Waking the undead: implications of a soft explosive model for the timing of placental mammal diversification

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ABSTRACT. The explosive, long fuse, and short fuse models represent competing hypotheses for the timing of placental mammal diversification. Support for the explosive model, which posits both interordinal and intraordinal diversification after the KPg mass extinction, derives from morphological cladistic studies that place Cretaceous eutherians outside of crown Placentalia. By contrast, most molecular studies favor the long fuse model wherein interordinal cladogenesis occurred in the Cretaceous followed by intraordinal cladogenesis after the KPg boundary. Phillips (2016) proposed a soft explosive model that allows for the emergence of a few lineages (Xenarthra, Afrotheria, Euarchontoglires, Laurasiatheria) in the Cretaceous, but otherwise agrees with the explosive model in positing the majority of interordinal diversification after the KPg mass extinction. Phillips (2016) argues that rate transference errors associated with large body size and long lifespan have inflated previous estimates of interordinal divergence times, and further suggests that most interordinal divergences are positioned after the KPg boundary when rate transference errors are avoided through the elimination of

calibrations in large-bodied and/or long lifespan clades. Here, we show that rate transference errors can also occur in the opposite direction and drag forward estimated divergence dates when calibrations in large-bodied/long lifespan clades are omitted. This dragging forward effect results in the occurrence of more than half a billion years of ‘zombie lineages’ on Phillips’ preferred timetree. By contrast with ghost lineages, which are a logical byproduct of an incomplete fossil record, zombie lineages occur when estimated divergence dates are younger than the minimum age of the oldest crown fossils. We also present the results of new timetree analyses that address the rate transference problem highlighted by Phillips (2016) by deleting taxa that exceed thresholds for body size and lifespan. These analyses recover all interordinal divergence times in the Cretaceous and are consistent with the long fuse model of placental diversification. Finally, we outline potential problems with morphological cladistic analyses of higher-level relationships among placental mammals that may account for the perceived discrepancies between molecular and paleontological estimates of placental divergence times.

Keywords: divergence time; ghost lineage; long fuse model; placental mammal; zombie lineage

Abbreviations: KPg, Cretaceous-Paleogene; PAML, phylogenetic analysis by maximum likelihood; PAUP, phylogenetic analysis using parsimony

1. Introduction

The radiation of placental mammals in relationship to the KPg boundary (~66 Ma) is one of the most contentious problems in paleontology and systematics. Archibald and Deutschman (2001) suggested three competing models for placental diversification. The explosive model, which is favored by many paleontologists (e.g., O’Leary et al., 2013), posits interordinal and intraordinal diversification after the KPg boundary. This model is underpinned by morphological cladistic analyses that place Cretaceous eutherians outside of crown Placentalia (Wible et al., 2009; O’Leary et al., 2013; Zhou et al., 2013; Chester

et al., 2015). The long fuse model agrees with the explosive model in positing most intraordinal diversification after the KPg boundary, but positions nearly all interordinal diversification before the KPg boundary. Support for the long fuse model derives from a wide array of molecular timetree analyses (Hasegawa et al., 2003; Springer et al., 2003, 2005; Delsuc et al., 2004; Meredith et al., 2011; dos Reis et al., 2012; Lartillot and Delsuc, 2012; Slater, 2013; Emerling et al., 2015; Foley et al., 2016; Tarver et al., 2016). Archibald and Deutschman's (2001) third model, the short fuse model, posits interordinal and some intraordinal diversification well before the KPg boundary. This model is supported by Bininda-Emonds et al.'s (2007) analysis of a supertree phylogeny with local molecular clocks.

Advocates of the explosive model have argued that both long fuse and short fuse models are in direct conflict with the fossil record because of their implied ghost lineages (O'Leary et al., 2013). However, ghost lineages are a logical extension of an incomplete fossil record and cannot be dismissed out of hand (Springer and Lilje, 1988; Strauss and Sadler, 1989; Marshall, 1990; Springer, 1990; Teeling et al., 2005; Johnson et al., 2006; Meredith et al., 2008). Also, the explosive model is predicated on the accuracy of morphological cladistic analyses that place Cretaceous eutherians outside of Placentalia. Morphological cladistics has a poor track record of recovering superordinal clades of even extant placental mammals and is prone to cluster taxa together based on ecomorphological convergence. Furthermore, most morphological studies utilize matrices in which many of the taxa (fossils) are missing the majority of the characters because of incomplete fossil preservation (Springer et al., 2007a, 2008, 2013; Sansom and Wills, 2013). Finally, the explosive model requires viral-like rates of evolution in mammalian lineages during the interval immediately following the KPg boundary (Springer et al., 2013).

Most recently, Phillips (2016) proposed a fourth model, the soft explosive model, which allows for cladogenic separation of the four major clades of placental mammals (Afrotheria, Xenarthra, Laurasiatheria, Euarchontoglires) in the Cretaceous, but otherwise agrees with the explosive model in positioning the bulk of interordinal diversification in Placentalia after the KPg boundary. Phillips (2016) argued that support for the long fuse model in previous timetree analyses results from rate transference errors that inflate

estimates of interordinal divergence times, and that most interordinal divergences are positioned after the KPg boundary when rate transference errors are avoided by eliminating calibrations in large-bodied/long lifespan clades that are the source of these errors. Here, we discuss fundamental problems with Phillips' (2016) timetree analyses and show that they result in 'zombie' lineages, which are the antithesis of ghost lineages and occur when estimated divergence dates are younger than minimum ages implied by the fossil record. We show that when divergence dates in large-bodied/long lifespan clades are not calibrated and are underestimated (i.e., too young), as in Phillips (2016), they can drag forward deeper nodes and result in estimates of interordinal divergence times that are in direct conflict with the fossil record. We also present the results of new timetree analyses that circumvent the rate transference problem highlighted by Phillips (2016) by deleting taxa that exceed thresholds for body size and lifespan. The results of these analyses again position all interordinal divergence times in the Cretaceous and support the long fuse model of placental diversification. Finally, we review potential problems with the results of morphological cladistic analyses of higher-level relationships among placental mammals that challenge the stem status of all Cretaceous placentals.

2. Methods

2.1. Molecular dating analyses

Molecular data analyses with Meredith et al.'s (2011) DNA data set were performed with the mcmctree package in PAML 4.8 (Yang 2007). Analyses were performed with both autocorrelated and independent rates, as well as with hard-bounded and soft-bounded calibrations. Each mcmctree analysis was run twice to check for convergence. As in Meredith et al. (2011), each gene was allowed to have its own model of sequence evolution following Meredith et al. (2011). We set 1 time unit = 100 million years. Analyses were run with cleandata = 0. Shape (α) and scale (β) parameters for rgene_gamma, which describes the gamma prior for the overall rate parameter μ , were as in Meredith et al. (2011). Similarly, shape and scale parameters for sigma_gamma, which describes the gamma prior for the rate-drift parameter (σ^2), were taken from Meredith et

al. (2011). Analyses were run for 100,000 generations following a burn-in of 10,000 generations. Each chain was sampled every 20 generations.

Timetree analyses with too few calibrations in large-bodied/long lifespan clades (Phillips, 2016) may drag divergence times of deeper nodes toward the present owing to underestimation of divergences in the large-bodied clades. Instead of dropping all or most calibrations in large-bodied clades, which would have the effect of forcing rates from small-bodied taxa onto their branches, we employed an alternate strategy (Springer et al., 2003) and excluded taxa with average adult body mass > 10 kg and/or maximum longevity > 40 years (thresholds suggested by M. Phillips, pers. comm.). Body size data are from Pantheria (Jones et al., 2009) and longevity data are from Magalhães and Costa (2009). The resulting topology included 122 of 169 taxa from Meredith et al. (2011) and excluded all members of Proboscidea, Sirenia, and Perissodactyla; all Cetartiodactyla except for *Tragul* (mouse-deer); all Anthropeoidea with the exception of *Callithrix* (marmoset); nine of 16 carnivorans including all three pinnipeds and *Ailuropoda* (giant panda); and assorted taxa in other clades such as *Pteropus* (flying fox), *Myrmecophaga* (giant anteater), and *Hydrochoerus* (capybara). After excluding these taxa, this 122-taxon data set retained at least one representative of all placental orders except for Proboscidea, Sirenia, Tubulidentata, and Perissodactya. Analyses were performed with an updated set of 62 calibrations that reflect newly described fossils and recommendations from a variety of other timetree studies (Table 1). Analyses were performed with all four combinations of hard-bounded versus soft-bounded constraints and autocorrelated versus independent rates. All four timetrees are available at TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19854>).

