses.

In the DF analysis, support values were generally higher than other analyses, even before pruning unstable taxa, with relatively good support for a Hyopsodontidae-Artiodactyla relationship, and very high support for an Arctocyonid-Creodont-Palaeanodontan clade. Atlantogenata, the Laurasiatherian affinity for "condylarths", the Phenacodontidae-Perissodactyla relationship, and a Triisodontidae-Carnivora relationship were also notably all supported. The DE and DP analyses were very stable once unstable taxa (*Lainodon*, *Macrocranion*, *Bisonalveus*, *Oreotalpa*, and *Chambius*) had been excluded from the strict consensus tree, with strong support for many higher-level relationships within the phylogeny.

Support for nodes within crown Placentalia were weaker when *Purgatorius* was constrained as a primate across placental nodes. In all analyses, the weakest area of support is within Ferae, where relative Bremer indicated almost equivocal support for the presence or absence of any given clade. The best-supported topologies are found in the DF analysis (Figure 2.4).

2(e) – ***Discussion***

2(e)(i) – *Resolving Placental Relationships*

While many relationships presented in this study are consistent across analyses, several remain poorly supported. Although *a posteriori* pruning of unstable taxa removes some of the uncertainty in relationships, there are several aspects of the tree that still remain to be confirmed with additional data. A phylogeny of a group with as much convergence as Placentalia will inevitably return nodes with relatively low support, but this broad and inclusive phylogenetic tree is an important step towards further refinement and clarification of the relationships and evolution of living and extinct placental mammals.

Among the topologies supported by these analyses, most support hypotheses that have been raised previously with varying levels of support. The nature of a wastebasket taxon, particularly one with such a long history as "Condylarthra", is that many hypotheses of internal and external relationships have been and are being put forward, based upon different lines of evidence. This study, in presenting the relationships supported by a broad skeleto-dental matrix combined with molecularly derived constraints, supports topologies which are largely consistent with at least some of the literature. While it must be acknowledged that many of the relationships presented in this paper will be controversial, it is largely because there is little consensus for the majority of the relationships of Paleocene placental mammals.

The plesiomorphic eutherians *Protungulatum* and *Purgatorius* are most parsimoniously resolved on the stem, except where constrained otherwise. This indicates, in the case of *Purgatorius*, that the tarsal characters which have been used to affine the genus with primates and their kin are perhaps convergent due to a similar, arboreal lifestyle. However, as Templeton's tests did not preclude alternative phylogenetic positions for either *Protungulatum* or *Purgatorius* within the crown, the hypothesis that these are crown placentals cannot be conclusively rejected.

This study strongly supports the polyphyly of "Condylarthra" and its status as a wastebasket taxon. However, several enigmatic Paleocene groups within this wastebasket, including Periptychidae, Pantodonta, and Mesonychia, have been resolved as monophyletic, as well as, for the most part, Arctocyonidae. Others, such as Phenacodontidae, Leptictida, and Cimolestidae are recovered as paraphyletic. The polyphyly of Hyopsodontidae, which has long been suspected (Zack*, et al.* 2005a; Cifelli 1983; Archibald 1998), is also supported here, with Pleuraspidotheriidae, Apheliscidae, and the 'true' hyopsodontids *Hyopsodus*, *Meniscotherium* and allies found to be entirely separate lineages.

This study also finds that a broad division can be drawn within Scrotifera between a loosely 'ungulatomorph' clade, including Artiodactyla, Perissodactyla, Hyopsodontidae, Phenacodontidae, and Pleuraspidotheriidae, and a remaining group of more insectivorous, omnivorous, and carnivorous taxa, including Chiroptera, Mesonychia, Palaeanodonta, Pholidota, Carnivora, Creodonta, Palaeoryctidae, and Arctocyonidae. Periptychidae and Pantodonta are more often within this latter grouping too, but are more equivocal in their placement, while Apheliscidae is occasionally reconstructed with Eulipotyphla.

The support for the relationship of Phenacodontidae to Perissodactyla is in agreement with the majority of the literature. The original definition of "Condylarthra" was originally as a subgroup of Perissodactyla, and was largely composed of phenacodontids (Cope 1884a; Rose 2006); phenacodontids and perissodactyls have been considered close relatives since (Radinsky 1966; Thewissen 1990; Zack 2009; Ladevèze*, et al.* 2010), although sometimes Phenacodontidae is thought to be sister to Altungulata (Kondrashov and Lucas 2012), a concept including perissodactyls as well as several afrotherian 'ungulates', and therefore in conflict with molecular topologies.

The placement of creodonts closer to pangolins than to carnivorans is typically not recovered by phylogenetic analyses. While Creodonta is today often thought of as a paraphyletic lineage leading to Carnivora (Flynn and Wesley-Hunt 2005), the distinctive carnivoran carnassial teeth are composed of the upper fourth premolar and the lower first molar, rather than solely molars as seen in Creodonta (Goswami 2010; Ungar 2010; Colbert and Morales 1991; Colbert 1933), suggesting a possible convergent acquisition of this phenotype. Additionally, monophyly of Creodonta is not always recovered (Polly 1996; Sole *et al.* 2009). A position within Ferae – the clade uniting Carnivora and Pholidota – is accepted (Smith and Smith 2001; MacIntyre 1966), but the relative positions of Pholidota, Carnivora, and Creodonta have been unclear.

Atlantogenata is strongly supported over Exafroplacentalia (Xenarthra + Boreoeutheria) or Epitheria (Afrotheria + Boreoeutheria) for the first time in an exclusively morphological analysis. While Atlantogenata has been supported by a wide range of molecular studies (e.g. Morgan*, et al.* 2013; Prasad *et al.* 2008; Song *et al.* 2012; Hallstrom and Janke 2008), analyses including morphology have tended to favour a xenarthran root (O'Leary*, et al.* 2013; Gaudin*, et al.* 1996). The concordance between topologies derived from previous molecular studies and this morphological study suggests that a solution to the conflict between data sources may be possible, despite the degree of convergence that is clearly present in the placental mammal phylogeny. Although molecular constraints were implemented in this tree, the topology at the root of Placentalia was left unconstrained, and Atlantogenata was unambiguously favoured.

More and more evidence is accruing that the diversification of the Laurasiatherian orders occurred extremely rapidly, (Zhou*, et al.* 2012; Hallstrom and Janke 2008) such that incomplete lineage sorting has been invoked as an explanation for lack of resolution (Hallstrom and Janke 2010). With the inclusion of Paleocene taxa, we have a window into the time during which this diversification was occurring, and are able to break the methodological constraints of using only extant data to peer back at events whose effects on the genome, have, over time, been overwritten and obscured. Use of molecular constraints which can overcome problems of homoplasy in morphological data help to reveal past patterns (Davalos *et al.* 2014), meaning that integration of palaeontological and neontological data is essential to answer questions of ancient relationships. This analysis represents an important first step in untangling the relationships of these extinct clades, and to understand the evolutionary and ecological context of the radiation of placental mammals. Later chapters will investigate the rates of morphological character evolution and changes in morphological disparity over the K-Pg boundary in order to ascertain whether the end-Cretaceous mass extinction had a discernible effect on the macroevolutionary patterns within eutherian mammals.

Some taxa are found in highly divergent positions on the phylogeny depending on analysis, and yet are very strongly supported, with relative Bremer supports (RBS) of 100 at the level of suboptimality measured. This is most apparent in the case of the henricosbornid notoungulate *Simpsonotus*, which is well supported as a stem artiodactyl (DP, RBS = 100), and a stem pangolin (DF, RBS=100) Additionally, it was less well resolved as a basal arctocyonid (CP, RBS=2), a stem bat alongside arctostylopids and mesonychids (CF, RBS=9), a stem pangolin again (CE, RBS=1) or a basal palaeanodont (DE, RBS=20). While consistently within Laurasiatheria, these positions are extremely morphologically and phylogenetically distinct. In this particular case, *Simpsonotus* is the only notoungulate represented in the data matrix, and is only known from a skull. Cladistic analysis of a single incomplete notoungulate, in a data matrix primarily designed to assess the relationships of "condylarths" has perhaps resulted in a limited set of characters that can affine it to any given close relative. Although henricosbornids are the most basal of notoungulates, their affinities with living mammals have not been clear from comparative anatomy – until recently (Welker*, et al.* 2015) the only data available. With two equally well supported topologies here for a taxon such as *Simpsonotus*, where the clade is present in all sampled suboptimal trees, analysis of the characters which support each node is required to distinguish alternative hypotheses.

Characters that support *Simpsonotus* close to artiodactyls are those which are indicative of an herbivorous ecology, with increases in lophs and crown height, whereas the characters that link *Simpsonotus* to palaeanodonts and pangolins are primarily reversals to primitive eutherian character states, such as a relatively lingual position of the paraconid.

Any phylogenetic topology is not in itself a result, but a hypothesis that comes from the data. Only by qualitative and qualitative assessment of the anatomy and by testing the implications of that hypothesis can a better picture of the relationships of the clade of interest be revealed. Where there is conflicting information, further work is needed to determine why one topology might be considered more reliable than another.

2(e)(ii) – *Dating the Origin of Placentalia*

As noted in previous studies including *Protungulatum* (O'Leary*, et al.* 2013; Wible*, et al.* 2007; Archibald *et al.* 2011), the phylogenetic position of that taxon is critical to the interpretation of the oldest known members of crown Placentalia. *Protungulatum* is known from both Paleocene and Cretaceous formations (Archibald*, et al.* 2011), and as such, the presence of *Protungulatum* within crown Placentalia would be evidence that the origin of placental mammals predates the K-Pg boundary. Where *Protungulatum* is resolved as a stem placental, the conclusions are more equivocal, as neither a Cretaceous nor a Paleocene origin for placental mammals can be ruled out. Nevertheless, given that the earliest "condylarths" are known from the first few hundred thousand years of the Paleocene (Lofgren*, et al.* 2004), and are consistently resolved not just within Placentalia but within Laurasiatheria, an explosive increase in evolutionary rate would be necessary for a radiation to occur entirely within the Paleocene. Estimates from extant taxa require a five-fold increase in background rates of morphological evolution to allow the placental mammal origin to be less than 66 million years ago (Beck and Lee 2014). This new topology, with broad sampling of temporally relevant taxa, makes it possible to robustly analyse the timing and rate of placental mammal divergences using Bayesian and maximum likelihood methods, which will be presented in Chapter Three.

Identifying the sister taxon to crown Placentalia is also relevant for dating its origin and estimating the effect of the mass extinction on mammal diversity. The sister taxon to crown Placentalia varied among analyses in this study, but was always either a member of the now paraphyletic Leptictida – *Gypsonictops* + *Leptictis* or *Prodiacodon*, with the lattermost found on the stem of Atlantogenata in some most parsimonious trees, or a *Protungulatum*-*Purgatorius* clade, in analyses where *Purgatorius* was not constrained as a stem primate. *Gypsonictops*, the oldest and most rootward of the three leptictids, is known from the Late Cretaceous, while the other two genera are Paleocene. The presence of Cimolestidae and *Leptictis* on the stem implies that, minimally, three lineages of eutherian mammals (Placentalia, Cimolestidae, and a subgroup of Leptictida) survived the end-Cretaceous mass extinction; more if Placentalia had already begun to diverge in the Late Cretaceous.

Additionally, there are several well-supported relationships within Placentalia that provide minimum estimates for the divergence of orders which, based simply on first appearance dates, differ markedly in some cases from previous estimates. The earliest perissodactyl, *Hyracotherium*, is known from the earliest Eocene (e.g. Smith and Smith 2003), giving a minimum divergence date of Perissodactyla from its nearest relatives of 56 Ma. However, the earliest phenacodontid, *Tetraclaenodon*, is known from the Torrejonian (e.g. Scott *et al.* 2013). With a close relationship between Perissodactyla and Phenacodontidae, the minimum divergence date of Perissodactyla from its closest extant relatives would be 63 Ma, in the Early Paleocene. Such changes to internal estimates of divergence dates will impact further on the predicted date of divergence of crown Placentalia. The deep nesting within Laurasiatheria of Periptychidae, one of the earliest definitively crown placental clades from the first faunal substage of the Paleocene, would seem to support the hypothesis that either a rapid increase in evolutionary rate took place, or the origin of placental mammals predated the end-Cretaceous mass extinction.

2(f) – *Conclusions*

1 – An Atlantogenata-Boreoeutheria split is favoured over Epitheria or Exafroplacentalia at the root of Placentalia. While relatively common in molecular systematics, this topology is rarely supported using maximum parsimony and morphological data.

2 – No definitive crown placental mammal has yet been found from the Cretaceous, as *Protungulatum* is resolved as a stem eutherian, and therefore the Cretaceous occurrence of *Protungulatum* cannot be considered definitive proof of the Cretaceous origin for placental mammals.

3 – Cimolestidae and Leptictida are here resolved as stem eutherians, and both are paraphyletic with respect to crown Placentalia. The hypothesised relationship between Cimolestidae and Pantodonta is therefore not supported here.

4 – All "condylarth" taxa are laurasiatherian, with no taxa favoured as a stem paenungulate. The origin of the Afrotherian 'ungulates' therefore remains unresolved, and although some 'ungulate' taxa such as *Simpsonotus* are occasionally recovered on the stem of Afrotheria, the pattern is inconsistent and requires further analysis with a more representative sample of South American ungulates.

5 – Phenacodontidae is consistently resolved as a paraphyletic group from which Perissodactyla emerge, although the precise position of *Phenacodus* is consistently more parsimoniously resolved with members of Hyopsodontidae.

6 – Periptychidae and Pantodonta are sister taxa, and are more closely related to Ferae and Chiroptera than to Perissodactyla or Artiodactyla.

7 – Where there is lack of support for the relationships of Paleocene mammals, this is in large part due to the behaviour of a few highly unstable taxa.

CHAPTER THREE

DATING THE ORIGIN OF PLACENTAL MAMMALS AND RATES OF EVOLUTION OVER THE K-PG BOUNDARY

3(a) - *Abstract*

The effect of the end-Cretaceous (K-Pg) mass extinction on the evolution of many groups, including placental mammals, has been hotly debated. The fossil record suggests a sudden adaptive radiation of placentals immediately postdating the event, but molecular data implies little change in either clade origination rates or rates of character evolution. Here I use maximum likelihood methods to date a recent phylogenetic analysis of largely Cretaceous and Paleocene mammals and show that the crown group of Placentalia originated in the late Cretaceous, but most intraordinal diversification occurred during the earliest Paleocene. This analysis reconstructs fewer than ten placental mammal lineages crossing the K-Pg boundary. Moreover, I show that rates of morphological evolution in the five million year interval after the K-Pg mass extinction are three times higher than background rates during the Cretaceous. This suggests that the K-Pg mass extinction had a marked impact on the morphological evolution of placental mammals, supporting the view that an adaptive radiation occurred as lineages invaded vacant ecological niches during the earliest Paleocene.

3(b) - *Background*

The end-Cretaceous mass extinction occurred approximately 66 million years ago (hereafter, mya), and was the second largest extinction event in the history of life so far, wiping out some 75% of terrestrial species (Jablonski and Chaloner 1994). It marks a shift from non-avian dinosaur-dominated fauna (Brusatte *et al.* 2014) to purportedly mammal-dominated fauna (despite the greater modern taxonomic diversity of birds) (Wilson and Reeder 2005; Gaston and Blackburn 1997), and is therefore often thought of as the start of the so-called 'Age of Mammals' (Rose 2006). Within Mammalia, however, several groups of eutherian and metatherian mammals were also extinguished, with metatherian lineages seemingly more highly affected (Williamson *et al.* 2014). As there are no known unambiguous placental mammal fossils from the Mesozoic, a statement which remains true after the analyses of Chapter Two, the end-Cretaceous has been thought of as a turning point in mammal evolution, sparking an adaptive radiation at the beginning of the Paleocene (the ten million year (Ma) interval immediately following the mass extinction) that ultimately resulted in the diversity of mammals present today (Foote *et al.* 1999).

Most recent analyses dating the origins of Placentalia have focused on molecular data. The traditional use of clock or clock-like methods to reconstruct the origination dates of Placentalia, as well as placental subclades, have historically recovered dates in the 'mid' or even Early Cretaceous (Bininda-Emonds*, et al.* 2007; Springer*, et al.* 2003; Kumar and Hedges 1998; Eizirik *et al.* 2001), suggesting that the first crown-group members of Placentalia should be found before the end-Cretaceous mass extinction. However, as this is not borne out by the fossil record, either the fossil record must be substantially incomplete, or such reconstructed dates are unreasonably old. Although recent genomic analyses (dos Reis*, et al.* 2012) have reconstructed the youngest molecular estimates to date, and in general the reconstructed ages are progressively decreasing (Goswami 2012), they are still considered to be far older than supported by the fossil record, and run contrary to the conclusions of several fossil-based analyses, which have supported an origin close to the end-Cretaceous mass extinction (O'Leary*, et al.* 2013; Wible*, et al.* 2009). This is often due to the interpretation that, because there is no undisputed crown placental fossil from earlier than the Paleocene, the crown group must have originated in the Paleocene.

Molecular date estimates are by necessity calibrated using the age of well-resolved fossil species. However, because of the historic lack of resolution of the higher-level phylogeny of placental mammals, calibration points tend to be deeply nested within Placentalia, rather than capturing the dates of, for example, the superordinal divergences. Moreover, even in the case of the recent genomic analysis by dos Reis and colleagues (2012), calibration points were highly biased in clade selection towards Euarchontoglires, and towards Primates in general, with 9 of 13 calibration points within that single superorder. Nonetheless, fossils provide minimum age estimates only for any clade containing that fossil, and the clade is unlikely to be exactly as old as the oldest fossil member of the clade. Indeed, the conclusion of O'Leary and colleagues (O'Leary*, et al.* 2013) that crown Placentalia originated 64.85 mya has been criticised as relying on inappropriate and 'unjustified' methods for reconstructing internal node dates for the phylogeny (dos Reis *et al.* 2014).

An additional important consideration when assessing the timescale of placental evolution is the impact on evolutionary rate (Beck and Lee 2014). However, previous analyses of evolutionary rates have typically considered only single, continuous characters, which risks exclusion of potentially important morphological change. By including information regarding total amounts of morphological evolutionary change, two major questions may be answered: firstly, was there an increase associated with the origin of crown Placentalia, as would be expected with a key innovation that sparked a radiation, and, secondly, was there an increase in rate of evolution associated with the end-Cretaceous mass extinction, as would be expected under a model of ecological release?

Despite the popular conception that the K-Pg mass extinction resulted in an explosive radiation for mammals, few studies of mammals have conclusively shown any discernible change in evolutionary parameters at the end-Cretaceous mass extinction. Indeed, several studies have found no difference between the latest

Cretaceous and the earliest Paleocene in either lineage accumulation rate (Bininda-Emonds*, et al.* 2007; Meredith*, et al.* 2011) or body size evolution (Venditti*, et al.* 2011), a pattern which has also been recovered from molecular analyses of birds and acanthomorph teleosts (Near *et al.* 2013; Brown *et al.* 2008).

Another study found that the rate of body size evolution in placental mammals decreased at the end-Cretaceous mass extinction, with a change in the mode of evolution, representing a release of constraints previously imposed primarily by non-avian dinosaurs (Slater 2013). Certainly, the dawn of the Cenozoic brought a shift in mean body size for mammals (Alroy 1999). Additionally, a local-level faunal study showed a dramatic increase in the rate of per-lineage extinction at the last faunal substage of the Cretaceous, and a similarly large increase in per-lineage origination rates in the first faunal substage of the Paleocene (Wilson 2014). However, with the exception of this last example, few studies have included Paleocene taxa as a significant proportion of the data, despite such taxa representing the very forms that would have contributed to the putative adaptive radiation.

Here, I present a fossil-based analysis of the effect of the end-Cretaceous mass extinction on placental evolution. Specifically, I use the trees generated in Chapter Two to date the nodes using the most recent stochastic techniques (Bapst 2013), and provide answers to two major outstanding questions in placental mammal evolution: when did crown Placentalia originate, and was there a change in rates of discrete character evolution during the late Cretaceous and early Palaeogene?

3(c) – ***Methods***

The R (R Development Core Team 2010) code used to run all analyses in this chapter is available as supplementary information (Appendix 2.7, electronic supplementary information). Stage level time bins and stage-based taxon ranges for dating are provided here (Table 3.1, 3.2).

3(c)(i) – *Selecting a tree*

The phylogenies presented in Chapter Two represent the largest study to date to focus on the mammals of the Paleocene and Eocene, as well as a substantial sample of Cretaceous mammals. The advantages of using the results of such a study in an analysis concerning macroevolutionary patterns around the end-Cretaceous mass extinction are manifold. Firstly, and most importantly, the taxa sampled are proximal in time to the extinction event in question, meaning that rates of change are being measured semi-directly, rather than being inferred across several tens of millions of years of subsequent evolution, as would be the case for a tree including only extant taxa. Secondly, by including taxa which belong to groups with no living descendants, the effect can be measured across Eutheria, that is, avoiding the omission of those groups (such as Leptictida) that survived for several more epochs

Table 3.1 – Dates of the Cretaceous geological stages and Cenozoic North American Land Mammal Ages as used for dating the topologies and determining taxon occurrences.

STAGE	START TIME	END TIME	STAGE	START TIME	END TIME
BERRIASIAN	145	139.8	TIFFANIAN	60.2	56.8
VALANGINIAN	139.8	132.9	CLARKFORKIAN	56.8	55.8
HAUTERIVIAN	132.9	129.4	WASATCHIAN	55.8	50.3
BARREMIAN	129.4	125	BRIDGERIAN	50.3	46.2
APTIAN	125	113	UINTAN	46.2	42
ALBIAN	113	100.5	DUCHESNEAN	42	38
CENOMANIAN	100.5	93.9	CHADRONIAN	38	33.9
TURONIAN	93.9	89.8	ORELLAN	33.9	30.8
CONIACIAN	89.8	86.3	ARIKAREEAN	30.8	20.6
SANTONIAN	86.3	83.6	HEMINGFORDIAN	20.6	16.3
CAMPANIAN	83.6	72.1	BARSTOVIAN	16.3	13.6
MAASTRICHTIAN	72.1	66	CLARENDONIAN	13.6	10.3
PUERCAN	66	63.3	HEMPHILLIAN	10.3	4.9
TORREJONIAN	63.3	60.2	BLANCAN TO RECENT	4.9	0

before going extinct. The use of primarily extant taxa in reconstructing the past would result in a potentially tautological conclusion – there was no increase in extinction rates in those taxa which did not go extinct – and risks biasing interpretation of ancient events by only considering the taxa whose descendants happen to exist in that arbitrarily distant future that we call the present. Thirdly, the tree is derived from a single analysis of 177 taxa – the largest taxonomic sample in any morphological analysis of placental mammal phylogeny to date – meaning that the topology includes a wide variety of taxa, but relies on direct analysis of characters, thereby avoiding some of the issues of loss of phylogenetic signal and lack of resolution associated with supertree methods (Gatesy *et al.* 2002; McMorris and Wilkinson 2011; Kupczok *et al.* 2010).

Table 3.2 – Occurrences of each genus in this analysis in the time bins from Table 3.1. Stage 1 is the Berriasian, Stage 12 the Maastrichtian, Stage 13 the Puercan, and so on.

TAXON	FIRST STAGE	LAST STAGE	TAXON	FIRST STAGE	LAST STAGE
Peramus	1	1	*Mimatuta*	13	13
Deltatheridium	11	12	*Desmatoclaenus*	13	15
Sheikhdzheilia	6	7	*Protoselene*	13	15
Avitotherium	11	11	*Bunophorus*	17	18
Gallolestes	11	11	*Diacodexis*	17	18
Alostera	11	12	*Homacodon*	18	20
Parazhelestes	9	9	*Hyopsodus*	16	20
Aspanlestes	9	11	*Meniscotherium*	17	17
Zhelestes	8	9	*Phenacodus*	14	18
Paranyctoides	8	12	*Macrocranion*	15	20
Batodon	11	12	*Alsaticopithecus*	18	18
Maelestes	11	11	*Teilhardimys*	15	18
Bobolestes	6	7	*Apheliscus*	15	17
Bulaklestes	9	9	*Haplomylus*	15	19
Daulestes	8	9	*Hilalia*	18	18
Uchkudukodon	9	9	*Orthaspidotherium*	15	15
Kennalestes	9	11	*Pleuraspidotherium*	15	15
Asioryctes	11	11	*Poebrotherium*	21	23
Ukhaatherium	11	11	*Gobiohyus*	18	21
Kulbeckia	9	10	*Leptomeryx*	21	23
Lainodon	11	11	*Elomeryx*	21	24
Zhangolestes	5	7	*Indohyus*	18	20
Barunlestes	11	11	*Pakicetus*	17	19

Alymlestes	11	11	*Rodhocetus*	19	19
Zalambdalestes	11	11	*Aphronorus*	13	16
Cimolestes	11	15	*Pentacodon*	14	15
Puercolestes	13	13	*Conacodon*	13	13
Betonnia	13	13	*Anisonchus*	13	15
Eoryctes	17	17	*Periptychus*	13	15
Chacopterygus	13	13	*Ectoconus*	13	13
Procerberus	13	14	*Hemithlaeus*	13	13
Purgatorius	13	15	*Esthonyx*	16	18
Protungulatum	12	13	*Alcidedorbignya*	13	13
Gypsonictops	11	12	*Coryphodon*	16	18
Leptictis	20	22	*Pantolambda*	14	15
Prodiacodon	13	17	*Titanoides*	15	16
Asiostylops	14	14	*Cyriacotherium*	15	16
Arctostylops	15	16	*Lambdotherium*	17	18
Chaetophractus	26	28	*Litolophus*	16	16
Utaetus	15	15	*Molinodus*	13	13
Bradypus	28	28	*Haploconus*	13	14
Tamandua	28	28	*Tetraclaenodon*	14	15
Procavia	27	28	*Copecion*	15	18
Eritherium	15	15	*Ectocion*	14	18
Potamogale	28	28	*Eohippus*	17	17
Adapisorex	14	16	*Hyracotherium*	17	17
Rhynchocyon	23	28	*Homogalax*	17	17
Chambius	16	20	*Heptodon*	17	17
Todralestes	16	18	*Oxyclaenus*	13	14
Dilambdogale	21	21	*Loxolophus*	13	14
Widanelfarasia	22	22	*Eoconodon*	13	13
Lessnessina	17	17	*Goniacodon*	13	15
Tribosphenomys	15	16	*Hapalodectes*	15	18
Paramys	16	21	*Ankalagon*	14	14
Rhombomylus	17	17	*Pachyaena*	15	17
Gomphos	17	17	*Dissacus*	13	17
Ptilocercus	28	28	*Mesonyx*	18	19
Tupaia	25	28	*Sinonyx*	16	16
Cynocephalus	28	28	*Arctocyon*	14	15
Elpidophorus	14	15	*Claenodon*	14	15
Worlandia	16	16	*Anacodon*	15	18
Plagiomene	16	17	*Thryptacodon*	14	17
Bisonalveus	15	15	*Chriacus*	13	17
Notharctus	17	19	*Onychonycteris*	17	17
Adapis	20	21	*Icaronycteris*	16	18
Apatemys	17	21	*Didymictis*	15	19
Mixodectes	13	15	*Viverravus*	15	19
Elphidotarsius	14	15	*Protictis*	14	19
Cantius	17	19	*Uintacyon*	15	19

Saxonella	15	15	*Vulpavus*	15	20
Lambertocyon	15	16	*Miacis*	17	21
Escavadodon	14	14	*Wyolestes*	17	17
Onychodectes	13	13	*Prolimnocyon*	16	18
Didelphodus	17	20	*Pyrocyon*	17	17
Acmeodon	14	15	*Dipsalidictis*	16	17
Gelastops	13	15	*Tytthaena*	15	16
Solenodon	28	28	*Bessoecetor*	14	15
Parapternodus	17	17	*Palaeosinopa*	15	18
Leptacodon	13	17	*Pararyctes*	13	17
Wyonycteris	16	17	*Palaeoryctes*	13	16
Litocherus	14	15	*Aaptoryctes*	15	16
Centetodon	17	23	*Eurotamandua*	18	18
Blarina	28	28	*Palaeanodon*	16	17
Tubulodon	17	17	*Eomanis*	18	18
Domnina	19	23	*Pteropus*	28	28
Echinosorex	28	28	*Plesiadapis*	14	17
Uropsilus	28	28	*Simpsonotus*	15	15
Desmana	27	28	*Protolipterna*	15	15
Oreotalpa	21	21			

The data matrix from Chapter Two was used to generate sixteen sets of trees. In this chapter, the six sets of MPTs from constrained analyses – CFO, CEO, CPO, DFO, DEO, DPO – were used, totalling 643 most parsimonious trees. Further, as many results included trees with lengths specific to one or more decimal points, suboptimal topologies within a single full step of the most parsimonious trees were used in all analyses, in order to test over a wider variety of plausible evolutionary relationships – CFS, CES, CPS, DFS, DES, and DPS. Each set is derived from a different level of constraint constructed from the consensus phylogeny of extant placentals. This constraint minimally included the monophyly of each of the four superorders of placental mammals – Afrotheria (e.g. elephants, hyraxes, tenrecs, aardvarks), Xenarthra (sloths, armadillos, anteaters), Laurasiatheria (e.g. cats, bats, rhinoceroses, whales, shrews, pangolins), and Euarchontoglires (e.g. flying lemurs, tree shrews, rodents, rabbits, primates). Some additional constraints were imposed within each clade – for example, the division within Euarchontoglires between Glires (rodents, rabbits, pikas, hares) and Euarchonta (tree shrews, flying lemurs, primates). Laurasiatheria and Euarchontoglires were also constrained as sister taxa in the clade Boreoeutheria to the exclusion of Afrotheria and Xenarthra. Here, I analyse each of the six sets of trees separately, to determine whether the results are robust to the variation in topologies generated from these analyses.

3(c)(ii) – *Dating the phylogenies*

I dated the morphology-derived phylogenies using a stochastic method, "cal3" (Bapst 2013) which relies on the calculation of three rates: rate of sampling, which is a measure of the per-time probability of sampling a particular genus; rate of diversification, which is a measure of the rate of origin of taxa through time; and rate of extinction, which is a measure of the rate at which taxa disappear. This approach has been found to be significantly better than alternative methods typically used for estimating divergence dates and time-calibrating phylogenies for morphological and fossil-based datasets (Bapst 2014). For time bins, I used Cretaceous stages and Cenozoic North American Land Mammal Ages (NALMAs). I assigned first and last appearance time bins to each taxon, and analysed the strict consensus of each phylogeny.

