

Resolving the relationships of Paleocene placental mammals

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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 driven a 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 the relationships of the extant orders, hindering efforts to reconstruct robustly the origin and early evolution of placental mammals. Here we 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. We 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 pre-dates the Cretaceous–Palaeogene boundary. Our results support an Atlantogenata–Boreoeutheria split at the root of crown Placentalia, the presence of phenacodontids as closest relatives of Perissodactyla, the validity of 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 understanding fully the biotic dynamics associated with the end-Cretaceous mass extinction. The relationships presented here mark a critical first step towards accurate reconstruction of this important interval in the evolution of the modern fauna.

Key words: Placentalia, evolution, phylogeny, Palaeogene, radiation, Condylarthra, palaeontology.

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I. INTRODUCTION

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 & Chaloner, 1994), dramatically altering both terrestrial and marine ecosystems (Vajda, Raine & Hollis, 2001; Sessa *et al.*, 2012). Palaeontologists usually reconstruct this point as the beginning of the so-called ‘Age of Mammals’; prior to the K/Pg boundary, mammals were mainly small, terrestrial-to-arboreal insectivores with low ecological disparity (Goswami, 2012; Grossnickle & Polly, 2013), albeit with a few notable exceptions (Luo, 2007). By 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 (Osborn, 1902; Simpson, 1953; Alroy, 1999; Raia *et al.*, 2013). However, macroevolutionary studies of placental mammals of 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, Scott & Rankin, 2010), no extant order of placental mammal has an unambiguous representative during the Paleocene, minimally leaving a 10 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; they occur during the period of rapid ecological

diversification for placental mammals, but pre-date 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; Venditti, Meade & Pagel, 2011; Slater, 2013). All, however, have used data sets that mostly or entirely excluded Paleocene taxa, and therefore lack data from the important period during which an adaptive radiation would seem, from a strict reading of the fossil record, to have occurred. These analyses, which have mostly used divergence estimates from molecular dating techniques, have tended to favour a ‘mid’ to Late Cretaceous origin of placental orders and superorders (Springer *et al.*, 2003; Bininda-Emonds *et al.*, 2007; dos Reis *et al.*, 2012). However, despite numerous suggestions of Cretaceous placentals, no Cretaceous eutherian mammal has been unambiguously resolved within the placental crown (Wible *et al.*, 2009; Goswami *et al.*, 2011). The earliest definitive members of crown orders are mostly known from the Late Paleocene or Eocene. A Cretaceous origin would therefore require the existence of long ghost lineages. Additionally, it has been suggested that clock models suffer from artefacts resulting from historical changes in evolutionary rate (Beck & Lee, 2014). Estimating the date of origin of placental mammals and reconstructing their response to the end-Cretaceous mass extinction are therefore highly contingent on method and data set.

Addition of fossil data has also been shown to change results of analyses significantly in a wide range of macroevolutionary studies (Tarver & Donoghue, 2011; Pyron & Burbrink, 2012; Slater, Harmon & Alfaro, 2012; Wood *et al.*, 2013; Raj Pant, Goswami & Finarelli, 2014). The

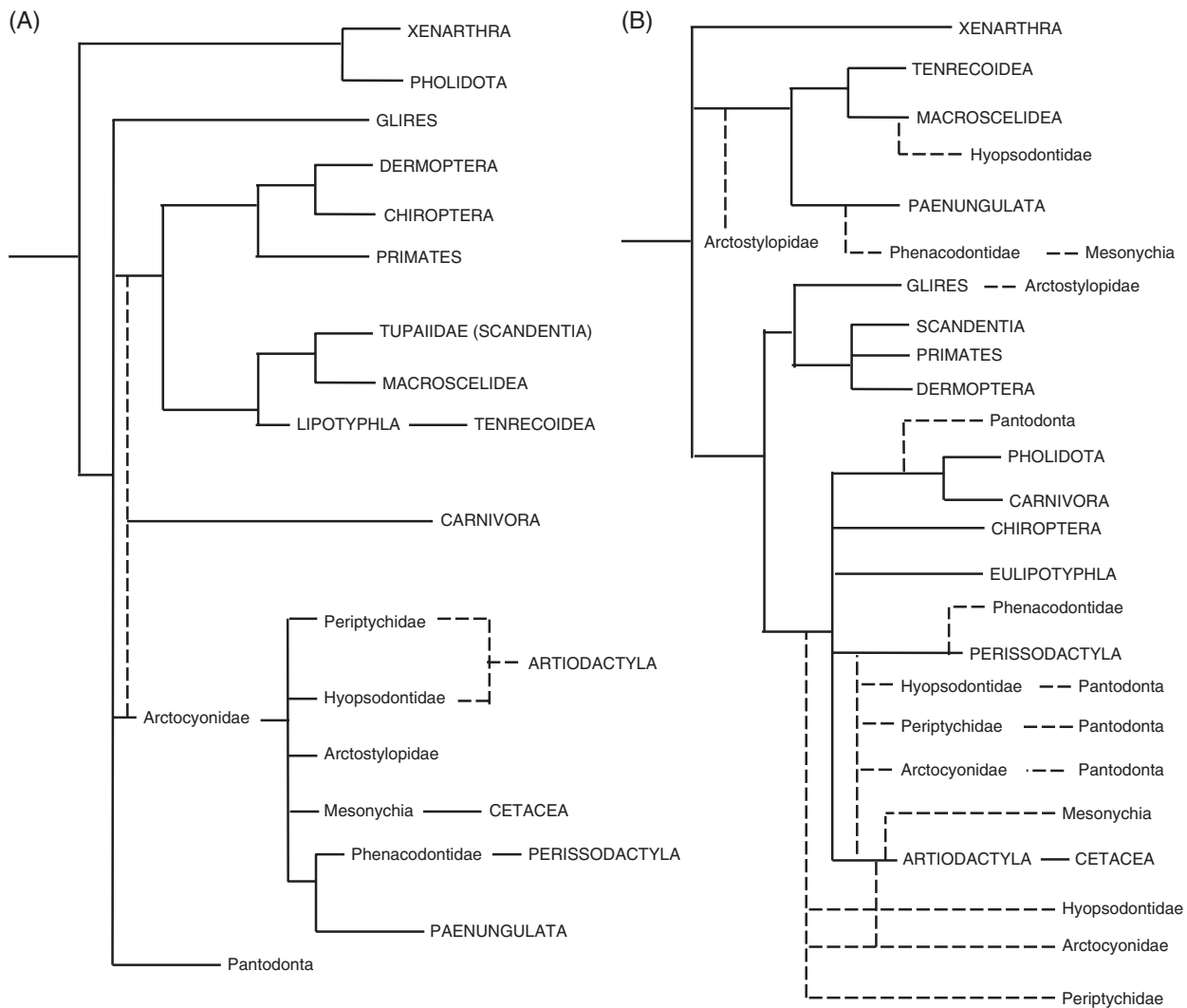


Fig. 1. A depiction, in broad terms, of changes in understanding of the relationships of placental mammals over the last 20 years. (A) Broad understanding of placental mammal relationships prior to the advent of molecular data. ‘Condylarth’ families were considered basal to Ungulata, a number of plesiomorphic 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.

inclusion of fossil data is, however, only possible where the phylogenetic relationships of those fossil forms is understood.

The phylogenetic relationships among extant placental mammals have a long history of study based on morphological data, with some degree of stability in tree topology for several decades (Gregory, 1910; Simpson, 1945; McKenna, 1975; Novacek, 1992). This traditional topology accommodated many of the Paleocene mammal clades in a relatively straightforward manner, such as ‘condylarths’ being identified as stem ungulates (Fig. 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,

Geisler, & Sanchez-Villagra, 2008 for a review of these). For instance, the distinction between the Afrotherian golden mole *Chrysochloris* and European moles was suggested, based on entirely morphological data, 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, 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, unguligrade mammal from the Palaeogene has been consigned (Archibald, 1998). Patently, these taxa must have ancestors, and extant orders likely 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 (Fig. 1B). For the most part, these ‘condylarth’ clades themselves are considered monophyletic, but the relationships among them, and between any ‘condylarth’ clade and extant orders are unknown.

Identifying the phylogenetic position of these enigmatic Palaeogene taxa with respect to extant orders and Cretaceous groups is therefore essential to understanding the timing of divergence of extant orders. Distinct Paleocene mammals first appear less than a million years after the K/Pg boundary, and if they are crown-placental mammals, this timing would imply that speciation between extant orders most likely occurred cryptically during the Cretaceous. Establishing how many mammalian lineages span the K/Pg boundary also allows for greater accuracy in assessing the role of mass extinctions in evolutionary dynamics more generally. Ascertaining the phylogenetic relationships of fossil forms will facilitate 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.

II. AIMS

Here, we present the results of the largest cladistic analysis of Palaeogene mammals to date, with the aim of resolving the relationships of some enigmatic groups of eutherian mammals. Inclusion of key representative taxa from this important period in placental evolution in a wide-reaching study is a crucial requirement for future analysis of the early evolution of this clade. Below, we provide a detailed overview of the early fossil record of placental mammals, followed by the new cladistic analysis and a discussion of its implications for resolving internal placental relationships and the origins of the group.

III. OVERVIEW OF THE FOSSIL RECORD OF EARLY PLACENTAL MAMMALS

(1) ‘Condylarthra’

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’.

(a) *Arctocyoniidae*

(i) *Composition.* Arctocyoniidae is composed of approximately 20 genera, including 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, 1980), or a synonym of *Arctocyonides* (Van Valen, 1978). Some recent studies (Williamson & Carr, 2007; De Bast & Smith, 2013) have hinted that the subfamilies of Arctocyoniidae may be polyphyletic, with the Oxycyleninae occurring at the base of crown placentals (although all taxa sampled in those analyses are certain or probable laurasiatheres), Arctocyoniinae 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 & Smith (2013, p. 971), arctocyoniids have ‘been used as a wastebasket for basal condylarths’; making arctocyoniids particularly enigmatic, as the general consensus is that ‘Condylarthra’ is itself a wastebasket taxon (Archibald, 1998).