2.2. Parsimony analysis

Maximum parsimony analyses of Wible et al.'s (2009) data set were performed with PAUP* 4.0a147 (Swofford, 2002). Analyses were performed after excluding *Almylestes* because of a high percentage (94.9) of missing data for this taxon. Searches for optimal trees, with or without phylogenetic constraints, employed 100 random addition sequences with tree-bisection and reconnection branch swapping. Trees with

minimum branch lengths of zero were collapsed using the “-amb” option in PAUP. Templeton and winning-sites tests were also performed with PAUP to compare parsimony scores for different trees to each other.

2.3. Molecular timetree diversification patterns and the fossil record

We used the R package paleobioDB (Varela et al. 2014) to acquire eutherian fossil data from each geological stage ranging from the Berriasian (Lower Cretaceous) to the Priabonian (Eocene). For each stage, we downloaded all records of eutherian families, genera, and species, recorded the standing diversity for each taxon, and quantified the number of new taxa in each category. We estimated new lineage accumulation rates for each stage by dividing the number of new lineages by the stage’s time duration, and then calculated the percentage increase or decrease across each stage boundary. Stage durations in millions of years were taken from version 2014 of the International Chronostratigraphic Chart (Cohen et al., 2013; www.stratigraphy.org). Next, we performed similar calculations (i.e., number of lineages, number of new lineages, and number of new lineages per million years for each stage, percentage increase or decrease across stage boundary) based on three timetrees: (1) Phillips’ (2016) preferred timetree (dR27b) using Meredith et al.’s (2011) DNA supermatrix encompassing 169 species and 27 calibrations from dos Reis et al. (2012), including updated maximum bounds for Chiroptera, Primates, and Rodentia; (2) Phillips’ (2016) reanalysis of Meredith et al.’s (2011) DNA supermatrix with 82 calibrations (Mer82c); and (3) Emerling et al.’s (2015) analysis of 388 species (Emer15). This last timetree included nearly all of the mammalian and outgroup taxa in Meredith et al.’s (2011) supermatrix, plus additional loci (38 total) and 77 fossil calibrations, many of which are updated from Meredith et al. (2011) and also described here. We used the 2010 version of the geological time scale to calculate rates for dR27b and Mer82c, and the 2014 version of the geological time scale to calculate rates for Emer15, because these authors employed different versions of the geologic time scale (www.stratigraphy.org). Emer15 records two speciation events prior to the end of the Lutetian that are not represented by Meredith et al.’s (2011) taxon

sampling (i.e., deep splits in Soricidae and Emballonuridae), so these were excluded from the analyses.

3. Results and Discussion

3.1. Zombie lineages and the “soft explosive model”

Phillips (2016) argued that correlations between life history and rates of molecular evolution will tend to inflate deep-level divergence estimates among placental mammals because calibrations in clades that have evolved large body size and/or extreme longevity could be susceptible to rate-shift identifiability errors, which may transfer crown rates to stem rates if deeper nodes are not tightly calibrated. Previously, Meredith et al. (2011) demonstrated that divergence time estimates for many nodes in Placentalia are too old when calibrations are exclusively from taxa with larger body sizes and relatively slow rates of molecular evolution. Similarly, Meredith et al. (2011) showed that divergence time estimates are too young for clades with larger body sizes and slower rates of molecular evolution when calibrations are limited to taxa with smaller body sizes and faster rates of evolution. Meredith et al.'s (2011) strategy to mitigate against these problems was to employ a dense network of calibrations at 82 nodes including both shallow nodes, some of which subtend clades with larger-bodied taxa (e.g., Proboscidea, Cetacea, Hominoidea), and deeper nodes where ancestral body size was presumably smaller (e.g., Paenungulata, Cetartiodactyla, Haplorhini). Meredith et al. (2011) also noted that hard-bounded calibrations are more effective than soft-bounded calibrations in mitigating dates that are significantly younger than the fossil record.

By contrast with Meredith et al. (2011), Phillips (2016) preferred timetrees that underpin his conclusion that most interordinal cladogenesis occurred after the KPg boundary, are based on a much sparser set of calibrations for 27 nodes from dos Reis et al. (2012), with and without three new maximum bounds that were applied to rodents, primates, and bats. Phillips (2016) eschewed hard-bounded constraints and performed these analyses with soft-bounded constraints. Phillips (2016) argued that his interordinal divergence estimates are more accurate than previous studies because rate transference

problems resulting from calibrations within large-bodied clades were mitigated. However, Phillips (2016) paid less attention to potential problems that may arise when divergence times are too young in clades with larger body sizes and longer generation times. Timetree analyses with too few calibrations in large-bodied/long lifespan clades, as is the case with Phillips' (2016) original and augmented calibration sets from dos Reis et al. (2012), result in divergence time estimates for numerous clades that are younger than their minimum ages implied by the fossil record. We refer to these lineages as 'zombie' lineages (Fig. 1). By contrast with ghost lineages, which occur when a lineage is inferred to exist before it is represented in the fossil record, zombie lineages occur when the origin of a crown clade is estimated by molecular timetree methods to post-date the appearance of an older crown fossil (Fig. 1). This circumstance suggests that the fossil specimen should not have been alive at the age before its origin estimated by geochronological methods. In popular culture, fictional individuals that are not alive and yet have the appearance of being alive are commonly referred to as the undead or zombies.

Importantly, divergence times of deeper nodes on Phillips' preferred timetrees appear to be dragged forward owing to underestimation of divergence times in uncalibrated clades with larger body sizes and/or longer lifespans (Fig. 2, Table 2). Inspection of Phillips' (2016) timetree shows that at least 61 of 136 internal nodes in Placentalia have estimated ages that are younger than minimum ages implied by the fossil record (Fig. 2, Table 2). This list includes numerous superordinal clades as well as clades that are characterized by taxa with smaller body sizes and/or relatively short lifespans. For example, Phillips' (2016) estimated age for the superordinal clade Afrotheria is 57.7 Ma, which is younger than the minimum age for the oldest stem proboscidean (*Eritherium*, 59.2 Ma) (Gheerbrant, 2009; Schmitt and Gheerbrant, 2016; Kocsis et al., 2014). Indeed, the minimum age for *Eritherium* implies that the minimum ages for the superordinal clades Hyracoidea + Proboscidea, Paenungulata, and Afrotheria should all be at least 59.2 Ma, but Phillips estimated age for Hyracoidea + Proboscidea is only 44.6 Ma. Similarly, Phillips estimated ages for Fereuungulata (Carnivora + Pholidota + Perissodactyla + Cetartiodactyla) and Variamana (Fereuungulata + Chiroptera) are only 61.5 and 61.6 Ma, respectively, yet the oldest stem carnivorans are from the middle

Puercan (65-64 Ma; Fox et al., 2010). Thus, Phillips' (2016) estimated divergence times for four superordinal clades in Laurasiatheria (Ostentoria, Zoomata, Fereuungulata, Variamana) are all younger than the oldest stem fossils for Carnivora (Fox et al., 2010).

Phillips (2016) noted that analyses with Meredith et al.'s (2011) calibrations resulted in ghost lineages in Boreoeutheria that total more than one quarter of a billion years. However his own preferred timetree, with distorted divergence times that are in striking conflict with the fossil record (Fig. 2), results in zombie lineages that exceed half a billion years. Four of these zombie lineages exceed 20 million years and are shown in bold in Table 2. Ghost lineages are inferred to exist but have no fossil record, whereas zombie lineages are the opposite of ghost lineages and have known fossil records that are incompatible with errant timetree dates. Ghost lineages are an expected product of an incomplete fossil record, whereas zombie lineages are logically impossible except in cases where minimum ages for fossils are inaccurate or fossils have been attributed to the incorrect taxonomic group. However, the zombie lineages with some of the largest dating errors (e.g., Perissodactyla, Ceratomorpha, Cetacea) have minimum dates that are based on unambiguously assigned fossils (Table 2). Phillips' (2016) preferred timetrees, which are based on a relatively sparse compilation of 27 calibrated nodes (dos Reis et al., 2012) relative to Meredith et al.'s (2011) 82 highlight the point that timetree analyses should include calibrations at more nodes, rather than fewer nodes, to assist with rate-shift identification errors that can drag uncalibrated nodes both backward and forward in time. Dos Reis et al.'s (2012) 27 calibrations were appropriate for their phylogenomic data set with 37 mammalian species, but these calibrations are insufficient to calibrate Meredith et al.'s (2011) data set encompassing 164 mammals and five outgroups.