When dating the phylogenies, polytomies were resolved randomly. For the six consensus phylogenies of the suboptimal trees, several large polytomies existed, due in large part to the existence of one or a few unstable taxa such as *Lainodon*, for which few characters could be scored. As a result, random resolution of polytomies produced several topologies that were not present in any of the trees that were used to make up the consensus. By testing several topologies, derived from multiple analyses, the sensitivity of the rate results to markedly different topologies could be tested. Polytomies within the six optimal sets of trees generally included only very few taxa, and tended to be closer to the tips; unusual topologies generated from randomisation would therefore be expected to have very little impact on any macroevolutionary pattern.

The taxonomic sample fairly represents the eutherian fossil record from the Cretaceous and Paleocene. Of the eutherian families, 67% of those from the Cretaceous are sampled, and 62% of Paleocene families. However, the numerical dominance of Paleocene taxa may have resulted in an overestimation of the sampling rate the Cretaceous fossil record. In order to test the effect of the assumed sampling rate, the calculations were rerun with an assumed sampling rate of 0.5% per million years. This is a highly conservative estimate of the completeness of at least the earliest Cenozoic mammalian fossil record, which has been estimated as approximately 40% for an interval length of one lineage million years (Foote and Raup 1996).

3(c)(iii) – *Calculating evolutionary rates*

Most analyses of how rates of morphological evolution change across the placental mammal phylogeny focus solely on a single character – typically continuous in nature, such as body size (Cooper and Purvis 2010; Evans *et al.* 2012) – and assess how that character changes over time. However, any single parameter is not necessarily a good descriptor of how the overall complement of morphological features shifts in time. If the end-Cretaceous extinction event had no effect on one character trait, that does not preclude radical changes in the evolution of other traits. As body size is correlated with several important variables concerned with life history and ecology (Damuth 1981; Gillooly *et al.* 2002; Kleiber 1947; McClain and Boyer 2009), it has typically been thought to be a useful and relatively easily measured indicator of the evolution of new niche occupation. It has therefore commonly been used in evolutionary studies (Benson *et al.* 2014a; Butler and Goswami 2008; Cooper and Purvis 2010), but it is still at least one stage removed from the raw changes themselves, and might not be correlated with other important morphological transitions. When attempting to understand the overall evolution of a group, it is perhaps more useful to assess the rate of change of a broad suite of characters, whether continuous or discrete. This is especially true during periods of adaptive radiation or dramatic evolutionary change, where selection pressures act in novel and sundry directions. I therefore apply methods to assess rates of evolution across the discrete characters that were used to generate the trees.

Where a character is discrete, either by definition of the character states or by necessity, it is not possible to measure the rate of change as easily as for continuous characters, because there are typically only two states, which means a change either occurs, or does not, with no possible gradation in between. While it might be theoretically possible to quantify the overall shape of the feature and measure, for example, the position of a shifting foramen through time, the required sample sizes to overcome both gaps in the fossil record and intraspecific variation are high enough to make this impractical. Moreover, those gaps in the fossil record may result in an apparent sudden jump from one state to another, missing out the crucial period of transition in the tradition of the punctuated equilibrists (Gould and Eldredge 1977), and preventing full identification of the variation. In fact, where characters follow the ideal scenario for phylogenetic analysis – changing only at a single node such that it represents an unambiguous synapomorphy for a subset of the tree – measuring rate of change of that character is impossible, because there is a single shift across the tree. More often this is not the case, as many characters possess at least some degree of homoplasy, but since any given branch can only ever, under all character optimisation protocols, have one change for any single character, assessing rates of evolution for individual discrete characters is impractical. However, taking a suite of discretised characters allows simultaneous optimisation of multiple transitions across the tree. Each character will have its own distribution of character state changes, and if these changes are summed for each branch across all characters, an estimation of rate of evolution on any given branch can be produced, being defined as the number of character state transitions per lineage million years.

Further, by using a dated phylogeny, it is possible to time-bin those branches and measure average rates of change over geological time.

I calculated rates of discrete character evolution in three ways, implementing the methods described in Lloyd *et al.* (Lloyd *et al.* 2012), and formalised in the freely available R package Claddis (Lloyd 2014). Rates of evolution were defined as the number of discrete character transitions per million years. As such, character transitions were optimised unambiguously using maximum parsimony. Those characters which were treated as ordered in the original data matrix were also ordered for this analysis, and character weightings were also preserved between analyses. It has been shown that the precise method of character optimisation has little effect on the degree of homoplasy in the tree (Agnarsson and Miller 2008). However, ACCTRAN will tend to place character states early on in the tree, disproportionately increasing rates of evolution on the stem, while DELTRAN will tend to put character change nearer the tips, increasing rates of evolution disproportionately within the crown. As a result, it is here considered most informative to only use unambiguous character transitions. For each of the twelve sets of dated phylogenies (ie both optimal and suboptimal), a sample of 50 trees was used to calculate evolutionary rates, giving a total sample of 600 dated phylogenies with associated evolutionary rates.

Firstly, the rates of individual branches were compared with a null hypothesis of equal rates of evolution across the tree, and those branches with significantly high or low rates of evolution were identified. In order to do this, the summed duration of all branches on the tree was calculated and considered to represent a continuum between 0 and 1, with each branch assigned to some percentage of that continuum in proportion to temporal duration. Randomly determined values between 0 and 1 were then drawn, with the same number of repetitions as optimised character transitions. Each randomly drawn number represents an expected character transition. Given the null hypothesis of an equal rate model, the number of character transitions on a branch will be proportional to the temporal duration of that branch.

For each branch, this procedure was repeated 1000 times. If a branch had more observed characters than expected (predicted by the randomisation) in at least 95% of the repetitions, that branch was considered to have significantly higher evolutionary rates than would be expected given a uniform rate across the tree. Those branches with rates significantly deviating from the null hypothesis were then identified to establish whether particular regions of the phylogeny contained branches of consistently higher rates of evolution.

Secondly, nodes were identified that subtended clades for which the average evolutionary rate differed significantly from the rest of the tree. At such nodes, it can be inferred that there is some intrinsic shift in background evolutionary rate, whether representing the onset of some key innovation or changing extrinsic circumstances.

Finally, rates of evolution were compiled across different time bins. Time bins used were geological stages for the Cretaceous and North American Land Mammal Ages for the Cenozoic. This distinction reflects the bias in geographic distribution of Palaeogene mammals in favour of North America, and the necessity as part of the available methodology of binning all taxa into known stages. By using NALMAs, uncertainty in dating of first and last appearances of individual genera can be addressed while still minimising the error introduced by inclusion of taxa which are known from stratigraphic bounds that do not wholly overlap with the defined bins. To assess the differences between time bins, the rate calculated for each branch within a given time bin were compiled. Because of the very short branch lengths sometimes calculated by the dating analysis, the median of these branch rates was preferred to the mean, as it is less sensitive to outliers. Median absolute deviation was calculated as a measure of error.

3(d) – *Results*

3(d)(i) – *Dating the Origin of Placentalia*

Crown Placentalia was estimated to have diverged in the latest Cretaceous (Figure 3.1, Table 3.3), contrary to the recent conclusions of O'Leary *et al.* (2013), and in agreement with the majority of recent statistical estimates (dos Reis*, et al.* 2012; dos Reis*, et al.* 2014; Meredith*, et al.* 2011). However, the dates reconstructed in this study are considerably younger than those predicted by any molecular analysis to date (Goswami 2012; Bininda-Emonds*, et al.* 2007; dos Reis*, et al.* 2012), with 95% of

Table 3.3 – Divergence dates for major clades within and including Placentalia. Mean, minimum, and maximum values are reported combined for all optimal (DFO, DEO, DPO, CFO, CEO, CPO) and suboptimal (DFS, DES, DPS, CFS, CES, CPS) topologies. 6000 dated phylogenies are therefore represented for each of optimal and suboptimal values. Suboptimal topologies are reconstructed as considerably older due to the random resolution of polytomies which exist across the base of Placentalia.

	OPTIMAL MEAN	OPTIMAL MINIMUM	OPTIMAL MAXIMUM	SUBOPTIMAL MEAN	SUBOPTIMAL MINIMUM	SUBOPTIMAL MAXIMUM
AFROTHERIA	59.74	57.47	62.46	69.71	37.28	124.77
XENARTHRA	60.94	57.91	65.36	73.27	57.66	124.21
ATLANTOGENATA	60.94	57.91	65.36	73.27	57.66	124.77
LAURASIATHERIA	65.97	65.11	66.90	78.24	62.24	115.73
EUARCHONTOGLIRES	65.34	63.69	66.88	71.30	62.19	119.31
BOREOEUTHERIA	66.18	64.91	67.54	78.59	62.33	119.31
PLACENTALIA	66.62	64.91	69.10	83.99	62.33	124.77

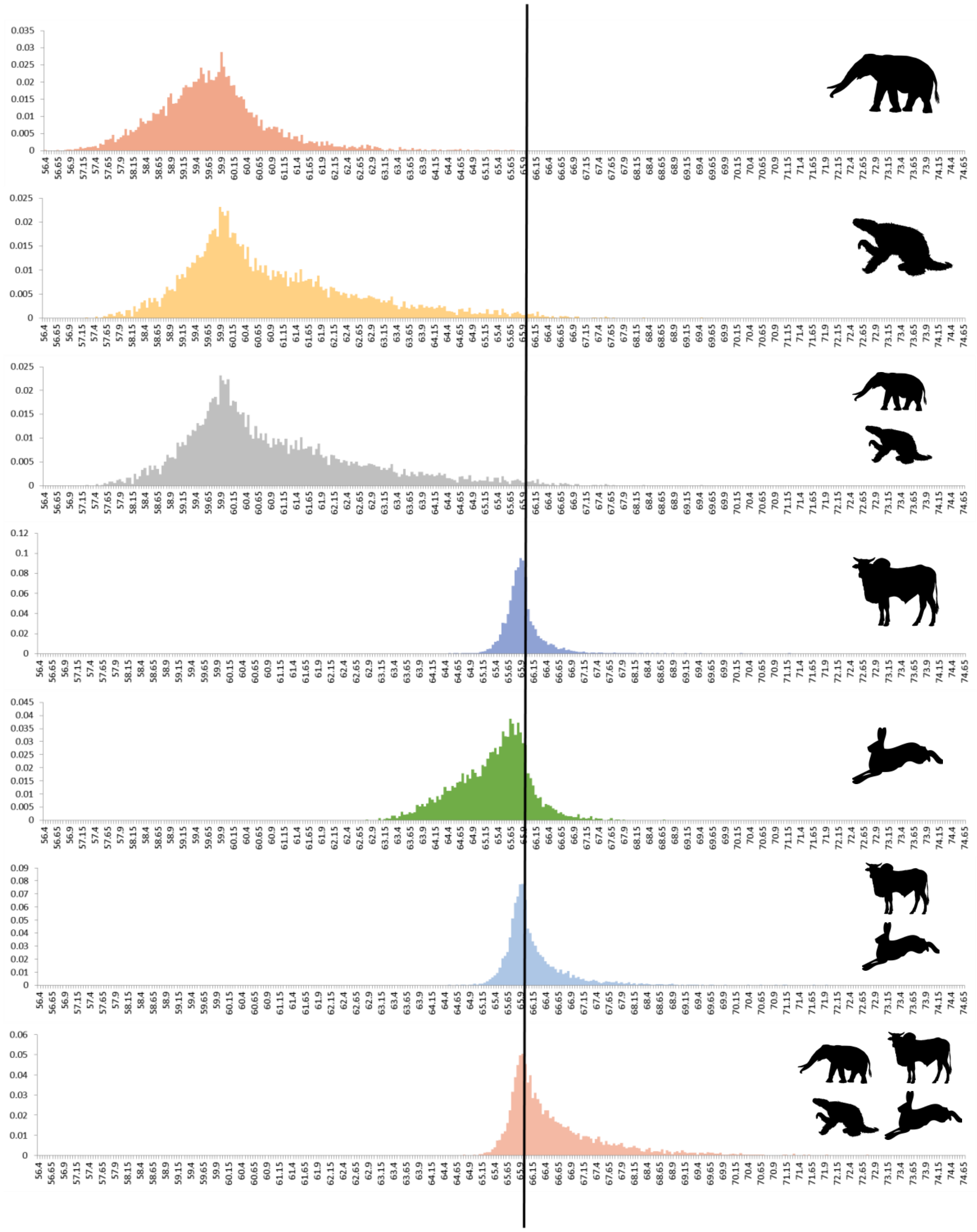


Figure 3.1 – Distributions of reconstructed dates from all optimal (DFO, DEO, DPO, CFO, CEO, CPO) topology analyses for major superordinal level clades as a result of dating with cal3, totalling 6000 dated trees. From top to bottom: Afrotheria, Xenarthra, Atlantogenata, Laurasiatheria, Euarchontoglires, Boreoeutheria, Placentalia. With the exception of Laurasiatheria, Boreoeutheria and Placentalia, the mean age is significantly lower than 66 million years. For Placentalia, the mean age is significantly older than 66 million years. Silhouettes from PhyloPic (www.phylopic.org).

estimates for the origin of crown Placentalia younger than 69.5 mya for optimal topologies. Although some reconstructions for the origin of Placentalia range into the Paleocene, 69.4% (Figure 3.1) of estimates predate the K-Pg boundary of 66 mya, and the mean is significantly older than the K-Pg mass extinction (Table 3.4).

Internal crown divergences that are reconstructed as having occurred prior to the end-Cretaceous mass extinction include that between Boreoeutheria and Atlantogenata, and between Euarchontoglires and Laurasiatheria (Figure 3.1, Table 3.4). Whether Laurasiatheria began to diverge prior to the K-Pg boundary is presently unclear as the estimated dates do not differ significantly from 66 mya, with 95% confidence interval between 66.7 and 65.45 million years ago. Other eutherian lineages that also survived the extinction event include *Protungulatum*, Leptictida, and Cimolestidae. These results were consistent regardless of nuanced differences in tree topology due to alternative constraint models, or sampling rate. However, the inclusion of suboptimal trees resulted in the generation of some high-level polytomies due to the behaviour of some unstable taxa, which resulted in a very wide distribution of divergence date estimates (Table 3.3).

Table 3.4 – Results of t-tests testing the difference between the mean of reconstructed divergence dates derived from all 6000 dated optimal phylogenies and the end-Cretaceous mass extinction 66 million years ago. All seven clades were distributed with significantly different means (although, in the case of Laurasiatheria, this was only true for two of the six optimal constraint topologies when tested separately. The node representing the last common ancestor of Placentalia and of Boreoeutheria were the only crown-group nodes reconstructed as having diverged in the Cretaceous.

	MEAN	T-STATISTIC	P-VALUE	K VS PG
AFROTHERIA	59.74	-435.989	<0.0001	Paleocene
XENARTHRA	60.94	-229.269	<0.0001	Paleocene
ATLANTOGENATA	60.94	-229.269	<0.0001	Paleocene
LAURASIATHERIA	65.97	-5.279	<0.0001	Paleocene
EUARCHONTOGLIRES	65.34	-69.310	<0.0001	Paleocene
BOREOEUTHERIA	66.18	22.294	<0.0001	Cretaceous
PLACENTALIA	66.62	46.075	<0.0001	Cretaceous

3(d)(ii) –*Rates of Evolutionary Change*

In all topologies, the null hypothesis of a uniform rate of evolution across the tree was conclusively rejected. Assessment of evolutionary rates suggested that, across all 6000 dated optimal trees, the branch leading to crown Placentalia possessed higher rates than would be expected by chance.

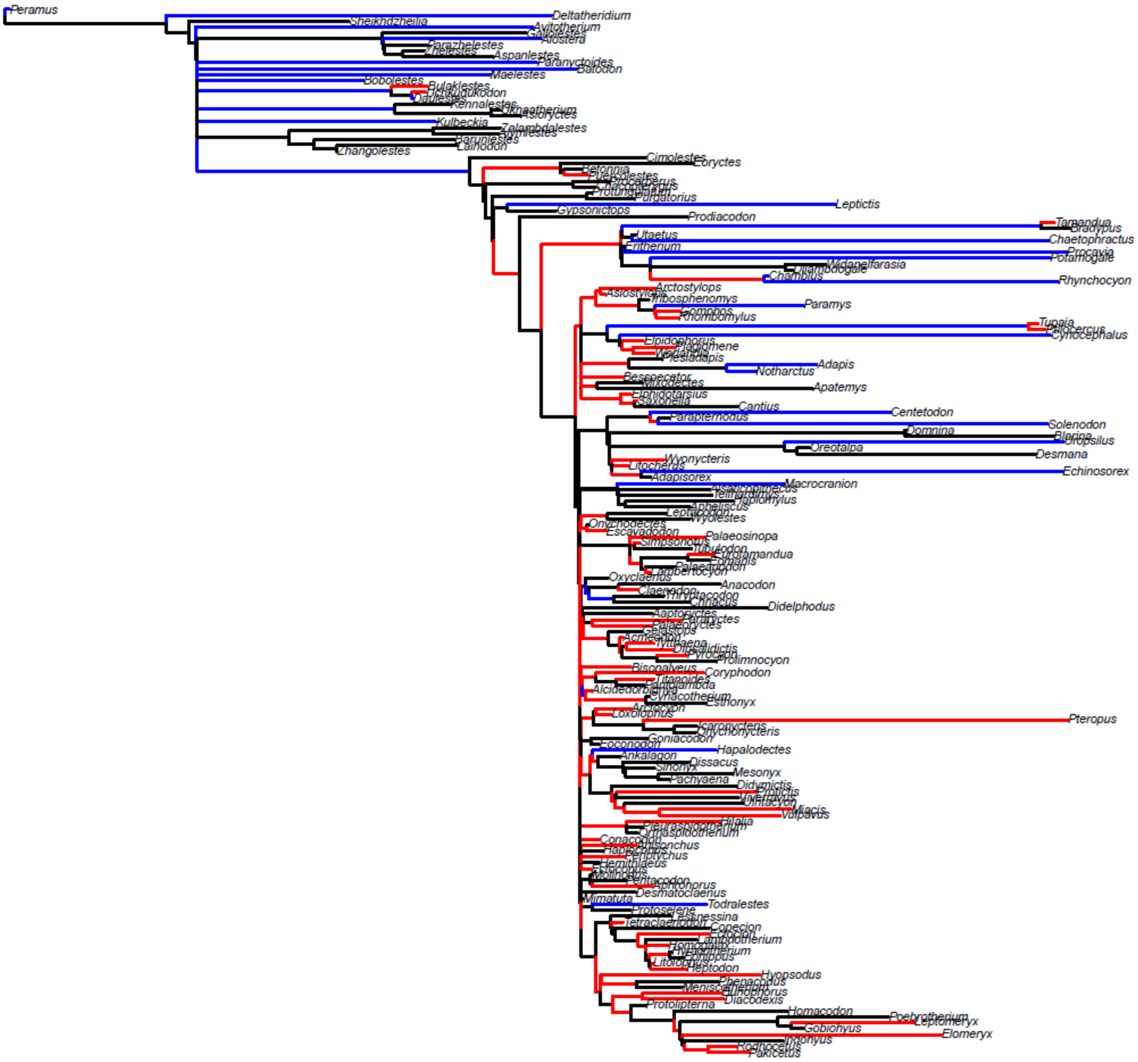


Figure 3.2 – Exemplar time-scaled phylogeny (DFO) with branches coloured according to whether they have significantly lower (blue) or higher (red) evolutionary rates than would be expected given an equal rate model. Black branches are those for which no significant difference in rate from an equal rate model was observed.

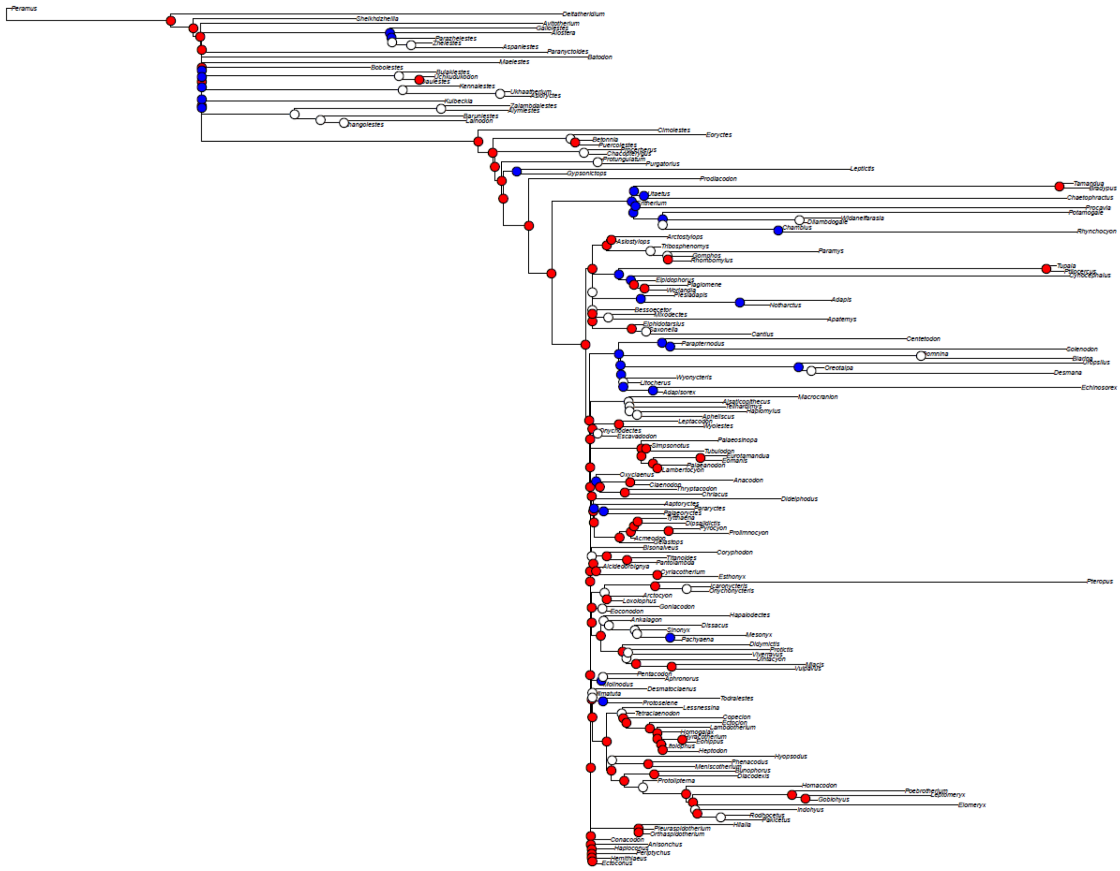


Figure 3.3 – Exemplar time-scaled phylogeny (DFO) with nodes coloured according to whether the clade for which they are the last common ancestor has significantly lower (blue) or higher (red) evolutionary rates than the remainder of the tree. White circles subtend clades with no significant difference in rate from an equal rate model.

With the exception of a few branches leading to the origin of Zalambdalestidae during the Early Cretaceous, all branches with increased rates were associated either with placental mammals or on branches leading to placental mammals (Figure 3.2).

Crown Placentalia was found to have a significantly higher intrinsic background rate of evolution than the rest of the tree. This was also true of several higher clades which encompass Placentalia, including all sequentially larger nodes from Placentalia to that denoting the last common ancestor of the most basal cimolestids and Placentalia (Figure 3.3). Within Placentalia, several nodes also show an increase in evolutionary rate, with the notable exceptions of Atlantogenata and Euarchontoglires, which have, when they are significant at all, significantly reduced evolutionary rates. This implies that the large increase in evolutionary rates is driven primarily by a radiation within Laurasiatheria. When assessing differences in evolutionary rates among time bins, North American Land Mammal Ages in the early Palaeogene – in particular, those during the Paleocene – had significantly higher rates than those in the rest of the Cretaceous (Figure 3.4). Rates during the Cretaceous and after the Eocene are significantly lower than would be expected under an equal-rate model.

3(e) – *Discussion*

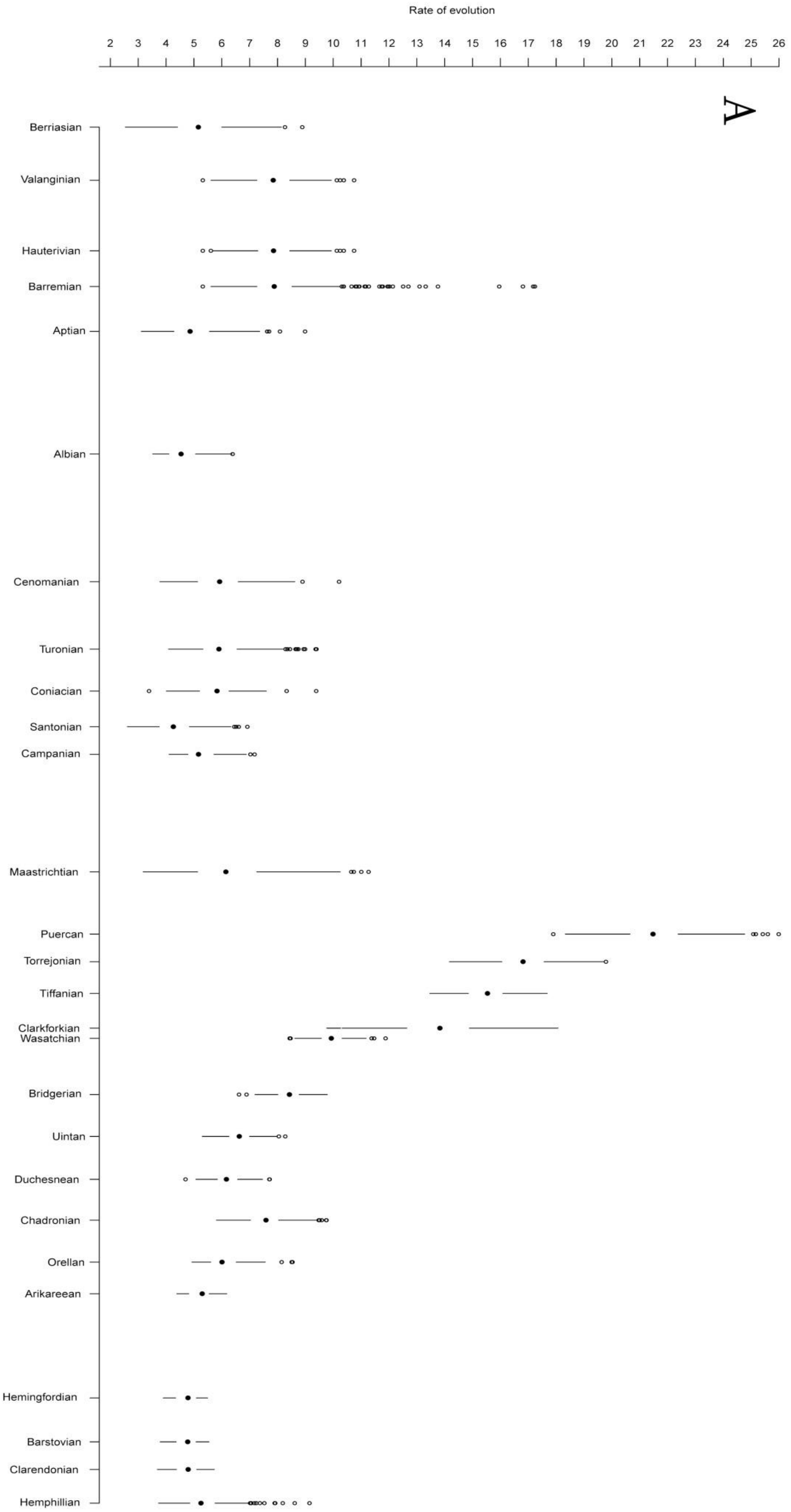
The results presented here indicate that, although the origin of crown Placentalia occurred in the latest Cretaceous, and although some diversification of lineages had occurred prior to the end-Cretaceous mass extinction, intraordinal diversification of placental mammals did not, in general, begin until after the end-Cretaceous mass extinction. The date of origin of crown Placentalia is here reconstructed within the Cretaceous, although still at least 15 million years younger than the youngest estimate from molecular data (dos Reis*, et al.* 2012). Although no tree reconstructed a crown placental in the Cretaceous, the earliest fossil placentals are found within the first few hundred thousand years after the end-Cretaceous mass extinction. Even with estimated sampling intensities twice those which have been calculated before (Foote and Raup 1996), the early diverging branches of crown Placentalia are pushed back into the Cretaceous. Indeed, artificially modifying the sampling rate here has very little impact on the reconstructed divergence dates for all higher clades. This has important ramifications for our understanding of the quality of the eutherian fossil record at the end of the Cretaceous. It has been hypothesised that the lack of unambiguous fossil crown placental mammals during the Late Cretaceous is due to a preservational bias, as is the case for fluctuations in Cretaceous dinosaur diversity (Lloyd *et al.* 2008). Fossilisation requires an environment in which sediment is deposited and in which tissues are not broken down by biotic or chemical means, effectively precluding the finding of fossil vertebrates from tropical rainforest or mountainous regions, among others. The “Garden of Eden” hypothesis for placental mammals suggests that an unsampled ecosystem or region of the world that has not been preserved housed the first placental mammals, and that the apparent radiation is in fact geographic dispersal (Foote*, et al.* 1999).

If a derived Campanian placental mammal fossil were to be discovered in some hitherto unsampled region, this would, of course, result in the estimated divergence dates being pushed back in time, and interordinal divergences would be considered to be significantly within the Cretaceous. It is partly to ensure that any reconstructed divergence dates were as accurate as possible given the data that the earliest members of each clade were selected. In the case where there is a gap between the first real member of a clade and the first sampled member of a clade, this could present some problems for the analysis if sampling is assumed to be high. As sampling rate is one of the factors that is included in the calculation of the divergence dates in the first place, this was easily testable by artificially assuming an extremely low sampling rate for eutherian mammals throughout the tree.

That the reconstructed dates for different levels of sampling rate are so similar very strongly indicates that the Garden of Eden hypothesis, brought about from incomplete fossil sampling, is not the case. If sampling is assumed to be 0.5%, as was tested here, there is a 99.5% of any given taxon being missing from a time bin. This is as true of the internal nodes as of the tips, meaning that the internal divisions of Placentalia for which no stem fossils are known might be expected to be reconstructed as closer in age to the divergence between Placentalia and its sister taxon. This is not the case; the internal divergences within Placentalia are reconstructed as being nearly simultaneous with the end-Cretaceous mass extinction, even assuming that 99.5% of the eutherian fossil record is missing. While crown placentals from the Cretaceous are here predicted to exist, substantial diversification of the internal orders is rejected by the data, suggesting that even undersampled regions or unfavourable environments for preservation are unlikely to have been a “garden of Eden” for placental mammals.