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

(iii) *Ecology.* The species *Arctocyon primaevus* was originally described as being aquatic (de Blainville, 1841), and has been variously hypothesised as being 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 an almost complete postcranial specimen, 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 munak* and *Anacodon* – might have been semifossorial, based on morphological features of the astragalus (Gould & 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. Large canines are often present, and the premolars are relatively sharp, but the molars are bunodont, suggesting a largely omnivorous dietary niche.

(b) *Periptychidae*

(i) *Composition.* Periptychidae is composed of approximately 15 genera, divided among the subfamilies Periptychinae, Anisonchinae, and Conacodontinae (Archibald, Schoch & Rigby, 1983), the latter of which comprises *Conacodon* and *Oxyacodon*. According to 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.

(ii) *Proposed relationships.* Periptychids are represented by several North American genera, such as *Periptychus*, *Anisonchus*, *Ectoconus*, and others, and, in the case of *Periptychus*, are among the earliest known crown-placental mammals (Prothero, 1998; Lofgren *et al.*, 2004). They first appear in the San Juan Basin as immigrants (Clemens, 2010; Wilson, 2014) approximately 500000 years after the end-Cretaceous mass-extinction event, and are, as a result, usually thought to be basal among ‘condylarths’ (Prothero, 1994).

(iii) *Ecology.* Periptychid condylarths are characterised by highly bunodont, square molars which are of roughly equal size along the tooth row. As they are considered to be both temporally early and phylogenetically basal, they show the first adaptations to a herbivorous lifestyle.

(c) *Hyopsodontidae*

(i) *Composition.* Depending on interpretation, Hyopsodontidae may be treated as synonymous with Mioclaenidae (Williamson & Weil, 2011). Some authors prefer Mioclaenidae to be an entirely separate group, an interpretation backed up with some cladistic evidence (Ladevèze, Missiaen & Smith, 2010). In that analysis, 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 all ‘condylarth’ lineages. In total, there are 15 genera of hyopsodontid. The type genus, *Hyopsodus* is primarily Eocene, and is found across all Laurasian land masses.

(ii) *Proposed relationships.* 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 placed them with either afrotheres – whether hyracoids (Godinot, Smith & Smith, 1996) or macroselideans (Tabuce *et al.*, 2001) – or with the enigmatic South American ungulates (Cifelli, 1983; de Muizon & Cifelli, 2000). The characters that have linked hyopsodontids to this large variety of clades are mostly dental, although in the case of the macroselidean relationships this depends on the assumption that apheliscid ‘condylarths’ fall within Hyopsodontidae, and is supported primarily 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’.

(iii) *Ecology.* 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 & Dashzeveg, 2003).

Analysis of the braincase of *Hyopsodus lepidus* has indicated that it possessed strong abilities to detect the positions of acoustic stimuli accurately, 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, Argot & Gilissen, 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 & 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.

(d) *Mioclaenidae*

(i) *Composition.* Those that subscribe to the viewpoint that mioclaenids are a separate family place all 10 mioclaenid genera in the subfamily Mioclaeninae (e.g. Zack *et al.*, 2005b). Regardless of phylogenetic topology, mioclaenids are considered by all to be monophyletic.

(ii) *Proposed relationships.* Mioclaenidae are a little known group of archaic ungulates considered by some to be a subgroup or synonym of Hyopsodontidae (Williamson & Weil, 2011). Originally erected as a monospecific family (Osborn & Earle, 1895), it includes several taxa from across North America and Europe, as well as a few in South America.

(iii) *Ecology.* The most recent summary of the characters which define Mioclaenidae was a reanalysis of two genera – *Bomburia* and *Ellipsodon* – by Williamson & 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). Mioclaenids also have relatively enlarged premolars, similar to periptychids, which are thought to indicate a diet consisting of tough vegetation (Rose, 2006).

(e) *Pleuraspidotheriidae*

(i) *Composition.* 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*.

(ii) *Proposed relationships.* Ladevèze *et al.* (2010) hypothesised that Pleuraspidotheriidae are closest relatives to arctocyonids such as *Chriacus*, in a group also including the basal artiodactyls, but their taxonomic sampling was very low, and only very few representatives of each supposed group were present. 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 modern orders, and little has been proposed concerning the relationships of this family.

(iii) *Ecology.* The basicranial morphology of pleuraspidotheres 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). 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).

(f) *Phenacodontidae*

(i) *Composition.* Phenacodontidae is composed of 14 North American genera, the best known and most complete of which are the phenacodontine phenacodontids *Phenacodus*, *Tetraclaenodon* and *Copecion* (Osborn, 1898; Thewissen, 1990; Kondrashov & Lucas, 2012). Meniscotheriidae, once considered separate, is now generally included within Phenacodontidae (Rose, 2006) as the subfamily Meniscotheriinae (Simpson, 1937), and includes *Ectocion* and *Meniscotherium*.

(ii) *Proposed relationships.* 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 comprising Paenungulata,

Phenacodontidae and Perissodactyla, while Kondrashov & Lucas (2012) found phenacodontids to be paraphyletic to Perissodactyla, Paenungulata, and Hyracoidea. While Perissodactyla is certainly not closely related to Paenungulata, being consistently resolved as being in a totally different superorder by molecular methods (Springer *et al.*, 2004), 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 – both Paenungulata (e.g. Rose *et al.*, 2014) and Perissodactyla (e.g. Kondrashov & Lucas, 2012) have been considered the closest living relatives of phenacodontids in recent years, whether phenacodontids are considered paraphyletic or monophyletic. Indeed, *Phenacodus* and *Meniscotherium* have also been found to be close relatives of Artiodactyla (Wible *et al.*, 2007).

(iii) *Ecology.* 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). 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. The forelimb 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 & Lucas, 2012). This hypothesis is borne out by the morphology of the hind limb, which is far more specialised for terrestriality, although not cursoriality (Kondrashov & Lucas, 2012). The third trochanter on the femur is a cursorial adaptation, as is the weakening of the deltopectoral crest of the humerus.

(g) *South American native ungulates (SANUs)*

(i) *Composition.* 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' (McKenna, 1975). 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 (de Muizon & Cifelli, 2000), surviving into the Late Pleistocene (MacFadden & Shockey, 1997). Across all five orders, there are well over 200 named genera, many of which are known from multiple species (McKenna & Bell, 1997).

(ii) *Proposed relationships.* Although some hypotheses have suggested that SANUs are more closely related to Afrotheria (Agnolin & Chimento, 2011), or descended from 'condylarths' (de Muizon & Cifelli, 2000), recent analysis of protein sequences from subfossil material (Buckley, 2015; Welker *et al.*, 2015) has indicated that the closest extant relatives of both Notoungulata (represented by *Toxodon*) and Litopterna (represented by *Macrauchenia*) are

stem Perissodactyla, a result which is consistent with a recent morphological analysis incorporating Notoungulata (Beck & Lee, 2014), which returned close relationships between notoungulates and perissodactyls. As morphological analyses have been inconsistent in terms of the relationships of these unusual taxa, this particular topology raises many biogeographical questions. Cladistic analysis of the morphology of SANU postcrania has supported a relationship between a notoungulate–lioptern clade and phenacodontids (Horovitz, 2004), with astrapotheres most closely related to periptychids. Relationships among orders of SANU are unclear, with Billet (2010) finding a notoungulate–astrapotheres clade and non-monophyletic Liotoperna.

(iii) *Ecology.* Ecologically, the SANUs are remarkably diverse, with analogues of several artiodactyl and perissodactyl clades, most clearly emphasised in the similarity between liopterns, 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.

(2) Other placental non-ungulate clades

In addition to the condylarths, there are several other controversial and enigmatic mammal groups represented by Paleocene 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 (Lopatin, 2006; Wible *et al.*, 2007). Both show relatively basal general morphology, but also bear specialisations that have driven hypotheses of relationships to extant clades.

(a) *Leptictida*

(i) *Composition.* Leptictida was first identified as a superorder 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. Novacek (1986) provided an extensive and comprehensive morphological characterisation of the group, reduced the rank to ordinal status, and proposed a position within Insectivora. In McKenna & Bell (1997), Leptictida was a diverse assemblage of taxa including several additional Cretaceous mammals such as *Zhelestes*, *Gypsonictops*, *Lainodon* and *Gallolestes*, and also Kennalestidae. The traditional leptictid forms such as *Prodiacodon* and *Leptictis* were also included in Leptictida, as well as the European Pseudorhynchocyonidae.

In light of further analysis, the taxonomic composition of Leptictida has been revised as a more restricted group. Archibald, Averianov & Ekdale (2001) provided evidence that *Gypsonictops* was part of a separate clade from *Zhelestes* and its kin, implying that Leptictida was at least paraphyletic. In that study, both clades were resolved within the placental crown, 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, Cifelli & Luo (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. The composition of Gypsonictopidae was also reduced by the removal of *Zhelestes*, as well as other forms previously allied to Leptictida such as *Lainodon*. The newly constructed Zhelestidae was allied with Ungulatomorpha, well within the crown of placental mammals.

An extensive study of Cretaceous mammalian affinities by Wible *et al.* (2007) further modified the position of Leptictida. Here, rather than being crown-group placental mammals, *Leptictis* and *Gypsonictops* were placed at the crownward end of the placental stem, more derived than Zalambdalestidae but less than *Protungulatum*. Meehan & Martin (2010), however, favoured inclusion of Leptictida in the abandoned grouping 'Insectivora'. They noted that the morphology of leptictidans was highly convergent to that of extant macroscelideans, due to similar ecological specialisations to insectivory, digging, and saltatory locomotion.