Even with its numerous zombie lineages that are in direct conflict with the fossil record, Phillips' (2016) timetree (Fig. 2) also retains a variety of ghost lineages that are older than the fossil record, albeit with smaller discrepancies than most other studies (Meredith et al., 2011; dos Reis et al., 2012; Slater, 2013). Some of the most prominent ghost lineages on Phillips' (2016) tree occur in clades with notoriously poor fossil records including Lemuriformes and Chiroptera. In the case of Lemuriformes, Phillips' (2016) estimate for the most recent common ancestor of this clade is 36.8 Ma, but the oldest fossils are only from the Holocene and are only 11.7 thousand years old

(Paleobiology Database). Similarly, the chiropteran family Craseonycteridae (bumble bats) does not have a fossil record, but Phillips' age for the most recent common ancestor Craseonycteridae and Megadermatidae is 36.8 Ma and implies a ghost lineage of this duration.

3.2. Timetree analyses without larger-bodied and long lifespan taxa

Timetree analyses with reduced taxon sampling (122 of 169 taxa from Meredith et al., 2011) are reported in Figure 3 and Table 3. Figure 3 shows the timetree based on autocorrelated rates with hard-bounded constraints. The results of four different analyses with different combinations of hard-bounded versus soft-bounded constraints and autocorrelated versus independent rates are shown in Table 3. Timetrees in nexus format are available at TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19854>). By contrast with Phillips (2016) analyses that retained large-bodied and long-lived taxa without calibrations, the results of our analyses recovered Cretaceous dates, including 95% credibility intervals, for all interordinal divergences within Placentalia (Fig. 3, Table 3). These dates are younger than in Meredith et al.'s (2011) 169-taxon timetree, but are generally in good agreement with dos Reis et al.'s (2012) estimated dates that firmly support the long fuse model (Fig. 3, Table 3). For example, Meredith et al.'s (2011, table S6) mean date for Placentalia is ~101.4 Ma, whereas our date for this clade based on analyses with 122 taxa is ~92.0 Ma (Table 3). Similarly, dos Reis et al. (2012, table 1) obtained a mean date of 90.9 Ma for Placentalia based on four different analyses. By contrast, our estimated divergence dates for interordinal divergences are in direct conflict with Phillips' (2016) soft explosive model. Importantly, the soft explosive model of diversification is contradicted if interordinal divergences within Afrotheria, Laurasiatheria, and Euarchontoglires pre-date the KPg by even a small amount of time (e.g., 100,000 years), let alone several million or even tens of millions of years, because pre-KPg divergences preclude a role for the KPg in promoting interordinal diversification. In this context, O'Leary et al. (2013) suggested that the early Paleocene *Protungulatum donnae* (64.85 Ma) is well nested inside of Laurasiatheria. However, Archibald et al. (2011) reported a new species of *Protungulatum* from Late Cretaceous rocks in Montana

that are at least 300,000 years older than the KPg extinction that resulted in the final extirpation of non-avian dinosaurs. If *Protungulatum* is a crown laurasiatherian, then several interordinal divergences in Laurasiatheria are immediately pushed back into the Cretaceous in direct conflict with both the explosive and soft explosive models.

3.3. Body size and lifespan in ancestral placental mammals

Phillips (2016) assumed that all Cretaceous eutherians were small (<500 g) insectivores or omnivores based on existing paleontological evidence (e.g., O'Leary et al., 2013). However, fossils do not provide conclusive evidence regarding the ancestry of extant mammals because it is not straightforward to link Cretaceous and Paleocene fossils to modern placental lineages (Romiguier et al., 2013). By contrast with Phillips (2016), Romiguier et al. (2013) estimated body size and life span in early placental mammals based on ancestral reconstructions of two aspects of genome dynamics, GC content and dN/dS ratio, which are correlated with life history traits. Romiguier et al. (2013) estimated that early placental mammals had life spans > 25 years and body masses > 1 kg. These estimates are more similar to most primate, cetartiodactyl, and carnivoran species than to smaller and shorter-lived mice and shrews (Romiguier et al., 2013). Romiguier et al.'s (2013) results reinforce the important point that rate-shift identifiability errors may push and pull in both directions depending on which nodes are calibrated. Indeed, Phillip's (2016) preferred timetree presents many intraordinal divergences that may drag forward interordinal divergences because they are younger than minimum dates implied by the fossil record (Fig. 2, Table 2). Some of the most striking differences include Whippomorpha, Cetacea, Odontoceti, Mysticeti, Perissodactyla, Ceratomorpha, Pinnipedia, Otariidae + Odobenidae, Anthropoidea, Catarrhini, Platyrrhini, Hominoidea, Proscidea, and Sirenia (Fig. 2, Table 2).

3.4. Divergence times, morphological cladistics, and the fossil record

Phillips (2016) suggests that there is a perplexing mismatch between the diversification pulse identified by Meredith et al. (2011) at ~83 Ma and the absence of

such a pulse in the fossil record because eutherian species richness is virtually unchanged in Campanian fossil faunas (~84-71 Ma) and only one new family appears during this interval. We disagree with this conclusion based on our analysis of the eutherian fossil record in the Cretaceous (see section 3.5). Also, Halliday and Goswami's (2016) analysis of morphological diversity suggests that eutherians showed an increase in morphological disparity in the Campanian. At the same time, the pulse of diversification suggested by Meredith et al.'s (2011) analyses allows for, but does not require, the emergence of multiple orders and families appearing in the fossil record during this time. Rather, some or all of the emergent lineages with living descendants may have remained morphologically similar to each other until after the KPg boundary when morphological diversification occurred in the wake of the KPg extinction. Further, Meredith et al.'s (2011) analyses were based on a pure birth model and only queried patterns of diversification in the ancestry of extant Placentalia, not all of Eutheria as implied by Phillips.

Meredith et al.'s (2011) finding that the ancestors of extant placental mammals did not experience a significantly increased diversification rate after the KPg mass extinction does not imply that the same is also true for the entirety of Placentalia, which includes extinct placental lineages (e.g., *Purgatorius*, creodonts) that left no descendants. Finally, Phillips (2016) incorrectly suggests "Meredith et al.'s (2011) molecular diversification analyses instead suggest a decline across the KPg and throughout the Paleocene." Meredith et al.'s (2011) diversification analyses with both TreePar and Laser, which were performed to identify the locations of temporal shifts in the diversification rate of mammalian lineages with extant descendants, failed to show any significant shifts in diversification rates at or near the KPg boundary.

Phillips (2016) acknowledges that palaeontologists have recovered Cretaceous zhelestids and zalambdalestids within crown Placentalia (Archibald, 1996; Archibald et al., 2001), but then suggests that this argument for ancient placental origins is invalid because both zhelestids and zalambdalestids have been recovered as stem eutherians in more recent cladistic analyses (Wible et al., 2009; Zhou et al., 2013). These arguments ignore many problems with morphological cladistic analyses for recovering higher-level relationships among eutherian mammals (Springer et al., 2007a, 2008, 2013). The most

comprehensive phenomic data sets that are available for diverse fossil and living mammals are those of O’Leary et al. (2013), which comprises 4541 phenomic characters for 86 fossil and living mammals, and Halliday et al. (2015), which includes 680 morphological characters for 177 fossil and extant taxa. Phylogenetic analyses with O’Leary et al.’s (2013) phenomic data set are in striking disagreement with analyses based on molecular data. Instead of recovering extensively validated molecular clades such as Afrotheria, Afrosoricida, Paenungulata, Boreoeutheria, Laurasiatheria, and Eulipotyphla, O’Leary et al.’s (2013) phenomic tree provides robust support for a wide range of polyphyletic taxa including an “insectivore” group, a “spiny hedgehog” group, and “ant and termite eating” group, a “tree dwelling” group, an “ungulate” group, and a “cud chewing” group (Springer et al., 2013). These results are not surprising given that the global theater for mammalian evolution includes similar habitats in far-flung regions of Earth that promoted the evolution of remarkable ecomorphological convergence (Springer et al., 2013). Similarly, Halliday et al.’s (2015) morphological tree exhibits numerous instances of polyphyletic groups that conflict with well-supported molecular clades or extant mammalian orders with living and fossil representatives, including Afrotheria, Paenungulata, Macroscelidea, Boreoeutheria, Laurasiatheria, Variamania, Eulipotyphla, Talpidae, Ostentoria, Euarchontoglires, and Scandentia. While some of the problems with ecomorphological convergence for living taxa may be overcome with combined analyses that include large molecular data sets, or by enforcing molecular scaffolds, these approaches may not be adequate for accurately placing extinct taxa that lack molecular data (see below). A related problem is that few coded anatomical characters are available for extant mammals in comparison to fossil mammals (Guillerme and Cooper, 2016). This issue may compromise the accuracy of morphological cladistic analyses with mammalian data sets that include both fossils and living taxa