Here, speciation and extinction rates were assumed to be, on average, essentially equal, though this is not necessarily the case in reality (Ricklefs 2007). However, estimating the precise geological period in which an extinction occurs is a non-trivial problem, meaning that it is not possible to directly infer extinction rates from a dated phylogeny whose tips represent first appearances. Certainly, extinction rates cannot be estimated with any certainty from ultrametric phylogenies (Rabosky 2010), but, rather than the inclusion of additional arbitrary constants in an analysis derived from a non-ultrametric tree, the null model must be that net speciation is equal to zero. Moreover, there is support in the fossil record for speciation and extinction rates tracking one another across palaeontological timescales (Stanley 1979), and as a result, this assumption is justifiable. Adaptive radiations follow periods of elevated extinction (Wagner and Estabrook 2014), and the K-Pg is associated with local level increases in both speciation and extinction rates in placental mammals (Wilson 2014).

The phylogenetic position of the enigmatic genus *Protungulatum* has been considered an important question, and has therefore been a topic of extensive debate – opinions are split as to whether it represents a crown placental (O'Leary*, et al.* 2013) or a more basal eutherian (Wible*, et al.* 2007). Where it is supported as a placental, a Cretaceous origin for crown placental mammals is assured, as there is a single Cretaceous occurrence of *Protungulatum* in the latest Maastrichtian. Where it is considered a non-placental eutherian, it is normally phylogenetically very close to the crown. Here, all topologies used conclude that *Protungulatum* is not a crown placental mammal, meaning that all members of Placentalia known to date are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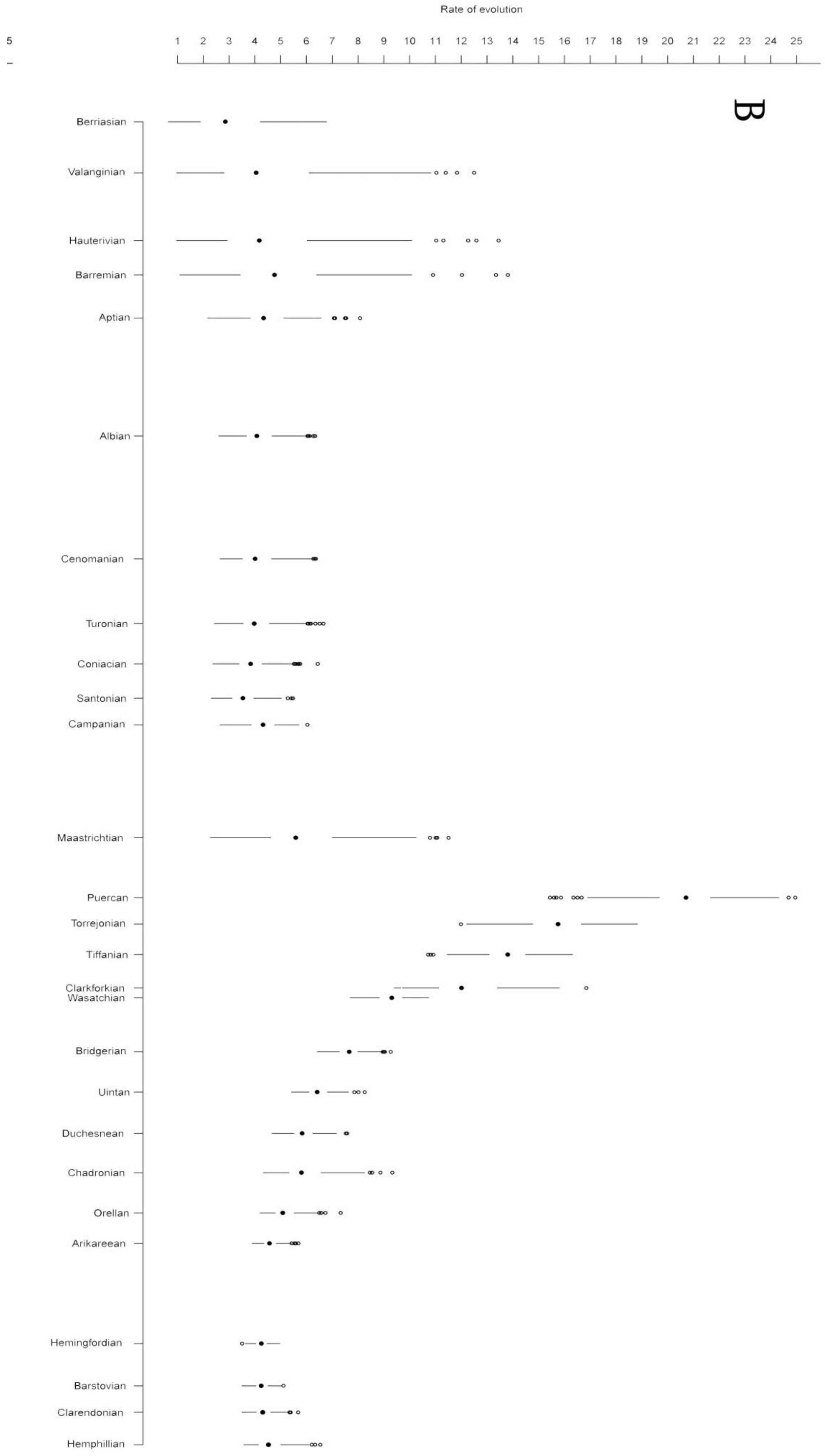
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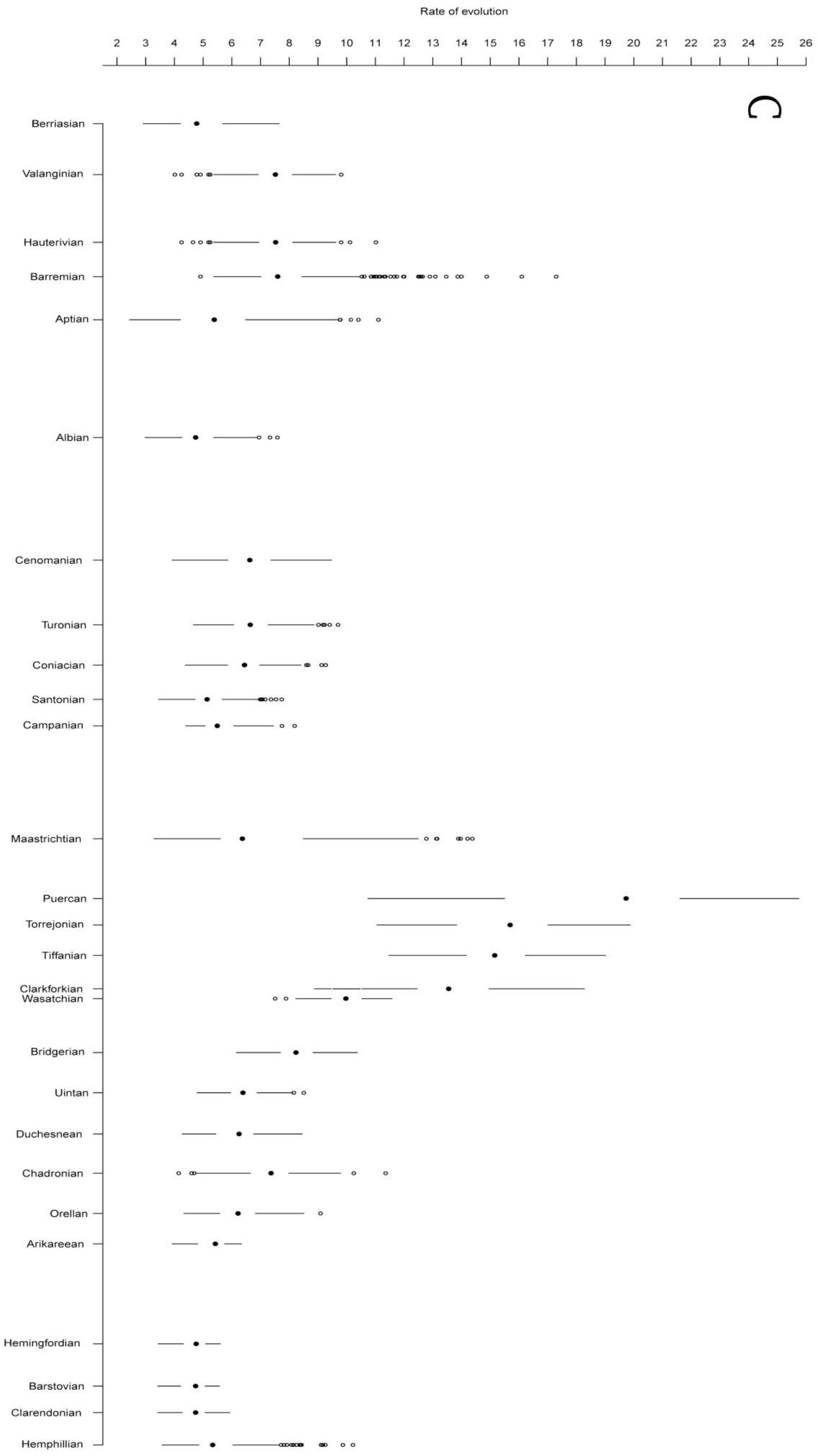
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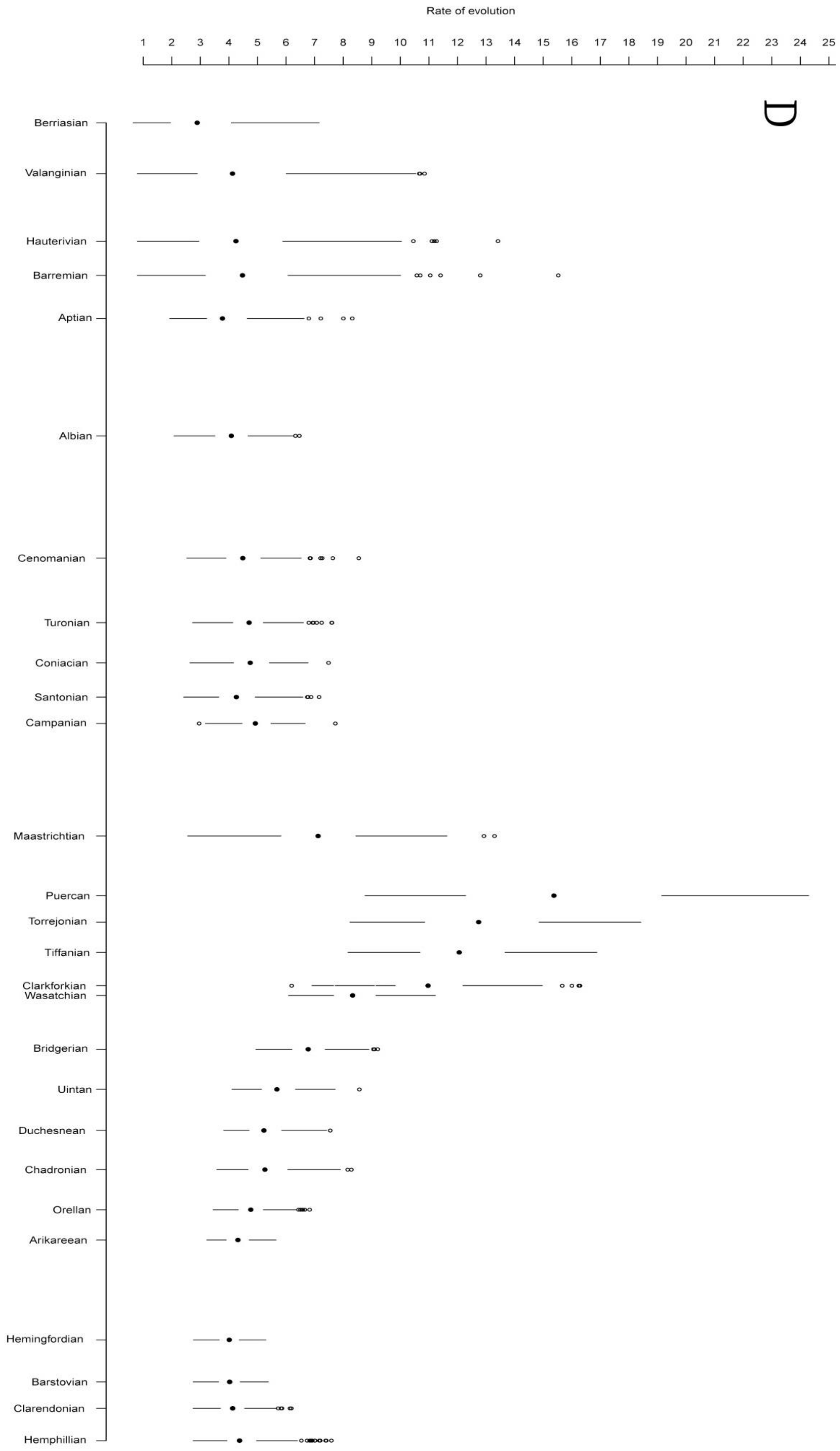
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Figure 3.4 – Four graphs of evolutionary rate through time. A and B depict rates through time calculated from the consensus of optimal (DFO, DEO, DPO, CFO, CEO, CPO) topologies only from the six different original phylogenetic analyses. C and D depict rates from a strict consensus of suboptimal (DFS, DES, DPS, CFS, CES, CPS) topologies that are nonetheless within a single phylogenetic step, and therefore represent a more divergent set of trees. A and C assume that the estimated sampling rate is accurate, which implies that the fossil record is relatively good throughout the tree. B and D, conversely, assume that the fossil record is conservatively poor. All four sets of analyses show the same broad pattern of low Cretaceous rates with a two- to four-fold increase at the end-Cretaceous mass extinction, with rates through time for suboptimal topology and low sampling analyses varying to a greater degree.

Palaeogene or younger. The dates estimated here for the divergence of *Protungulatum* and crown Placentalia are approximately 75 mya, which is nine million years prior to the end-Cretaceous mass extinction, and approximately six million years before the estimated origin of placentals. The lack of an unambiguous Cretaceous placental does leave a temporal gap of approximately five million years between this estimate of the time of origin of Placentalia and the first confirmed fossil placentals in the earliest Palaeogene (Kondrashov and Lucas 2006). This gap is much smaller than those suggested by molecular-derived dates, and indeed even a larger gap need not be a problem if evolutionary rates are taken into account. The age of Placentalia, as reconstructed by Bayesian and clock-like methods, has been shown to be sensitive to evolutionary rate, with a predicted ten- to twenty-fold increase in evolutionary rate of morphological characters required to bring the date of origin into the Paleocene (Beck and Lee 2014). In the nine million years between the divergence of Placentalia from *Protungulatum* and the extinction event, a little lineage diversification occurred in Placentalia. Per lineage rates of origination remain constant until the end-Cretaceous mass extinction, when, in the earliest Paleocene, a dramatic increase in species origination rates occurs (Figure 3.5) following a similarly large per-lineage extinction rate, consistent with the local-scale patterns found by Wilson (2014) in the San Juan Basin.

Concomitant with this increase in per-lineage speciation rate is an increase in the rate of evolution of morphological characters. While there is some small increase during the Maastrichtian, usually found in highly suboptimal topologies, the maximum rates of discrete character evolution occur during the earliest Paleocene. This combination of high speciation rates and elevated rates of character evolution is suggestive that placental mammals radiated immediately in the wake of the K-Pg mass extinction. The pattern observed here in mammals is also consistent with a recent genomic network analysis on the early radiation of birds (Jarvis *et al.* 2014), which found that the majority of the internal diversification of crown birds occurred in a short space of time at the beginning of the Paleocene.

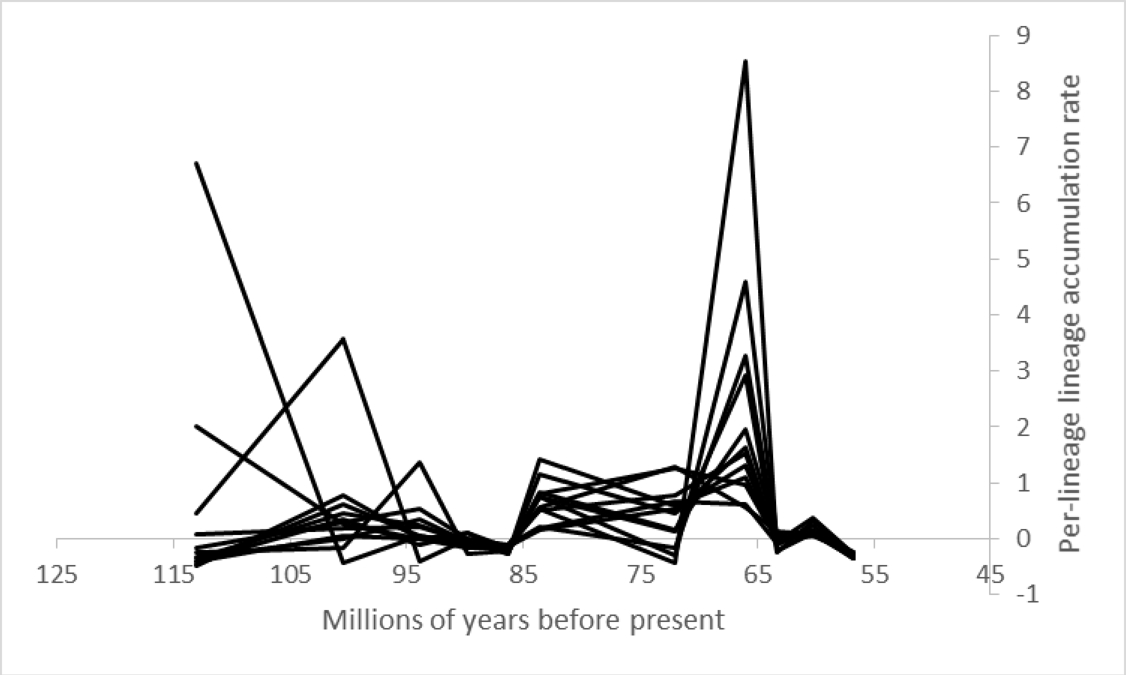


Figure 3.5 - Lineage accumulation rate per bin through time. Each line represents one of the twelve sets of dated trees. Per-lineage accumulation rate increased drastically at the boundary between the Cretaceous and the Palaeogene.

When an unrealistically conservative sampling rate of 0.5% per million years was applied, the node divergence estimates were pushed to older dates, but still within the error of those dates generated from the cal3 method itself, which estimated unrealistically high sampling rates of 84%. It would be expected that lowering the sampling intensity would result in greater uncertainty in the dating of the origin of these nodes. However, that the results are relatively similar across different sampling regimes suggests that the signal of a radiation is very strong, and that the dating is being driven by the other parameters – diversification and extinction. As a result, it is possible to conclude that the inclusion of Late Cretaceous and Paleocene mammals in this analysis, from which more accurate diversification rates could be determined, are driving the reduction in the predicted age of origination of crown Placentalia. The taxonomic sample of eutherian mammals that are known from Late Cretaceous and Paleocene strata is relatively complete in this analysis – that is, all major clades for which fossils are known from this time are represented. Thus, insofar as the fossil record can be considered to be a reliable indicator of diversity, the apparent rapid Palaeogene diversification represents a real event in placental mammal evolution. Indeed, a high Palaeogene rate of body size evolution, declining towards the present, has been identified through analyses of constructed fossil phylogenies, even when discounting Paleocene, flying, and aquatic taxa (Raia*, et al.* 2013).

The majority of the Cretaceous has significantly lower evolutionary rates than would be expected from a null hypothesis of equal rates, but this is likely a result of an elevated estimation of what constitutes a background rate as a result of the extreme deviation from the background pattern observed in the Palaeogene. Post-Eocene rates are also lower than those of the Paleocene, but this is an artefact generated by lower taxonomic sampling. Specifically, each extant order is represented by only a few taxa, and therefore later radiations are masked. There is no equivalent lack of sampling in Cretaceous mammals; that there are fewer taxa included is a reflection of the lower taxic richness at that time (Newham *et al.* 2014).

A complication for the calculation of evolutionary rates concerns the completeness of the individual placental mammal genera themselves. When reconstructing ancestral character states in order to determine the number of transitions on each branch, missing data can be a problem. Real transitions that are unsampled will be undetected, or, depending on the method of character optimisation used, will be reconstructed earlier or later than they occurred in reality. Furthermore, if a particular temporal bin is relatively undersampled (either from taxon selection or missing fossil data), this could result in branches with longer durations, as the missing taxa would break the long branhces. If combined with higher Cretaceous missing data, the result of this analysis might have fewer character transitions than in reality placed onto branches that are longer than in reality, artificially reducing reconstructed rates of evolution. In this case, the increase in evolutionary rates into the Paleocene could be seen as simply an artefact of missing data. However, as mentioned before, the sampling of available fossil data from the Cretaceous is higher than in the Palaeogene, sampling rates do not strongly impact the reconstructed dates, and there is no reason to suspect that Cretaceous eutherians are significantly less complete than their Paleocene counterparts – on average, Cretaceous members of the dataset are 39.3% complete, and Palaeogene members are 41.8% complete in terms of number of characters that can be scored.

These results are found across all topologies tested, which indicates that both the origination date and increase in rates are well supported for early crown Placentalia regardless of the particular arrangement of the internal superorders and orders. This stability of the result regardless of the specific topology used in each analysis is important, as it strongly suggests that, irrespective of the ultimate resolution for the phylogenetic topology of the root of crown Placentalia, the macroevolutionary story is robust.

The beginning of the increase in mammalian evolutionary rates at the end of the Cretaceous occurs during a period where, in North America at least, many dinosaur groups were already in decline, although the pattern across clades and space was complex (Brusatte*, et al.* 2012), and it is likely that the final extinction was sudden (Brusatte*, et al.* 2014). The debate over whether the end-Cretaceous was a catastrophic sudden event or the accumulation of several factors further stressing ecosystems to the point of collapse is important in the context of interpreting the apparent onset of mammalian diversification prior to the Cretaceous-Palaeogene boundary. The eruption of the Deccan volcanic province, which began approximately 250,000 years prior to the Cretaceous-Palaeogene boundary (Schoene *et al.* 2014) has been implicated in the ecological changes that occurred around this time (Courtillot *et al.* 1986; Courtillot and Fluteau 2010).

A second interpretation returns to the idea that the initial diversification of placental mammals occurred in some as yet unsampled region of the world, or some unsampled ecosystem (Maas and Krause 1994). The effect of sampling on reconstructed dates in this analysis aside, this hypothesis is difficult to assess without analysis of the completeness of the available fossil record, and without extensive sampling of other geographic regions where basal placental (or derived non-placental eutherian) mammals may have diversified, such as Africa and India. India has thus far yielded eutherians, but no early placentals (Goswami*, et al.* 2011), while the earliest placental mammal known from Africa is the basal afrothere *Ocepeia*, from the Middle Paleocene (Gheerbrant*, et al.* 2014). Madagascan mammals from the Cretaceous have to date included gondwanatheres and multituberculates (Krause 2013; Krause *et al.* 1997; Krause *et al.* 2014), but no eutherians. The abrupt faunal turnover at the K-Pg suggests that the majority of novel species were immigrants (Wilson 2014), as there are no clear ancestors to taxa such as periptychid "condylarths" in the preceding strata. Given the remarkable continuity of the San Juan Basin over this period (Butler *et al.* 1977), it must be concluded that either morphological evolution occurred so quickly as to be geologically invisible, or that there is significant bias in either preservation or collection of Cretaceous mammals. It has previously been suggested that, in order for there to be no known placental mammals during the Cretaceous, the sampling of mammals during that interval would have to be orders of magnitude worse than the Palaeogene (Foote*, et al.* 1999). The relative completeness of the Cretaceous and Palaeogene fossil records is currently under investigation, but the view that this discrepancy is unreasonably large, and that therefore crown placental mammals can only have predated the end-Cretaceous mass extinction by a small time, is supported by the dates reconstructed here.

As I have stated elsewhere, the inclusion of Paleocene taxa in the analysis of the K-Pg mass extinction is essential in order to accurately reconstruct the evolutionary patterns that occurred during that interval, as well as the processes that shaped them. This principle can be extended to any major event in the history of life, and demonstrates the indispensable utility of fossils in the reconstruction of past events. In answer to the two questions posed in the introduction to this paper, the evidence from morphology and phylogeny rejects the supposition that the origin of crown Placentalia was in particular a source of increased evolutionary rate – rather, this occurred within the radiations at the superordinal and ordinal level. Secondly, the end-Cretaceous mass extinction is contemporaneous with a dramatic increase in evolutionary rate in eutherian mammals.

CHAPTER FOUR

MORPHOLOGICAL DISPARITY OF EUTHERIANS ACROSS THE END-CRETACEOUS MASS EXTINCTION

4(a) – *Abstract*

In the aftermaths of mass extinction events, and during radiations of clades, there is often a decoupling of taxonomic diversity and morphological disparity. The placental mammal radiation after the end-Cretaceous mass extinction is the archetypal adaptive radiation, but the change in overall morphological disparity across this important boundary has not been quantified. By extending morphologies back using ghost lineages from a previously derived phylogeny, I assess three measures of morphological disparity during the Late Cretaceous and Palaeogene. I find that the end-Cretaceous mass extinction immediately precedes an increase in sums of range of occupation of morphospace, but that there is no change in mean pairwise distance from the Maastrichtian to the Puercan – the first North American Land Mammal Age of the Paleocene, nor in sums of variance. Instead, increases in variance-based metrics lag behind range-based metrics and taxonomic diversity, suggesting that the response of mammals to the K-Pg event was characterised by early radiation, increasing overall morphospace occupation, and then subsequent specialisation, as tracked by increased dissimilarity.

4(b) – *Introduction*

Mass extinction events have long been suggested to be important drivers of evolutionary novelty. The term ‘adaptive radiation’, coined by Osborn (1902) in specific reference to the sudden appearance in the fossil record of a whole suite of new species, and new morphologies, of mammals in the earliest Cenozoic, has often been applied in this context. Adaptive radiations, in essence, are an evolutionary process in which a clade undergoes an increase in lineage diversification as a result of adapting to a number of new niches (Schluter 2000), with divergent selection for specialisation to those niches promoting reproductive isolation (Rice 1987; Barton 2010), and hence speciation. During the course of an adaptive radiation, then, it should be expected that the disparity of a clade – a measure of morphological variation (Wills *et al.* 1994) – should increase as the clade fills new regions of morphospace (Foote 1994). An increase in disparity through time has been observed in several groups, across different metrics of disparity - morphometric (Young *et al.* 2010), biomechanical (Stubbs *et al.* 2013), and cladistic (Thorne *et al.* 2011), where some form of evolutionary radiation has been identified. However, it has also been suggested that a general feature of radiations is an initial decoupling between disparity and taxic diversity (Foote 1997b; Ruta *et al.* 2013), a pattern that has been observed in a number of invertebrate groups (Bapst *et al.* 2012; Hopkins 2013), where speciation increases taxic richness early on, while changes in morphological disparity react more slowly.

At first sight, an increase in disparity would appear to have occurred during the original adaptive radiation – the Paleocene diversification of placental mammals. There is an association between cladistic and functional measures of disparity (Anderson and Friedman 2012). However, Grossnickle and Luo (2014) concluded that there was no statistical change in the disparity of lower molar shape across the Cretaceous-Palaeogene boundary in eutherians. In a separate study, evidence from morphometric analysis of lower jaws supported a previous decrease in mammal disparity during the mid-Cretaceous (Grossnickle and Polly 2013). This is perhaps unexpected, given that the first carnivorous eutherians, as well as the first large-bodied herbivores, arose in the early Paleocene. One might expect molar shape disparity to increase markedly with the origin of novel ecological dietary niches.

Ecological release in terms of body size evolution of eutherians has also been identified (Slater 2013), concluding that the end-Cretaceous mass extinction allowed mammals to radiate into a greater range of body sizes than had previously been available thanks to a loss of competition from the generally larger dinosaurs. This line of evidence, too, would imply that the end-Cretaceous mass extinction would be expected to result in an increase in overall measures of disparity.

One method for assessing disparity other than morphometric or biomechanical disparity is cladistic disparity (Wills*, et al.* 1994; Foote 1992). Cladistic disparity measures determine the amount of difference in discrete morphological characters across phylogenies. Cladistic characters have been used to measure disparity in radiations of echinoderms (Foote 1992), dinosaurs (Brusatte *et al.* 2008), gnathostomes (Anderson and Friedman 2012), and crocodylomorphs (Toljagic and Butler 2013) and allow testing of the disparity of all morphological features.

By measuring three metrics of disparity across a phylogeny of Cretaceous and Paleocene mammals, I aim to determine whether the end-Cretaceous mass extinction affected the measure of total cladistic disparity in eutherian mammals.

4(c) – *Materials and methods*

4(c)(i) – *Source of the tree*

Previously, I have used Paleocene taxa to establish the phylogenetic relationships of the early crown placental mammals in Chapter Two, subsequently dating those phylogenies in Chapter Three using first and last appearance dates of taxa derived from the Palaeobiology Database (www.paleobiodb.org) and calculating rates of morphological evolution. Here, I use the twelve sets of dated topologies from

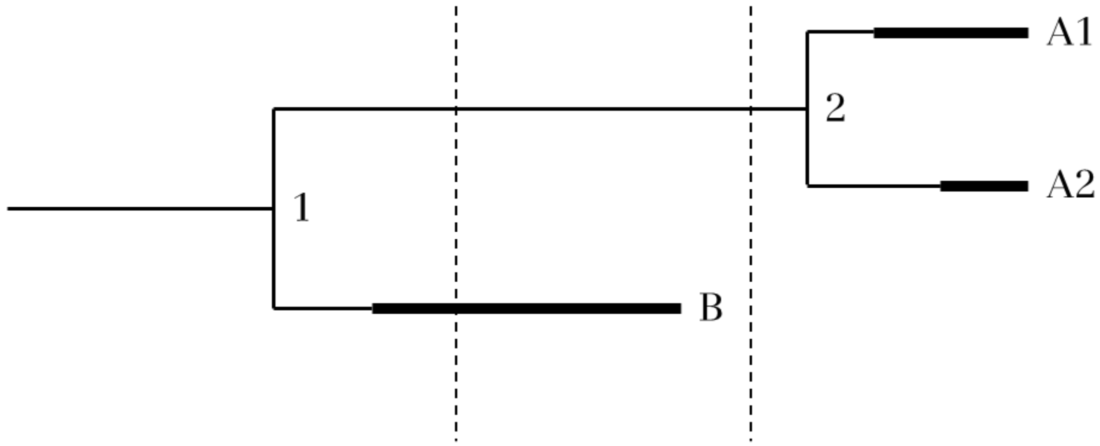
Chapter Three to infer the presence of ancestral morphologies in time bins through ghost lineages.