Recently, the European Eocene–Miocene Pseudorhynchocyonidae – a subgroup of Leptictida *sensu* McKenna & Bell (1997) – has been separated from Leptictida entirely, instead placed closer to Palaeanodonta and Pantodonta (Hooker, 2013). However, an unrooted version of the tree from this analysis is entirely consistent with a monophyletic Leptictida to the exclusion of Palaeanodonta and Pantodonta. The order Leptictida currently consists of three families: Gypsonictopidae, a monogeneric family containing only *Gypsonictops*; Leptictidae, consisting of several North American genera; and Pseudorhynchocyonidae. In total, the clade contains 16 genera. Although there is largely a consensus on the taxonomic composition of Leptictida, 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.

(ii) *Proposed relationships.* The leptictids are one of the few orders of mammals definitively to 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 (Kielan-Jaworowska *et al.*, 2004; Meehan & Martin, 2010). Leptictida, therefore, 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 within the placental radiation, it would provide conclusive proof of the early (pre K/Pg) origin of placental mammals.

The initial discovery of *Leptictis haydeni* was 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' (Leidy, 1868, p. 315). Leidy placed them within the order Insectivora, and they were first identified as a separate family with the name Leptictidae by Gill (1872).

(iii) *Ecology.* Leptictida are a specialised Laurasian group, occurring throughout northern North America from the Cretaceous to the Oligocene, with some examples – the Mongolian *Praolestes* (Matthew, Granger & Simpson, 1929), European pseudorhynchocyonids such as *Pseudorhynchocyon* (Filhol, 1892), and a Spanish specimen of *Leptictis* (Crusafont-Pairo & Golpe Posse, 1975) – from the Eocene of Europe and Paleocene of Asia. They are characterised by their long hind limbs, superficially resembling jerboas and sengis, although this is probably an entirely convergent adaptation to a similar ecological niche of a hopping insectivore–omnivore (Rose, 1999b).

(b) *Cimolestidae*

(i) *Composition.* There are 13 genera within Cimolestidae, seven of which are monospecific. 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 to 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. Paleocene and Cretaceous forms of *Cimolestes* may not be the same genus, with some concluding that Carnivora and Creodonta were independently derived from *Cimolestes* (Lillegraven, 1969; McKenna, 1975).

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

The Cretaceous cimolestids include only the three genera mentioned above. By the earliest Paleocene, the group had diversified to include the South American *Alcidedorbignya*, and the Laurasian *Puercolestes*. Some also include the Paleocene taxon *Procerberus* in the cimolestid lineage (Williamson, Weil & Standhardt, 2011), although *Procerberus* has also been considered to be a very basal eutherian (Kielan-Jaworowska, Bown & Lillegraven, 1979), and still others favour a relationship with Leptictida (Sloan & Van Valen, 1965).

Considering *Procerberus* as a stem eutherian mammal need not necessarily remove *Procerberus* from the cimolestids, however, because 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 (Hunt & Tedford, 1993). Given that 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 demonstrate 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 80 Ma), 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 among eutherians (Archibald *et al.*, 2001; Ekdale, Archibald & Averianov, 2004). Because 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 Placentalia, only *Solenodon* possesses a prootic canal, which appears to be a result of convergence (Wible *et al.*, 2009).

(iii) *Ecology.* Cimolestids have in general been considered to have incipiently carnassial teeth (Rana & 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 suggest a scansorial habit (Szalay & Decker, 1974).

(c) *Pantodonta*

(i) *Composition.* Pantodonta is composed of several families, the most diverse of which is the Coryphodontidae, which includes 18 species from seven genera. Although the relationships among these families are not well established, there is evidence for the existence of a grouping of exclusively North American pantodonts, the Pantolambdaoidea, which includes Cyriacotheriidae, Pantolambdodontidae, Pastoralodontidae, and Titanoideidae (Simons, 1960). In total, Pantodonta includes approximately 35 genera (McKenna & Bell, 1997).

(ii) *Proposed relationships.* The pantodonts, for the purposes of this introduction, are considered separately from the Cimolestidae, although they are regarded as a suborder in McKenna & 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 pantodonts being related to either an assortment of unusual South American ungulates or Paenungulata – the Afrotherian

lineage including proboscideans, sirenians and hyracoids. Pantodonts appeared in the Early Paleocene, with a largely global distribution, and survive to the Middle to Late Eocene, whereupon they became extinct approximately 33 Ma.

(iii) *Ecology*. Pantodonts include some of the largest terrestrial mammals of the period – the coryphodonts – 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 abundant components of North American Eocene faunas, being common enough to be a stratigraphic indicator for several North American Land Mammal Ages (NALMAs) (Robinson *et al.*, 2004), but have smaller representation throughout the Paleocene.

(d) *Creodonta*

(i) *Composition*. The status of the 16 genera of Creodonta has long been considered controversial, and the precise composition of the group has changed radically across the history of the literature. 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 (Morlo, Gunnell & Polly, 2009; Zack, 2011). 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 developmental repatterning.

(ii) *Proposed relationships*. 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 & 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.

(iii) *Ecology*. Creodonts were arguably the most specialised placental carnivores, with some members of the group achieving a hypercarnivorous state and modifying their entire molar row to carnassials (Stucky & 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 of the former by the latter (Wesley-Hunt, 2005).

(e) *Mesonychia*

(i) *Composition*. Mesonychia was traditionally composed of the Asian family Didymoconidae, the semiaquatic Hapalodectidae, and the most speciose member of the

clade, Mesonychidae, which includes 19 of the 29 mesonychian genera (Carroll, 1988). Didymoconidae has subsequently been removed from the clade (Meng, Suyin & Schiebout, 1995; Lopatin, 2001), but both hapalodectids and mesonychids remain, with hapalodectids considered more derived than mesonychids. The best known of the mesonychians, *Sinonyx*, *Mesonyx* and *Dissacus*, are all mesonychid mesonychians. The giant mammal *Andrewsarchus* has historically been considered to be a mesonychian or a close relative (Osborn, 1924; Tabuce, Clavel & Antunes, 2011), but competing hypotheses have suggested that *Andrewsarchus* may in fact be a cetancodontomorph artiodactyl (Spaulding, O’Leary & Gatesy, 2009) or an arctocyonid ‘condylarth’ (Van Valen, 1978).

(ii) *Proposed relationships*. Mesonychians are an enigmatic group of ‘archaic ungulate’, often considered separate from the ‘condylarths’. 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, particularly the double pulley astragalus that cemented the position of Cetacea within Artiodactyla, separate from mesonychians (Gingerich *et al.*, 2001; Thewissen *et al.*, 2001). The precise position of the mesonychids with respect to extant clades has been unclear; they have been thought of as stem artiodactyls (Theodor & Foss, 2005) or stem to the clade comprising Artiodactyla and Perissodactyla (Spaulding *et al.*, 2009). Conservatively, they have been grouped with triisodontids and oxyclaenids in the basal placental group Acroedi, and sister to the arctocyonid ‘condylarths’ (Tabuce *et al.*, 2011).

(iii) *Ecology*. 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 & Rose, 1995).

(3) Paleocene representatives of extant placental clades

(a) *Afrotheria* (elephants, hyraxes, dugongs, aardvarks, tenrecs, sengis, golden moles)

The earliest afrotherians known from the fossil record are found in the Middle Paleocene. The species *Ocepeia daouiensis* is known from the Selandian (61.6 to 59.2 Ma) of Morocco, and possesses a mosaic of characters suggesting 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).

(b) *Xenarthra* (sloths, armadillos, anteaters)

The location and phylogenetic affinities of the earliest xenarthran is controversial. The earliest member of the crown group that is not disputed is the already highly derived

Late Paleocene or Early Eocene armadillo *Utaetus*, which is found from the Casamayoran of Argentina (Ameghino, 1902; Rose, 2006). More controversial is the inclusion of the Asian Paleocene genus *Emanodon* (Ding, 1987), supposedly part of the suborder Eumantodonta (McKenna & Bell, 1997). This controversy is in part because it occurs on a different continent from other xenarthrans, with the exception of the only other putative xenarthran from Guangdong, *Asiabradypus*. This taxon, however, was considered by Rose *et al.* (2005) to be an animal of unknown affinity, ‘irrelevant to xenarthran origins’. Xenarthrans have historically been grouped together on the basis of simplistic characters such as a lack of teeth. There are few examples of positive characters, with the exception of the additional articulations of the vertebrae which characterise them as xenarthrous, and a relatively highly variable vertebral number (Asher *et al.*, 2011). No clear affinity with typical xenarthran characters has been definitively shown for *Emanodon*, and Gaudin (1999, p. 30) suggested that the articulations of the vertebrae of *Emanodon* ‘only vaguely resembles that characteristic of most true xenarthrans’.

(c) *Euarchontoglires* (rodents, rabbits, pikas, primates, tree shrews, flying lemurs)

The fossil record of Euarchontoglires in the Paleocene is limited to rodents and primates. The earliest lagomorph (rabbits, hares, pikas) and scandentian (tree shrews) fossils are known from the early to mid Eocene of China and Mongolia (Yongsheng, 1988; Lopatin & Averianov, 2008), while the earliest dermopteran (flying lemur) is known from the Late Eocene of Thailand (Rage *et al.*, 1992).

(i) *Rodentia* (mice, squirrels, porcupines, guinea pigs, beavers, voles). The earliest definitive rodents are known from the Paleocene, with *Tribosphenomys* a close outgroup to Rodentia (Meng & Wyss, 2001) and *Paramys*. 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.