Phillips (2016) cited two studies in support of his conclusion that hypotheses of Cretaceous placental origins are invalid: Wible et al. (2009) and Zhou et al. (2013). Wible et al.’s (2009) analyses were based on a data matrix comprised of 69 taxa and 408 characters, including 11 extant placentals with three genera (*Chaetophractus*, *Bradypus*, *Tamandua*) in Xenarthra, four (*Orycteropus*, *Rhynchocyon*, *Procavia*, *Potamogale*) in Afrotheria, one (*Ptilocercus*) in Euarchontoglires, and three (*Blarina*, *Sorex*, *Solenodon*)

in Laurasiatheria. Major problems with the phylogenetic placement of extant taxa on Wible et al.'s (2009) tree include Afrotheria polyphyly, Eulipotyphla paraphyly, and Boreoeutheria paraphyly. Moreover, taxa that are traditionally regarded as stem carnivorans (*Vulpavus*, *Miacis*) and a stem "artiodactyl" (*Gujaratia* = *Diacodexis*) fall outside of crown Placentalia (misplaced on Wible et al.'s [2009] tree). In addition, many of the clades on Wible et al.'s (2009) tree have low support scores (e.g., decay index for Placentalia = 1 step). It is more costly to enforce a well-supported molecular scaffold (Afrotheria, Xenarthra, (Laurasiatheria, Euarchontoglires)) with Wible et al.'s (2009) data (+26 steps, six trees) than it is to constrain a sister-group relationship between Glires and Cretaceous zalambdalestids (+25 steps, six trees). Templeton and winning-sites tests reject all six trees with the molecular scaffold, whereas only four of six trees with zalambdalestids + Glires are rejected by one or both tests (Table 4). Given these results it is difficult to argue, as Phillips (2016) has done, that Cretaceous eutherians are definitively excluded from crown Placentalia.

Zhou et al.'s (2013) analyses included ten extant placentals: three genera in Laurasiatheria (*Erinaceus*, *Felis*, *Canis*), two in Euarchontoglires (*Rattus*, *Oryctolagus*), and five in Xenarthra (*Bradypus*, *Tamandua*, *Dasyurus*, *Chaetophractus*, *Euphractus*). Of these, *Erinaceus* was recovered as the sister taxon to all remaining placental genera. Zhou et al.'s (2013) morphological tree is in conflict with the monophyly of Laurasiatheria and Boreoeutheria, which are among the most robust superordinal clades of placental mammals based on analyses with diverse molecular and phylogenomic data (e.g., Madsen et al., 2001; Murphy et al., 2001a,b; Springer et al., 2004, 2005, 2007a,b; Wildman et al., 2007; Nishihara et al., 2009; Meredith et al., 2011; Romiguier et al., 2013; Tarver et al., 2016). Following Phillips' (2016) logic do the results of Wible et al. (2009) and Zhou et al. (2013) invalidate Afrotheria, Laurasiatheria, Eulipotyphla, and Boreoeutheria? Is *Gujaratia*, with its "double trochleated astragalus" that is diagnostic for "artiodactyls", outside of crown Placentalia? Are *Vulpavus* and *Miacis*, with their carnassial teeth that are diagnostic of Carnivora, outside of crown Placentalia? We suggest that the answer to these rhetorical questions is no, and that morphological cladistic analyses remain problematic for higher-level mammalian relationships because of rampant ecomorphological convergence, diachronous terminals that create opportunities for long-

branch misplacement, and missing data problems (Springer et al., 2007a, 2008, 2013; Fig. 4). Specifically, random homoplasy on long branches leading to extant taxa (“the pull of the Recent”) may create a morphological analog of the long-branch problem with molecular data so that increased homoplasy on extant tips may mislead phylogenetic analyses that include both extant and extinct taxa (Wang et al., 2005). Homoplasy resulting from parallel evolutionary constraints will be more severe than garden-variety long-branch misplacement because parallel evolutionary constraints can result in correlated homoplasy that affects multiple characters (e.g., characters related to eating ants and termites; Fig. 4). Homoplasy resulting from parallel evolutionary constraints (e.g., on functional anatomy) has previously been suggested as the cause of anomalous phylogenetic relationships for carnivorans (Wang et al. 2005; Finarelli 2008) and rodents (Rodrigues et al. 2011, Lazzari et al. 2008).

Potential problems with morphological cladistic analyses of higher-level relationships among placental mammals have also been demonstrated in pseudoextinction analyses with combined supermatrices (i.e., molecules and morphology) that queried the phylogenetic position of extant orders of placental mammals after recoding molecular data as missing (Springer et al., 2007a). For example, when odd-toed ungulates (Order Perissodactyla) were treated as extinct they clustered inside of Afrotheria as the sister to Hyracoidea. Similarly, when armadillos (Order Tubulidentata) and pangolins (Order Pholidota) were recoded as extinct these orders were allied with Xenarthra rather than placed within Afrotheria and Laurasiatheria, respectively. Carnivorans, in turn, were recovered as the sister taxon to all other placental mammals when recoded as extinct. These results are difficult to reconcile with the results of molecular data, but are nevertheless the best-supported hypothesis in pseudoextinction analyses (Springer et al., 2007a).

Along these lines, Sansom and Wills (2013) showed that the inevitable bias of the fossil record to preserve biomineralized (hard) morphological characters systematically distorts phylogeny. Specifically, this bias results in ‘stemward slippage’ so that fossils are significantly more likely to move towards the root of the tree than away from the root. The net result of stemward slippage is that fossils will be artificially deployed to deeper branches on the tree, in some cases below the crown clade to which they belong, so that

divergence dates will be underestimated (Sansom and Wills, 2013). Given this suite of concerns (i.e., parallel evolutionary constraints, long versus short branches on trees with diachronous terminals, incomplete fossil specimens, results of pseudoextinction analyses, stemward slippage with biomineralized characters), we strongly disagree with Phillips' (2016) conclusion that cladistic analyses and the fossil record invalidate the inclusion of Cretaceous eutherians inside of crown Placentalia. Instead, we suggest that the apparent conflict between molecular and paleontological dates for the placental mammal radiation may result from systematically distorted morphology-based phylogenies for fossil and extant taxa, and do not discount the possibility that 85-90 Ma zalambdalestids or other Cretaceous forms are crown rather than stem eutherians. If even a handful of Cretaceous eutherians have been inaccurately placed outside Placentalia in morphological cladistic analyses because of the abovementioned problems, then there is effectively no disagreement between the fossil record and molecular timetrees with Cretaceous interordinal divergences.

3.5. Molecular timetree diversification patterns and the fossil record

To undergird his argument in favor of tightening maximum calibrations to mitigate against upward rate transference problems, Phillips (2016) demonstrated that his preferred timetree (dR27b), based on updated calibrations from dos Reis et al. (2012), places most interordinal cladogenic events in the species rich Paleocene. By contrast, the more heavily calibrated Mer82c tree positions most of these cladogenic events in the far less speciose Campanian–Maastrichtian (Late Cretaceous). This is taken by Phillips (2016) as evidence that the dR27b tree better fits the diversification of fossil placental mammals documented in the wake of the KPg mass extinction. This assumption is unwarranted, primarily because interordinal diversification need not take place in the Paleocene to be consistent with the fossil record, as the spike in Paleocene diversity may have been driven by intraordinal diversification instead. What is more pertinent to Phillips' (2016) hypothesis is whether or not the timetree of interest records an increase in the rate of new lineages in the earliest Paleocene relative to the latest Cretaceous.

When examining eutherian fossil diversity in the Paleobiology Database, we found that the Danian (66.0-61.6 Ma) records an upsurge in the accumulation of new lineages: 29 new families, 128 new genera and 248 new species compared to just two, 13 and 20, respectively, in the Maastrichtian (Fig. 5A, Supplementary Fig. 1). This corresponds to respective rates of 6.59, 29.09 and 56.36 new lineages per million years (NL/Myr), resulting in +1910%, +1265% and +1619% rate increases. These rate increases represent the largest for each taxon category in every stage we examined (Cretaceous–Eocene), testifying to the magnitude of the post-KPg diversification event on eutherian diversity. We found that the Mer82c tree recorded a very slight rate decrease from the Maastrichtian to the Danian (-0.65%), whereas the dR27b tree showed a rate increase (15.91%), suggesting that Phillips’ preferred timetree matches the K/Pg event better than the former (Fig. 5B, Supplementary Fig. 1). However, Mer82c records a greater number of new lineages (six versus four) in the Danian, and therefore implies a higher rate for the accumulation of new lineages than dR27b (1.36 vs. 0.91 NL/Myr). Furthermore, dR27b’s greatest rate increase (+237%) occurs in the Maastrichtian (72.1-66.0 Ma), immediately prior to the KPg boundary. We also evaluated a timetree (Emer15) reported by Emerling et al. (2015), which included more species (388) and updated calibrations relative to Meredith et al. (2011). Like dR27b, Emer15 records a greater number of new lineages in the Danian compared to the Maastrichtian, but the number of new lineages (seven), rate (1.59 NL/Myr), and rate increase (+61.7%) are all higher than dR27b (Fig. 5B). This is despite the fact that Emer15 records all but one placental interordinal cladogenic event prior to the KPg boundary, consistent with the long fuse model.