4(c)(ii) – *Cladistic Disparity*

Many methods that have attempted to reconstruct changes in disparity have used only those taxa which are present in the fossil record. However, this is problematic, because, even where taxa are unknown from the fossil record, they may often be known to be present thanks to reconstructed ghost lineages. Several authors (Wills 1998; Brusatte *et al.* 2011) have identified this problem and corrected for it by reconstructing ancestral states for ancestral nodes, and including those hypothetical morphologies in the time bins in which they were reconstructed as occurring.

While an improvement on most previous methods, this is not necessarily ideal, however, as, firstly, an ancestral node will only be sampled in a single bin. It is a hypothetical combination of character states which, by definition, has no fossil record, and is therefore represented as solely a point in time. Tip taxa can be considered to appear from their first to last appearance, and, depending on the method used to reconstruct extinction time (if any), even beyond these. However, this is not possible for ancestral nodes. The second problem, related to the first, is that this still does not fully account for ghost lineages.

Where ghost lineages are small, and the fossil record relatively complete in the period of interest, there is no problem. Ancestors are binned either with their oldest descendant (the "conservative" method) or with their oldest sister taxon (the "punctuational" method), depending on method (Brusatte*, et al.* 2011; Brusatte*, et al.* 2012). Theoretically, however, it is possible to imagine a situation where a tree spans three time bins. In the first is Node 1, an ancestor of Clade A and Clade B. Clade B is



	Bin 1	Bin 2	Bin 3
Richness	1	1	2
“Conservative”	1	1	3
“Punctuational”	2	1	2
“Extended Punctuational”	2	2	3

Figure 4.1 – A comparison of different measures of disparity on a hypothetical, previously dated phylogeny. In this three time bin example, traditional richness methods, as well as those corrections applied by Brusatte *et al.* (2011) will fail to recognise the morphology of the branch leading from Node 1 to Node 2 when assessing disparity. Only by treating the ancestral morphology as occurring along the entire branch can the total morphological disparity of the time bin be assessed, including all the data. Thick lines represent species occurrences; thin lines represent ghost lineages. The root itself is not counted, as the reconstruction of characters at the root node is dependent on the next outgroup, which is not sampled.

known from the first and second time bins. Clade A has two members, which diverge at Node 2 in the third time bin. These two members are known only from the third time bin.

This situation is perfectly consistent with the application of the method of Brusatte *et al.* (2012), but potentially throws up some undesirable circumstances. In the first time bin, we measure Node 1 and Clade B. In the second we measure Clade B. In the third, we measure Node 2, and both members of Clade A. Despite the fact that the morphology between Nodes 1 and 2 must have existed in the second time bin, it is still not sampled by these methods, and as such will tend to underestimate disparity in such bins (Figure 4.1).

Where phylogenies are dated using methods other than simply reconstructing the bins in which they appear on the basis of the raw fossil record (i.e. without applying suitable statistical corrections based on sampling), the incidence of ghost lineages which pass through time bins without speciation is much higher. This is especially true for trees which possess a combination of extinct and extant taxa, with some large time difference between the majority of the extinct clades and the present.

Therefore, the most desirable situation is that the ghost lineages must be included in the calculations of disparity for the time bins through which they pass. I assume for mathematical simplicity that the particular combination of character states along the ghost lineage is that of the daughter node or taxon. In comparison with the "conservative" and "punctuational" methods of Brusatte *et al.* (2011), this is perhaps best described as an "extended punctuational" approach. This assumes that all morphological change occurs at speciation, and while this is unlikely to be strictly true in all cases, it is certainly true that speciation by necessity involves some degree of change. By assuming that all character state transitions occur at the beginning of a branch which crosses a time-bin boundary, character transitions that may have actually occurred on the portion of a branch after that boundary are reconstructed as occurring prior to that event. This approach will, as a result, push morphologies backwards in time, and tend to bias analyses by reconstructing changes as occurring earlier than they otherwise might. However, failure to apply this correction will falsely reduce disparity in intermediate time bins.

4(c)(iii) – *Ancestral State Reconstruction*

Ancestral states were reconstructed for every state for every node using maximum likelihood methods as implemented in the R packages ape (Paradis *et al.* 2004) and Claddis (Lloyd 2014), using the discrete character data matrix from Chapter Two. Ordered multistate characters were treated as such for all character reconstruction and calculation of disparity metrics, and, to ensure internal consistency, character weightings were identical to those which generated the initial phylogeny on which these analyses are based. Although the morphological distributions of ancestral nodes are hypothetical reconstructions, they represent real, living organisms. It would be expected that these ancestors have autapomorphies of their own, but these cannot be coded as the taxa have not been sampled. If autapomorphies were to be coded for terminal taxa, this would not be comparable to those ancestors, and bins with a higher proportion of internal nodes would tend to have artificially reduced morphological disparity (Brusatte*, et al.* 2011). As a result, no autapomorphic characters for any genus were coded.

4(c)(iv) – *Time-binning Data*

Ancestral character distributions were assigned to the branches leading to each node, and branches were treated as occurring in every time bin through which they pass, including those in which they originate and end. Time bins used were geological stages for the Cretaceous, and North American Land Mammal Ages (NALMA) for the Cenozoic. The division of nodes into the time bins through which their ancestral branch passed was carried out using code written for R (Appendix 2.8, electronic supplementary information) using functions from the package paleotree (Bapst 2012).

Using biostratigraphic over geochronological divisions is preferable, for two reasons. Firstly, the known uncertainty in sampling the ages of taxa is, with few exceptions, within a stage- or NALMA-level interval. This means that error in the precise temporal position of a taxon is minimised by using the divisions that best reflect the known temporal distribution of the sampled taxa. Dating using 'cal3' requires a single sequence of non-overlapping consecutive time bins in which observations can be placed. No single sequence of bin divisions can accurately reflect the uncertainty in dating for all fossil taxa. As there is a sampling bias in the fossil record favouring North American taxa, especially with regards to the evolution of eutherian mammals, it is most sensible to use NALMAs. While there will still be uncertainty in the placing of Cenozoic taxa from outwith North America, the use of NALMAs over European or South American land mammal ages means that any additional error introduced by this method is minimised. Secondly, as these divisions were used to assess the dating of the phylogeny in the first place, it is more consistent to use the same time bins.

As longer time bins represent a greater amount of sampling of the fossil record, it would be expected that longer time bins might have higher levels of disparity, because there is a greater chance of finding more morphologically extreme taxa. As a result, all analyses were also carried out on equal length time bins of 2 million years from 90 to 38 million years ago (from the Coniacian stage to the Duchesnean NALMA, temporally roughly equivalent to the Bartonian stage). Division of time in this way provides a more fine-scale approach that is more robust to sampling, but risks dividing the data up more finely than the uncertainty in the dating of the fossil taxa would permit.

4(c)(v) – *Calculating Disparity*

After calculating ancestral state values for all characters and all nodes using maximum likelihood, a distance matrix of all tips and nodes was generated. Under the methods described above, the morphologies for each tip and node were assigned to the ancestral branch leading to that tip or node. Principal Coordinates Analysis (PCO) was applied to this distance matrix in order to generate a multidimensional morphospace within which measures of disparity could be assessed. Three metrics of disparity were calculated for each time bin, and for each phylogenetic tree. The mean pairwise Gower dissimilarity between all nodes and the sum of variances of PCO scores on all axes were used as variance-based metrics of disparity . Gower disparity accounts well for heterogeneous data, such as the combination of continuous and discrete characters, as in this dataset, hence it is preferred over a raw distance measure. Sums of ranges of PCO scores were also calculated, but this latter measurement is highly susceptible to sample size (Foote 1997a; Butler *et al.* 2012).

To avoid the possibility of the lower taxonomic richness of the Cretaceous biasing the estimates of sums of ranges, simulated PCO coordinate data was generated under a normal distribution in order to determine above which level of sampling any biases would be minimal. This ensures that the differences observed between bins are a result of real differences in morphological diversity, and not simply an indication of lineage richness. Sums of ranges were then corrected by dividing the observed sum for each bin by the expected for a bin of the same sample size, given the number of morphologies present.

Time-binned distance matrices involved in calculating mean pairwise distances were bootstrapped such that taxa were randomly sampled with replacement, and new distance matrices generated, with 1000 replicates. Mean pairwise distance was calculated for each bootstrapped matrix, and 5% and 95% percentiles were ascertained. Adjacent time bins with non-overlapping 95% confidence intervals were considered to represent significant increases or decreases in cladistic disparity. All disparity measures and bootstrapped matrices were generated in R using existing and newly written code (Appendix 2.8, electronic supplementary information).

4(d) – ***Results***

On generating simulated range size data, bins were found to increase in sum of range disparity with number of sampled morphologies, asymptoting at a sampling level of approximately 40 branches per bin (Figure 4.2). Therefore, all estimations of disparity using sums of PCO ranges were restricted to those bins which contained more than 40 reconstructed morphologies. This constraint restricted interpretation of the sum of range data to the interval between the Maastrichtian and the Uintan inclusive. As mean pairwise distances are less affected by sample sizes, all bins with the exception of those with only a single morphology represented (where disparity is equal to zero by dint of there being no difference between a morphology and itself) were sampled.

Individually, PCO axes represented extremely low proportions of overall variation between taxa. For example, PCO1 and PCO2 together represented only 3% of total variation. Therefore, interpretation of the meaning of any single axis is not informative (Figure 4.3).

Even with axes representing very low proportions of overall variance, sums of ranges (SOR) are able to be calculated across all PCO axes. In SOR of PCO axis scores, across all levels of constraint, disparity of eutherian taxa remains relatively low during most of the Cretaceous, before increasing during the Maastrichtian and Puercan. Values for the sum of ranges of PCO scores increase by about 60% across these two time bins (Figure 4.4).

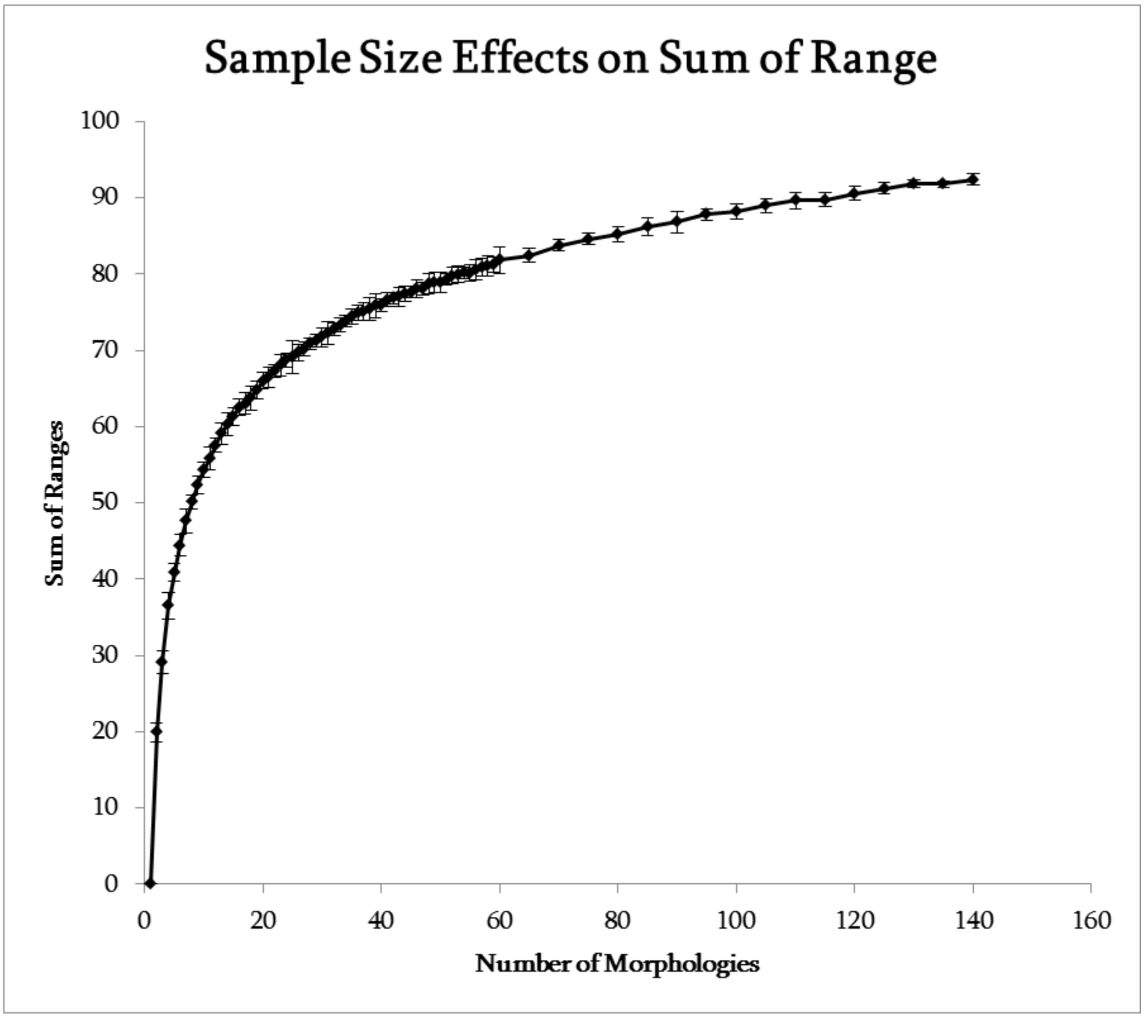


Figure 4.2 – Effect of sample size on sums of ranges. Morphologies sampled were normally distributed across 353 simulated PCO axes. If all taxa were randomly distributed according to the PCO axes, an increase in sum of ranges would still be apparent for time bins with larger numbers of morphologies present. Sums of ranges for every integer from 1 to 60 was sampled ten times, and every five integers thereafter to 140 morphologies.

Conversely, mean pairwise distance (MPD) and sums of variances (SOV) showed no significant change in disparity over the end-Cretaceous mass extinction, both considering stage-level (Figures 4.5, 4.6) and equal bins (Figure 4.7). However, significant increases in MPD were found from the Puercan to the Torrejonian in all optimal topologies, and from the Torrejonian to the Tiffanian in all discrete

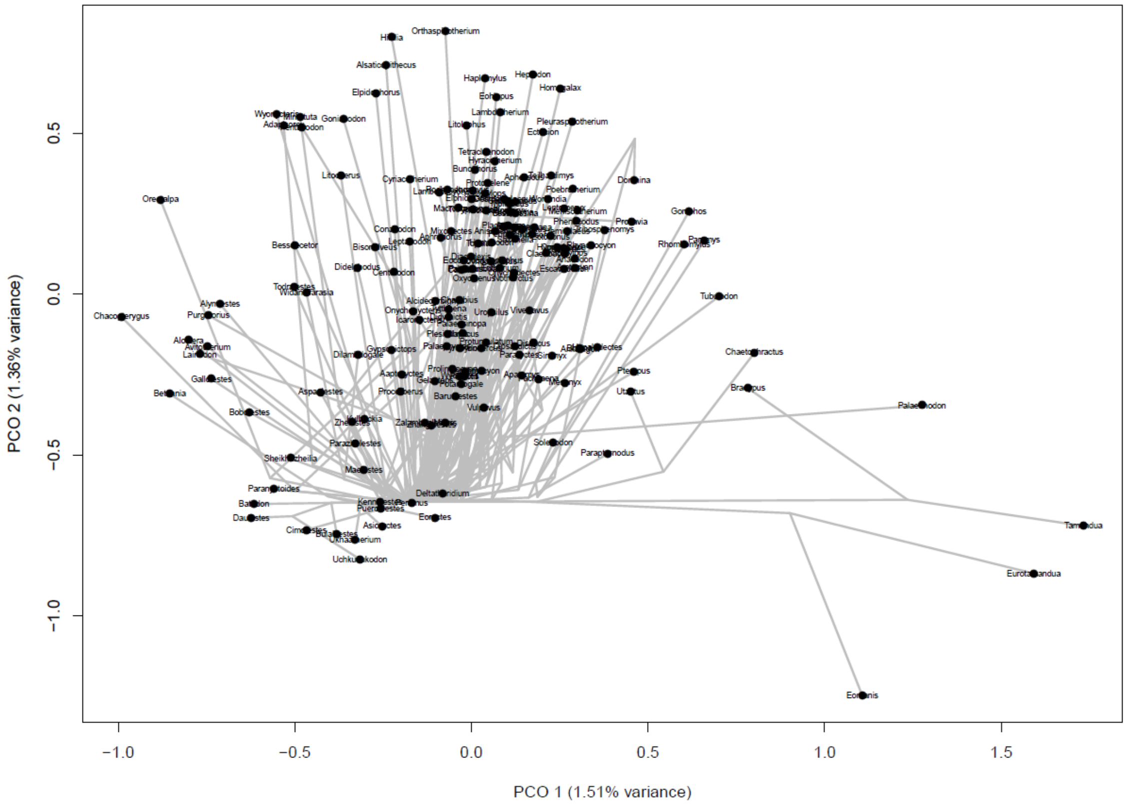


Figure 4.3 – PCO plot of the first two coordinates axes for the cladistic distance matrix. Black circles represent terminal tips, and grey lines the reconstructed ancestral states. Apart from a distinct group of edentulous mammals (the xenarthrans and pangolins), which occupy the bottom right of the plot, no clear distinction can be drawn, and even then, the proportion of variance explained by each axis is remarkably low.

character optimal topologies. After the beginning of the Eocene, there was no significant change across any single time bin, and, while MPD continued to increase across every bin, the rate of increase decelerated as time bins approach the present. In the Cretaceous, the Campanian represents a significant increase in mean pairwise distance in most topologies, with disparity decreasing once more into the Maastrichtian.

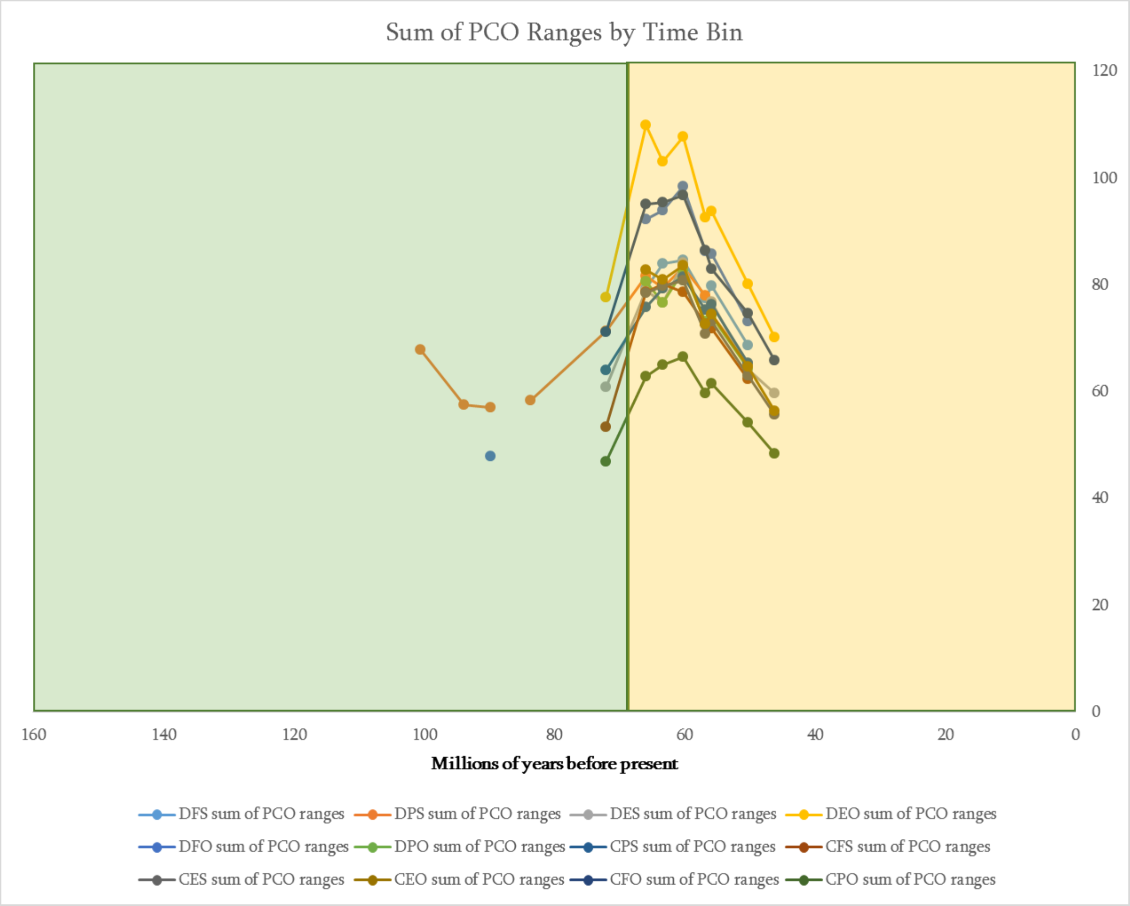


Figure 4.4 – Time-binned measures of sum of ranges on 353 PCO axes for all sets of trees, both optimal and suboptimal topologies. Due to small numbers of branches, and the sensitivity of sum of range analysis to sample sizes, the only Cretaceous bin that was able to be sampled was the Maastrichtian. In all analyses the Puercan contains a larger occupied region of morphospace than the Maastrichtian, with Paleocene bins being higher in range-based disparity than later Eocene and Neogene bins. Abbreviations refer to the sets of trees used for reconstruction of disparity, and are composed of three elements – 'C' or 'D' refer to whether the trees were derived from continuous or discrete datasets. 'E', 'F', and 'P' refer to the level of constraint used in the generation of the tree. 'O' and 'S' refers to whether the trees are MPTs – "Optimal" – or within a single parsimony step – "Suboptimal". Hence, 'DFO' refers to the optimal topologies derived from a discrete dataset analysed under a full constraint.

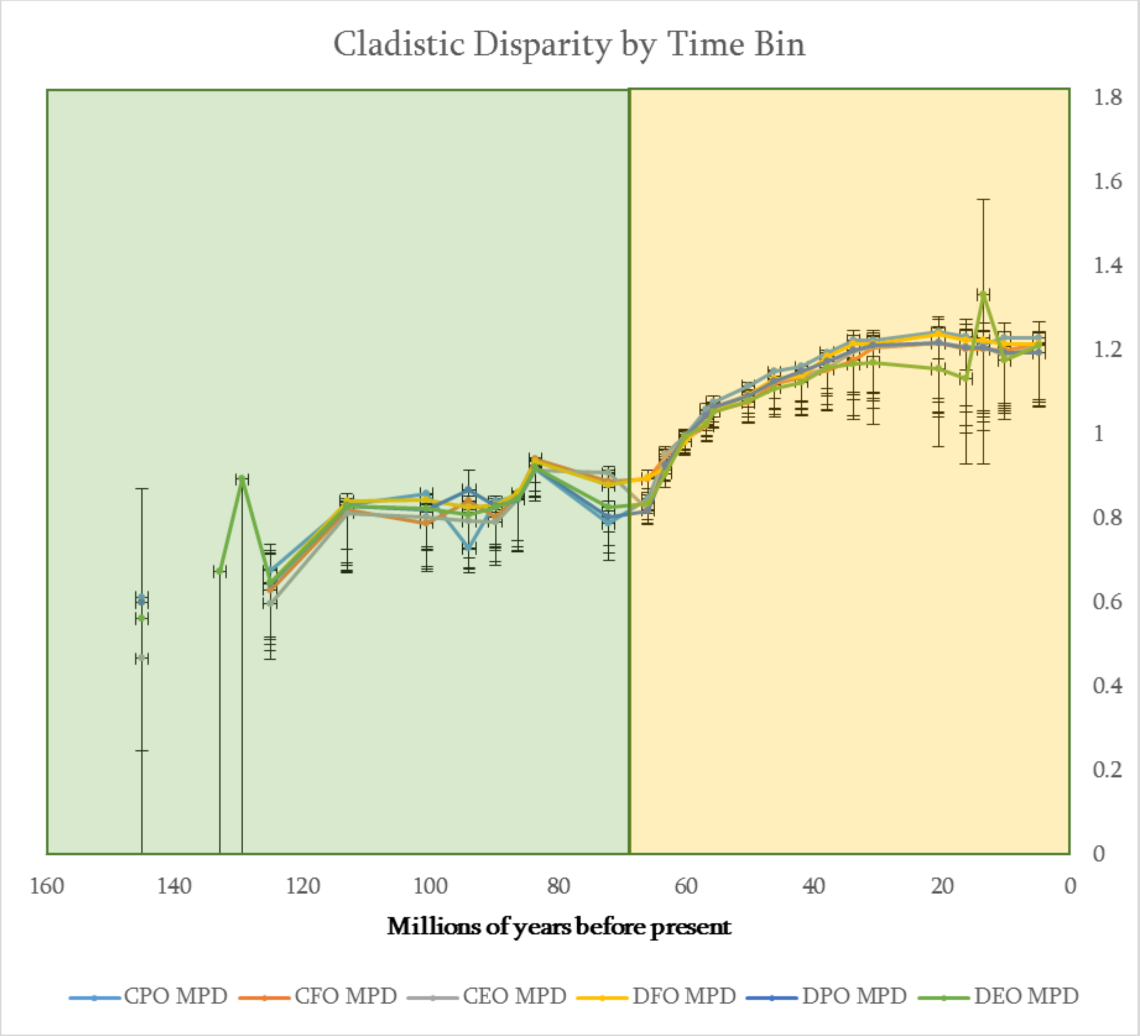


Figure 4.5 - Time-binned measures of mean pairwise distance. Coloured points and lines represent the mean pairwise distance between morphologies represented in that bin for each of the six sets of most parsimonious trees derived from continuous/discrete data, and each of three constraint topologies. Error bars are 95% bootstrap confidence intervals. The green period of time is the Cretaceous, and the orange the Paleocene. There is no change between the last Cretaceous bin (Maastrichtian) and the first Paleocene bin (Puercan), but subsequent radiation in the Paleocene causes mean pairwise disparity to rise. MPD = Mean Pairwise Dissimilarity. The other abbreviations refer to the sets of trees used for reconstruction of disparity, and are composed of three elements – 'C' or 'D' refer to whether the trees were derived from continuous or discrete datasets. 'E', 'F', and 'P' refer to the level of constraint used in the generation of the tree. 'O' refers to trees that are optimal for their level of constraint. Hence, 'DFO' refers to the optimal topologies derived from a discrete dataset analysed under a full constraint.

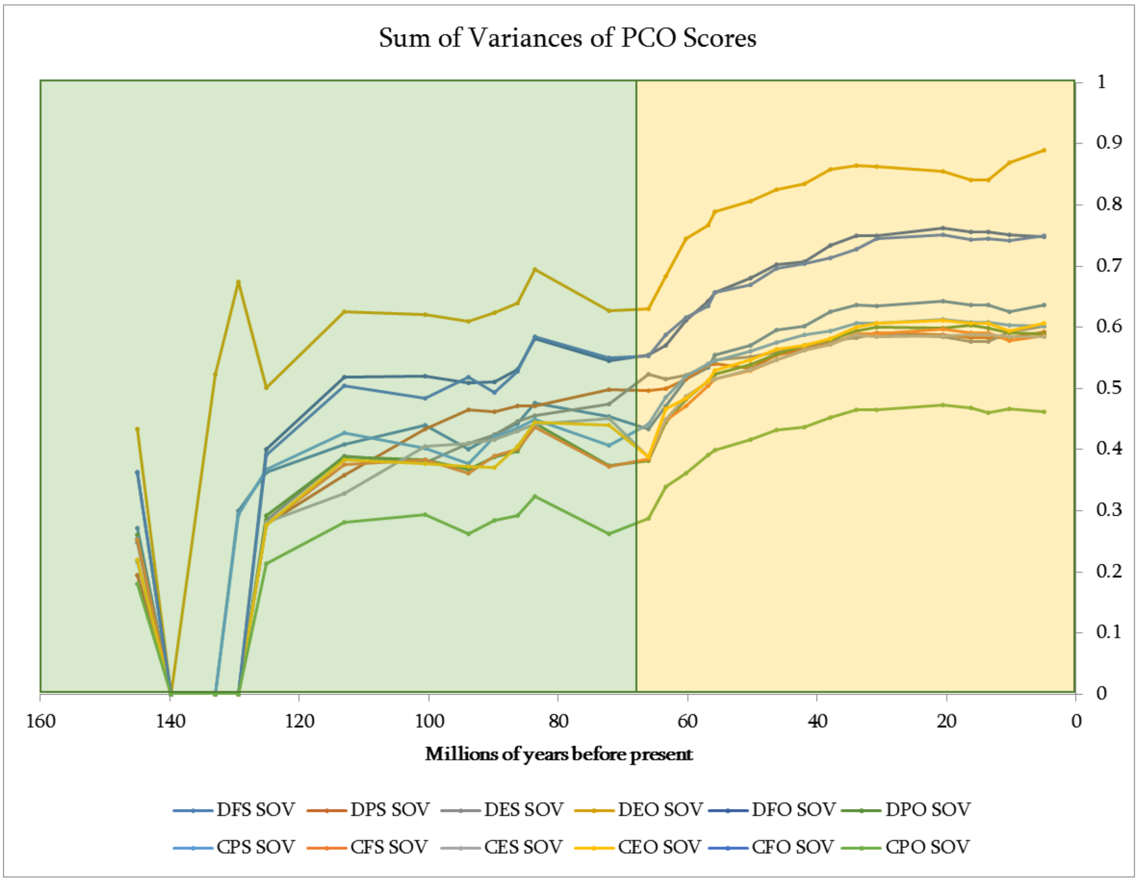


Figure 4.6 – Sums of variances of all 353 PCO axes for each set of trees, including both optimal and suboptimal topologies. The Campanian is a Cretaceous high, but there is no change across the end-Cretaceous mass extinction in any analysis. In the Cenozoic, variance in the PCO space increases, asymptoting approximately 40 million years before the present. SOV = Sum of Variances. The other abbreviations refer to the sets of trees used for reconstruction of disparity, and are composed of three elements – 'C' or 'D' refer to whether the trees were derived from continuous or discrete datasets. 'E', 'F', and 'P' refer to the level of constraint used in the generation of the tree. 'O' and 'S' refers to whether the trees are MPTs – "Optimal" – or within a single parsimony step – "Suboptimal". Hence, 'DFO' refers to the optimal topologies derived from a discrete dataset analysed under a full constraint.