(ii) *Primates* (apes, monkeys, lemurs, lorises, tarsiers). While there are no definitive crown primates in the Paleocene, there is strong evidence of the presence of plesiadapiforms. These taxa 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 – for example, grasping hands and a good depth of vision (Rose, 2006). *Purgatorius* is a putative plesiadapiform based on teeth (Clemens, 2004), and recently, tarsal material (Chester *et al.*, 2015). However, its relationships to modern forms has been controversial, with some analyses reconstructing *Purgatorius* outside of Placentalia (Wible *et al.*, 2009). If the Cretaceous Indian genus *Deccanolestes* is, as some have suggested, closely related to purported euarchontans, such as nyctitheres (Hooker, 2001, 2014) or adapisoriculids (Smith, De Bast & Sigé, 2010), then *Deccanolestes* would represent a Cretaceous occurrence of a euarchontan. However, while

Deccanolestes has been shown to be more closely related to adapisoriculids (Goswami *et al.*, 2011), neither group fell within Placentalia. Nyctitheres, by contrast, appear to be more closely related to eulipotyphlans (Manz *et al.*, 2015).

(d) *Laurasiatheria*

(i) *Carnivora* (cats, dogs, bears, otters, badgers, mongooses, hyaenas). The earliest stem carnivorans are the genera *Ravenictis* and *Pristinictis*, which are from the earliest Paleocene (Fox & Youzwshyn, 1994). These earliest forms have relatively unspecialised molars, suggesting a generalised omnivorous diet with only limited specialisation to true carnivory, although *Pristinictis* has been considered a primitive member of Viverravidae. Miacidae and Viverravidae, both relatively derived carnivorans, are both known from the Late Paleocene (Meehan & Wilson, 2002; Sole & Smith, 2013).

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

(ii) *Pholidota* (pangolins). Pholidotans are known from the middle Eocene of Europe, being represented by the two genera *Eomanis* and *Eurotamandua*, both from the Messel Pits of Germany (Storch, 1978; Rose *et al.*, 2005). Already relatively derived, a relationship with the Paleocene palaeonodons has been proposed (Rose, 1999a; Gaudin, Emry & Wible, 2009).

(iii) *Eulipotyphla* (shrews, hedgehogs, moles). Eulipotyphla include much of what once was ‘Insectivora’, the basalmost wastebasket taxon of placental mammals from which all others were supposed to have derived (McKenna, 1975). Now recognised as a derived group within Laurasiatheria, if morphologically plesiomorphic, the split between Eulipotyphla and Scrotifera is generally considered to be the basalmost division within Laurasiatheria (Waddell *et al.*, 1999; Nishihara, Hasegawa & Okada, 2006; Zhou *et al.*, 2012), although some earlier molecular analyses support a sister relationship between Eulipotyphla and Chiroptera (Onuma *et al.*, 2000). Combined morphological and molecular analyses consistently have been 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 (Stanhope *et al.*, 1998; Tabuce, Asher & Lehmann, 2008).

If nyctitheres are eulipotyphlans (Manz *et al.*, 2015), the earliest eulipotyphlans in the fossil record are the earliest Paleocene nyctitheres such as *Leptacodon* (Van Valen & Sloan, 1965), with putative but controversial members of the group in the latest Cretaceous (Antunes, Sigogneau-Russell & Russell, 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).

(iv) *Chiroptera* (bats). The first chiropteran fossils are of already relatively derived bats from the Green River Formation of the Early Eocene of Wyoming – *Onychonycteris*

funneyi (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.

(v) *Perissodactyla* (horses, rhinoceroses, tapirs). 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 forms (Eberle, Rzebczynski & Greenwood, 2014). The earliest equid, *Hyracotherium*, underwent a dramatic taxonomic revision in 2002 (Froehlich, 2002), with the separation of the genus into many new (and resurrected) genera. Tapirs and rhinoceroses, which are monophyletic to the exclusion of equids (Froehlich, 1999), are represented in the earliest Eocene by *Heptodon* (Radinsky, 1965) and *Hyrachyus*, respectively. *Heptodon* is known primarily from North America, where the majority of perissodactyl evolution occurred, although there are reports of the genus from China (Chow & Li, 1965). *Hyrachyus* is known from Europe and Asia, but has also been reported from the Caribbean (Domning *et al.*, 1997). Along with these crown 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 & Lapergola, 2011).

(vi) *Artiodactyla* (cattle, deer, giraffes, camels, pigs, hippopotamuses, whales). *Artiodactyla* is another extant order 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*. Represented by near-complete specimens (Rose, 1982b; Orliac, Benoit & O'Leary, 2012b), *Diacodexis* is known from layers immediately above the Paleocene–Eocene boundary (Smith, Smith & Sudre, 1996). It 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).

IV. NEW PHYLOGENETIC ANALYSIS OF CRETACEOUS AND PALAEOGENE PLACENTAL MAMMALS

(1) Materials

(a) Taxonomic sample

A broad sample of 177 eutherian taxa was selected in order to evaluate robustly hypotheses of relationships across Placentalia. For both extant orders and extinct groups of unknown affinity, taxa were selected based on several criteria, with particular preference for 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 that extensive evolutionary change has inevitably occurred within each clade 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.

Terminals were coded at genus rather than species level, to increase character completeness for fossil taxa. 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 the potential issue of including poorly supported genera. *Cimolestes* has been suspected to be polyphyletic – Scott (2010, p. 197) states ‘evidence for the monophyly of (*Cimolesta*) is weak, as is evidence for monophyly of *Cimolestes* Marsh, 1889 itself – but is here treated as a single terminal. 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 represent *Cimolestes*, and are coded into the same terminal to maximise completeness of this important taxon. Completeness and quality of fossil material was also taken into account in taxonomic sampling, with preference for taxa with a higher proportion of codable characters. 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, 904 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 (see online Supporting information, Appendix S1). In total, 177 genera were coded, comprising 130 Palaeogene, 29 Cretaceous, and 18 extant taxa.

(b) Characters

In total, 680 morphological characters – 48 of which are continuous – were coded for the 177 taxa, resulting in two matrices, one traditionally discrete (Appendix S2), and one with continuous characters treated as such (Appendix S3).

Characters were derived from four major sources – the PhD thesis of 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 *et al.* (2011) focusing on the Cretaceous–Palaeogene group Cimolestidae, which ultimately descends from the Wible matrix for Cretaceous eutherians (Wible *et al.*, 2007, 2009); a matrix used for establishing the relationships of the Palaeogene ‘ungulate’ mesonychia (Geisler & 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 S4).

(2) Methods

(a) Treatment of continuous characters

There is much debate over the benefits of using continuous traits in morphological phylogenetic analysis (Rae, 1998; Wiens, 2001; Goloboff, Mattoni & Quinteros, 2006). 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, we weight the continuous characters such that the difference between the maximum and minimum values for the trait is equivalent to a single step. Coded values for each terminal taxon were generated through measurement of multiple specimens where possible (Appendix S1) and calculation of the mean value of those measurements. This approach 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 directly to compare the accuracy of the topology by tree length alone when comparing data sets 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, discrete, ordered, multistate 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. We modified the weights of continuous and discretized characters using TNT (Goloboff *et al.*, 2006; Goloboff, Farris & Nixon, 2008).

(b) Constraints on tree topology

Placentalia is known to display a high level of morphological homoplasy, with adaptive radiations in different groups leading to occupation of similar niches (Madsen *et al.*, 2001), with concomitant morphological similarities. As a result, relationships derived from solely morphological data have often been in conflict with those derived from molecular data, with homoplasy overriding phylogenetic signal at higher phylogenetic levels (Lee & Camens, 2009). As noted above, this issue of homoplasy has long been appreciated, with certain traditional placental groupings (ungulates and insectivores) identified as being particularly suspect (Asher *et al.*, 2008). The most obvious failure of morphological phylogenetic analyses of Placentalia is the lack of support for the major placental ‘superorders’ – Afrotheria, Xenarthra,

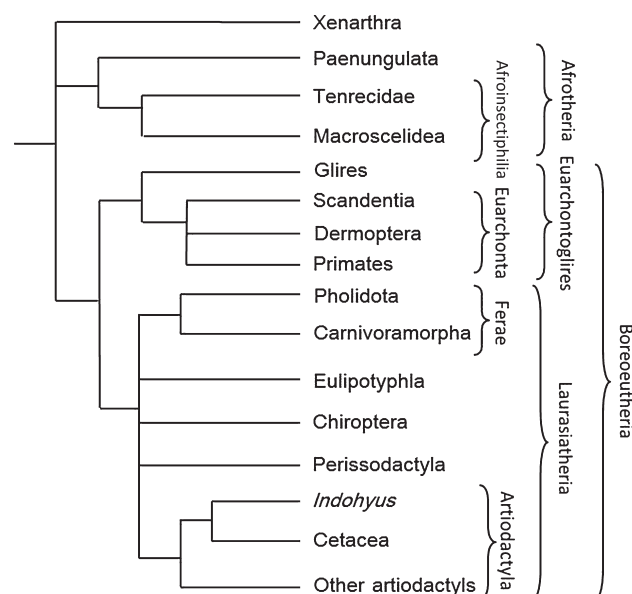


Fig. 2. The constraint applied to all analyses, derived from the molecular understanding of the relationships of extant placental mammal groups. In CM and DM analyses, Xenarthra was composed of *Chaetophractus*, *Bradypos* and *Tamandua*; Paenungulata: *Eritherium* and *Procavia*; Tenrecidae: *Potamogale*; Macroscelidea: *Chambius* and *Rhynchocyon*. Glires was composed of *Tribosphenomys*, *Paramys* and *Gomphos*; Scandentia: *Tupaia* and *Philocercus*; 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 other 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 *Elphidotarsius*, *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.