Among the different timetrees that we examined, dR27b (2010 Geological Timescale [GT]; KPg = 65.5 Ma) records only one new lineage (at 64.58 Ma) during the 1-million year interval after the KPg boundary, and no further speciation events until the end of the Danian when there are three cladogenic events between 61.6 and 61.22 Ma. However, there are four new lineages in the 2-million year interval prior to the KPg boundary (67.56-65.58 Ma), following a cladogenic drought of 4.7 million years. Similarly, Mer82c (2010 GT) records six cladogenic events in the 2-million year interval preceding the KPg boundary (67.5-65.54 Ma) following 3.6 million years of no

cladogenesis, and a further six at the end of the Danian (61.99-61.22 Ma). Notably, both timetrees show qualitatively similar patterns near the KPg boundary, although pre-Selandian cladogenic events for dR27b are interordinal, whereas Mer82c records numerous intraordinal cladogenic events during the same time period. Compared to Mer82c and dR27b, Emer15 (2014 GT; KPg = 66 Ma) appears to provide the best fit to a model of placental diversification in the immediate wake of the KPg extinction event. After four million years of no new crown placentals, a new lineage appears at 67 Ma and two speciation events occur immediately before the KPg between 66.13 and 66.04 Ma. Subsequently there is a relatively steady accumulation of additional lineages (seven) during the Danian. Similar to Mer82c, many of these cladogenic events reflect intraordinal rather interordinal diversification. Together, these results suggest that placental interordinal cladogenesis in the Cretaceous and an increased accumulation of placental lineages following the KPg boundary need not be mutually exclusive.

A second and related contention of Phillips (2016) concerns the long fuse model's placement of many of the placental interordinal cladogenic events in the Campanian. Indeed, both Mer82c and Emer15 record numerous speciation events during the Campanian, with 15 and 12 new lineages, respectively, compared with only three and one in the previous stage. While the long timespan of the stage may partially explain this pattern (11.5 myr 2014 GT, 12.9 myr 2010 GT), Emer15 still records a large rate increase (+182%) (Fig. 5B) after correcting for stage duration. Even Phillips' (2016) preferred timetree (dR27b) estimates that the first three crown placental cladogenic events occurred during the Campanian. Phillips (2016) states that this "most profound" diversification event (in the Campanian) inferred by the molecular consensus "leaves no trace in the fossil record" as "eutherian species richness is virtually unchanged" in this stage. Contrary to Phillips (2016), the Paleobiology Database indicates that this stage had the highest number of new families (four), genera (16) and species (21) in the Cretaceous. The previous stage, the Santonian, had zero new families and genera and one new species, with a standing diversity of only two families, one genus and two species. Prior to that, the Coniacian records no new families and only three new genera and species. Among 15 stages (Aptian–Priabonian), the Campanian increase in the rate of new species accumulation (+393%) was third highest, behind only the Turonian (+865%) and the

Danian (+1619%). While not as remarkable as the Danian, Campanian diversification was relatively extensive and may be associated with interordinal diversification in Placentalia if morphological cladistic analyses have misplaced some Cretaceous eutherians outside of crown Placentalia, as argued above. In this context, Halliday and Goswami (2016) utilized a set of morphology-based timetrees to estimate the change in eutherian morphological disparity through time. Despite using trees that assumed an origin for Placentalia near the KPg boundary, Halliday and Goswami (2016) consistently recovered an increase in eutherian morphospace during the Campanian, which had the highest disparity estimates during the entirety of the Cretaceous. Stemward slippage and other problems with cladistic analyses (e.g., diachronous terminals), coupled with morphometric analyses of Mesozoic mammals and mammaliaforms (e.g., Chen and Luo, 2013; Gill et al., 2014; Halliday and Goswami, 2016), suggest that Campanian placentals with diverse specializations may be hidden in plain sight, or perhaps will be uncovered with more extensive sampling (e.g., Luo et al., 2007).

3.6. Conclusions

The soft explosive model (Phillips, 2016) was proposed as a solution to the longstanding debate over the timing of placental mammal diversification. Unlike the long fuse model, which posits all or most interordinal diversification in the Cretaceous, followed by most intraordinal diversification after the KPg mass extinction, the soft explosive model positions most interordinal and all intraordinal diversification after the KPg mass extinction. Meredith et al. (2011) suggested that timetree analyses should include more calibrations, rather than fewer, because lineage-specific rate variation can result in misleading divergence times when fossil calibrations are sparsely or unevenly distributed throughout the tree and are limited to taxa with either fast or slow rates of molecular evolution. Phillips (2016) addressed rate transference problems in Placentalia by omitting calibrations in most clades with large body size and/or long lifespan, and recovered most interordinal divergences after the KPg boundary. However, Phillips' (2016) soft explosive model results in more than 500 million years of zombie lineages, which occur when estimated divergence dates are younger than reliable minimum ages

that are implied by crown fossils. Importantly, Phillips' (2016) interordinal divergence dates are dragged forward by divergence dates in clades with large body size and/or long lifespan that are too young. Zombie lineages are not unique to Phillips' (2016) study. For example, Sato et al. (2016) obtained a date of 58.6 Ma for the most recent common ancestor of Eulipotyphla (hedgehogs, moles, shrews, solenodons), but this date is younger than the oldest erinaceid (hedgehog) fossil (Benton et al., 2015).

By contrast with Phillips (2016), we employed an alternate approach to the rate transference problem (Springer et al., 2003) and deleted taxa with large body size and/or long lifespan, and recovered all placental interordinal divergences in the Cretaceous. These results are in good agreement with other recent timetree studies that support the long fuse model of placental mammal diversification (dos Reis et al., 2012; Emerling et al., 2015; Tarver et al., 2016). Potential problems with morphological cladistic analyses of higher-level relationships among placental mammals, including inaccurate phylogenies, stemward slippage, and the “pull of the Recent”, may account for the perceived discrepancies between molecular and paleontological estimates for the timing of placental diversification.

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Legends for Figures

Fig. 1. Depiction of ghost (A) versus zombie (B) lineages. A. True tree and divergence time for extant sister taxa 1 and 2. Individual fossil occurrences are plotted by age and define the observed stratigraphic ranges (green rectangles) of taxa 1 and 2. The older range of Taxon 1 requires a ghost lineage for Taxon 2 (pink rectangle). If the true divergence time for taxa 1 and 2 is older than the oldest fossil for either lineage, then additional ghost lineages (red rectangles) are required for Taxon 1 and Taxon 2. B. The estimated divergence time between taxon 1 and taxon 2 is younger than the minimum age for this divergence as defined by the fossil record. The difference between the minimum age required by the oldest fossil and the estimated age on a timetree is a zombie lineage (blue rectangle).

Fig. 2. Zombie lineages in Phillips' (2016) preferred tree, which is based on 27 calibrations from dos Reis et al. (2012) and new maximum bounds for Chiroptera, Primates, and Rodentia. Branches with zombie lineages, which have parent nodes that are younger than minimum ages implied by fossils, are highlighted with red branches. Paintings by Carl Buell.

Fig. 3. Timetree for 117 mammalian taxa from Meredith et al. (2011) after excluding 47 taxa with body size > 10 kg and/or lifespan > 40 years. The RAxML phylogram for timetree analyses was obtained by deleting 47 taxa from Meredith et al.'s (2011) 169-taxon, DNA tree that exceed threshold criteria for large body size and long lifespan. Bootstrap support percentages and Bayesian posterior probabilities for the original tree are provided in Meredith et al. (2011). The timetree is based on mcmctree with autocorrelated rates and hard-bounded constraints. Calibrated nodes (Table 1) within Mammalia are shown with filled black circles. Interordinal divergences within Placentalia are denoted with open red circles and are all in the Cretaceous (see Table 3

for 95% credibility intervals). Interordinal divergence times based on other combinations of autocorrelated versus independent rates and hard-bounded versus soft-bounded constraints are provided in Table 3. The KPg boundary is denoted with a dashed blue line. Non-mammalian outgroups are not shown. Paintings by Carl Buell.