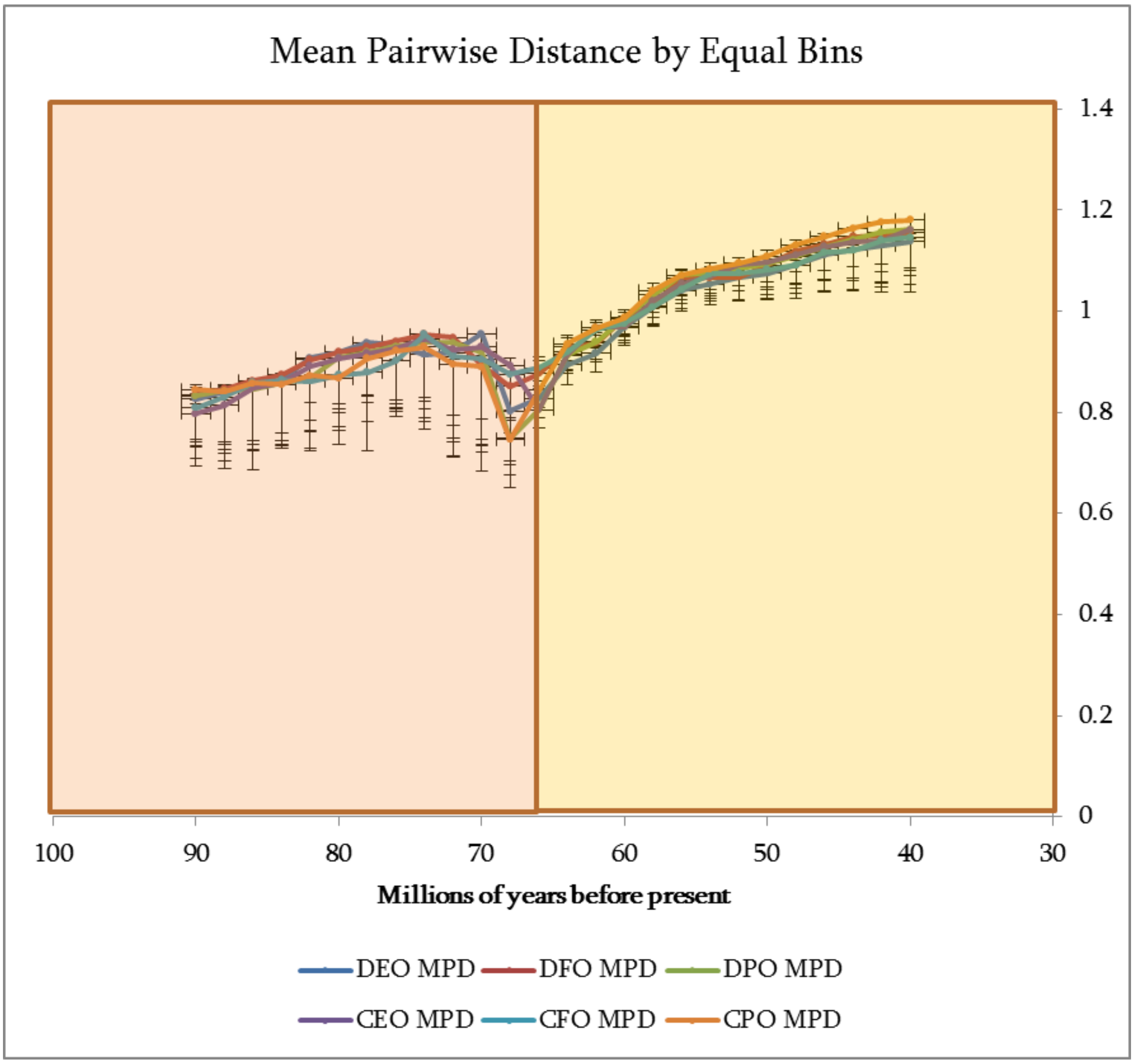


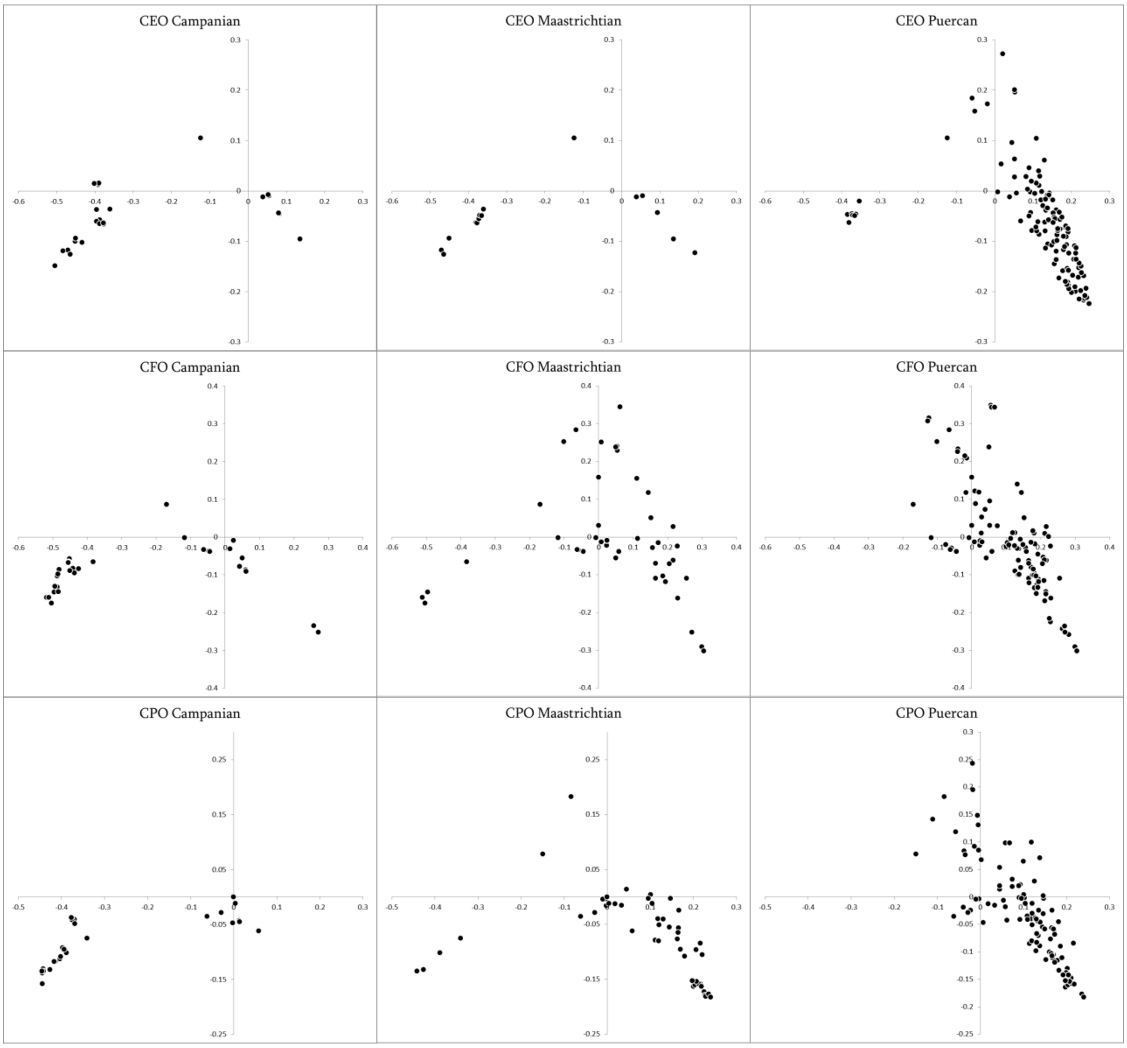
Figure 4.7 – Mean pairwise distance across all morphologies reconstructed as being present in each two million year time bin. The finer scale pattern observed here shows little change over the end-Cretaceous mass extinction, and a subsequent immediate increase. The decrease observed from the Campanian to the Maastrichtian is here found to be restricted to the period of the Maastrichtian after 70 million years ago; this may be due to the uniform distribution within stages applied to first and last appearance dates when dating the tree. The other abbreviations refer to the sets of trees used for reconstruction of disparity, and are composed of three elements – ‘C’ or ‘D’ refer to whether the trees were derived from continuous or discrete datasets. ‘E’, ‘F’, and ‘P’ refer to the level of constraint used in the generation of the tree. ‘O’ refers to trees that are optimal for their level of constraint. Hence, ‘DFO’ refers to the optimal topologies derived from a discrete dataset analysed under a full constraint.

4(e) – *Discussion*

When the first two PCO axes are plotted against one another, and those morphologies present in the Campanian, Maastrichtian and Puercan bins placed in the same morphospace, there is a distinct shift from one region of morphospace to another (Figures 4.8, 4.9). The majority of the initial diversification of Placentalia occurs within the area of the morphospace already occupied by Placentalia and their close relatives, similarly to the idea that an adaptive radiation occurs along the genetic multivariate axis for which there is most variation (Schluter 1996). While each axis explains very little of the overall variation in cladistic characters, it is indicative that the Maastrichtian represents a loss of diversity in part of the eutherian tree, and the beginnings of taxonomic diversification elsewhere.

That each PCO axis represents such low percentages of the total variation is expected. Ideally, all morphological characters used in the generation of a cladistic data matrix are uncorrelated, meaning that each character should represent an orthogonal axis in the first place. Some correlation might be expected due to unidentified developmental association between characters and simple biological noise, but the low percentage for the first PCO axis is not of itself a cause for concern. Summation of ranges and variances is still meaningful, as long as it encompasses most or all of the PCO axes, while keeping in mind the observation that the former is more susceptible to low sample sizes (Butler*, et al.* 2012; Foote 1997a).

Of the taxa in this database, five are last known from the Maastrichtian: the outgroup *Deltatheridium*, *Alostera*, *Paranyctoides*, *Batodon* and *Gypsonictops*. *Deltatheridium* is an outgroup taxon representing Metatheria (marsupials and their stem relatives), and will therefore not be considered further. *Alostera* is the latest


CEO Campanian

CEO Maastrichtian

CEO Puercan

CFO Campanian

CFO Maastrichtian

CFO Puercan

CPO Campanian

CPO Maastrichtian

CPO Puercan

Figure 4.8 – Morphospaces of Principal Coordinates 1 and 2, for morphologies within each time bin and for optimal topologies of continuous characters. Rows represent differing topologies, while columns represent the Campanian, Maastrichtian, and Puercan. In each, the cluster representing zalambdalestids, zhelestids, asioryctitheres, and other basal eutherians (to the left of the origin) undergoes sequential losses in diversity during from the Campanian into the Maastrichtian, while the cluster representing cimolestids, leptictids and placentals (at and to the right of the origin) undergoes sequential diversifications.

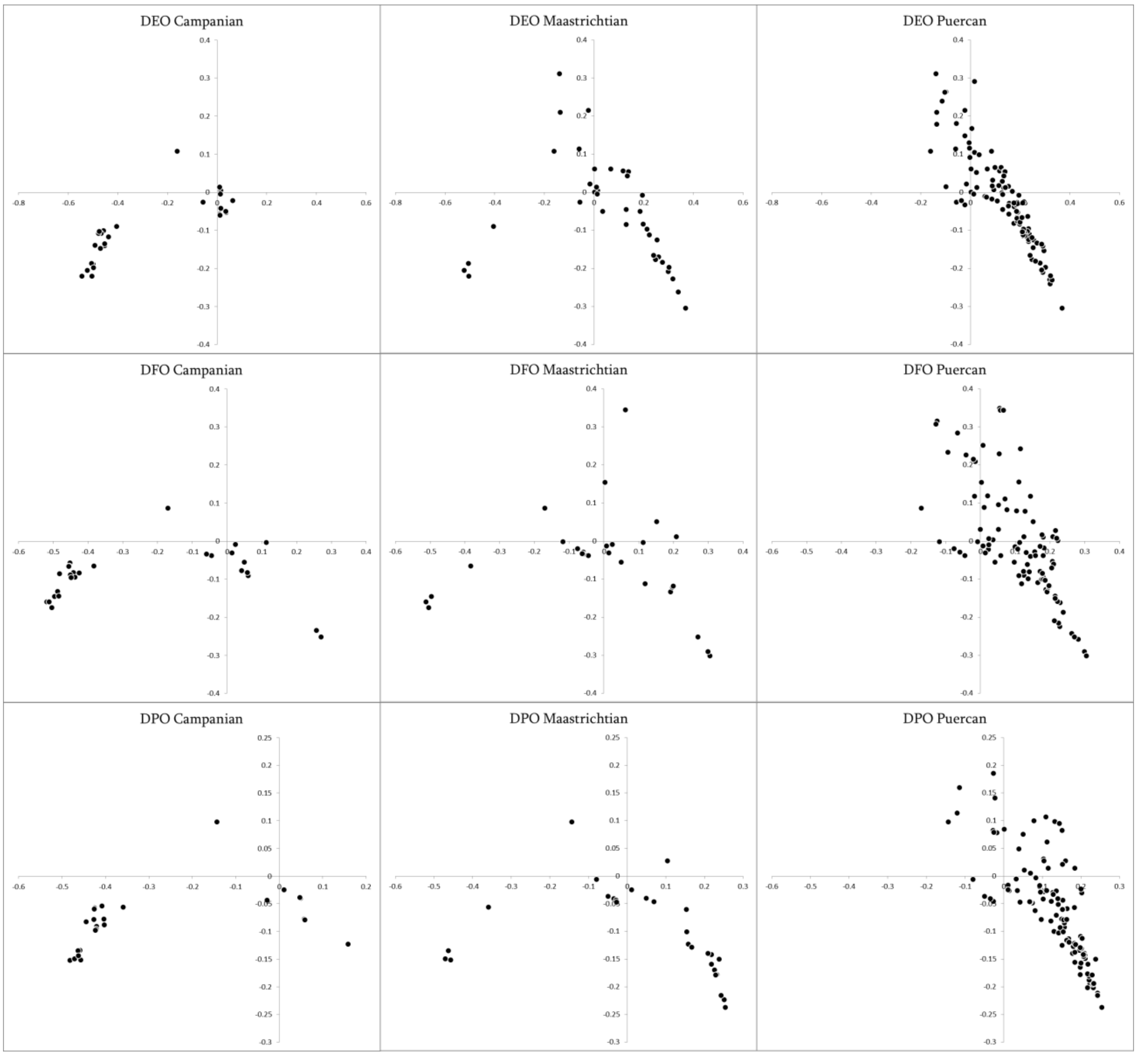


Figure 4.9 – Morphospaces of Principal Coordinates 1 and 2, for morphologies within each time bin and for optimal topologies of discrete characters. Rows represent differing topologies, while columns represent the Campanian, Maastrichtian, and Puercan, and show a pattern almost identical to Figure 4.8.

known zhelestid (W*ania chowi*, a Paleocene form which was described as a zhelestid (Wang 1995), was considered an anagalid by McKenna and Bell (1997) a remnant of an earlier Cretaceous radiation. *Paranyctoides* is a morphologically plesiomorphic eutherian of unclear affinities. *Batodon*, also has unknown relationships (Wood and Clemens 2001), but has been considered a cimolestid (Kielan-Jaworowska*, et al.* 2004; Williamson*, et al.* 2011). However, that group was not resolved as monophyletic in the analyses which generated the trees from which these results are based (see the results in Chapter Two). *Gypsonictops* is an early leptictid – a group which survived the end-Cretaceous mass extinction, eventually becoming extinct in the Neogene.

Those branches that pass through the Maastrichtian, then, include a few disparate remnants of earlier radiations, as well as several internal branches which connect the close relatives of crown Placentalia, and the earliest divergences within the crown. As a result, overall morphological space occupation increases, as some novel characters associated with the rise of placentals expand the boundaries of the morphospace. However, as taxonomic increase is almost exclusively clustered in the region of the morphospace containing the close relatives and ancestors of crown Placentalia, the mean distance between any pair of randomly selected taxa is smaller. Additionally, the Campanian marks the final appearance of a large number of taxa more distantly related to crown Placentalia, which results in the region of the morphospace occupied by such taxa as *Alostera* becoming heavily depauperated.

There is a clear disjunct between patterns of SOR and MPD measures of morphological disparity within eutherian mammals through time. A reduction in MPD but an increase in SOR in the Maastrichtian would suggest that, while the total occupation of morphospace is increased, the majority of the variation is within a small portion of that morphospace, with higher clustering. Where there is an extinction event, this would come about from taxic selectivity, where certain portions of the morphospace are reduced, or from localised diversification, where several closely related, recently diverged taxa cluster morphologically. It is known that large but peripheral subgroups contribute the greatest amount to measures of disparity (Foote 1993a), which seems to be the case for Placentalia. Similar patterns of a reduction in variance based metrics of disparity from the Campanian to the Maastrichtian is known for ceratopsian and hadrosaurian dinosaurs (Brusatte*, et al.* 2012), but they also show decreases in range-based metrics, unlike eutherian mammals, and the pattern is spatially restricted to North America. There is no reason, however, to suspect that a pattern holding true for an already highly diverse, large-bodied clade such as Dinosauria would be also true of the relatively species poor, small-bodied eutherians. Additionally, previous simulations of evolutionary radiations have suggested that low ecological diversity is to be expected at the beginning of a radiation, even where the group is relatively taxon-rich (Mitchell and Makovicky 2014).

The rise in SOR disparity in the Maastrichtian relative to the earlier Cretaceous stages reflects those placental lineages which were reconstructed as diverging prior to the end-Cretaceous, leading to nodes such as the last common ancestors of Atlantogenata, Euarchontoglires, and the orders within Laurasiatheria. That there is some disparification apparent in the Maastrichtian implies that some increase in morphological diversity occurred with the division of Placentalia into the four superorders, before markedly increasing further with intra-superordinal diversification during the Paleocene. No fossils are known which represent stem members of any of the four superorders, but the reconstruction provided in Chapter Three and here predicts that these hypothetical ancestors, which represent the beginnings of the morphological diversification that occurred in eutherian mammals, were present in the latest Cretaceous and into the very earliest Paleocene.

Sampling of the Late Cretaceous eutherian fossil record is certainly not complete. Although the nature of a cladogram is to treat every sampled taxon as a terminal rather than speculating on ancestor-descendant relationships, the lack of any fossil which breaks the internal branches of Placentalia (ie, a stem atlantogenatan) tells us that part of the earliest placental diversification is missing from the fossil record. This has some implications for interpreting the results from this analysis. Range-based metrics of disparity are sensitive to sample size; inclusion of additional taxa, presently unsampled, would be likely to increase estimates of overall range-based disparity during this time. Variance-based metrics are less sensitive to sample size, but if there were to be an entire, unsampled community of eutherian mammals in, for example, India, which was unrelated to the crown group or the known stem clades, this would add an additional cluster of points in morphospace, distinct from the others. In theory, this would result in increased variance and mean pairwise distance. Although important for the discussion of overall patterns of eutherian evolution, such a clade would not affect the conclusions concerning Placentalia. The only ways in which incomplete sampling could affect interpretations of the patterns of disparity in the early evolution of Placentalia would be if a definitive Campanian (for example) placental taxon were to be discovered. In that case, the reconstructions of divergence dates of clades would be altered, the binning of internal branches would change, and the overall patterns of disparity would all change. As discussed in previous chapters, it is very unlikely that this is the case, due to the degree to which the completeness of the Cretaceous fossil record would have to be worse than that of the Paleocene (Foote*, et al.* 1999).

Reductions in MPD following taxon-selective extinction events are known (Bapst*, et al.* 2012), even where the surviving taxon subsequently radiates, as this is indicative of a selective extinction (Foote 1993b). However, here it is necessary to explain why the reduction in MPD occurs prior to the end-Cretaceous mass extinction.

The general pattern of increasing mean pairwise distance over time is a result of the accumulation over time of synapomorphies, which therefore result in the suite of characters at any given node being more and more divergent. The rate at which there is an increase in mean pairwise distance is therefore a measure of rate of accumulation of synapomorphies. The decelerating increase in morphological disparity through the Cenozoic is consistent with observations from invertebrate radiations that, barring disturbances such as the immediate aftermath of extinction events, rates of evolution decline over time (Foote 1999; Wagner 1995). This pattern supports Simpson's (1944) early burst model of adaptive radiations in rate of evolution, but contrasts in that the model predicts high morphological disparity but low taxonomic diversity early in a clade's evolution, whereas here there is low initial disparity and high taxonomic diversity.

It is possible that the sustained high mean pairwise distance later in the Cenozoic is a result of the sampling of the dataset. As the majority of sampled taxa are from the Paleocene or Eocene, those that persist until the Recent represent relatively disparate members of the total diversity, as extinction has pruned out the intermediate taxa (Hopkins 2013).

That there is no change in mean pairwise distance, nor in summed variance in morphospace, across the end-Cretaceous mass extinction is perhaps surprising. However, this is simply an indication that the extinction event itself was not selective within Eutheria with regard to morphology. Angiosperms show a similar pattern (Lupia 1999) of changes in taxonomic richness but not variance-based measures of disparity. However, unlike the eutherian pattern of increased range occupation but no change in variance, many vertebrate groups, such as lizards (Longrich *et al.* 2012) and multituberculates (Levering 2013) show a dramatic decrease in range occupation across the end-Cretaceous mass extinction, although teleost fish show a sudden increase in range occupancy and number of lineages (Friedman 2010). While metatherian mammals were severely affected by the extinction event (Williamson*, et al.* 2014), the results from this study appear to suggest that eutherians went remarkably unscathed, with those groups which went extinct already in severe decline during the latest Cretaceous. This is in accord with the observation that subsampled taxonomic richness declines substantially from the Campanian to the Maastrichtian (Newham*, et al.* 2014).

1(f) – *Conclusions*

The end-Cretaceous mass extinction undoubtedly had an impact on the evolution of eutherian mammals and the radiation of what would become crown Placentalia. The earliest Paleocene is here shown to be a period in which the range of morphologies of those earliest placental taxa expanded greatly. However, taking Eutheria as a whole, the story is more complicated. Parts of the eutherian tree were already in decline prior to the end-Cretaceous mass extinction event, with the beginnings of a taxic turnover in the Maastrichtian from archaic eutherians like zhelestids and zalambdalestids to the more derived forms such as leptictids and the progenitors of Placentalia. This is manifested in the decline in mean pairwise dissimilarity from the Campanian to the Maastrichtian. The rise in sum of ranges reflects the beginning of the diversification of Placentalia, with new synapomorphies exploring novel regions of morphospace. In the Paleocene, mean pairwise dissimilarity increased as the adaptive radiation resulted in placental mammals specialising ecologically. Although the extinction event caused the loss of those more basal (with respect to Placentalia) eutherians, a transition within eutherian mammals was already underway, paving the way for the subsequent radiation.

CHAPTER FIVE

TESTING THE INHIBITORY CASCADE MODEL IN MESOZOIC AND CENOZOIC MAMMALIAFORMES

5(a) – *Abstract*

Background

Much of the current research in the growing field of evolutionary development concerns relating developmental pathways to large-scale patterns of morphological evolution, with developmental constraints on variation, and hence diversity, a field of particular interest. Tooth morphology offers an excellent model system for such 'evo-devo' studies, because teeth are well preserved in the fossil record, and are commonly used in phylogenetic analyses and as ecological proxies. Moreover, tooth development is relatively well studied, and has provided several testable hypotheses of developmental influences on macroevolutionary patterns. The recently-described Inhibitory Cascade (IC) Model provides just such a hypothesis for mammalian lower molar evolution. Derived from experimental data, the IC Model suggests that a balance between mesenchymal activators and molar-derived inhibitors determines the size of the immediately posterior molar, predicting firstly that molars either decrease in size along the tooth row, or increase in size, or are all of equal size, and secondly that the second lower molar should occupy one third of lower molar area. Here, I tested the IC Model in a large selection of taxa from diverse extant and fossil mammalian groups, ranging from the Middle Jurassic (~176 to 161 Ma) to the Recent.

Results

Results show that most taxa (about 65%) fell within the predicted areas of the Inhibitory Cascade Model. However, members of several extinct groups fell into the regions where m2 was largest, or rarely, smallest, including the majority of the

polyphyletic "condylarths". Most Mesozoic mammals fell near the centre of the space with equality of size in all three molars. The distribution of taxa was significantly clustered by diet and by phylogenetic group.

Conclusions

Overall, the IC Model was supported as a plesiomorphic developmental system for Mammalia, suggesting that mammal tooth size has been subjected to this developmental constraint at least since the divergence of australosphenidans and boreosphenidans approximately 180 Ma. Although exceptions exist, including many 'condylarths', these are most likely to be secondarily derived states, rather than alternative ancestral developmental models for Mammalia.

5(b) – ***Background***

5(b)(i) – *Inhibitory Cascade Model*

Tooth morphology is used extensively in the study of mammalian evolution because teeth are generally well-preserved in the fossil record and contain a large amount of phylogenetically and ecologically important information (Bergqvist 2003). With the explosion of the field of 'evo-devo' over the last few decades (Müller 2007), new data on tooth development have provided broad hypotheses on the mechanisms generating the diversity of morphologies observed in mammalian teeth (e.g. (Polly 2005; Salazar-Ciudad and Jernvall 2010)). These hypotheses have, however, rarely been applied to palaeontological datasets, due to the difficulty of discerning developmental mechanisms in the fossil record (but see (Sanchez 2012) and references therein).

Across mammals, molar buds develop sequentially from the anteriormost to the posteriormost (Butler 1939; Gaunt 1963). In a recent study, Kavanagh *et al.* (2007)

examined lower molar development in extant murid rodents, demonstrating that explantation of lower molar buds delayed development of posterior molars, but that early severance of posterior molar buds restored the rate of growth. In the framework of their model, termed an 'Inhibitory Cascade' (IC), the growth of each developing molar bud is affected by the balance between an inhibitor present in the adjoining anterior molar and a mesenchymal activator. A key feature of the IC Model is that the changes in size along the molar sequence will be cumulative – in other words, the development of the third lower molar (m3) is affected both by m2 and m1. The parameters of this cumulative relationship, determined experimentally, predict that, should the IC Model be a primary control on mammalian tooth sizes, m2 will occupy one third of total molar occlusal area, regardless of whether m1 is larger than m3 or vice versa. The second lower molar, then, will always be intermediate in size, or all three molars will be the same size. They further demonstrated that this pattern was broadly applicable across murid rodents. A third prediction suggested is that there is a correlation between the position of a taxon in the molar morphospace and its diet. Specifically, they state that "the most equal molar proportions are found in herbivorous taxa and the least equal in faunivorous taxa" (see Figure 5.1), and demonstrate this prediction with one example each of a faunivorous, omnivorous, and herbivorous murid, although this is not tested statistically across murids.

As a developmental mechanism, the IC Model is unusual in providing testable predictions regarding morphologies which are readily preserved in the fossil record. This applicability to taxa that are only available as fossilised remains and hence generally excluded from such analyses allows for robust testing of the origin of the mechanism itself. Teeth are among the best preserved elements of a mammalian skeleton and make up a significant proportion of specimens found in mammalian assemblages (e.g. (Bown and Kraus 1981)). For this reason, many extinct taxa that

Figure 5.1 – Illustrations of molar size decreasing and increasing posteriorly. On the left is *Pentacodon occultus*, a cimolestid, which are generally regarded as being faunivorous, and on the right, *Hyracotherium sp.*, the earliest known equid, a browsing herbivore. In each, m1 is coloured yellow, m2 green, and m3 red. *Pentacodon* displays the typical pattern for an insectivorous-carnivorous mammal, with the posterior molars much smaller in area. *Hyracotherium* displays the typical pattern for a herbivores, with the posteriormost molar much larger than the first or second. In each case, m2 is intermediate in size between the other two.

are known solely from a lower molar series can be included in an analysis of the IC Model, thus greatly increasing the potential dataset available for study.

A small number of studies have tested the predictions of the IC Model in a variety of fossil and extant mammalian groups (Polly 2007; Asahara 2013). The predictions of the IC Model have been found to, for the most part, be applicable to Rodentia (Labonne *et al.* 2012) as a whole, and South American ungulates (Wilson *et al.* 2012), although in each case, several taxa fell outside of the expected area. Thus far, the largest deviation from the predictions of the IC Model has been found in canids (dogs and their kin) (Asahara 2013), but also in arvicoline rodents (voles and lemmings) (Renvoise *et al.* 2009), leading the latter authors to conclude that the IC Model might not be generalisable even across rodents. In contrast, an analysis of 29 mammals, mostly extant placental mammals but also including two marsupials and some extinct taxa, suggests that the IC Model held true for all variation across the sample, although there were some outliers (Polly 2007). The distribution of taxa in that study also supported the prediction that taxa with different diets would fall into distinct regions of the molar morphospace, with herbivorous forms bearing relatively larger m3, and faunivorous relatively larger m1, although this was again not tested statistically. That the IC Model has been supported in detailed analysis of two disparate groups (the South American notoungulates and most rodents), as well as a phylogenetically broad sample of predominantly extant mammals, suggests that this developmental mechanism may have been established early in mammalian evolution.

In this study, I test the applicability of the IC Model within a large sample of extant and extinct boreosphenidans (the clade including extant marsupials, placentals, and their stem relatives) and australosphenidans (the clade including monotremes and their stem relatives). These lineages are estimated to have diverged approximately 180 million years ago (Ma) and encompass all of extant mammalian diversity (Luo *et al.* 2001; Kielan-Jaworowska*, et al.* 2004). Thus, the sample has sufficient phylogenetic breadth to assess the hypothesis that the IC Model is a common and ancestral model of mammalian tooth development and that it was established early in mammalian evolution.

5(c) – ***Methods***

5(c)(i) – *Taxonomic Sampling*

A total of 154 specimens were included in the present study (Appendix 2.9, electronic supplementary information), comprising 132 genera within 23 orders. The majority of these taxa are eutherians, including placental mammals and their stem relatives. Within placental mammals, the four superorders were all sampled. The “southern” superorders Xenarthra (sloths, armadillos and anteaters) and Afrotheria (elephants, hyraxes, sirenians and allies) were each represented by two genera. Euarchontoglires was represented by two scandentians (tree shrews), two dermopterans (colugos), three primates and ten rodents. The best sampled of the four superorders was Laurasiatheria, with three sampled from Carnivora (cats, dogs, bears and allies), ten from Perissodactyla (horses, rhinoceroses, and tapirs), fifteen from Eulipotyphla (shrews, moles and allies), and seventeen from Artiodactyla (cows, pigs, camels and allies).