Euarchotheria, and Laurasiatheria, each of which are very well supported in most molecular studies (Stanhope *et al.*, 1998; Springer *et al.*, 2003; Bininda-Emonds *et al.*, 2007; Prasad *et al.*, 2008; dos Reis *et al.*, 2012; Morgan *et al.*, 2013). In order to incorporate the uncontroversial aspects of topology for living placentals provided by molecular studies, we constrained the relationships among extant clades with a topological scaffold that is consistent with the vast majority of molecular analyses of placental mammals (Fig. 2). Using molecular constraints can help to correct for morphological homoplasy, and allow the truly synapomorphic morphological features to have a stronger effect.

Rather than constraining taxa, many phylogenetic analyses have used a total-evidence approach to explore the relationships of groups, incorporating both molecular and morphological data. While this tactic would be possible for these fossil groups, the aim of this study was to elucidate the relationships among the placental mammals of the Paleocene and their affinities with extant orders. Total-evidence analyses require a substantial proportion of extant taxa. As noted above, we have included earlier and more basal members of extant clades as representatives, as they are less morphologically derived, and are therefore more likely to possess more useful synapomorphies relevant to the diversification of Placentalia, and concomitantly fewer homoplastic traits.

In applying molecular constraints, we allowed for areas of uncertainty such as the topology of the Laurasiatherian orders (Hu, Zhang & Yu, 2012) and the relationships between Boreoeutheria, Atlantogenata and Xenarthra (Murphy *et al.*, 2007; Nishihara, Maruyama & Okada, 2009), discussed further below, by treating them as unresolved polytomies within the scaffold. Two levels of constraint were implemented; one imposed a ‘minimum’ constraint, including a limited subset of exemplar taxa as representatives of the extant orders. For example, while both *Pakicetus* and *Rodhocetus* are undoubtedly closest relatives in this data set, both being stem cetaceans, only *Rodhocetus* was included in the constraint. This approach 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 morphological data with a minimal constraint. Exemplar taxa were selected on the basis of both morphological completeness and the level of support for inclusion within a group. For example, within Chiroptera, the extant *Pteropus* was included in the minimum constraint due to high completeness relative to *Onychonycteris* and *Icaronycteris* (both of which are indisputably bats), while within Carnivoramorpha, the genera *Miacis* and *Viverravus* were selected as representatives of Miacidae and Viverravidae respectively. The second approach constrained all taxa which are unequivocally accepted as stem members of the extant orders (Fig. 2) in recent analyses focusing on those groups, in order to ensure that well-established and evidenced relationships were maintained in these analyses.

Each node that has been constrained is justified on the basis of multiple previous phylogenetic analyses. The ‘four-clade model’ of placental relationships is now well established (Asher, 2007; Murphy *et al.*, 2007; Wible *et al.*, 2007), but the nature of the relationship between Xenarthra, Afrotheria, and Boreoeutheria, the well-accepted grouping of Laurasiatheria and Euarchontoglires (Delsuc *et al.*, 2002; Asher & Helgen, 2010) is unclear (Hallstrom *et al.*, 2007; Murphy *et al.*, 2007; Morgan *et al.*, 2013; Teeling & Hedges, 2013). As a result, the scaffold is constrained to allow any topology between these three groups. Within Afrotheria, the basal separation of ‘ungulate-grade’ from ‘insectivore-grade’ organisms is well established (Tabuce *et al.*, 2008; Asher & Helgen, 2010), and therefore was also constrained. The division between Glires and Euarchonta is supported by a

number of analyses, but the relationships within the orders of Euarchonta differ among them (Waddell, Kishino & Ota, 2001; Nie *et al.*, 2008). As a result, Primates, Dermoptera, and Scandentia, all certainly monophyletic, were allowed to vary in their interrelationships within Euarchonta. Within Laurasiatheria, there is no clear consensus for the relationships of the orders (Hallstrom *et al.*, 2011; Hu *et al.*, 2012), except that Carnivora and Pholidota are likely to be sister taxa (Nishihara *et al.*, 2006; Zhou *et al.*, 2012). Raoellid artiodactyls (including *Indohyus*) are considered to be closer relatives of cetaceans than other artiodactyls in this analysis (Bajpai, Thewissen & Sahni, 2009), and as a result, the topologies within Artiodactyla were also constrained to reflect this basal division.

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 & 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 & Hunter, 2014), although counterarguments suggest that this more basal position has resulted from inadequate sampling of plesiadapiforms and early Primates (Chester *et al.*, 2015), 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.

In implementing these constraints, 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 & Bell, 1997), in order to ensure that trees were rooted appropriately.

In total, we 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 (MPTs). For brevity, we refer to these eight analyses using the following abbreviations: CU and DU represent the continuous and discretised unconstrained analyses. CM and DM 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.

(c) 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 random and exclusive sectorial searches, drift (rejection factor 50) and tree fusing, dumping fused trees for computational ease due

Table 1. Numbers of most parsimonious trees (MPTs), their lengths, the number of suboptimal trees within a single step, and consistency (CI) and retention (RI) 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	CM	CF	CP	DU	DM	DF	DP
No 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
No 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

to the size of the data set. This was followed by a round of traditional tree bisection and reconnection (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 350–500 h of computing time. Multistate characters were treated as ordered where meristic or where they represented a morphological sequence in which one or more states are discrete intermediates between end-member states (Wilkinson, 1992). For example, character 325 describes the position of the palatine foramen, and has the ordered states ‘within palatine’, ‘between palatine and maxilla’ and ‘within maxilla’ (see Appendix S4). 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 MPTs were also recovered.

(d) *Templeton’s tests*

Templeton’s test (Templeton, 1983) allows alternative, suboptimal topologies to be compared in order to ascertain whether the additional length is significantly longer than the optimal topology, and therefore can be rejected as unsupported by the data. Where two competing hypotheses for the phylogenetic placement of a taxon exist, Templeton’s tests are therefore a useful way to determine whether a data set supports one hypothesis strongly over another. Pairwise Templeton’s tests were conducted on each set of MPTs for both discrete and continuous data sets using Microsoft Excel.

(e) *Bremer support*

Relative Bremer supports were calculated by searching for suboptimal trees at increasing levels of suboptimality until the storage limit of 99999 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 a score of 100 clades that are always present. For example, a score of 50 would indicate that the number of trees that contradicted the clade was half that of the number that supported the clade. Values of 0 or below result in the node being collapsed, as they are contradicted by a majority of trees.

Relative Bremer support holds the advantage over absolute Bremer support of taking into account contradictory and favourable evidence for a clade, rather than just favourable evidence (Goloboff & Farris, 2001). Additionally, because they vary within the same scale, measuring a ratio, results can be directly comparable across trees. As a result, it has been argued that relative Bremer support is a superior metric of node support to absolute Bremer support (Goloboff & Farris, 2001).

V. RESULTS

(1) Phylogenetic topology

The MPTs resulting from the six constrained analyses were generally consistent with each other. For clarity, only the results from three analyses will be discussed in detail – the discrete, unconstrained tree (DU), and both continuous and discrete trees, with the full constraint applied (CF and DF). Details of the differences between these trees and those derived from alternative constraints (the ‘minimum’ constraint and full constraint incorporating *Purgatorius*) may be found in Appendix S5. Numbers of MPTs, number of suboptimal trees within a single step of the MPTs, and tree metrics are summarised in Table 1.

(a) *Unconstrained analyses*

The topology of the unconstrained analysis (Fig. 3, see online Fig. S1) contained many of the groupings that have been generally supported by previous morphological analyses, and failed to recover Eulipotyphla as a monophyletic group to the exclusion of other laurasiatherians. Afrotheria was recovered as polyphyletic and Chiroptera allied with a reduced Euarchontoglires. Aspects of the topology such as these demonstrate the need for constraining relationships among extant clades to those that are well supported by both molecular and phenotypic data sets, such as the four superorders. Results were consistent between discretised and continuous characters.

(b) *Fully constrained analyses*

When full constraints were implemented as described in Section IV.2b, the precise topology of extant clades varied