Fig. 4. Illustration of long-branch misplacement resulting from diachronous terminals, which is intensified by correlated homoplasy. A. The true evolutionary tree showing relationships among taxa W, X, Y, Z. Taxa X and W represent extant species and taxa Y and Z represent fossil species. Taxa X and Y are united by one shared derived character without homoplasy (character 9). Taxa W and Z are united by two shared derived characters without homoplasy (characters 10 and 11). Taxa X and W share eight homoplastic characters, four of which (1-4) result from random homoplasy on long branches and four of which (5-8) are the result of parallel evolutionary trends that create opportunities for correlated homoplasy. The minimum fossil constraint for the split between taxa X and W is based on taxon Y. B. The reconstructed tree based on parsimony deltran optimization. The presence of homoplasy results in a reconstructed tree that fails to recover true evolutionary relationships. Instead, random homoplasy (characters 1-4) on the long branches X and W attracts these taxa together. Long branch misplacement is further exacerbated when there are parallel evolutionary constraints (characters 5-8). In the reconstructed tree, the minimum age for the split between X and W is incorrect and provides an underestimate of the true minimum age because Y and Z are outside of the crown clade.

Fig. 5. Plots that indicate the number of new lineages in each geological stage from the Cenomanian through the Lutetian. A. New fossil eutherian taxa as recorded by the Paleobiology Database. B. New lineages based on molecular timetrees. Arrows indicate rate changes relative to the previous geological stage: small arrows = 50-99.9%; medium arrows = 100-999.9%; large arrows $\geq 1000\%$. Infinity signs show instances where the previous stage had no new lineages, and -100% indicates zero new lineages in the current stage. dR27b = Phillips' (2016) timetree (169 taxa) based on 27 calibrations from dos Reis (2012) with modified maximum constraints for Chiroptera, Primates, and Rodentia;

Mer82c = Phillips' (2016) reanalysis of Meredith et al.'s (2011) DNA supermatrix (169 taxa) with 82 calibrations (Mer82c); and Emer15 = Emerling et al.'s (2015) timetree (388 species) with calibrations at 77 nodes; Coniacia = Coniacian; Santon = Santonian; Selan = Selandian; Thanet = Thanetian.

Glossary

Ghost lineage: a lineage that is inferred to exist based but lacks a fossil record.

Zombie lineage: a lineage that has a fossil record that is older than a molecular divergence time estimate.

Figure 1

- = true divergence time between taxon 1 and 2
- = estimated divergence time between taxon 1 and taxon 2

☛ = fossil occurrence

■ = observed taxon range

■ = ghost lineage implied by fossil record of sister lineage

■ = ghost lineage resulting from incomplete fossil record in both lineages

■ = zombie lineage resulting from crown fossil(s) that are older than timetree estimate

Figure 2

— = branches with parent node on Phillips' (2016) timetree that is younger than minimum fossil age (= zombie lineages)

— = branches with parent node on Phillips' (2016) timetree that is older than minimum fossil age

Figure 3

Figure 4

A. TRUE TREE

B. RECONSTRUCTED TREE

Figure 5

(A) Number of New Eutherian Fossil Taxa by Stage

(B) Number of New Lineages by Stage

Table 1

Table 1. Calibrations used in molecular dating analyses.

Clade	Oldest crown fossil	Minimum age	Maximum age	References for oldest fossil(s) and discussion of calibration
1. Actinopterygii + Sarcopterygii	<i>Guiyu oneiros</i>	420.7	444.9	Benton et al. (2015)
2. Tetrapoda	<i>Lethiscus stocki</i>	337	351	Benton et al. (2015)
3. Amniota	<i>Hylonomus lyelli</i>	318	332.9	Benton et al. (2015)
4. Sauropsida	<i>Protorosaurus speneri</i>	255.9	295.5	Benton et al. (2015)
5. Neognathae	<i>Vegavis iaai</i>	66.0	86.8	Benton et al. (2015)
6. Mammalia	<i>Ambondro mahabo</i>	164.9	227	Luo et al. (2001, 2015); Woodburne et al. (2003); Bi et al. (2014); Krause et al. (2014); Benton et al. (2015); Emerling et al. (2015)
7. Monotremata	<i>Obdurodon insignis</i>	25.0	121	Rowe et al. (2008); Meredith et al. (2011); Emerling et al. (2015)
8. Caenolestidae	None	0	15.97	Goin et al. (2007, 2009); Emerling et al. (2015)
9. Didelphimorphia + Australidelphia	<i>Peradectes</i>	65.18	83.8	Horovitz et al. (2009); Emerling et al. (2015)
10. Didelphidae	<i>Micoureus laventicus</i>	11.608	20.44	Goin (1997); Emerling et al. (2015)
11. Didelphimorphia	<i>Micoureus laventicus</i>	11.608	66.0	Emerling et al. (2015)
12. Dasyuromorphia	<i>Barinya wangala</i>	15.97	54.65	Wroe (1999); Emerling et al. (2015)
13. Peramelidae	cf. <i>Peroryctes</i>	4.36	23.8	Turnbull et al. (2003); Emerling et al. (2015)
14. Peramelemorphia	cf. <i>Peroryctes</i>	4.36	54.65	Godthelp et al. (1992); Turnbull et al. (2003); Emerling et al. (2015)
15. Burramyidae + Phalangeridae	<i>Eocuscus sarastamppi</i>	25.0	54.65	Case et al. (2009); Emerling et al. (2015)
16. Petauridae +	<i>Paljara</i> sp. A	25.5	54.65	Woodburne et al. (1993); Emerling et al. (2015)

Pseudocheiridae				
17. Macropodidae + Potoroidae	<i>Bulungamaya delicata</i>	24.7 ^A	54.65	Woodburne et al. (1993); Kear et al. (2007); Kear and Pledge (2008); Meredith et al. (2011); Emerling et al. (2015)
18. Placentalia	<i>Purgatorius</i>	65.2	131.5	Benton et al. (2009); Chester et al. (2015)
19. Chrysochloridae	<i>Amblysomus julianae</i>	1.7	33.9	Avery (2001); Seiffert et al. (2007); Emerling et al. (2015)
20. Macroscelidea	<i>Myohyrax</i>	15.97	56.0	McKenna and Bell (1997); Tabuce et al. (2008); Emerling et al. (2015)
21. Hyracoidea	<i>Dendrohyrax</i>	6.08	11.62	Pickford and Hlusko (2007); Emerling et al. (2015); Springer et al. (2015)
22. Xenarthra	<i>Riostegotherium</i>	47.8	66.0	Bergqvist et al. (2004); Woodburne et al. (2014); Emerling et al. (2015)
23. Pilosa	<i>Pseudoglyptodon chilensis</i>	31.5	66.0	Emerling et al. (2015)
24. Tardigrada	Megalonychidae fossils	15.97	41.3	Emerling et al. (2015)
25. Prionodontidae + Felidae	<i>Proailurus lemanensis</i> , <i>Stenogale julieni</i>	28.1	41.3	Hunt (1998); Wesley-Hunt and Flynn (2005); Holliday (2007); Emerling et al. (2015)
26. Carnivora	<i>Hesperocyon gregarious</i>	38.0	66.0	Wesley-Hunt and Flynn (2005); Benton et al. (2009); Spaulding and Flynn (2009); Emerling et al. (2015)
27. Musteloidea	<i>Promartes</i>	24.8	38.0	Finarelli (2008); Paleobiology Database
28. Ostentoria	<i>Ravenictis</i>	64.0	83.8	Fox et al. (2010)
29. Craseonycteridae + Megadermatidae	<i>Saharaderma</i>	33.9	47.8	Eiting and Gunnell (2009); Emerling et al. (2015)
30. Hipposideridae + Rhinolophidae	<i>Hipposideros</i>	38.0	56.0	Gunnell and Simmons (2005); Eiting and Gunnell (2009); Emerling et al. (2015)
31. Chiroptera	<i>Tachypteron</i>	47.8	66.0 ^B	Storch et al. (2002); Ravel et al. (2012); Emerling