In addition to those taxa known to fit unambiguously within extant placental orders, several stem taxa and taxa of uncertain affinities were included. Among those sampled taxa of less certain affinities are three genera of Arctostylopidae, a group which has traditionally been placed with the notoungulates (e.g. (Zheng 1979)), but which more recent studies place near the stem of Glires (rodents, rabbits and pikas) (Missiaen *et al.* 2006). Notoungulates (two representatives) is one of several South American ungulate clades (Billet 2011) generally treated as Mammalia *incertae sedis* (Billet 2010), although they have been reconstructed as close to Afrotheria based on shared dental, vertebral and astragalar synapomorphies (Agnolin and Chimento 2011). Cimolestidae (11 representatives) is a diverse order, thought to be ancestral or closely related to Ferae (e.g. Lopatin 2006), the clade containing the extant orders Carnivora and Pholidota (pangolins), but have also been placed as a stem placental clade (e.g. Rose and Von Koenigswald 2005), as has Leptictida (Wible*, et al.* 2007; Goswami*, et al.* 2011; Meehan and Martin 2010), of which there are three representatives in this dataset. Pantodonta (6 representatives) are sometimes considered to be related to Cimolestidae (e.g. McKenna and Bell 1997), and are reconstructed by others as comprising an entirely separate order of placental mammal (e.g. (Scott 2010)). Plesiadapiformes, of which there were two genera in this dataset, are often, but not uncontentiously, considered to be close to the origin of Primates (Bloch *et al.* 2007a). Also included in this dataset were two palaeanodonts, a group which has been considered ancestral to pangolins (Kondrashov and Agadjanian 2012), and two creodonts, which are often reconstructed as a paraphyletic group of stem carnivorans (e.g. (Flynn and Wesley-Hunt 2005; Morlo*, et al.* 2009; Zack 2012)). By far the most troublesome polyphyletic grouping is that of "Condylarthra" (seventeen representatives), as well as "Acreodi" (five representatives), which have been commonly referred to as "archaic ungulates" (Archibald 1998). Once thought to be ancestral to the now abandoned group "Ungulata" (a polyphyletic collection of extant hoofed mammals), these Palaeogene omnivores and herbivores have been suggested to be ancestral to several extant placental clades. For instance, phenacodontid "condylarths" have been affiliated with perissodactyls (Penkrot *et al.* 2008) as well as Afrotheria (Asher 2007). Arctocyonid "condylarths" such as *Chriacus* have been suggested to be ancestral to artiodactyls (Rose 1996), with "Acreodi" often suggested as ancestral specifically to Cetacea (Geisler 2001). Apheliscid "condylarths" have recently been suggested to be ancestral to Macroscelidea (elephant shrews or sengis), within Afrotheria (Tabuce*, et al.* 2001; Zack*, et al.* 2005a).

Lastly within the eutherian sample were two genera of Zhelestidae, a small, herbivorous clade that has been placed as stem placentals, outside of the crown group, in a recent analysis (Wible*, et al.* 2007), but have also been considered primitive "ungulatomorphs" by some (e.g. (de Muizon and Cifelli 2000)).

Four unambiguous members of the placental stem were included (*Zalambdalestes*, *Bobolestes*, *Montanalestes*, and *Zhangolestes*), as was a single metatherian (*Asiatherium*) and two members of the therian stem lineage (*Arguimus* and *Kielantherium*), all of which are from the Cretaceous (145 to 66 Ma).

Finally, outside of Theria, a sample of Jurassic and Cretaceous australosphenidan mammals were included, comprised of two Cretaceous members of Monotremata (*Kollikodon* and *Steropodon*) and two members of the sister group

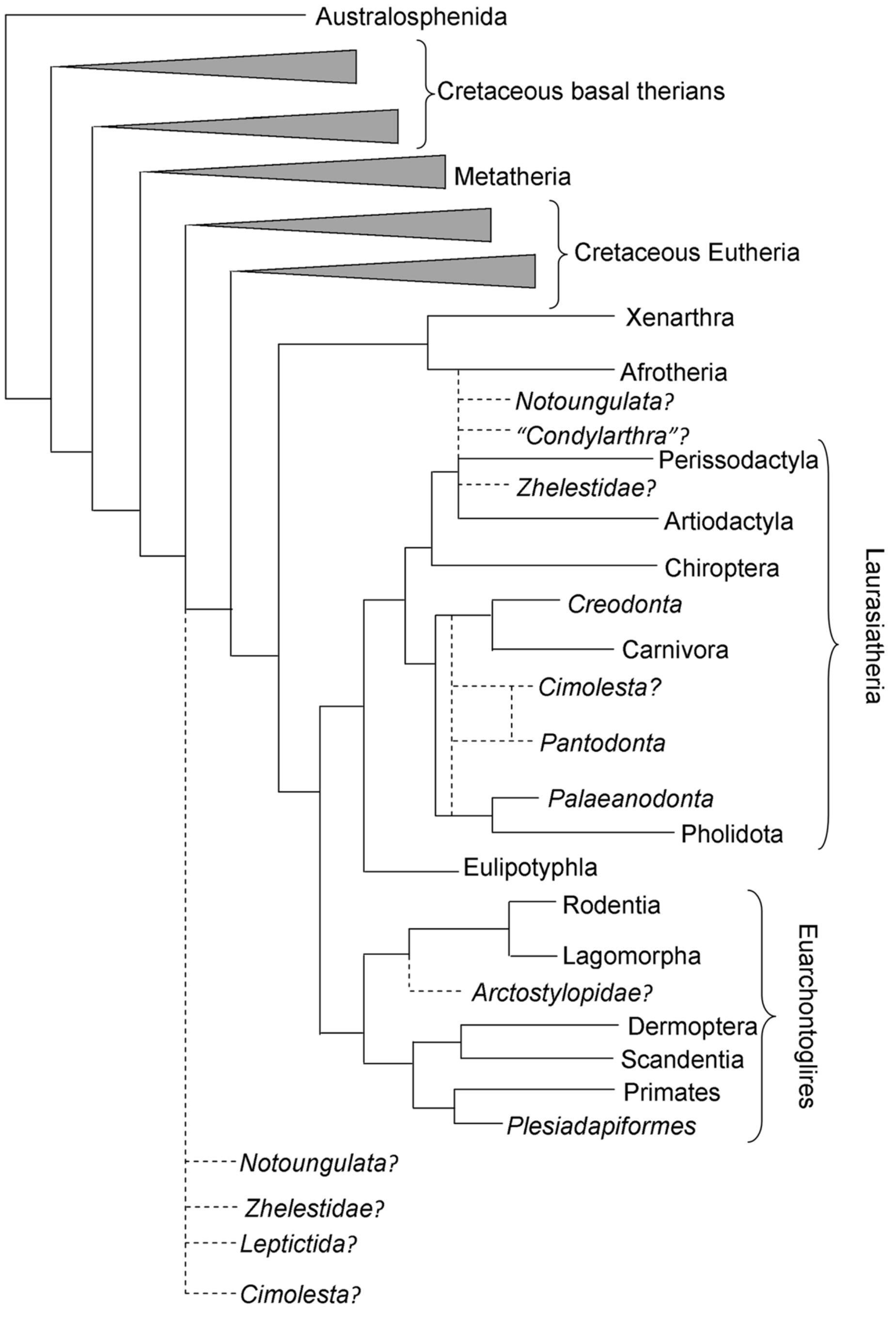


Figure 5.2 – High level phylogeny of mammals, including all groups used in this study. Dotted lines represent possible affinities or where groups may be polyphyletic. Italicised taxonomic names are extinct groups, some of which are likely polyphyletic. Tree topology modified from Asher and Helgen (2010),with extinct group placement based on various recent analyses or compilations (Agnolin and Chimento 2011; Bloch*, et al.* 2007a; Kondrashov and Agadjanian 2012; de Muizon and Cifelli 2000; Lopatin 2006; McKenna and Bell 1997; Missiaen*, et al.* 2006; Rose and Von Koenigswald 2005; Zack*, et al.* 2005a). This tree is intended to be illustrative of the diversity of groups covered in this analysis, and is not derived from any single phylogenetic analysis.

Ausktribosphenida (*Asfaltomylos* and *Ausktribosphenos*). These extinct forms are generally considered to be closely related to modern monotremes (echidnas and the platypus) (Luo*, et al.* 2001; Martin and Rauhut 2005), although this has been disputed by some (Rich *et al.* 2002), and represent the final major division of crown mammalian diversity. Sampling, therefore, covers the majority of crown mammalian clades (see Figure 5.2).

All time periods from the Cretaceous to the Recent were well-represented in this sample. One taxon (*Asfaltomylos*) is known from the Middle Jurassic (174 to 163 Ma), 14 are known from the Cretaceous (145 to 66 Ma), 95 from the Palaeogene (66 to 23 Ma), and 25 from the Neogene (23 to 2.6 Ma). 9 taxa are extant. Twelve genera are known from both the Palaeogene and Neogene or from both the Neogene and Recent.

5(c)(ii) – *Measurements*

Measurements of lower molar length and width were obtained from the literature, either from published measurements or specimen images, or directly from museum specimens (both high-quality casts and original material) (Appendix 2.9, electronic supplementary information). Area was estimated for each tooth as the product of length and width, following the method of both Polly (Polly 2007) and Wilson (Wilson*, et al.* 2012). For specimens that were measured directly, length and width were obtained from occlusal-view photographs in ImageJ v1.45s (Rasband 1997-2012). In addition, measurements for several taxa were obtained from the Palaeobiology Database (www.paleodb.org) on the 13th of May 2012, using the taxonomic group name 'Mammalia' and the following parameters: Taxonomic resolution = 'certainly identified to genus', Body Parts = 'm1, m2, m3', with 'all parts must be measured' ticked. Output fields were 'length', 'width', 'specimens measured'. All measurements were corrected for size by using the ratio of respective tooth area to that of m1 area, such that a posterior decrease in molar sizes would give values lower than 1, and an increase would give values larger than 1. Only specimens with two or all three adjacent molars present were included in the final dataset, and where multiple specimens were available, averages of molar ratios were analysed. All taxa which were composed solely of isolated molars, regardless of whether all three were represented, were removed from the dataset, due to inability to control for intraspecific variation. Ratios of m1:m2, m2:m3 and m1:m3 were quantified for each specimen, and averages of these ratios were then calculated for each genus. For taxa with more than three lower molars, only the first three were measured. Taxa with fewer than three lower molars were excluded from the analysis. Taxa for which either length or width were unavailable due to preservation were also excluded, such that length was not used as a proxy for area in any of the analyses.

While the approach used here, and in the studies noted above, estimated tooth area as a product of maximum length and width, some other studies (Kavanagh*, et al.* 2007; Labonne*, et al.* 2012; Renvoise*, et al.* 2009; Asahara 2013) have measured tooth occlusal area directly. In order to establish the comparability of these area measurements, I also directly measured molar area in 41 genera (41 specimens) for which specimens were available. For this analysis, only values from the second lower molar were used, in order to reduce non-independence in the dataset, and molar area was measured from occlusal-view photographs using the outline tool in ImageJ v1.45s (Rasband 1997-2012).

5(c)(iii) – *Data analysis*

Correlations among measurements of tooth size

For many fossil taxa, the nature of their preservation results in two-dimensional specimens, for which tooth widths (and hence areas) are unable to be assessed, except where preservation is in occlusal aspect. These specimens cannot be plotted in a tooth area ratio graph, although there is the potential for important size information to nonetheless be extracted. In order to identify whether molar length or width alone could be used as an accurate proxy for area, and hence increase the sample size in future studies, non-parametric Spearman Rank correlation analyses were performed among the relative lengths, widths and areas (scaled against the respective measure for m1) for each pair of molars. A strong length-area correlation would support the use of length as a proxy for molar area, and would imply that the major axis of increase in size is the antero-posterior axis. Such a result would further mean that the length ratios between teeth should follow the same pattern as area, although with differing regression parameters. All analyses were conducted in R (R Development Core Team 2010).

Testing the Inhibitory Cascade Model

Each taxon was plotted in a morphospace described by the ratios of molar areas of m2:m1 and m3:m1, as in previous studies (e.g. (Kavanagh*, et al.* 2007; Polly 2007)), and a reduced major axis linear regression line was calculated (Figure 5.3). This regression line was then compared with the model predicted by Kavanagh *et al.* (Kavanagh*, et al.* 2007), as well as with the regression line of their original dataset, using 95% confidence intervals to test whether the two datasets were significantly different from one another or from the IC Model.

In order to test the second prediction of the IC Model – that m2 should occupy one third of total molar occlusal area – the proportion of total molar area occupied by m2 was calculated for all 154 specimens (132 genera) included in this study. Averages of this proportion were then taken for each genus. A two-tailed Student's t-test was used to test whether the mean proportion of occlusal area taken up by the m2 was significantly different from 33%. This was then compared with the murine data

((Kavanagh*, et al.* 2007), supplementary information), to which the same method was applied.

Phylogeny and Diet

Non-parametric MANOVA were conducted in R (R Development Core Team 2010) using the 'adonis' command line in the 'vegan' package (Dixon 2003), in order to test for significant clustering of different dietary guilds and of taxonomic orders within the morphospace. The 101 taxa from higher-level groups with five or more representatives (with a pooled Creodonta-Carnivora group and a Primates-Plesiadapiformes group) were included in the analysis of phylogenetic clustering, comprising 10 groups in total. Phylogenetic group and dietary assignments are detailed in Appendix 3. Decisions on taxonomic grouping follow McKenna and Bell (1997) where possible, and otherwise refer to the original descriptive literature for any given genus. Dietary information was extracted from the Paleobiology Database where possible, and otherwise directly from the original descriptive literature. Where dietary assignments were not available for a particular genus, family- or subfamily-level dietary estimates were used. Because precise diets can be difficult to discern in extinct organisms and are continually debated, broad categories (folivorous, carnivorous, omnivorous, insectivorous, frugivorous and durophagous) were used, which, despite some inevitable overlap, should be relatively accurate. Moreover, some inaccuracy in dietary assignations should not obscure a strong pattern with regard to morphospace position and diet, if one exists.

5(d) – ***Results***

5(d)(i) – *Correlations of Measurements*

Significant positive correlations were found between all pairings of tooth length, width and product area, for ratios of m2 and m1, as well as of m3 and m1 (Table 5.1).

Unsurprisingly, the strongest correlations were of length or width with area, reflecting the dependence of the area measurement on length and width, while correlations between length and width were markedly weaker.

Table 5.1 - Correlations between size parameters in lower molars. Pairwise Spearman Rank Correlation analysis between length, width and area values. Data used are ratios of m2/m1 and m3/m1 to control for absolute size differences.

CORRELATION	SAMPLE SIZE	S-STATISTIC	P-VALUE	RHO
LENGTH:WIDTH, m2/m1	130	300091.2	<<0.001	0.4214
LENGTH:WIDTH, m3/m1	121	136839.2	<<0.001	0.6430
LENGTH:AREA, m2/m1	130	80543.3	<<0.001	0.8447
LENGTH:AREA, m3/m1	121	22257.7	<<0.001	0.9419
WIDTH:AREA, m2/m1	130	99563.7	<<0.001	0.8080
WIDTH:AREA, m3/m1	121	57711.7	<<0.001	0.8494

The single strongest correlation observed was between length and area, particularly for m3:m1 ratios, suggesting that tooth length can reasonably be used as a proxy for tooth area. Spearman rank correlation analysis of the two different methods of measuring area, directly from specimen images or as the product of length and width, was highly significant (rho = 0.9878, p<<0.001), suggesting that product area is an accurate means of estimating tooth area.

5(d)(ii) – *Comparison of IC Model with Previous Studies*

In the morphospace defined by m2/m1 against m3/m1, the majority of taxa (86 of 132) fell within the region predicted by the IC Model, although many specimens were found to be outside this region (Figure 5.3). This observation is consistent with, although slightly higher than, other studies, in which 12-20% fall outside the predicted region (Polly 2007; Labonne*, et al.* 2012). Of the 46 taxa which fell outside this 'm2 intermediate' region, 39 fell in the area in which m2 was the largest lower molar; only 7 displayed an m2 that was the smallest of the three molars. 30 genera

Table 5.2 – Comparison of regression parameters in different analyses. A comparison of the parameters of the IC Model, and linear regressions for three previous analyses of the IC Model, as well as this study.

MODEL SOURCE	SLOPE	SLOPE 95% CI	INTERCEPT	INTERCEPT 95% CI
IC MODEL	2.000	n/a	-1.000	n/a
KAVANAGH *et al.* (2007) (MURINE RODENTS)	2.150	1.772:2.688	-1.219	-1.651:-0.925
RENVOISÉ *et al.* (2009) (ARVICOLINE RODENTS)	1.390	1.208:1.555	-0.313	-0.407:-0.213
ASAHARA (2013) (CANIDAE)	0.450	0.376:0.515	-0.080	-0.104:-0.037
THIS STUDY (MAMMALIA)	2.303	2.007:2.655	-1.455	-1.863:-1.113

exhibited molars that decreased in size posteriorly, and 56 exhibited molars increasing in size posteriorly. The 95% confidence intervals of the slope and intercept parameters (Table 5.2) overlapped with those of the murine study (Kavanagh*, et al.* 2007), but were significantly different from those of the arvicoline study (Renvoise*, et al.* 2009). The regression parameter confidence intervals of this study were, however, significantly different from the theoretical parameters of the IC Model (Table 5.2).

Table 5.3 – m2 area as a proportion of total occlusal area. A comparison between the proportion of total lower molar occlusal area (m1 + m2 + m3) taken up by m2, in the IC Model's prediction, a previous analysis, and this study.

DATA SOURCE	T	DF	m2 AREA AS %	95% CI	P-VALUE
IC MODEL	n/a	n/a	33.33	n/a	1
KAVANAGH *et al.* (2007) (MURINE RODENTS)	5.702	28	34.84	34.30:35.38	<0.001
THIS STUDY (MAMMALIA)	3.898	129	34.58	33.94:35.22	<0.001

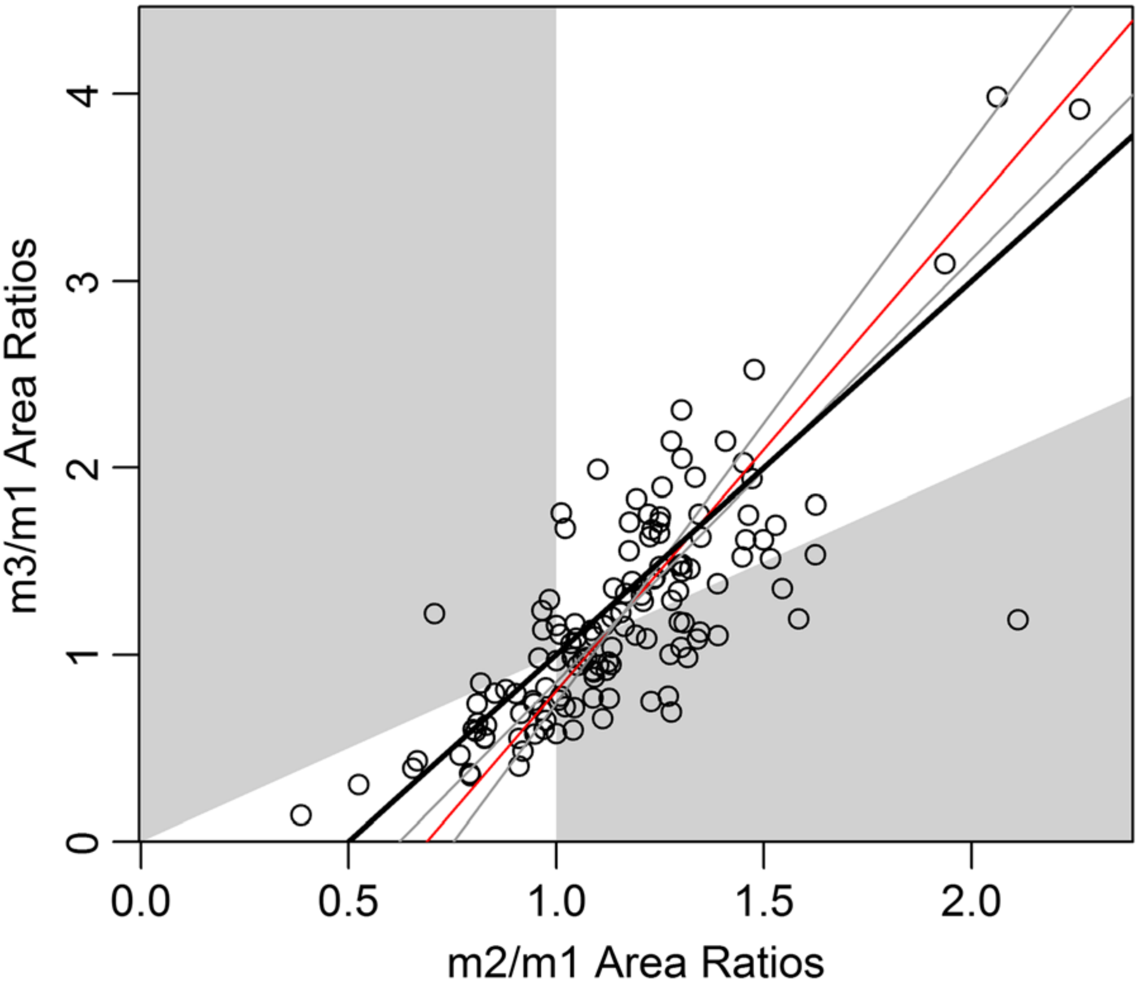


Figure 5.3 – Lower molar area ratios plotted for 132 mammalian genera, with regression line. The black line represents the IC Model as predicted by Kavanagh *et al.* (Kavanagh, *et al.* 2007), with the white areas representing the predicted possible areas under the strict IC Model. Grey regions are outside the predicted areas of the model, and represent regions of the graph where m2 is either the largest lower molar (bottom-right) or the smallest (top-left). 65.2% of sampled taxa fall within the predicted area. The thin red line is the reduced major axis regression line, with 95% confidence bands in blue on either side.

Mean second lower molar area was 34.58%, similar to the 1/3 of total molar area predicted by the IC Model. However, both this study and the murine data give a value slightly higher and significantly different from the predicted value, although, as with the regression parameters, the two studies were not significantly different from one another (Table 5.3). In both cases, m2 comprised slightly more than one third of total molar occlusal area.

5(d)(iii) – *Phylogeny and Diet*

Above the ordinal level, a non-parametric MANOVA suggested that taxonomic groups are significantly distinct in morphospace (Table 5.4). This pattern appears to be driven largely by the Carnivora-Creodonta and Artiodactyla groupings, which are

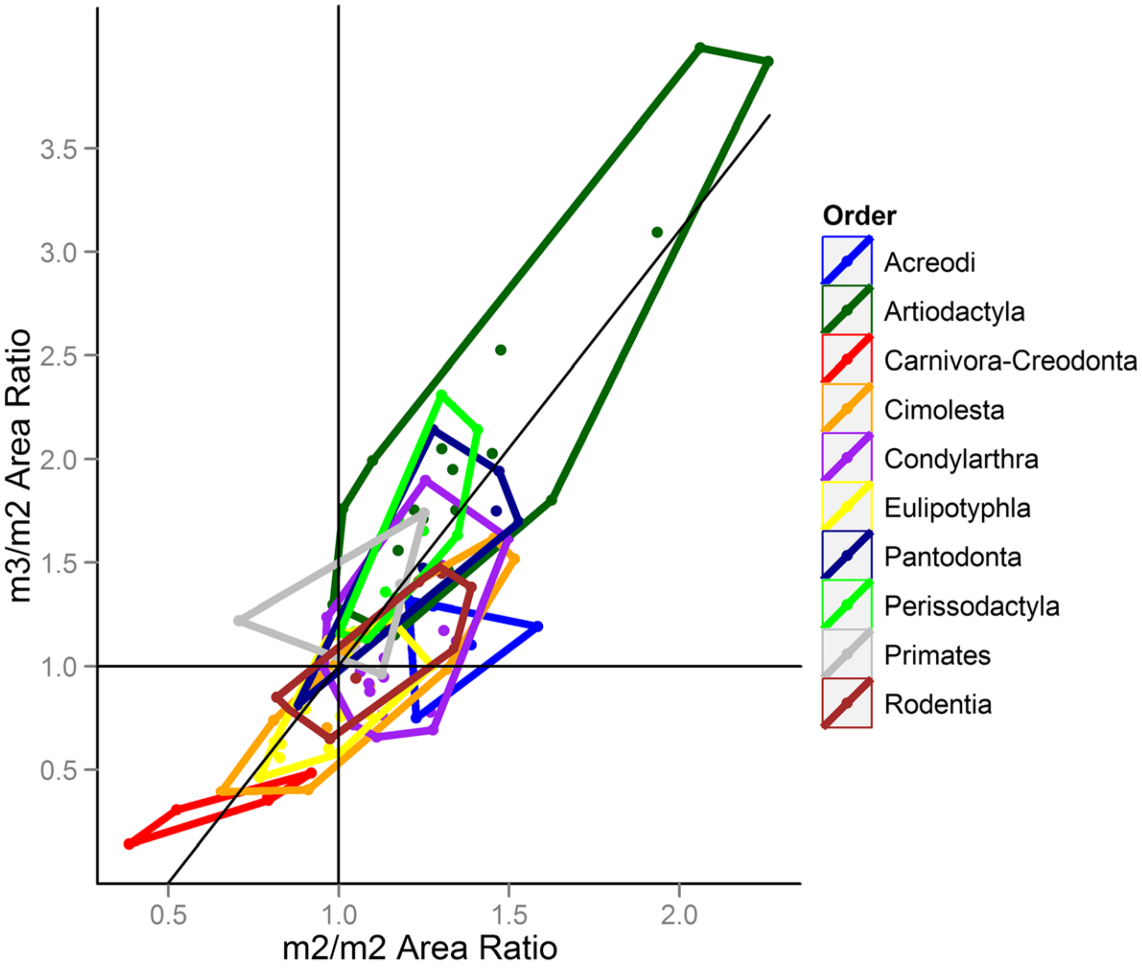


Figure 5.4 – Minimum area polygons for the ten taxonomic groupings. Only groups with more than five genera were included in this analysis. Carnivora and Creodonta have been grouped together as possibly closely-related carnivorous placentals; Primates and Plesiadapiformes are also grouped together. Non-parametric MANOVA results in a highly significant clustering by taxonomic group ($p<0.001$), even when removing the most extreme members of Artiodactyla. The only group to overlap with the range of the carnivorous placental grouping is Cimolestidae. "Condylarths" and Acreodi are clustered together in an area distinct from that occupied by Artiodactyla and Perissodactyla, with only three "condylarths" overlapping in range with the extant ungulate groups, showing that "archaic" and extant ungulates possess clearly distinct tooth morphologies.

particularly distinct from other taxonomic divisions (Figure 5.4). Despite this statistically significant cohesion of taxonomic divisions, there is considerable overlap among several groups. For example, the minimum area polygon for Cimolestidae overlaps at least partially with all other taxonomic divisions. While clustering of orders was apparent in the dental morphospace, for example between rodents and primates – the two largest groups comprising Euarchontoglires – the relationships between these broad taxonomic groupings is not sufficiently well-resolved to identify any inter- or intraordinal patterns. Nonetheless, these results demonstrate

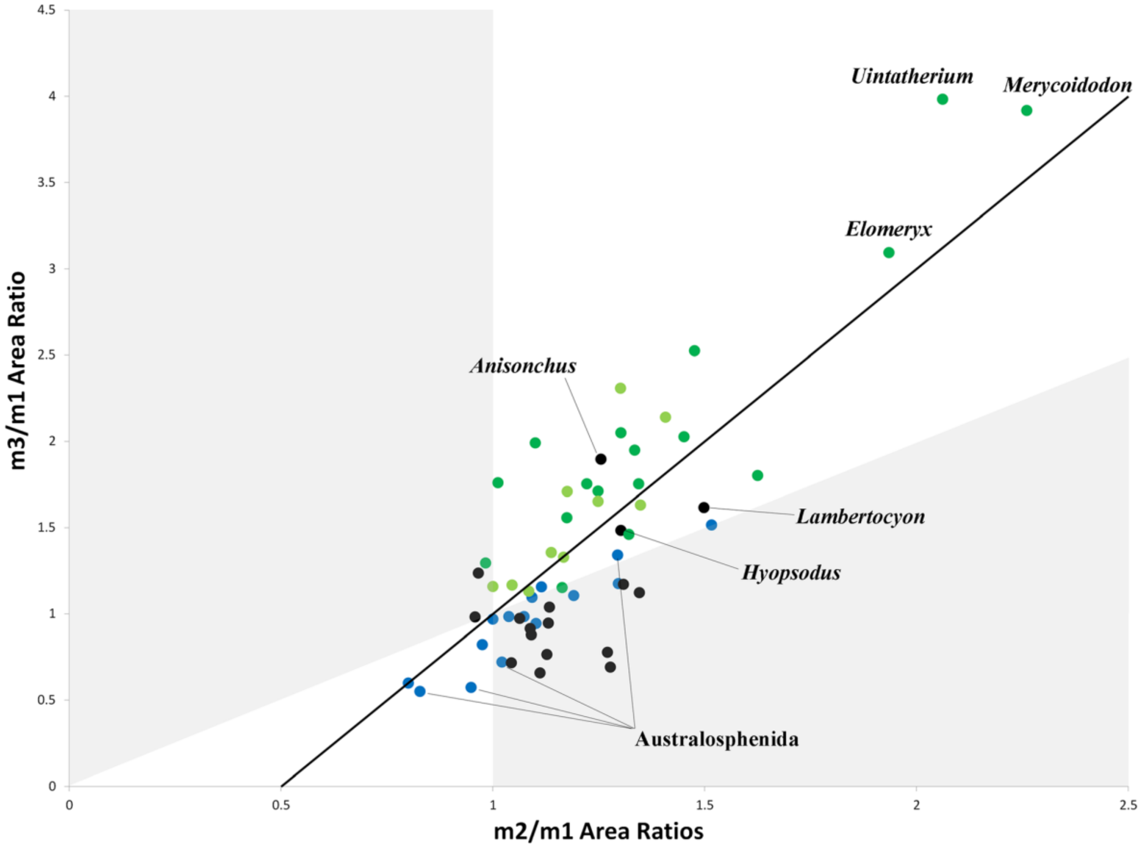


Figure 5.5 – Morphospace positions for Mesozoic mammals and the extant and "archaic" ungulates. Mesozoic mammals (coloured in blue) are found near the centre (1,1) of the morphospace, closer to the plesiomorphic conditions of equal-sized molars. "Condylarths", coloured black, are found mostly in the region of the morphospace where m2 is the largest molar, and are separate from Artiodactyla (dark green) and Perissodactyla (light green), with the exceptions of *Hyopsodus*, *Anisonchus* and *Lambertocyon*, all of which possess molars that increase in size posteriorly. Artiodactyla show the most extreme increase in molar size, with *Uintacyon*, *Elomeryx* and *Merycoidodon* exhibiting six-fold or more increases in molar area from m1 to m3.

that basal groups (australosphenidans, stem therians and stem placentals) consistently occupy the very centre of the morphospace (Figure 5.5), where tooth size is equal or subequal along the tooth row. The majority of the polyphyletic "condylarths" clustered together in the dental morphospace, but with the exception of the hyopsodontid *Hyopsodus*, arctocyonid *Lambertocyon* and periptychid *Anisonchus*, fell in a distinct region from the extant ungulate clades, Artiodactyla and Perissodactyla.