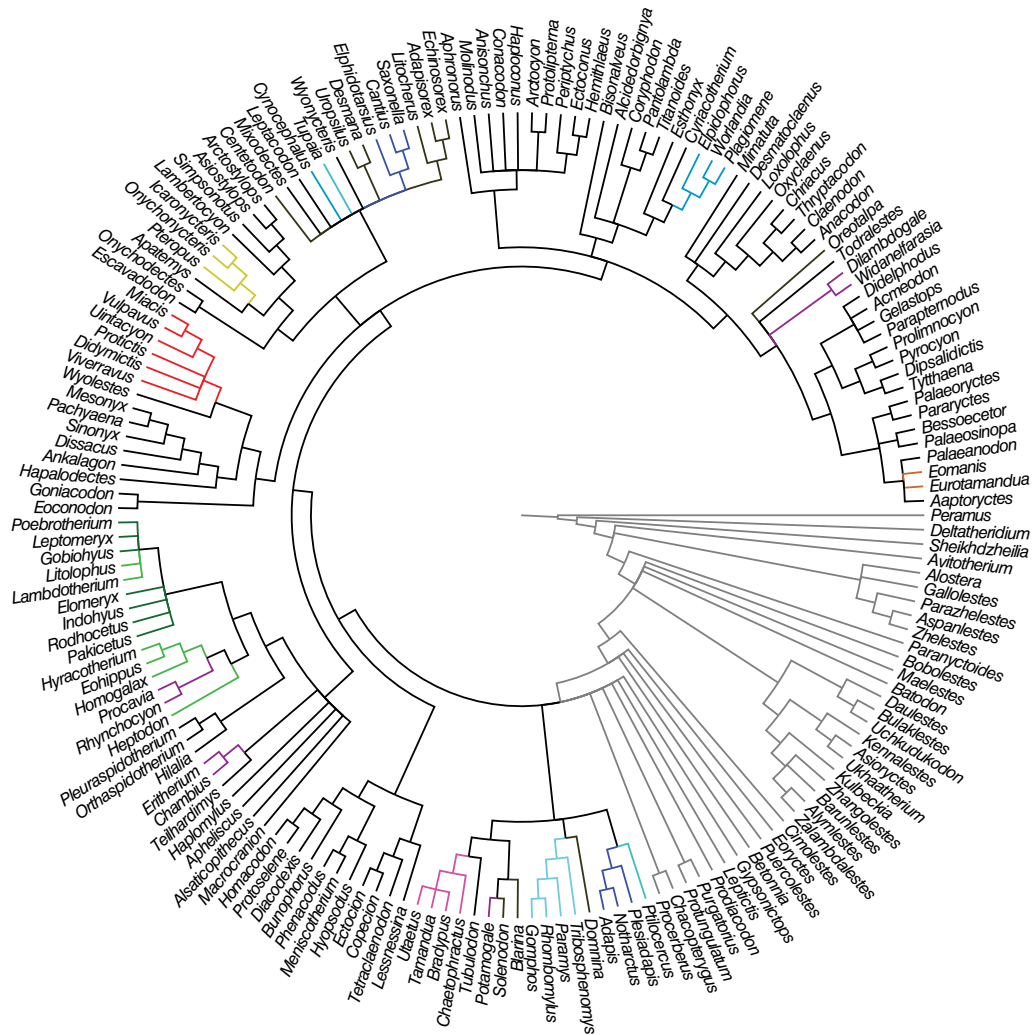


Fig. 3. Strict consensus of all discrete, unconstrained (DU) trees within one step of the most parsimonious trees. Colours represent members of extant orders as follows: pink, Xenarthra; purple, Afrotheria; sky blue, Glires; light blue, Scandentia; mid-blue, Dermoptera; royal blue, primates; brown, Eulipotyphla; dark green, Artiodactyla; light green, Perissodactyla; yellow, Chiroptera; orange, Pholidota; red, Carnivora.

where there was uncertainty, for example in the relationships among the laurasiatherian orders (Fig. 4, see online Figs S2–S6). Nonetheless, topological relationships of the clades of interest were generally consistent among all constrained analyses. The retention and consistency indices were similar in the constrained and unconstrained analyses (Table 1), indicating that the level of homoplasy in the unconstrained tree was almost as high as when relationships were constrained.

Below, we discuss relationships of clades of interest, and the synapomorphies that support them. Full lists of synapomorphies for major recovered clades are found in Appendix S6.

(c) 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’. *Purgatorius* was found consistently as sister taxon to *Protungulatum*, as in Wible *et al.* (2007), with both taxa immediately stemward of a paraphyletic Leptictida. Zhelestidae was recovered in a basal stem-placental position as opposed to being a stem member of an ‘ungulate’ clade within the crown. The monophyly of Zhelestidae was supported by the presence of a metaconid on p4 (Character 131), the separation of a relatively small paraconid from the metaconid (19, 20, 214), a hypoconulid close to the entoconid (236) and a mandibular ramus that deepens below the molars (263). Zalambdalestidae, too, was recovered as a monophyletic group of stem placentals, and was supported by several unambiguous synapomorphies, including the development of an enlarged, procumbent lower first incisor with an extensive root (72, 74, 76), a more anterior position of the posteriormost mental foramen (261), the lack of an ectoflexus on any upper molar (160), an uneven

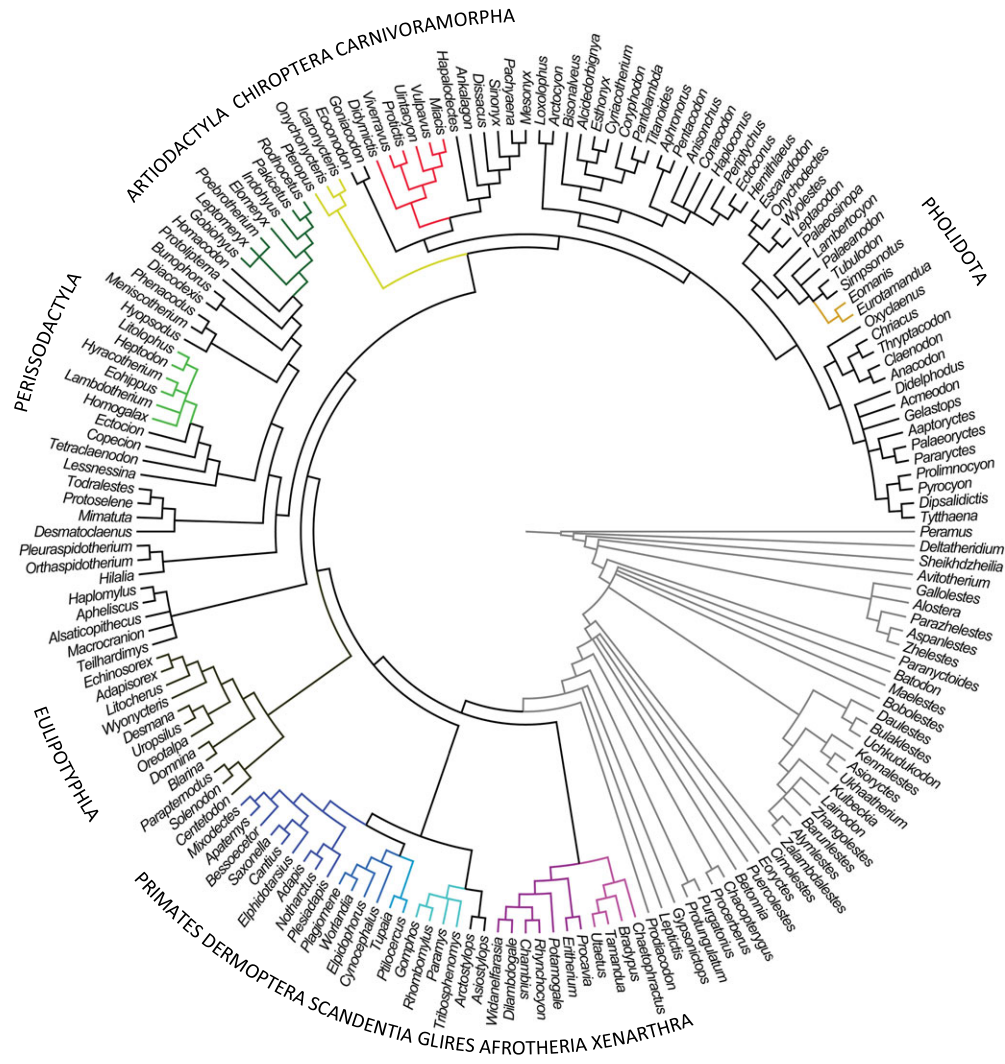


Fig. 4. Strict consensus of trees derived from the discrete data set with the full constraints applied (DF analysis). Colours are as in Fig. 3.

distribution of enamel on the incisors (256), and the presence of a separate metaconid on the fourth premolar (131).

(d) *Cimolestidae*

Cimolestids were found to be diphyletic in all analyses; one group, consisting of *Cimolestes*, *Procerberus*, *Chacopterygus*, *Betomnia* 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*. The inconsistency in the composition of this group means that there are few synapomorphies that are supported across all analyses. However, a premaxilla that extends beyond the canine (293), sharp, gracile molar cusps (138), and a small ectopterygoid process (387) are consistently reconstructed where this broadly carnivorous grouping is recovered as monophyletic.

(e) *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 (112), a developed cristid obliqua (230), and the presence of a hypoconule on upper molars (206). In the CF and DF analyses, *Prodiacodon* was found to be the sister taxon to crown Placentalia, with *Gypsonictops* and *Leptictis* the next closest relatives, rendering Leptictida paraphyletic with respect to Placentalia.

(f) *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 constrained 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 result is consistent with many recent genetic and genomic analyses of placental mammals (Hallstrom *et al.*, 2007; Murphy *et al.*, 2007; Kuntner, May-Collado & Agnarsson, 2011). Morphological synapomorphies for Atlantogenata were inconsistent across different analyses, due to the shifting relationships of other taxa. Those which remain across the majority of analyses were dental – typically related to the simplification of the molars – which poses problems for identifying these traits in edentulous taxa such as the majority of Xenarthra. Commonly reconstructed synapomorphies of Atlantogenata included loss of the pre- and postcingula (109, 110), as well as a vertical lingual face of the protocone (191), and the presence of a hypoconid on the second lower molar (232). In the DF and CF analyses, 26 and 25 synapomorphies, respectively, supported Atlantogenata, of which 21 were common to both (Appendix S6). Examples of these are postcranial characters including an increase in the number of thoracic vertebrae (524), a rounded rather than ovoid radial head (560), and a shortened astragalar neck (630), as well as many additional losses in cheek tooth complexity. However, no taxon was consistently resolved on the stem of either Atlantogenata or Boreoeutheria.

Although Laurasiatheria and Euarchontoglires were each constrained to form monophyletic clades in all analyses, they were 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 (393), the opening of the cavum epiptericum (419), the loss of the hypotympanic sinus (452), and, where present, more distal re-entrant grooves on the molars (257). Eulipotyphla was supported as the most basal extant order within Laurasiatheria in all constrained analyses, but the relationships among other laurasiatherian orders were more variable. With the exception of the minimum constraints analyses, the next most basal division within Laurasiatheria was between Euungulata (Artiodactyla and Perissodactyla) and a Chiroptera–Ferae (Carnivora and Pholidota) clade. Characters supporting Euungulata include a flattened ulnar facet on the radial head (560), the lack of a paraconid on the lower molars (213) or a preparacrista on the upper molars (164), and an elongate calcaneal tubercle (656), while the Chiroptera–Ferae clade was supported by a loss of a postpalatine torus (328), a laterally exposed mastoid region (508), three sacral vertebrae (527), and an inferior petrosal sinus that was housed between the petrosal, basisphenoid and the basicranium (476).