	<i>franzi</i> , <i>Witwatia sigei</i> , <i>Dizya exsultans</i>			et al. (2015); Phillips (2016)
32. Emballonuridae + Nycteridae	<i>Tachypteron franzi</i> ^C	47.8	59.2	Storch et al. (2002); Emerling et al. (2015); Phillips (2016)
33. Molossidae + Vespertilionidae + Miniopteridae	<i>Wallia scalopidens</i>	38.0	56.0	Eiting and Gunnell (2009); Lim (2009); Emerling et al. (2015)
34. Molossidae + Vespertilionidae + Miniopteridae + Natalidae	<i>Wallia scalopidens</i>	38.0	56.0	Eiting and Gunnell (2009); Lim (2009); Emerling et al. (2015)
35. Yangochiroptera	<i>Tachypteron franzi</i> , <i>Witwatia sigei</i> , <i>Dizya exsultans</i>	47.8	61.6	Storch et al. (2002); Ravel et al. (2012); Emerling et al. (2015)
36. Furipteridae + Noctilionidae	<i>Noctilio lacrimaelunaris</i>	5.332	33.9	Cozzuol (2006); Emerling et al. (2015)
37. Phyllostomidae + Mormoopidae	Mormoopid, gen. et sp. nov.	28.1	41.3	Morgan and Czaplewski (2003); Gunnell and Simmons (2005); Czaplewski et al. (2008); Emerling et al. (2015)
38. Erinaceidae	<i>Neurogymnurus indricotherii</i> , <i>Palaeoscaptor acridens</i>	28.1	47.8	Meredith et al. (2011)
39. Erinaceidae + Soricidae	<i>Adunator ladae</i>	61.6	83.8	Benton et al. (2009, 2015); Meredith et al. (2011); dos Reis et al. (2012); Emerling et al. (2015)
40. Primatomorpha	<i>Purgatorius</i>	65.2	83.8	O’Leary et al. (2013); Chester et al. (2015); Emerling et al. (2015)
41. Primates	Numerous	38.0 ^D	66.0 ^D	Williams et al. (2010); Benton et al. (2015)

	eosimiids (e.g., <i>Eosimias</i>)			
42. Haplorhini	Numerous eosimiids (e.g., <i>Eosimias</i> , <i>Phenacopithecus</i>)	38.0	59.2 ^E	Williams et al. (2010); Emerling et al. (2015)
43. Strepsirrhini	<i>Saharagalago misrensis</i>	38.0	56.0	Seiffert et al. (2003); Emerling et al. (2015)
44. Galagidae + Lorisidae	<i>Saharagalago misrensis</i>	38.0	56.0	Seiffert et al. (2003); Emerling et al. (2015)
45. Lagomorpha	Tarsals from Vastan mine	53.7 ^F	61.6	Rose et al. (2008); Emerling et al. (2015); Kapur and Bajpai (2015); Phillips (2016)
46. Rodentia	<i>Acritoparamys</i> , <i>Paramys</i>	56.0	66.0	Benton et al. (2015); Emerling et al. (2015)
47. Sciuromorpha to Hystricognathi	<i>Acritoparamys</i>	56.0	66.0	Korth (1994); Anderson (2008); Janis et al. (2008); Emerling et al. (2015)
48. Sciuromorpha	<i>Eoglimiravus</i>	47.8	61.6	Meredith et al. (2011); Emerling et al. (2015)
49. Aplodontidae + Sciuridae	<i>Spurimus</i>	45.7	59.2	Flynn and Jacobs (2008a); Meredith et al. (2011)
50. Diatomyidae + Ctenodactylidae	<i>Fallomus</i>	28.3	47.8	Dawson et al. (2008); Meredith et al. (2011); Emerling et al. (2015)
51. Hystricognathi	<i>Cachiyacuy contamanensis</i>	40.94	56.0	Hartenberger (1998); Antoine et al. (2011); Emerling et al. (2015); Phillips (2015)
52. Phiomorpha + Caviomorpha	<i>Cachiyacuy contamanensis</i>	40.94	56.0	Hartenberger (1998); Antoine et al. (2011); Emerling et al. (2015); Phillips (2015)
53. Caviidae + Dasyproctidae	<i>Asteromys</i> , <i>Chubutomys</i>	24.5	38.0	Vucetich et al. (1999); Campbell and Frailey (2004); Frailey and Campbell (2004); Emerling et al. (2015)
54. Chinchillidae + Dinomyidae	<i>Eoviscaccia</i>	24.5	38.0	Vucetich et al. (1999); Emerling et al. (2015)

55. Chinchillidae + Dinomyidae + <i>Abrocoma</i> + Octodontoidea	<i>Sallamys</i> , <i>Xylechimys</i> , <i>Deseadomys</i>	24.5	38.0	Flynn and Swisher (1995); Flynn and Wyss (1998); Vucetich et al. (1999); Emerling et al. (2015)
56. Octodontoidea	<i>Sallamys</i> , <i>Xylechimys</i> , <i>Deseadomys</i>	24.5	38.0	Flynn and Swisher (1995); Flynn and Wyss (1998); Vucetich et al. (1999); Emerling et al. (2015)
57. Ctenomyidae + Octodontidae	<i>Xenodontomys</i> , <i>Palaeoctodon</i> , <i>Chasicomys</i>	9.07	33.9	Vucetich et al. (1999); Zárate et al. (2007); Emerling et al. (2015)
58. Anomaluromorpha + Myomorpha ^G	<i>Erlianomys</i>	54.0	61.6	Li and Meng (2010)
59. Myomorpha (Muroidea + Dipodoidea)	<i>Pappocricetodon</i>	45.0	59.2	Beard et al. (1994); Emerling et al. (2015)
60. Castorimorpha + Anomaluromorpha + Myomorpha	<i>Erlianomys</i>	54.0	66.0	Li and Meng (2010); Meredith et al. (2011)
61. Geomyoidea	<i>Proheteromys</i>	31.4	41.3	Flynn et al. (2008); Meredith et al. (2011); Emerling et al. (2015)
62. Scandentia	<i>Ptilocercus</i> ^H	34.0	66.0	Emerling et al. (2015); Li and Ni (2016)

^AKear and Pledge (2008) recovered Macropodoidea with 100% bootstrap support, but within this clade there was only 51% support for an association of the advanced bulungamayine *Bulungamaya* with Macropodidae. Nevertheless, *Bulungamaya* is three nodes upwards from the macropodoid node and shares four unambiguous apomorphies with Macropodidae to the exclusion of Potoroidae and more primitive bulungamayines. Kear and Pledge's (2008) recommendation that Potoroidae and Bulungamayinae be treated as *incertae sedis* within Macropodoidea is concerned with the association of basal bulungamayines (*Ngamoroo*, *Purtia*, *Wakiewakie*) with either potoroids or macropodids + advanced bulungamayines.

^BWe used maximum age suggested by Emerling et al. (2015).

^CPhillips (2016) suggests that the placement of *Tachypteron franzeni* is highly speculative, but Storch et al. (2002) reported that the “proportions of the strikingly narrow wing, the outline of the flight membranes and external ear, the morphology of the postcranial skeleton, and the relative cochlea size of *T. franzeni* and extant *Taphozous* species are almost identical” and that *T. franzeni* represents the oldest unequivocal record of Emballonuridae.”

^DBenton et al. (2015) suggest a minimum age of 56.0 for crown Primates (Euprimates) based on the inclusion of the late Paleocene *Altiaatlasius* in this clade, but this taxon may be a stem euprimate (Bloch et al., 2007; Williams et al., 2010). Similarly, Benton et al. (2015) suggested a maximum age of 66.0 Ma for Primates based on early Paleocene deposits that have yielded fossils of plesiadapids, paromomyids, and carpolestids, which are reconstructed as being more closely related to crown primates than to Scandentia or Dermoptera.

^EThe maximum age for Haplorhini allows for the possibility that the late Paleocene *Altiaatlasius* from Morocco is a stem anthropoid (Williams et al. 2010).

^FKapur and Bajpai (2015) provide an updated age for the Vastan tarsals (Rose et al., 2008) that are associated with Leporidae.

^GThe minimum for Myomorpha + Anomaluromorpha is established by *Erlianomys*, which is the oldest stem Myodonta at ~54 Ma (Li and Meng, 2010). The stratigraphic bounding maximum (*sensu* Meredith et al., 2011) is 61.6 Ma.

^HLi and Ni (2016) described *Ptilocercus* fossils from the early Oligocene (~34.0 Ma) of China, which establish a minimum age for crown Scandentia. The putative scandentian *Eodendrogale parva* is slightly older (~38.0 Ma), but the original fossil specimens are missing (Ni and Qui, 2012) and the published illustrations of Tong (1998) do not provide sufficient evidence for allocating *E. parva* to Scandentia (Ni and Qui, 2012). We followed Emerling et al. (2015) for the maximum age of 66.0 Ma.

Table 2

Table 2. Compendium of zombie lineages implied by Phillips' (2016) preferred timetree^A.