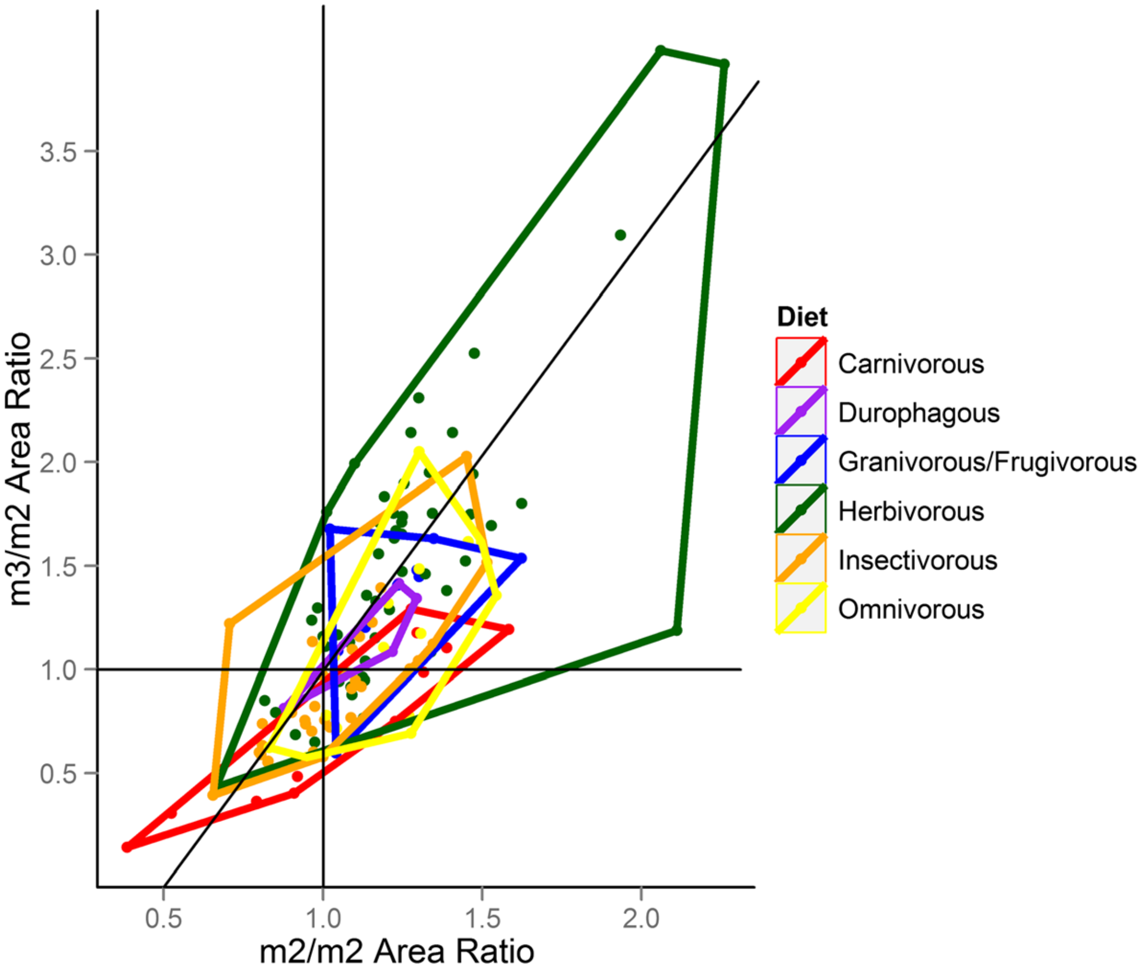


Figure 5.6 – Minimum area polygons for 132 genera divided into six dietary types. The data show a similarity to the predicted distribution from Kavanagh *et al.* (Kavanagh*, et al.* 2007), with more faunivorous dietary types placed in the bottom left of the morphospace, and more herbivorous dietary types in the top right.

The division in morphospace position of dietary groups was also found to be statistically significant (Table 5.4, Figure 5.6). Once again, however, there is overlap of minimum area polygons for all pairs of taxonomic divisions. The statistical determination, both in the case of diet and taxonomic divisions, of degree of clustering depends primarily on the variance of the positions of the taxa within each division. As a result, minimum area polygons can overlap substantially while still representing significantly different distributions of morphospace coordinates. Such analyses of variance are often susceptible to outliers, and so the five outlying and likely herbivorous taxa (the artiodactyls *Uintatherium*, *Merychyus*, *Merycoidodon*, and *Elomeryx*, and the arctostylopid *Palaeostylops*) were excluded from a second, otherwise identical analysis. While the F-statistic was lowered, the degree of cohesion of the groups remained highly significant, suggesting that there is a robust relationship between relative tooth areas and diet.

Table 5.4 – Morphospace clustering due to diet and phylogeny. Results of non-parametric MANOVA testing clustering due to phylogeny and diet in the morphospace. All results were highly significant. Sample sizes were 132 genera for of Phylogeny and Diet, 101 for the limited phylogenetic groupings (5+ representatives per group), and 127 for the reduced dietary analysis (without extreme outliers, of which four were artiodactyls and one an arctostylopid).

TEST	DF	SUM SQS	MEAN SQS	F	R^2	P-VALUE
PHYLOGENY	24	2.088	0.087	5.764	0.564	<0.001
PHYLOGENY (5+)	9	1.706	0.190	12.595	0.555	<0.001
DIET	5	0.922	0.184	8.351	0.248	<0.001
DIET (REDUCED)	5	0.736	0.147	7.768	0.243	<0.001

5(e) – *Discussion*

The results of this study are consistent with the hypothesis that the IC Model of lower molar development is the plesiomorphic condition for Mammalia. Furthermore, this study is wholly consistent with, and resembles closely, the results from a recent study that focused on rodents (Labonne*, et al.* 2012). While murids made up the majority of the rodents in this study, Labonne *et al.* (Labonne*, et al.* 2012) used a broader phylogenetic sampling of rodent taxa, which spanned the same range of molar ratios as do all mammals. This correspondence strongly suggests that a common developmental mechanism underlies the development of all mammalian teeth, rather than being specific to rodents.

Deviations from the parameters of the IC Model have been identified in a few clades – such as arvicoline rodents (Renvoise*, et al.* 2009) and canids (Asahara 2013), both of which show a significantly lower slope than predicted by the IC Model. This latter group's deviation from the model has been hypothesised to relate to the presence of the specialised m1, which forms part of the carnassial pair of slicing teeth. In each case, however, the observed data fell within the region of morphospace consistent with the predictions of an inhibitory cascade, even if the parameters of the regression line differed. High variability has also been noted in South American ungulates (Wilson*, et al.* 2012), with two groups (Astrapotheria and Interatheriidae) deviating significantly from the IC Model, as well as falling outside of the predicted region of morphospace.

In the IC Model, the value of the slope is determined by the degree to which the effect of the activator/inhibitor mechanism is changed in the m3:m1 ratio with respect to the m2:m1 ratio. It can therefore be described as representing the change in effect of the inhibitory cascade mechanism along the tooth row. In the pure IC Model, the expected value is 2, meaning that the change is cumulative and additive; m3 has had twice the effect of the activator/inhibitor balance as has m2. The difference in gradient of the slope, then, if expressed in terms of the change of effect through the molar series, would suggest that, through evolutionary time, the degree to which the effect changes along the tooth row is easily modified, and the morphologies of murine rodents, arvicoline rodents and canids may be explained through relatively small changes in this balance.

That 65% of sampled taxa in this study fell within the area predicted by the model suggests that the IC Model is indeed a common pattern underlying mammalian molar development. This percentage rises to 75% of taxa if excluding the 22 ‘archaic ungulates’, 18 of which fell in the m1<m2>m3 region of the morphospace. These ‘condylarths’ are considered by most to represent a polyphyletic group (e.g. (de Muizon and Cifelli 2000)), so their close proximity to one another, and distinct position in the morphospace from the extant ungulate clades, Artiodactyla and Perissodactyla, is notable. This observed separation between ‘archaic’ and extant ungulates suggests that these taxa may utilise distinct molar developmental mechanisms, with the ‘archaic’ ungulates representing a deviation from the common mammalian pattern. While this result is not necessarily surprising, as ‘condylarths’ are not as a whole considered to represent the ancestral group for modern ungulates, the observed tight clustering of the sampled condylarths, along with the sampled representatives of Acreodi (*Eoconodon, Ankalagon, Oxyclaenus, Sinonyx* and *Mesonyx*), is surprising. It is, however, plausible that the clustering of the ‘Condylarthra’ reflects their shared omnivorous to herbivorous dietary condition, rather than phylogenetic proximity, since dietary groups were also strongly clustered within the molar morphospace. A well-supported tree is required to analyse the real association between phylogeny, diet and dental morphospace proximity. Ongoing work to resolve the position of Paleocene condylarths within the broader placental mammal tree should ultimately allow for a more robust test of phylogenetic clustering within this dataset, and provide insight into whether this grouping represents a taxonomic or ecological signal, if either.

Apparent differences from the IC Model in previous studies may be largely due to limited taxonomic focus. For example, our data show that both arvicolines

(Renvoise*, et al.* 2009) and murines (Kavanagh*, et al.* 2007), while distinct in relative molar size from one another, fall within the range of observed variation for mammals as a whole, as well as within the region of morphospace that the IC Model predicts. While variation in the regression parameters of subgroups is high (Wilson*, et al.* 2012), the IC Model is generally consistent with the higher-level pattern observed across Mammalia. That the second prediction of the IC Model is not upheld, with the second molar being slightly, albeit significantly larger than would be expected, is not unsurprising given that the majority of taxa which fall outside of the predicted area do so with m2 as the largest tooth. Again, the data are consistent with the murine data collected by Kavanagh *et al.* (Kavanagh*, et al.* 2007), which indicates further that, while some deviations are apparent, the patterns observed for the majority of mammalian subgroups are consistent with that for Mammalia as a whole.

Despite the significant clustering of dietary groups, molar ratios likely do not provide a useful predictive tool for estimating diet in extinct organisms, as there is extensive overlap of several dietary groups in the central region of the molar morphospace (Figure 5.6). However, if molar proportions fall in the more extreme regions of the space (i.e., when m1>>m2>>m3 or vice versa), a prediction of herbivory (where m3 is largest) or carnivory (where m3 is smallest) could be made with reasonable confidence. Additional complications arise from the inherent association between phylogeny and diet, especially as some extinct genera in this study were assigned diets based on those of con-familial genera where more specific data were unavailable. An explicitly phylogenetic analysis, which will only be possible once a resolved phylogenetic tree is available, as well as better understanding of diet in many of these taxa, would greatly improve the ability to distinguish these two effects.

Another interesting aspect of molar development that is not considered here concerns the role of the premolars. Labonne *et al.* (Labonne*, et al.* 2012) demonstrated that loss of the lower fourth premolar in some taxa appeared to remove a spatial constraint on the development of the lower first molar. This loss would then affect the development of the first molar to a far greater extent that the more posterior molars, enabling a proportionally larger m1. None of the taxa included in this study are known to lack a fourth premolar, with the exception of the single metatherian genus, which, like all metatherians, has only three premolars. The effect should not influence the results presented here, but is important for future studies to take into account.

In conclusion, the results presented here corroborate the hypothesis that the Inhibitory Cascade Model is plesiomorphic to Mammalia as a whole. Although exceptions do exist, including many ‘condylarths’ these are more likely to represent secondarily derived states, rather than alternative ancestral conditions for the broader clade, as nearly all basal Mammaliaforms fall within the predicted area for the model. That the IC Model applies to mammalian taxa ranging from Jurassic and Cretaceous australosphenidans (*Asfaltomylos*, *Ausktribosphenos*, *Kollikodon*, and *Steropodon*) to early Cretaceous stem therians (*Arguimus*, *Bobolestes*, and *Kielantherium*), to a diverse sample of Cretaceous to Recent eutherians, including crown placentals, suggests that this developmental constraint predates the divergence of Australosphenida and Boreosphenida (marsupial and placental mammals and their stem groups) approximately 180 mya (Luo*, et al.* 2001; dos Reis*, et al.* 2012). As many of the most basal taxa in this analysis fall near the centre of the molar morphospace, where all three lower molars are near-equal in area, one could further hypothesise that a trend along the predicted regression line towards either a larger m1 or a larger m3 corresponds with dietary specialisation through mammalian evolution. Better resolved phylogenetic trees of living and extinct mammals are required to further reconstruct the trajectory of molar size evolution across

Mammalia, but further work on the distribution of these changes, as well as the effect of different ecological parameters, will provide important new information and models to reconstruct the evolution of mammalian dental morphology and diversity both today and in the fossil record.

CHAPTER SIX

CONCLUSIONS

6(a) - *Key findings*

6(a)(i) – *Phylogenetic relationships of enigmatic Paleocene mammals*

A major aim of this thesis was to establish the relationships among the earliest crown placental mammals. In particular, it aimed to derive the relationships of those mammals whose phylogenetic position with respect to the crown group were unknown, such as leptictids, cimolestids, and the genera *Purgatorius* and *Protungulatum*. In all cases, these taxa were found to be most parsimoniously resolved on the placental stem, and not as part of the crown group. However, constraining *Purgatorius* as a stem primate, as is commonly thought (Clemens 2004; Fox and Scott 2011), did not result in a significant increase in length.

Additionally, this thesis aimed to resolve the relationships of the patchwork collection of "archaic ungulates", including "condylarths", mesonychians, pantodonts, and the South American Native Ungulates. Some groups, such as the Phenacodontidae, were very strongly allied to an extant clade – in this case, Perissodactyla, confirming previous hypotheses (Radinsky 1966). Others were less well resolved, although a basal position for periptychids and a polyphyletic Arctocyonidae were both reasonably consistent across analyses. Within the extant lineages, the relationships among the superorders was very strongly resolved in favour of Atlantogenata, with no support whatsoever for the two competing hypotheses of Epitheria or Exafroplacentalia. This is an unusual result for morphological analyses, but not for molecular analyses (Hallstrom*, et al.* 2007; Prasad*, et al.* 2008; Morgan*, et al.* 2013). Inclusion of Paleocene taxa allows the long morphological branches between the extant superorders to be broken into shorter ones, and character polarities resolved such that the most basal division within Placentalia is strongly resolved in these analyses. As yet, there are still no known members of the stems of any of the four major superorders of crown Placentalia, nor of Boreoeutheria nor Atlantogenata, with both Cimolesta and Leptictida resolved as non-placental eutherians.

6(a)(ii) – *Dating the origin of Placentalia*

In Chapter Three, the phylogenies generated in Chapter Two were used to calculate the divergence dates of the major nodes within crown Placentalia, as well as the crown node itself. The mean reconstructed origination date for crown Placentalia was 66.35 million years ago, statistically significantly older than the end-Cretaceous mass extinction, meaning that the origin of the crown group predated the mass extinction event, albeit by as little as a few hundred thousand years.

The origins of Boreoeutheria, too, was reconstructed as having occurred prior to the end-Cretaceous mass extinction, whereas the origin of Laurasiatheria could not be considered statistically significantly different from that event. All other major divergences within the crown group were found to be statistically significantly younger than the end-Cretaceous mass extinction.

The diversification of crown Placentalia mostly, then, happened in the Paleocene, in agreement with the traditional interpretation of the fossil record that there was a real taxonomic diversification and adaptive radiation in eutherians in the earliest Cenozoic.

The divergence of Placentalia from its closest relatives – such as *Protungulatum*, *Purgatorius* and Leptictidae – was reconstructed as occurring some nine million years before the end-Cretaceous. Despite conservatively low sampling rates, 95% of placental occurrences were reconstructed after 69 million years ago, three million years prior to the Cretaceous-Palaeogene boundary, leaving a gap of three million years where it should be expected that we should find early crown placental mammals, and a gap of six million years where there should be non-placental eutherians that are closer to Placentalia than *Protungulatum*.

6(a)(iii) – *Rates of evolution across the K-Pg boundary*

Given a dated phylogeny, many macroevolutionary parameters can be tested across that tree. Chapter Three, in addition to dating the phylogeny, assessed the rates of discrete character evolution across the Cretaceous and Paleocene. Rates were found to significantly increase across the end-Cretaceous mass extinction, in a pattern that was robust to topology.

Overall, the Cretaceous had significantly lower evolutionary rates than would be expected from an equal rates model, while the Palaeogene was characterised by significantly higher rates which peaked in the Puercan, before declining slowly towards the Middle Eocene. Rates of evolution from the Oligocene onwards could not be accurately calculated due to a lack of sampling from those time bins.

Across the phylogeny, the branches involved in the diversification of Euarchontoglires, as well as Scrotifera (non-eulipotyphlan laurasiatheres), and the branch leading to Atlantogenata were all characterised by significantly increased rates relative to an equal rate model. Eulipotyphla, Dermoptera, Scandentia, and the branches within Xenarthra and Afrotheria all had significantly low rates, although these may be due to long branches in which little diversification was sampled.

On a node-based analysis, crown Placentalia was found to have significantly higher evolutionary rates than non-placental eutherians, implying that there was some hereditary shift in the inherent rate of evolution of crown Placentalia.

6(a)(iv) – *Disparity across the K-Pg boundary*

Three measures of disparity were calculated across the trees in Chapter Four. While sums of ranges of the PCO axes significantly increased across the end-Cretaceous mass extinction, even when accounting for biases introduced by sampling errors, there was no change in variance-based metrics of disparity between the Maastrichtian and the Puercan. However, by the time of the Torrejonian, mammals occupied significantly more disparate ecological niches; an increase that was repeated into the Tiffanian, before the rate of increase decelerated to a new stable level of mammalian morphological disparity, significantly higher than any stage of the Cretaceous.

The increase in sum of range measures of disparity at the beginning of the Paleocene represents the exploration of new cladistic morphospace by the earliest crown placental mammals. The rapid accumulation of synapomorphies that was demonstrated in Chapter Three resulted in novel ecologies and the increase in overall morphospace occupation. The depauperation of many eutherian groups at the end of the Campanian, and their subsequent extinction at the Cretaceous-Palaeogene boundary resulted in the mean distance between those taxa which remained being reduced. As a result, variance-based metrics were reduced in the Maastrichtian and only began to increase once again when the radiation of placental mammals was underway, and new regions of cladistic morphospace were being explored.

The phylogenies generated in Chapter Two therefore support the contention that the end-Cretaceous mass extinction was a time at which mammals underwent a strong increase in disparity of characters, and rapidly accumulated new morphologies, diversifying by the end of the Paleocene to the levels of diversity and ecological disparity that are observed in the present day.

6(a)(v) – *Conservation of developmental patterns across Mammalia*

As the majority of characters used in the cladistic analysis of mammals are dental, understanding how the dentition develops both ontogenetically and through evolutionary time is an important consideration. Chapter Five, therefore, tested a model of lower molar development – the Inhibitory Cascade model (Kavanagh*, et al.* 2007), a central prediction of which is that the second of the three lower molars should be intermediate in size between the other two. This model is slightly modified in marsupials and their metatherian ancestors, which have four molars. It was found that the mechanisms underlying the development of the lower molars – an internal stimulator of growth and an external inhibitor – were conserved not only within eutherian mammals, but also across metatherians, and even australosphenidans – the clade including monotremes. The Inhibitory Cascade Model could therefore be said to be plesiomorphic to Mammalia, and to have existed for at least 180 million years, with evolution from an ancestral state of equal sized molars to highly divergent forms, within the same constraint.

In general, herbivorous taxa possess molars that increase in area more posteriorly, while carnivorous and insectivorous taxa have molars that decrease in area posteriorly. Exceptions such as the majority of "condylarths" tend to have a second lower molar that is larger than both the first and third, with very few cases of second molars being smaller. This is hypothesised to be due to an early cessation of growth in the third molar, which is considered a less difficult modification to the developmental pathway than prolonged growth in the case of sequentially smaller molars. As “condylarths” represent the earliest exploration of specialist herbivores for placental mammals, it is possible that this early cessation is a result of historical contingency, having recently evolved from insectivorous ancestors, with their tendency to have reduced posterior molars.

6(b) – ***Broader context***

6(b)(i) – *Explaining the mammalian radiation in terms of an adaptive radiation*

An adaptive radiation, as has been discussed in previous chapters, must have certain characteristics. Schluter (2000) defined an adaptive radiation as “the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage” (Schluter 2000, page 10). He went on to describe the four features that are necessary (and sufficient) to determine that a clade underwent an adaptive radiation: common ancestry, phenotype-environment correlation, trait utility, and rapid speciation. The last of these – rapid taxic diversification, where per-lineage speciation rates outstrip per-lineage extinction rates quite significantly – is obvious in the post K-Pg placental fossil record. According to the analyses conducted here, and the dating of the placental mammal phylogeny, at the beginning of the Paleocene, the rate of speciation is between 56% and 850% higher than the rate of extinction, comfortably qualifying the appearance of placental mammals at the beginning of the Paleocene as a radiation. Similarly, common ancestry is easy to determine, as eutherian mammals are certainly monophyletic – the differences from metatherian mammals being straightforward to identify, and there being a long period from the divergence of metatherians and eutherians.

The second and third requirements according to Schluter are more difficult to quantify. Certainly, the mammals of the Paleocene were more ecologically diverse than their Cretaceous ancestors. Additionally, the disparity analyses presented in Chapter Four indicate that there was a Paleocene increase in total range occupation, followed by an increase in mean pairwise distance – a combination that certainly suggests divergent selection. However, the correlation between morphological disparity and ecological disparity, or between morphological disparity and the degree to which niche partitioning occurred, is not here explicitly tested.

Bruce Lieberman (2012) defines adaptive radiations still more stringently, arguing that the rapid morphological changes must be driven by selection, and must be acting on novel morphologies – true 'adaptations' rather than 'exaptations'. As I showed in Chapter Three, the rate of character acquisition increases remarkably at the end-Cretaceous mass extinction, suggesting that, if selection occurred, there were certainly plenty of novel morphologies on which it can act. In placentals, it has been suggested that a Brownian motion (ie, non-selective drift) model was in force after the end-Cretaceous mass extinction for body size evolution (Slater 2013), implying that selection was not an important factor in that parameter. Further study is certainly needed to identify whether changes in particular parameters for Paleocene placentals can be well characterised by models with selection parameters, such as trended or Ornstein-Uhlenbeck processes.

Asking whether the radiation of mammals is truly an adaptive radiation therefore requires more work, but the presence of this dataset – both in terms of included cladistic characters and phylogenies, from which ghost lineages can be derived to add in data otherwise unavailable from the fossil record – is invaluable in the possible future exploration of this question.

6(b)(ii) – *Understanding the placental phylogeny*

The two internal nodes of the tree containing all extant placental mammals which are most problematic are the root itself and the origins of Laurasiatheria. Each of the four superorders of Placentalia, and each of the seven orders of Laurasiatheria appear, already relatively highly derived in morphology, in the late Paleocene or early Eocene. Those taxa which are intermediate in time between the Cretaceous eutherians and the derived Eocene placentals, and which share mosaic patterns of features that prevent easy assignment of each group to the stem of an extant order, have here been able to inform on some of these nodes. In particular, providing the first morphology-derived trees that favour Atlantogenata over Epitheria suggests that this is the real topology of the node, consistent with as the majority of recent molecular analyses. In the case of the laurasiatherian orders, all "condylarths" are found to be ancestral to one or more laurasiatherian order, rather than being split across Artiodactyla, Perissodactyla and Paenungulata, as would have been thought thirty years ago. Understanding the patterns of relationships is important in detailing character polarities, and understanding what selection pressures were in place for the first ten million years of the Cenozoic.

By creating the largest such database to date, the biggest wastebasket taxon of mammals – "Condylarthra" – can be emptied, and the higher-order systematics of placental mammals will be improved. This is unlikely to be the final revision to the placental family tree, and several nodes remain poorly resolved, but there are clear general patterns which are an improvement over all previous studies.

6(c) – *Future Directions*

6(c)(i) – *Biogeography*

With the conclusion from this thesis that the main division of Placentalia is into the Gondwanan Atlantogenata and the Laurasian Boreoeutheria, a question that immediately arises is that of the biogeographical history of Placentalia. Models involving continental vicariance to explain the distribution and relationships of the extant placentals can be discounted immediately, as the continental breakup of Gondwana preceded the dates reconstructed in this thesis by tens of millions of years, if not more (Geiger *et al.* 2004; McLoughlin 2001).

The methods for reconstructing biogeographical change have improved considerably in recent years, with the most up-to-date techniques using Bayesian and maximum likelihood methods to assess the probabilities of certain patterns of dispersal in a variety of clades (Matzke 2014; Matzke 2013).

That no stem member of Xenarthra, Afrotheria, or Atlantogenata is known may be in part due to a relatively low amount of sampling from the Southern Hemisphere. Mammal evolution in the southern hemisphere is little known, and although the South American Native Ungulates are relatively common, their relationships are particularly enigmatic. While here there is support for SANUs being closely related to the two major extant 'ungulate' clades, and therefore part of the northern radiation of placental mammals, the origins of Xenarthra and Afrotheria are likely to have been in the south. Further searching in the Gondwanan continents might result in finds which will throw light on this difficult period within placental evolution.

There is a ten million year gap, still, between the divergence of Atlantogenata and Boreoeutheria, and the divergence of Afrotheria and Xenarthra. Identifying the morphology of the taxa that bridge this large gap would permit a more detailed understanding of the early evolution of the southern members of crown Placentalia. Paleocene sites are known from South America, Africa, Antarctica, Madagascar, and India, but do not have a large amount of outcrop, and have not yet produced more basal members of the superorders, with the exception of *Ocepeia* (Gheerbrant*, et al.* 2014). The only solution to this lack of definitive stem Atlantogenatan fossils is further sampling effort. If there are early members of these groups preserved in the fossil record, they will ultimately be found.

6(c)(ii) – *Genomic data*

Although the trees generated in Chapter Two improve our understanding of the relationships of placental mammals by some way, constraints were needed to enforce known relationships from the molecular data. However, imposing constraints, rather than letting the data dictate the results without being influenced, is obviously a suboptimal research position to take. One way around this is to include, *a priori*, the molecular data, and allow the combination of molecular and morphological data to inform on the relationships of the groups.

Including entire genomes is more reliable that taking smaller samples, and the genome database for placental mammals is relatively large. By including morphological information for all the taxa which have genome data available, the potential for accurately resolving relationships of this database would be increased manifold. The use of total-evidence approaches to assess the likelihood of trees, simultaneously estimating dates and phylogeny, is a direction in which the data matrix generated from this thesis will go. The recent development of new Bayesian methods for dating morphology-derived trees without the flawed assumption of a morphological clock permits this to take place.

6(c)(iii) – *Completeness*

The completeness of the Cretaceous, and in particular, the Maastrichtian, is a possible source of error in reconstructing some of these results. While Foote *et al.* (1999) concluded that the difference in completeness of the Cretaceous and Paleocene fossil records required for the origin date of placental mammals to be reconstructed tens of millions of years prior to the end-Cretaceous mass extinction is such as to make those early dates unlikely, this measure focused primarily on number of species. However, not all fossil species are equally complete in terms of morphology. Where certain portions of the body are missing, there are fewer opportunities to identify synapomorphies, and as a result, a smaller chance of identifying placental crown group members.

The processes of fossilisation cause loss of phylogenetically informative characters that have been shown to cause taxa to appear more basally on the tree. (Sansom *et al.* 2010; Sansom and Wills 2013). This need not be a problem where the number of sampled characters is large (Wiens 2006). Indeed, in many cases, incomplete taxa are able to be placed in a phylogeny with accuracy and with strong support for their position (Wiens 2003; Wiens and Morrill 2011; Kearney and Clark 2003), and even that, under certain conditions, incomplete taxa can help to break artefacts associated with long branch attraction (Roure *et al.* 2013). However, this phenomenon of "stemward slippage" has been found to occur under all conditions where there is more than 6% missing data (Sansom 2015). Incomplete taxa are not necessarily more phylogenetically unstable (Kearney 2002), meaning that stemward slippage may be difficult to identify in empirical examples.

If it can be shown that the Late Cretaceous eutherian taxa possess significantly fewer phylogenetically informative characters, and are potentially subject to stemward slippage, then it would suggest that these taxa might be placed more basally in the tree. If, however, there is little difference in completeness of taxa between the Maastrichtian and the earliest Paleocene, then the fact that we recover a large number of taxa which are definitively crown-group placentals in the latter but not the former is an indication that the reconstruction of latest Cretaceous origins for Placentalia are likely to be better supported.

6(c)(iv) – *Exploring the use of network analyses on morphological data*

Where lack of resolution suggests that homoplasy is a problem, such as in early placental mammal evolution, it is often the case that no topology is particularly more strongly resolved than another. This being true, support indices for particular nodes are very poor, and little in the way of a conclusion can be reached.

One reason that has been put forward for this is that modelling the evolution of taxa as a strict, bifurcating tree may not necessarily reflect the real history of clades. A recent advance in molecular analysis of complex genomic datasets is network analysis, which allow the generation of phylogenies which do not fit a traditional tree model. In the simplest situation, where all characters (or base pair/amino acid sites) support the same topology, a network analysis will result in a single, bifurcating tree. However, in cases where there is some degree of horizontal gene flow – whether this means between individuals, as in many single celled organisms, or with incomplete lineage sorting, as has been proposed for the divergences among the four superorders of placental mammals (Hallstrom and Janke 2010) – network analyses are able to provide alternative hypotheses on genetic datasets that are more complex than those that can be generated from phylogenetic trees alone (Bapteste, *et al.* 2013).

The assumptions that underlie models of molecular evolution are very different from those that underlie morphological evolution. Molecular mutation is a well-understood process which largely follows probabilistic and stochastic laws. Morphology is, however, more directly exposed to selection, and what might be considered a unit change in morphology is often derived from multiple locus changes at the molecular level. Nonetheless, morphologies are capable of being incompletely sorted as much as genetic data are; ultimately, it is genetic changes that drive a large proportion of morphological change.

By thinking of species in a more pluralistic way (a species being a continuum of morphologically and genetically similar individuals), and by taking into account the possibility of conflicting phylogenetic signal being a real biological effect, and not simply a matter of homoplasy in its strictest sense, network analyses provide a potentially fruitful way of addressing the patterns of relatedness within rapid radiations, providing that the models used to calculate the relationships are modified such that the assumptions match what we know about morphological evolution. This could be a way, for example, to tease apart the most likely patterns of relatedness among the Laurasiatherian orders, which is still uncertain, even after including Paleocene taxa.