Euarchontoglires was supported unambiguously by an extended ectopterygoid process of the alisphenoid (386), an anteriorly expanded tegmen tympani (447), a small and shallow stapedius fossa (463), and a reduction to three sacral vertebrae from four (527). The most common division within Euarchonta is a Scandentia–Dermoptera clade to the exclusion of Primates; this is supported by five consistent and

unambiguous synapomorphies. These are a reduction in the number of lower incisors (57), a loss of contact between the jugal and lacrimal (339), the absence of a sagittal crest (372), the presence of the interparietal (373), and a fused scaphoid and lunata (575).

(g) ‘Condylarths’

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. Phenacodontidae was not recovered as monophyletic. One group (*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* and *Meniscotherium* were found among hyposodontids in all analyses. With the exception of the presence of a mesostyle (148), there was no single synapomorphy that was unambiguously associated with a node subtending perissodactyls and the three phenacodontids when all analyses were considered. Nonetheless, several character states, such as a strong metalophid (221), highly molarised premolars (118, 119) and the loss of upper molar conular cristae (184) 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, sister to Scrotifera (the clade comprising all laurasiatherian orders except Eulipotyphla) in all analyses except CM and DP. Hyposodontids are placed, in all analyses except CM and DM, as the sister taxon to Artiodactyla. Periptychidae and Pantodonta are consistently found to be sister taxa, more closely related to Ferae and Chiroptera than to other Laurasiatherian orders. Arctocyonidae was polyphyletic in the DF and CF analyses, 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.

(h) Other Paleocene taxa

The close relationship between Creodonta and Carnivora was consistently supported, with other pseudocarnivorous genera such as *Gelastops*, *Acmeodon*, *Wyolestes* and *Didelphodus*, as well as Palaeoryctidae, also placed as close relatives to this grouping. Moreover, palaeonodonts are found to be sister taxa to Pholidota (represented here by *Eomanis* and *Eurotamandua*), supported by a strong teres tubercle (544), a central process of the radial head (559), a shallow olecranon fossa (573), and no iliopubic eminence (587).

The enigmatic South American meridiungulates are represented in this study by the henricosbornid notoungulate *Simpsonotus* and the early litoptern *Protolipterna*. *Protolipterna* was resolved alongside archaic dichobunid artiodactyls in

most analyses. *Simpsonotus*, however, had a less consistent position, being found next to Palaeonodonta in DF, CM and CP, but on the atlantogenatan stem with Arctostylopidae in DP, on the chiropteran stem with Arctostylopidae in CF, and close to Artiodactyla in DM. As the sampling in this study does 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. Neither *Protolipterna* nor *Simpsonotus* were resolved as close relatives of Perissodactyla, contrary to recent evidence from protein sequences (Welker *et al.*, 2015).

The relationships of Arctostylopidae are extremely poorly understood (Zack, 2004), but this group has been thought to be related to Glires, Notoungulata, or Artiodactyla (Cifelli, Schaff & McKenna, 1989; McKenna & Bell, 1997). Affiliation with Glires, supported by the DF analysis, was supported by mandibular and postcranial characters such as a single mental foramen (259), a space between m3 and the coronoid process (264), and a rotated sustentacular facet of the astragalus (626). A relationship with Notoungulata was supported in the CF and DP analyses by reduction of the metacone and protocone (9, 12), as well as smaller canines (83, 86), reduced protocristid (223), and a more even-sized tooth row (137). A more focused study of this enigmatic and rare family is required to resolve the character conflict between this hypothesis and that implied by an Arctostylopidae–Glires clade.

(2) Templeton's tests

Templeton's tests were used to compare all pairwise combinations of MPTs – a total of 42 comparisons. The lengths of all constrained topologies were found to be significantly longer than those of unconstrained trees for a given data set (Table 2), with the latter bearing no relationship to the known topologies of placental mammal phylogenies derived from molecular data. This result suggests that morphological data cannot of itself accurately reconstruct placental phylogeny without application of constraints, due to substantial differences between topologies resulting from constrained and unconstrained analyses. Nonetheless, the constraints that were applied are based upon well-established relationships that are consistently retrieved from both molecular and combined morphological–molecular analyses, and so are justified in this context.

Among the constrained topologies, no significant differences were found in either discrete or continuous character optimisations using the same constraints (Table 2), and for each data set, no particular constraint resulted in significantly longer trees than any other constraint. When different constraints and data types were compared in concert, significant differences were found between DM and CM under the discrete data set. In this case, the continuous topologies were significantly longer due

to the trees derived from the discrete data set better fitting the discretised data. All other differences in length between combinations of data set and constraint were not significant.

(3) Relative Bremer support

Relative Bremer support was low for several nodes across all trees (see online Figs S7–S12). The lack of support is in large part due to a few very unstable taxa, as confirmed by application of the 'Pruned trees' option in TNT, which identifies taxa that, when removed, result in the resolution of polytomies (Table 3). When relative Bremer supports were calculated after pruning these unstable taxa from the suboptimal topologies, the level of support increased markedly. In the CF analysis, many higher-level relationships were strongly supported, being found in all suboptimal topologies to the storage limit of 99999 trees. Well-supported relationships included the placement of all 'condylarths' within Laurasiatheria, the monophyly of Euungulata, the closest relatives of Perissodactyla being phenacodontids, and the affinity of Hyopsodontidae with Artiodactyla. Additionally, the placement of triisodontids with Arctocyonidae as a sister clade to Carnivora and Creodonta was very strongly supported. When *Eoryctes* was excluded, Atlantogenata was supported 100% of the time, as was the paraphyletic relationship of Leptictida with respect to crown Placentalia.

In the CM analysis, node support was in general weaker, although monophyly of many Paleocene clades was conserved. *Ectocion*, *Copacion* and *Tetraclaenodon* were still strongly supported as sequential closest relatives to perissodactyls. After excluding unstable taxa (*Lainodon*, *Oxyclaenus* and *Hilalia*) from the CM analysis, Atlantogenata was well supported, but laurasiatherian clades generally received poorer support than in the other analyses (see online Fig. S11).

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–palaeonodontan clade. Atlantogenata, the laurasiatherian affinity for 'condylarths', the relationship between Perissodactyla and some phenacodontids, and a Triisodontidae–Carnivora relationship were also notably all supported. The DM and DP analyses were very stable once unstable taxa (*Lainodon* and *Oreotalpa* in the former; *Eoryctes*, *Molinodus* and *Lainodon* in the latter) had been excluded from the strict consensus tree, with strong support for many higher-level relationships within the phylogeny.

Supports for nodes across crown Placentalia were weaker when *Purgatorius* was constrained as a primate. In all analyses, the weakest area of support was within Ferae, where relative Bremer indicated almost equivocal support for the presence or absence of any given clade. The best-supported topologies across the entire eutherian tree were found in the DF analysis (Fig. 4, see online Fig. S7).

Table 2. Results of Templeton's tests, comparing each set of topologies under both discrete and continuous data sets. Of all constrained topologies, the only comparison that was considered to be significantly different is that between the discrete (DM) and continuous (CM) minimum constraints under the discrete data set

Data set	Shorter topology	Longer topology	W	n	z	P value (two-tailed)
Continuous	CU	CF	22398	406	4.73	<0.0001
Continuous	CU	CP	20772	414	4.26	<0.0001
Continuous	CU	CM	23174	421	4.64	<0.0001
Continuous	CU	DF	20294	423	4.03	0.0001
Continuous	CU	DP	24412	429	4.75	<0.0001
Continuous	CU	DM	19465	407	4.1	<0.0001
Continuous	CM	CF	1071	327	0.31	0.7566
Continuous	CM	CP	1451	345	0.39	0.6965
Continuous	CM	DF	342	353	0.09	0.9283
Continuous	CM	DP	2856	353	0.74	0.4593
Continuous	CM	DM	2733	327	0.8	0.4237
Continuous	CF	CP	1184	294	0.41	0.6816
Continuous	CF	DF	1838	313	0.57	0.5687
Continuous	CF	DP	2207	305	0.72	0.4715
Continuous	CF	DM	2009	329	0.58	0.5619
Continuous	CP	DF	370	201	0.22	0.8259
Continuous	CP	DP	1842	305	0.6	0.5485
Continuous	CP	DM	999	358	0.25	0.8026
Continuous	DF	DM	2389	360	0.6	0.5485
Continuous	DP	DM	5259	380	1.23	0.2187
Continuous	DF	DP	161	301	0.05	0.9601
Discrete	DU	DF	35176	410	7.33	<0.0001
Discrete	DU	DP	37655	414	7.73	<0.0001
Discrete	DU	DM	34198	425	6.75	<0.0001
Discrete	DU	CF	40483	421	8.1	<0.0001
Discrete	DU	CP	38274	420	7.69	<0.0001
Discrete	DU	CM	41344	430	8.02	<0.0001
Discrete	DM	DF	4359	348	1.16	0.246
Discrete	DM	DP	5911	370	1.44	0.1499
Discrete	DM	CF	5980	324	1.77	0.0767
Discrete	DM	CP	5623	348	1.5	0.1336
Discrete	DM	CM	7540	321	2.27	0.0232
Discrete	DF	DP	1049	296	0.36	0.7188
Discrete	DF	CF	439	306	0.14	0.8887
Discrete	DF	CP	1751	194	1.12	0.2627
Discrete	DF	CM	3334	339	0.92	0.3576
Discrete	DP	CF	1397	302	0.46	0.6455
Discrete	DP	CP	2756	302	0.91	0.3628
Discrete	DP	CM	1865	346	0.5	0.6171
Discrete	CF	CP	1613	284	0.58	0.5619
Discrete	CF	CM	2282	316	0.7	0.4839
Discrete	CM	CP	1274	334	0.36	0.7188

p -values significant at an alpha level of 0.05 are in bold.