6(c)(v) – *Hidden support in morphological analyses of eutherian mammals*

Relevant to this is the concept of hidden support (Gatesy *et al.* 1999) where a clade, otherwise unsupported by any individual data partition, is supported by the total evidence analysis. This has been found to be extremely prevalent in molecular analyses of placental mammals (Gatesy and Springer 2014), where it may be an artefact. The theory behind hidden support suggests that phylogenetic signal common to all data partitions, however weak, indicates that the signal is real. Homoplasy, it is argued, is unlikely to result in the same phylogenetic signal in a large number of data partitions. Where a high value for a hidden support metric results from homoplasy, this is identifiable (Thompson *et al.* 2012). It would therefore be useful to partition this dataset and investigate the levels of hidden support in the origin of crown placental mammals from a morphological perspective.

6(c)(vi) – *Covariation of characters*

It has been recently suggested that teeth are worse indicators of phylogenetic relationships than bone, with lower consistency and retention indices for characters (Sansom 2014), and that therefore they may not be able to accurately resolve relationships of extinct mammals. Understanding whether this is an inherent quality of teeth or simply a reflection of inappropriate treatment by researchers is clearly crucial, and is something which needs to be further investigated.

The mammal fossil record is dominated by dental material, due to the layer of enamel that surrounds teeth, making it more resistant to destruction than bone. Moreover, the cheek teeth (molars and premolars) of mammals are highly complex structures, adapted for grinding and shearing food material, possessing an array of basins, cusps and ridges. The variation in features of the teeth, particularly of the cheek teeth, means that it is possible to identify a single isolated tooth to genus or even species level (Gingerich 1974), even in the absence of other morphological information. As a result of this high degree of variation, complexity, and preservation potential, mammal molars have been extensively used – in cladistic data matrices that palaeontologists use for assessing the phylogeny of mammals, teeth typically make up 25-40% of coded characters (e.g. (Wible*, et al.* 2007; Zack*, et al.* 2005a)). There is a large amount of convergence in placental mammal evolution, as was demonstrated in Chapter Two, and it is therefore critical to determine which characters are more likely to be displaying homoplastic signals, and which represent the true topology.

In order to be a useful cladistic character, a trait must fulfil two basic criteria – independence and heritability. It has long been suspected that mammal tooth morphology does not fulfil either of these criteria. In particular, independence of tooth characters has been questioned (Davalos*, et al.* 2014), with multiple examples of developmentally linked traits, which are often treated as separate in analyses, despite having the same genetic basis (Kangas *et al.* 2004). In shape, the molar region is more highly integrated as a module than other parts of the skull (Goswami 2006). While there are several good reasons for concern, the degree to which morphological cladistic characters derived from the dentition are non-independent, and to what extent this degree of non-independence differs from other portions of the skeleton, is unknown. Additionally, heritability – that is, the degree to which the morphology of a feature depends on constraints set by ancestry – is more questionable in teeth than in other regions of the body. Dental morphology is strongly linked with diet, which leads to the possibility that dental characters are more prone to convergence due to adaptation to similar diets. Dental and skeletal characters often support trees that are mutually incompatible (Lopez-Martinez *et al.* 1998), meaning that one set of data is necessarily convergent. However, certain factors controlling tooth morphology can be highly heritable, with the existence of developmental models that are conserved across extant mammals, such as the Inhibitory Cascade Model presented in Chapter Five.

Are tooth characters truly being over-atomised in mammals? If they are, to what extent does this bias our interpretation of the fossil record, and can this be corrected for? If our treatment of them has little effect, it there something intrinsic about tooth characters that precludes them from being as phylogenetically informative as osteological characters?

By using principal coordinate ordinations, correlations among characters in partitioned versions of the data matrix generated as part of this thesis can be quantified (Goswami and Polly 2010), measuring relative non-independence of character partitions. Evolution of discrete characters could then be simulated across virtual trees, and sampled appropriately to account for incomplete preservation and the incomplete fossil record. By duplicating characters, non-independence of data can be simulated at a variety of levels, with repeated phylogenetic analyses generating most parsimonious trees. Similarity to the true tree can be calculated by comparing numbers of identical nodes or shared n-taxon statements. By repeating with several degrees of non-independence, the effect of over-atomisation of characters on the accuracy of phylogenetic reconstruction can be assessed, and comparisons made with the mammal fossil record.

The degree to which a character may be considered phylogenetically informative differs with taxonomic scope of the analysis. A highly heritable character is useless if it does not vary within the group of interest. Equally, a character that varies among and within subclades of the clade of interest is simply homoplastic. Any given character will therefore become uninformative at some scale, with more rapidly evolving traits, such as those more controlled by ecology, decaying at more recent divergences. Using the mammalian cladistic datasets previously collected, it is possible to calculate the relative accuracy of partitions in reconstructing relationships of different ages, independently established by molecular means. If the age at which teeth become less accurate is much more recent than for osteological traits, this would confirm the conjecture that teeth are more ecologically sensitive, and would establish a general method for choosing appropriate cladistic characters for assessing relationships of a certain age. By establishing the relative efficacy of dentition as a source of phylogenetic information, it will be possible for future research to be conducted within a solid understanding of the limitations of particular datasets, as well as more specifically allowing more robust tests of the relationships of early placental mammals, thereby throwing light on the mechanics of the adaptive radiation after the end-Cretaceous mass extinction.

6(d) – *Summary*

The inclusion of Paleocene taxa in the study of the effect of the end-Cretaceous mass extinction results in an increased ability to finely resolve key questions in mammalian evolution. By incorporating data from those taxa that were temporally close to, or involved in, the Cenozoic radiation of mammals, finer-scale resolution of relationships, identification of character polarity, and increased support for certain interordinal relationships have been shown to be possible. Moreover, the incorporation of these taxa into the broader placental mammal phylogeny allowed the testing of big macroevolutionary questions regarding the effect of a mass extinction event on clade evolution. Without Paleocene taxa, some of which have no living descendants, the degree to which evolutionary change has been effected by biotic and abiotic factors will be missed. Extant mammals capture a large amount of the diversity of Placentalia, but in order to understand the events that occurred in the past, the sampling of taxa coincident with those events is essential. Where previous analyses suggested that the end-Cretaceous mass extinction is not associated with any major change in evolutionary mode or tempo, or with any increase in lineage accumulation, the presence of contemporaneous taxa in the analysis results in the conclusion that there was an adaptive radiation, as has been thought from the traditional interpretation of the fossil record for some time. An increase in evolutionary rate, an increase in lineage accumulation, and a decelerating increase in morphological disparity through the earliest portion of the Cenozoic support the contention that global ecosystem recovery, and the re-emergence of large-bodied vertebrates as major members of those ecosystems, was in large part due to shifting evolutionary parameters in placental mammals that resulted in an archetypal example of an adaptive radiation.

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APPENDICES

APPENDIX 1 - ABBREVIATIONS

Dentition

This thesis follows the convention that lower teeth are denoted by lower case letters, and upper teeth by upper case letters. As a result, "m2" refers to the second lower molar, while "I3" refers to the third upper incisor.

Institutional Abbreviations

AMNH – American Museum of Natural History, New York
BMNH – Natural History Museum, London (outdated, used on specimen identifiers)
CUZM – Cambridge University Museum of Zoology, Cambridge
FMNH – Field Museum of Natural History, Chicago
NHM-UK – Natural History Museum, London
NMNH – Smithsonian National Museum of Natural History, Washington
ROM – Royal Ontario Museum, Toronto
UCLGMZ – Grant Museum of Zoology, London
UMMP – University of Michigan Museum of Paleontology, Ann Arbor
YPM – Yale Peabody Museum, New Haven

APPENDIX 2 – ELECTRONIC SUPPLEMENTARY INFORMATION

The following files can be found on the CD which is submitted along with this thesis. All files can be opened with either a text editor such as Notepad, a spreadsheet reader such as Excel, or an application capable of opening pdf files.

Appendix 2.1 – List of specimens coded in matrix

This file includes every single specimen used in the coding of this matrix, complete with specimen number, genus and species level affiliation, and the literature from which codings were assessed, where relevant, including the figure number. Full references for the codings are found in the references tab and below. Where a specimen viewed in person was a cast, and where a specimen was coded both from the literature and subsequently in person, this has been noted. The following taxa were in part coded from the literature as well as from specimens observed in person.

Aaptoryctes (Gingerich 1982), *Alcidedorbignya* (de Muizon and Marshall 1992), *Alymlestes* (Averianov 1997; Averianov 2000), *Anacodon* (Cope 1884b), *Anisonchus* (Van Valen 1978) *Apatemys* (Beard and Dawson 2009), *Apheliscus* (Gingerich 1994; Zack*, et al.* 2005b), *Aphronorus* (Boyer and Georgi 2007), *Arctocyon* (Kondrashov and Lucas 2006), *Arctostylops* (Cifelli*, et al.* 1989), *Asioryctes* (Kielan-Jaworowska 1975), *Asiostylops* (Zheng 1979), *Aspanlestes* (Averianov 1997), *Avitotherium* (Cifelli 1990), *Barunlestes* (Kielan-Jaworowska 1975), *Batodon* (Wible*, et al.* 2009), *Betonnia* (Williamson*, et al.* 2011), *Bisonalveus* (Gingerich 1983a), *Bulaklestes* (Archibald and Averianov 2006), *Cantius* (Rose and Walker 1985), *Chacopterygus* (Williamson*, et al.* 2011), *Chambius* (Tabuce *et al.* 2007), *Chriacus* (Van Valen 1978), *Cimolestes* (Wible*, et al.* 2009; Fox 1994), *Claenodon* (Kondrashov and Lucas 2006), *Conacodon* (Middleton and Dewar 2004), *Copecion* (Gingerich 1990), *Coryphodon* (Gingerich 1990), *Cyriacotherium* (Rose and Krause 1982), *Daulestes* (Archibald and Averianov 2006), *Deltatheridium* (Averianov 1997; Rougier *et al.* 1998), *Desmatoclaenus* (Kondrashov and Lucas 2006), *Dilambdogale* (Seiffert 2010), *Dipsalidictis* (Gunnell and Gingerich 1991), *Dissacus* (O'Leary 1998; Thewissen 1991), *Domnina* (Kihm and Schumaker 2008), *Ectocion* (Gingerich 1987), *Elomeryx* (Lihoreau *et al.* 2009), *Eoconodon* (Van Valen 1978), *Eomanis* (Gaudin*, et al.* 2009), *Eoryctes* (Thewissen and Gingerich 1989; Bloch *et al.* 2004), *Escavadodon* (Rose and Lucas 2000), *Gallolestes* (Lillegraven 1976), *Gobiohyus* (Coombs and Coombs 1977), *Gomphos* (Asher *et al.* 2005), *Goniacodon* (St Clair *et al.* 2010; Van Valen 1978), *Gypsonictops* (Cifelli 1990), *Hapalodectes* (O'Leary 1998; Ting and Li 1987), *Haplomylus* (Gingerich 1994; Zack*, et al.* 2005b; Beard and Dawson 2009), *Hemithlaeus* (Kondrashov and Lucas 2006), *Heptodon* (Holbrook and Lapergola 2011), *Hilalia* (Maas *et al.* 2001), *Homogalax* (Holbrook and Lapergola 2011), *Hyopsodus* (Stock 1934), *Hyracotherium* (Holbrook and Lapergola 2011), *Icaronycteris* (Novacek 1987; Jepsen 1966), *Indohyus* (Cooper *et al.* 2012; Thewissen*, et al.* 2007), *Kennalestes* (Kielan-Jaworowska 1975), *Kulbeckia* (Averianov 2000), *Lambdotherium* (Holbrook and Lapergola 2011), *Leptacodon* (Gingerich 1987), *Lessnessina* (Hooker and Dashzeveg 2003), *Litocherus* (Novacek *et al.* 1985; Gingerich 1983a), *Litolophus* (Bai *et al.* 2010), *Macrocranion* (Novacek*, et al.* 1985), *Maelestes* (Wible*, et al.* 2009), *Mesonyx* (O'Leary 1998), *Miacis* (Qi *et al.* 1989; Gingerich 1983b; Heinrich 1997), *Mimatuta* (Van Valen 1978), *Molinodus* (de Muizon and Cifelli 2000), *Onychonycteris* (Simmons*, et al.* 2008), *Oreotalpa* (Lloyd and Eberle 2008), *Oxyclaenus* (Kondrashov and Lucas 2006; Middleton and Dewar 2004), *Pakicetus* (Nummela *et al.* 2006; Gingerich and Russell 1981), *Palaeoryctes* (Bloch*, et al.* 2004), *Palaeosinopa* (Beard and Dawson 2009), *Pantolambda* (Lucas and O'Neill 1981), *Paramys* (Korth 1988), *Paranyctoides* (Archibald and Averianov 2001; Averianov and Archibald 2013; Cifelli 1990), *Parapternodus* , *Periptychus* (Cope 1884a), *Plagiomene* (Rose 1982a), *Pleuraspidotherium* (Thewissen 1991), *Poebrotherium* (Scott 1891), *Procerberus* (Middleton and Dewar 2004), *Prodiacodon* (Rose 1999b), *Protictis* (Meehan and Wilson 2002; Flynn and Galliano 1982), *Protoselene (Kondrashov and Lucas 2006)*, *Protungulatum* (Van Valen 1978), *Puercolestes* (Williamson*, et al.* 2011), *Purgatorius* (Fox and Scott 2011; Fox 2011), *Pyrocyon* (Gingerich and Deutsch 1989), *Rhynchocyon* (Zack, et al. 2005a), *Rodhocetus* (Spaulding *et al.* 2009; Gingerich *et al.* 2001; Gingerich *et al.* 1994), *Saxonella* (Fox 1984; Fox 1991), *Sinonyx* (Zhou *et al.* 1995), *Teilhardimys* (Tabuce *et al.* 2006), *Tetraclaenodon* (West 1970), *Todralestes* (Gheerbrant 1991), *Tribosphenomys* (Meng *et al.* 1994), *Tubulodon* (Kalthoff *et al.* 2011), *Tytthaena* (Gingerich 1980), *Uchkudukodon* (Archibald and Averianov 2006), *Uintacyon* (Gingerich 1983b; Heinrich 1997), *Ukhaatherium* (Horovitz 2000, 2003), *Viverravus* (Gingerich 1987), *Widanelfarasia* (Seiffert and Simons 2000; Seiffert *et al.* 2007), *Worlandia* (Rose 1982a), *Wyolestes* (Beard and Dawson 2009; Gingerich 1981), *Wyonycteris* (Gingerich 1987), *Zalambdalestes* (Wible *et al.* 2004), and *Zhangolestes* (Zan *et al.* 2006).

Appendix 2.2 – Discrete character matrix

This matrix was used for the phylogenetic analyses which resulted in the DU, DF, DE, and DP sets of most parsimonious trees. It is formatted to be openable in TNT. Where a character cannot be coded due of absence of evidence, the character is coded as "?". Where a character cannot be coded because there is evidence of absence, it is coded as "-".

Appendix 2.3 – Continuous character matrix

This matrix was used for the phylogenetic analyses which resulted in the CU, CF, CE and CP sets of most parsimonious trees. It is formatted to be openable in TNT. Where a character cannot be coded due of absence of evidence, the character is coded as "?". Where a character cannot be coded because there is evidence of absence, it is coded as "-". Additionally, this matrix contains two batches of characters. The first 48 are continuous characters, while the remainder are discrete.

Appendix 2.4 – List of characters and character states

This file contains all 680 characters with descriptions of each character state, the proximal source of that character (the matrix from which the character is immediately derived), and the treatment of that character – whether it is continuous or discrete, and ordered or unordered. Where there is a gap for proximal source, the character was created by splitting previously coded characters into characters that are independent and exhaustive in definition.

Appendix 2.5 – List of synapomorphies for major clades of eutherian mammal

This file is formatted as an Excel file with six tabs, each representing one of the six constrained phylogenetic analyses. Each tab contains lists of unambiguous synapomorphies for major divisions within Eutheria, with the character state transitions listed. Those highlighted in bold are common across all constraint levels.

Appendix 2.6 – Bremer Support Trees

Due to being excessively large to display in paper format, the six Relative Bremer support trees are included as supplementary files. Values along each branch are Relative Bremer supports, which can be scored from -100 to 100, but collapse the node when less than 0. A relative Bremer support of 100 would indicate that a node is returned by every single topology that has been sampled. A relative Bremer support of -100 would mean that a node is not supported by any analysis. Many of the relative supports along these trees are very low and positive, which indicates that the topologies are slightly preferred by the dataset. Scores of 100 are marked with question marks, as it is unknown whether marginally more suboptimal topologies would result in less clear support. With the degree of suboptimality measured in these trees however, there is complete support for these nodes.

Appendix 2.7 – Rate of Evolution analysis code

This file includes the code that was used in R to date the phylogenies in Chapter Three, and calculate evolutionary rates. The code for dating the phylogeny and estimating the three rates that go into cal3 is not new, but is taken from the tutorial exercise of David Bapst at http://nemagraptus.blogspot.co.uk/2013/06/a-tutorial-to-cal3-time-scaling-using.html. The code that was used for conducting the rates analysis is a way of looping functions that already exist in paleotree (Bapst 2012) and generating the matrices on which calculations can be conducted.

Appendix 2.8 – Disparity analysis code

This file includes code for use in R for calculating disparity. It incorporates functions from Claddis (Lloyd 2014) to generate a set of distance matrices and PCO matrices on which calculations can be performed. There is also some novel code written specifically for time-binning the branch based morphologies as detailed in Chapter Four, as well as new code for bootstrapping distance matrices. It depends on Claddis, paleotree, (Bapst 2012), and ape (Paradis*, et al.* 2004).

Appendix 2.9 – Raw tooth measurements for Chapter Five

This file contains the raw data for each measured specimen with lower dentition, as well as calculated length:width ratios, and mean values for each genus. Literature used in the measuring of dentition, except those for which the data was directly downloaded from the Paleobiology Database, www.paleobiodb.org, is listed alongside each specimen, but is also listed below, as follows:

(Wilson 1985; de Muizon and Marshall 1992; Gingerich 1977; Rose *et al.* 1992; Gingerich *et al.* 1983; Lopatin and Averianov 2006; Martin and Rauhut 2005; Trofimov and Szalay 1994; Lucas and Tong 1988; Archibald and Averianov 2012; Zheng 1979; Rich *et al.* 1997; Gingerich and Childress 1983; Averianov and Archibald 2005; Tabuce*, et al.* 2007; Rose and Krause 1982; Seiffert 2010; Gunnell and Gingerich 1991; Geisler and McKenna 2007; Novacek*, et al.* 1985; Reguero *et al.* 2008; Ji *et al.* 2002; Zack*, et al.* 2005b; Zack 2011; Jenkins Jr and Schaff 1988; Hunter and Pearson 1996; Coombs and Coombs 1977; Maas*, et al.* 2001; Jepsen 1966; Bloch *et al.* 2007b; Luo *et al.* 2011; Lopatin and Averianov 2007; Flannery *et al.* 1995; Meehan and Martin 2010; Holbrook and Lapergola 2011; Gingerich 1983b; Tabuce*, et al.* 2006; de Muizon and Cifelli 2000; Lloyd and Eberle 2008; Middleton and Dewar 2004; Cifelli 1999; Suyin *et al.* 1987; Mills 1964; Ladevèze*, et al.* 2010; Gingerich 1996; Kondrashov and Lucas 2012; Gheerbrant 1991; Hu *et al.* 2005; Archer *et al.* 1985; Rich and Collinson 1973; Zan*, et al.* 2006; Zhou*, et al.* 1995; Gingerich 1981)

APPENDIX 3 – DIETARY ASSIGNMENTS FOR CHAPTER FIVE

Higher-level Taxon	Genus	m2/m1	m3/m1	Dietary Guild
Acreodi	*Oxyclaenus*	1.277466	1.291848	Carnivorous
Acreodi	*Eoconodon*	1.204445	1.318965	Omnivorous
Acreodi	*Ankalagon*	1.388943	1.103274	Carnivorous
Acreodi	*Dissacus*	1.22755	0.749695	Carnivorous
Acreodi	*Sinonyx*	1.583537	1.192988	Carnivorous
Afrotheria	*Dilambdogale*	1.12	0.918	Insectivorous
Afrotheria	*Microhyus*	1.544012	1.356229	Omnivorous
Arctostylopidae	*Asiostylops*	1.22449	1.632653	Herbivorous
Arctostylopidae	*Palaeostylops*	2.111111	1.188272	Herbivorous
Arctostylopidae	*Arctostylops*	1.447619	1.52381	Herbivorous
Artiodactyla	*Diacodexis*	1.163636	1.151515	Herbivorous
Artiodactyla	*Elomeryx*	1.934911	3.094428	Herbivorous
Artiodactyla	*Aepycamelus*	1.624569	1.801843	Herbivorous
Artiodactyla	*Bison*	1.334153	1.949436	Herbivorous
Artiodactyla	*Boreameryx*	0.983051	1.295455	Herbivorous
Artiodactyla	*Cranioceras*	1.247727	1.711201	Herbivorous
Artiodactyla	*Gentilicamelus*	1.32116	1.460795	Herbivorous
Artiodactyla	*Leptoreodon*	1.099696	1.991903	Herbivorous
Artiodactyla	*Longirostromeryx*	1.221675	1.752874	Herbivorous
Artiodactyla	*Merychyus*	1.4759	2.525208	Herbivorous
Artiodactyla	*Merycoidodon*	2.260009	3.918803	Herbivorous
Artiodactyla	*Miotylopus*	1.174734	1.558258	Herbivorous
Artiodactyla	*Yumaceras*	1.011934	1.760192	Herbivorous
Artiodactyla	*Indohyus*	1.302061	2.049702	Omnivorous
Artiodactyla	*Bunophorus*	1.343607	1.753942	Herbivorous
Artiodactyla	*Gobiohyus*	1.450855	2.027229	Insectivorous
Artiodactyla	*Uintatherium*	2.061123	3.983563	Herbivorous
Carnivora	*Vulpavus*	0.793003	0.35254	Carnivorous
Carnivora	*Vassacyon*	0.52381	0.305556	Carnivorous
Carnivora	*Parictis*	0.385109	0.141849	Carnivorous
Cimolesta	*Wyolestes*	1.316375	0.985692	Carnivorous
Cimolesta	*Aaptoryctes*	0.965517	0.702427	Insectivorous
Cimolesta	*Palaeoryctes*	1.089965	0.908304	Insectivorous
Cimolesta	*Cyriacotherium*	1.209026	1.287411	Herbivorous
Cimolesta	*Gelastops*	0.809668	0.739019	Insectivorous
Cimolesta	*Pentacodon*	0.654747	0.392493	Insectivorous
Cimolesta	*Esthonyx*	1.455882	1.617647	Omnivorous
Cimolesta	*Bessoecetor*	1.238095	1.414683	Durophagous
Cimolesta	*Simidectes*	0.90991	0.402495	Carnivorous
Cimolesta	*Palaeosinopa*	1.21746	1.08628	Durophagous

Cimolesta	*Peramus*	1.515704	1.515704	Insectivorous
Condylarthra	*Gingerichia*	1.345546	1.122363	Insectivorous
Condylarthra	*Hilalia*	1.133567	1.039275	Herbivorous
Condylarthra	*Molinodus*	1.30808	1.172411	Omnivorous
Condylarthra	*Oxyacodon*	1.063503	0.97393	Herbivorous
Condylarthra	*Pleuraspidotherium*	0.965217	1.237267	Herbivorous
Condylarthra	*Tetraclaenodon*	1.088011	0.915745	Herbivorous
Condylarthra	*Hyopsodus*	1.302345	1.485174	Omnivorous
Condylarthra	*Phenacodus*	1.131113	0.947063	Herbivorous
Condylarthra	*Ectocion*	1.127178	0.765293	Herbivorous
Condylarthra	*Haplomylus*	1.276786	0.692774	Omnivorous
Condylarthra	*Copecion*	1.090909	0.878788	Herbivorous
Condylarthra	*Lessnessina*	1.111034	0.657849	Omnivorous
Condylarthra	*Thryptacodon*	0.957983	0.983193	Omnivorous
Condylarthra	*Chriacus*	1.043478	0.717391	Omnivorous
Condylarthra	*Lambertocyon*	1.497899	1.617647	Omnivorous
Condylarthra	*Anisonchus*	1.254854	1.895884	Herbivorous
Condylarthra	*Loxolophus*	1.269899	0.7786	Omnivorous
Creodonta	*Galecyon*	0.919583	0.483991	Carnivorous
Creodonta	*Pyrocyon*	0.791344	0.363372	Carnivorous
Dermoptera	*Ignacius*	1.021317	1.67833	Granivorous/Frugivorous
Dermoptera	*Worlandia*	0.66482	0.432133	Herbivorous
Eulipotyphla	*Domnina*	1.011138	0.779061	Omnivorous
Eulipotyphla	*Entomolestes*	1.005503	0.756531	Insectivorous
Eulipotyphla	*Galerix*	0.768329	0.46194	Insectivorous
Eulipotyphla	*Litocherus*	0.810267	0.633806	Insectivorous
Eulipotyphla	*Litolestes*	0.80575	0.588923	Insectivorous
Eulipotyphla	*Macrocranion*	1.03538	1.060845	Omnivorous
Eulipotyphla	*Oreotalpa*	1.088566	0.768175	Insectivorous
Eulipotyphla	*Mesoscalops*	1	0.578947	Insectivorous
Eulipotyphla	*Proscalops*	0.970475	0.602482	Insectivorous
Eulipotyphla	*Leptacodon*	0.966667	1.133333	Insectivorous
Eulipotyphla	*Pseudotrimylus*	0.831447	0.622673	Omnivorous
Eulipotyphla	*Todralestes*	0.901961	0.793028	Insectivorous
Eulipotyphla	*Uropsilus*	1.273782	1.001597	Insectivorous
Eulipotyphla	*Mixodectes*	1.154543	1.226667	Insectivorous
Eulipotyphla	*Echinosorex*	0.82758	0.557748	Insectivorous
Leptictids	*Gypsonictops*	1.19109	1.105473	Omnivorous
Leptictids	*Leptictis*	1.3	1.040625	Insectivorous
Leptictids	*Megaleptictis*	0.909696	0.552056	Insectivorous
Metatheria	*Asiatherium*	1.295857	1.175364	Carnivorous
Australosphenida	*Asfaltomylus*	0.975075	0.823018	Insectivorous
Australosphenida	*Ausktribosphenos*	0.827426	0.552183	Insectivorous
Australosphenida	*Steropodon*	0.948542	0.575167	Omnivorous
Australosphenida	*Kollikodon*	1.293967	1.341463	Durophagous
Notoungulata	*Eohyrax*	1.229858	1.670201	Herbivorous

Notoungulata	*Pseudhyrax*	1.193498	1.834084	Herbivorous
Pantodonta	*Aphronorus*	0.878049	0.8125	Durophagous
Pantodonta	*Asiocoryphodon*	1.528572	1.694719	Herbivorous
Pantodonta	*Barylambda*	1.248884	1.472611	Herbivorous
Pantodonta	*Coryphodon*	1.276298	2.142247	Herbivorous
Pantodonta	*Heterocoryphodon*	1.462781	1.748371	Herbivorous
Pantodonta	*Titanoides*	1.470968	1.941346	Herbivorous
Perissodactyla	*Mesolambdolophus*	1.248027	1.652893	Herbivorous
Perissodactyla	*Hyracotherium*	1.348276	1.631034	Granivorous/Frugivorous
Perissodactyla	*Homogalax*	1.301502	2.309352	Herbivorous
Perissodactyla	*Xenicohippus*	1.407407	2.141414	Herbivorous
Perissodactyla	*Lambdotherium*	1.175676	1.710074	Herbivorous
Perissodactyla	*Aphelops*	1.08425	1.130587	Herbivorous
Perissodactyla	*Colodon*	1.166301	1.329808	Herbivorous
Perissodactyla	*Diceratherium*	1	1.158404	Herbivorous
Perissodactyla	*Equus*	1.044943	1.166482	Herbivorous
Perissodactyla	*Eohippus*	1.137842	1.356506	Herbivorous
Palaeanodonta	*Alocodontulum*	0.946237	0.737327	Insectivorous
Palaeanodonta	*Escavadodon*	0.943739	0.754991	Insectivorous
Plesiadapiforms	*Dryomomys*	0.706789	1.220088	Insectivorous
Plesiadapiforms	*Plesiadapis*	1.25	1.738636	Herbivorous
Primates	*Cantius*	1.125	0.9625	Herbivorous
Primates	*Craseops*	1.181989	1.393058	Insectivorous
Primates	*Mahgarita*	1.047431	1.088195	Granivorous/Frugivorous
Rodentia	*Alagomys*	1.133142	1.202381	Granivorous/Frugivorous
Rodentia	*Ammospermophilus*	1.302632	1.447368	Granivorous/Frugivorous
Rodentia	*Coloradoeumys*	0.817853	0.849555	Herbivorous
Rodentia	*Floresomys*	1.339286	1.083333	Herbivorous
Rodentia	*Jaywilsonomys*	1.388473	1.380439	Herbivorous
Rodentia	*Megapeomys*	0.85176	0.793476	Herbivorous
Rodentia	*Palaearctomys*	1.23445	1.406699	Granivorous/Frugivorous
Rodentia	*Pleurolicus*	1.050466	0.943149	Herbivorous
Rodentia	*Scottimus*	0.974346	0.649502	Herbivorous
Rodentia	*Spermophilus*	1.295933	1.478261	Granivorous/Frugivorous
Scandentia	*Ptilocercus*	1.62354	1.536051	Granivorous/Frugivorous
Scandentia	*Tupaia*	1.040605	0.597138	Granivorous/Frugivorous
Stem placentals	*Montanalestes*	1.114862	1.157463	Insectivorous
Stem placentals	*Zalambdalestes*	0.8	0.6	Insectivorous
Stem placentals	*Zhangolestes*	1.021407	0.722001	Insectivorous
Stem therian	*Arguimus*	1.092215	1.095593	Insectivorous
Stem therian	*Bobolestes*	1	0.969697	Insectivorous
Stem therian	*Kielantherium*	1.037706	0.985385	Insectivorous
Xenarthra	*Nothrotheriops*	1.008179	1.11096	Herbivorous
Xenarthra	*Pampatherium*	0.913978	0.685124	Herbivorous
Zhelestidae	*Aspanlestes*	1.073595	0.98454	Insectivorous
Zhelestidae	*Parazhelestes*	1.101857	0.945446	Insectivorous