Table 3. Unstable taxa pruned from each topology for the calculation of representatives

Level of Constraint	Continuous	Discrete
Unconstrained	n/a	<i>Lainodon</i> , <i>Pentacodon</i>
Minimum	<i>Hilalia</i> , <i>Lainodon</i> , <i>Oxycloenus</i>	<i>Lainodon</i> , <i>Oreotalpa</i>
Full	<i>Centetodon</i>	<i>Molinodus</i>
<i>Purgatorius</i>	<i>Prodiacodon</i>	<i>Eoryctes</i> , <i>Molinodus</i> , <i>Lainodon</i>

VI. DISCUSSION

(1) Comparison with previous studies

This study 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) was the PhD thesis of Zack (2009). However, several of the terminals in that analysis are composites of multiple 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, Lipscomb & Allard, 2003). Further, the Zack (2009) analyses presented trees derived primarily from dental and postcranial material. While cranial material, a rich source of data, was included in a single analysis, this was 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, and those that do have focussed primarily on ordinal- or family-level clades (e.g. Missiaen *et al.*, 2012; Chester & Bloch, 2013). 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 lousinid ‘condylarthrs’, but only including single members of Macroscelidea, Amphelimiridae, Adapisoriculidae, and outgroups (as in Hooker & Russell, 2012), it is possible to study the interrelationships of apheliscids and lousinids, but not possible to test alternative hypotheses of the relationships robustly between these taxa and the rest of the placental tree. The inclusion of a combination of living and fossil members of Placentalia in the present analysis advances our understanding of placental mammal origins, providing additional data, new resolution, and novel perspectives on the long-debated affinities of several enigmatic clades.

(2) Resolving placental relationships

Atlantogenata was strongly supported over Exafroplacentalia or Epitheria for the first time in an exclusively morphological analysis – albeit one incorporating constraints in other portions of the tree. While Atlantogenata has been supported by a wide range of molecular studies (e.g. Hallstrom & Janke, 2008; Prasad *et al.*, 2008; Song *et al.*, 2012; Morgan *et al.*, 2013), analyses including morphology have tended to favour a xenarthran root (Gaudin *et al.*, 1996; O’Leary *et al.*, 2013). 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 placental mammal morphology. Although molecular constraints were implemented in this tree, the topology at the root of Placentalia was left unconstrained, and Atlantogenata was recovered in all analyses. That there are dental synapomorphies at the node subtending Atlantogenata despite the extremely simplified dentition of xenarthrans can be explained by noting that the majority of dental characters that support Atlantogenata are concerned with structures that are lost in both Afrotheria and Xenarthra.

We found 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, Palaeonodonta, Pholidota, Carnivora, Creodonta, Palaeoryctidae and Arctocyoniidae, associated with Periptychidae and Pantodonta.

The polyphyly of ‘Condylarthra’ and its status as a wastebasket taxon are supported by a large number of morphological features. Several enigmatic Paleocene groups within this wastebasket, including Periptychidae, Pantodonta and Mesonychia, as well as, in a majority of analyses, Arctocyoniidae, are resolved as monophyletic sister taxa to extant clades. Others, such as Leptictida and Cimolestidae are recovered as paraphyletic with respect to extant clades. The polyphyly of Hyopsodontidae, which has long been suspected (Cifelli, 1983; Archibald, 1998; Zack *et al.*, 2005a), is also supported here, with Pleuraspidotheriidae, Apheliscidae and the ‘true’ hyopsodontids *Hyopsodus* and allies found to be entirely separate lineages (Fig. 4).

Although Phenacodontidae is here returned as diphyletic, the consistent support for the presence of phenacodontids as closest relatives of Perissodactyla is in agreement with the majority of the literature. The original definition of ‘Condylarthra’ was 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 has been identified as the sister group of Altungulata (Kondrashov & Lucas, 2012), a problematic grouping of perissodactyls and several afrotherian ‘ungulates’, which is in conflict with molecular topologies.

The placement of creodonts closer to pangolins than to carnivorans has not been recovered in previous phylogenetic analyses. While Creodonta has been suggested to be paraphyletic relative to Carnivora (Flynn & 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 (Colbert, 1933; Colbert & Morales, 1991; Goswami, 2010; Ungar, 2010), suggesting a possible convergent acquisition of this phenotype. Additionally, monophyly of Creodonta is not always recovered (Polly, 1996; Morlo *et al.*, 2009; Sole *et al.*, 2009). A position within Ferae – the clade uniting Carnivora and Pholidota – is accepted (MacIntyre, 1966; Smith & Smith, 2001), but the relative positions of Pholidota, Carnivora, and Creodonta have been unclear.

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 clarified with additional data, including the position of apheliscine condylarthrs and the topology of the enigmatic groups here resolved on the stem of Ferae. Indeed, evidence is accruing that the diversification of the laurasiatherian orders occurred extremely rapidly, (Hallstrom & Janke, 2008; Zhou *et al.*, 2012) such that incomplete lineage sorting has been invoked

as an explanation for lack of resolution in early placental relationships (Hallstrom & Janke, 2010).

Clearly, there is little consensus for the majority of the relationships of Paleocene placental mammals, and many of the relationships supported herein will continue to be debated. Many of the results from this analysis actually resurrect previous hypotheses from recent and more distant studies. 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 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 and provides new resolution to the placental tree.

With the inclusion of Paleocene taxa into a broad phylogenetic tree for eutherian mammals, we have a window into the time during which the placental 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 step in untangling the relationships of these extinct clades, and understanding the evolutionary and ecological context of the radiation of placental mammals. Ongoing work is focused on robustly dating the topologies produced in this phylogenetic analysis, and investigating 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.

(3) Implications for the timing of placental origins

As noted in previous studies including *Protungulatum* (Wible *et al.*, 2007; Archibald *et al.*, 2011; O’Leary *et al.*, 2013), the phylogenetic position of that taxon is critical to the interpretation of the oldest known members of crown Placentalia. *Protungulatum* (and *Purgatorius*) were most parsimoniously resolved on the stem of Placentalia, except where *Purgatorius* was constrained. However, Templeton’s tests do not reject alternative phylogenetic positions for either *Protungulatum* or *Purgatorius* within the crown. *Protungulatum* is known from both Paleocene and Cretaceous formations (Archibald *et al.*, 2011), and as such, the presence of this taxon within crown Placentalia would be evidence that the origin of placental mammals pre-dates 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 fivefold increase in background rates of morphological evolution to allow the placental mammal origin to be less than 66 million years ago (Beck & Lee, 2014). This new topology, with broad sampling of temporally relevant taxa, makes it possible to analyse the timing and rate of placental mammal divergences robustly.

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 either a member of the now-paraphyletic Leptictida in DP and CP, or a *Protungulatum*–*Purgatorius* clade in analyses where *Purgatorius* was not constrained as a stem primate. *Gypsonictops* is known from the Late Cretaceous, while the other two genera are Paleocene. The presence of Cimolestidae and *Leptictis* on the placental 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 oldest perissodactyl, *Hyracotherium*, is known from the earliest Eocene (e.g. Smith & 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, Spivak, & Sweet, 2013). With a close relationship found here between Perissodactyla and some members of Phenacodontidae, including *Tetraclaenodon*, 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 Peripitychidae, 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 pre-dated the end-Cretaceous mass extinction.

VII. CONCLUSIONS

(1) The majority of members of 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.

(2) 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.

(3) The closest relatives of crown perissodactyls are consistently found to be phenacodontids, although *Phenacodus* and *Meniscotherium* are more parsimoniously resolved with members of Hyopsodontidae, which are sometimes closer to Artiodactyla.

(4) Periptychidae and Pantodonta are sister taxa, and are more closely related to Ferae and Chiroptera than to Perissodactyla or Artiodactyla.

(5) 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 such as *Lainodon*.

(6) 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.

(7) 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 a Cretaceous origin for placental mammals.

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X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Fig. S1. Consensus topology deriving from the CU analysis.

Fig. S2. Consensus topology deriving from the DM analysis.

Fig. S3. Consensus topology deriving from the DP analysis.

Fig. S4. Consensus topology deriving from the CF analysis.

Fig. S5. Consensus topology deriving from the CM analysis.

Fig. S6. Consensus topology deriving from the CP analysis.

Fig. S7. Bremer support tree from the DF analysis.

Fig. S8. Bremer support tree from the DM analysis.

Fig. S9. Bremer support tree from the DP analysis.

Fig. S10. Bremer support tree from the CF analysis.

Fig. S11. Bremer support tree from the CM analysis.

Fig. S12. Bremer support tree from the CP analysis.

Appendix S1. Specimens 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.

Appendix S2. Matrix used for the phylogenetic analyses which resulted in the DU, DF, DM and DP sets of most-parsimonious trees, formatted to be openable in TNT.

Appendix S3. Matrix used for the phylogenetic analyses which resulted in the CU, CF, CM and CP sets of most-parsimonious trees, formatted to be openable in TNT.

Appendix S4. List of all 680 characters with descriptions of each character state, the proximal and ultimate sources of

that character, and the treatment of that character – whether it is continuous or discrete, and ordered or unordered.

Appendix S5. Additional topologies recovered in the DM, CM, DP and CP analyses.

Appendix S6. List of unambiguous synapomorphies of commonly recovered clades.

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