Clade	Phillips' Age (Ma)	Minimum Fossil Age (Ma)	Zombie Lineage (Ma)	Oldest Fossil	References for oldest fossil/age
Hyracoidea	3.12	6.08	2.96	<i>Dendrohyrax</i>	Pickford and Hlusko (2007); Emerling et al. (2015)
Proboscidea	1.27	6.8	5.53	<i>Loxodonta</i>	Vignaud et al. (2002); Lebatard et al. (2008); Emerling et al. (2015)
Hyracoidea to Proboscidea	44.63	59.2	14.57	<i>Eritherium</i>	Emerling et al. (2015)
Sirenia	5.74	41.3	35.56	<i>Eotheroides</i>	Vélez-Juarbe and Domning (2014, 2015); Springer et al. (2015)
Paenungulata	45.17	59.2	14.03	<i>Eritherium</i>	Gheerbrant (2009); Kocsis et al. (2014)
Tardigrada	13.74	15.97	2.23	<i>Imagocnus</i>	MacPhee et al. (2003)
Xenarthra	46.83	47.8	0.97	<i>Riostegotherium</i>	Bergqvist et al. (2004); Woodburne et al. (2014)
<i>Antilocapra</i> to <i>Okapia</i>	13.17	17.8	4.63	<i>Canthumeryx</i>	Theodor (2004); Drake et al. (1988); Emerling et al. (2015)
<i>Bos</i> to <i>Moschus</i>	12.06	18	5.94	<i>Eotragus</i>	Solounias et al. (1995); Emerling et al. (2015)
<i>Bos</i> + <i>Moschus</i> to <i>Cervus</i>	12.94	18	5.06	<i>Eotragus</i>	Solounias et al. (1995); Emerling et al. (2015)
Pecora	13.49	18	4.51	<i>Eotragus</i>	Solounias et al. (1995); Emerling et

					al. (2015)
Ruminantia	26.11	33.9	7.79	Lophiomerycidae	Janis and Theodor (2015)
<i>Megaptera</i> to <i>Eschrichtius</i>	2.53	7.246	4.716	<i>Plesiobalaenoptera</i>	Bisconti (2010)
Balaenopteroidea to Neobalaenidae	3.54	23.03	19.49	<i>Mauicetus</i>	Fordyce 2005; Boessenecker and Fordyce (2015)
Mysticeti	3.92	23.03	19.11	<i>Mauicetus</i>	Fordyce 2005; Boessenecker and Fordyce (2015)
Monodontidae to Phocoenidae	3.6	12.1	8.5	<i>Salumiphocoena</i>	Barnes (1976); Uhen et al. (2008); Emerling et al. (2015)
Delphinoidea	4.43	12.1	7.67	<i>Salumiphocoena</i>	Barnes (1976); Uhen et al. (2008)
<i>Inia</i> to <i>Pontoporia</i>	5.01	6.5	1.49	Iniid humerus	Gutstein et al. (2014)
Delphinoidea to <i>Inia</i> + <i>Pontoporia</i>	6.44	12.1	5.66	<i>Salumiphocoena</i>	Barnes (1976); Uhen et al. (2008)
Delphinoidea + <i>Inia/Pontoporia</i> to Ziphiidae	8.24	13.2	4.96	<i>Archaeoziphius</i>	Lambert and Louwye (2006)
Odontoceti minus Physeteroidea	8.46	15.97	7.51	<i>Prepomatodelphis korneuburgensis</i>	Barnes (2002)
Physeteroidea	6.26	13.82	7.56	<i>Idiophyseter</i>	Bianucci and Landini (2006); Paleobiology Database
Odontoceti	8.77	23.03	14.26	<i>Ferocetotherium</i>	Lambert et al., 2008; Gol'din and Marareskul, 2013
Cetacea	9.12	34	24.88	<i>Llanocetus</i>	Uhen (2010)
Whippomorpha	33.61	52.5	18.89	<i>Himalayacetus</i>	Meredith et al. (2011)
Cetruminantia	36.96	52.5	15.54	<i>Himalayacetus</i>	Meredith et al. (2011)

Cetruminantia + Suina	42.64	52.5	9.86	<i>Himalayacetus</i>	Meredith et al. (2011)
Cetartiodactyla	45.4	52.5	7.1	<i>Himalayacetus</i>	Meredith et al. (2011)
<i>Prionodon</i> to <i>Felis</i>	17.2	28.1	10.9	<i>Proailurus, Stenogale</i>	Emerling et al. (2015)
Felidae to Eupleridae	19.96	28.1	8.14	<i>Proailurus, Stenogale</i>	Holliday (2007)
Feliformia	24.11	28.1	3.99	<i>Proailurus, Stenogale</i>	Holliday (2007)
Mustelidae to Procyonidae	17.38	24.8	7.42	<i>Promartes</i>	Finarelli (2008)
Mustelidae + Procyonidae + Ailuridae	19.03	24.8	5.77	<i>Promartes</i>	Finarelli (2008)
Odobenidae to Otariidae	3.84	16.6	12.76	<i>Proneotherium</i>	Boessenecker and Churchill (2015)
Pinnipedeae	7.81	20.43	12.62	<i>Desmatophoca</i>	Demere et al. (2003)
Pinnipedeae + Musteloidea	24.08	24.8	0.72	<i>Promartes</i>	Finarelli (2008)
Arctoidea	24.35	28.1	3.75	<i>Cephalogale</i>	Banyue and Zhanxiang (2003); Wang et al. (2005); Finarelli (2008);
Caniformia	30.53	38	7.47	<i>Hesperocyon</i>	Wang and Tedford (1996); Spaulding and Flynn (2009)
Carnivora	36.68	38	1.32	<i>Hesperocyon</i>	Wang and Tedford (1996); Spaulding and Flynn (2009)
Ceratomorpha	25.28	53.7	28.42	<i>Cambaylophus</i>	Kapur and Bajpai (2015)
Perissodactyla	27.9	55.5	27.6	<i>Hyracotherium</i>	Woodburne et al. (2009)
Ostentoria	59.35	64	4.65	<i>Ravenictis</i>	Fox et al. (2010)
Zoomata	61.22	64	2.78	<i>Ravenictis</i>	Fox et al. (2010)
Hipposideridae to	28.5	38	9.5	<i>Hipposideros</i>	Gunnell and Simmons

Rhinolophidae					(2005); Eiting and Gunnell (2009)
Emballonuridae to Nycteridae	38.95	47.6	8.65	<i>Tachypteron</i>	Storch et al. (2002); Gunnell and Simmons (2005); Eiting and Gunnell (2009)
Noctilionoidea to Emballonuridae + Nycteridae	42.46	47.6	5.14	<i>Tachypteron</i>	Storch et al. (2002); Gunnell and Simmons (2005); Eiting and Gunnell (2009)
Erinaceidae to Soricidae	55.32	61.6	6.28	<i>Adunator</i>	Benton et al. (2009, 2015)
Erinaceidae + Soricidae to Talpidae	58.46	61.6	3.14	<i>Adunator</i>	Benton et al. (2009, 2015)
Eulipotyphla	59.12	61.6	2.48	<i>Adunator</i>	Benton et al. (2009, 2015)
Fereuungulata	61.48	64	2.52	<i>Ravenictis</i>	Fox et al. (2010)
Variamana	61.6	64	2.4	<i>Ravenictis</i>	Fox et al. (2010)
Hominoidea	9.74	12.68	2.94	<i>Sivapithecus</i>	Finarelli and Clyde (2004)
Catarrhini	15.55	20.55	5	<i>Afropithecus</i>	Finarelli and Clyde (2004); Harrison and Andrews (2009)
<i>Callithrix</i> to <i>Cebus</i>	8.35	11.8	3.45	<i>Aotus dindensis</i>	Setoguchi and Rosenberger (1987); Antoine et al. (2007); Springer et al. (2012)
<i>Callithrix</i> + <i>Cebus</i> + <i>Ateles</i>	9.41	11.8	2.39	<i>Aotus dindensis</i>	Setoguchi and Rosenberger (1987); Antoine et al. (2007); Springer et al. (2012)
Anthropoidea	21.7	28.1	6.4	<i>Aegyptopithecus</i>	Kay et al. (2008)
Lorisiformes	15.04	38	22.96	<i>Saharagalago</i>	Seiffert et al. (2003)

Lagomorpha	41.09	53.7	12.61	Vastan tarsals	Rose et al. (2008); Kapur and Bajpai (2015)
Octodontoidea	23.46	24.5	1.04	<i>Sallamys</i> , <i>Xylechimys</i> , <i>Deseadomys</i>	Vucetich et al. (1999); Flynn and Swisher (1995); Flynn and Wyss (1998); Emerling et al. (2015)
Aplodontidae + Sciuridae	40.28	45.7	5.42	<i>Spurimus</i>	Flynn and Jacobs (2008a)
Geomyoidea	27.01	31.4	4.39	<i>Proheteromys</i>	Flynn et al. (2008)
Castorimorpha	51.46	52.4	0.94	<i>Mattimys</i>	Flynn and Jacobs (2008b)

^APhillips' (2016) timetree based on 27 calibrations from dos Reis (2012) with modified maximum constraints for Chiroptera, Primates, and Rodentia. Zombie lineages that exceed 20 million years are highlighted in bold font.

Table 3

Table 3. Interordinal divergence times (millions of years) and 95% credibility intervals within Placentalia based on molecular dating analyses with mcmctree and Meredith et al.'s (2011) nucleotide data set for mammalian taxa after excluding 47 taxa that exceed body size and/or longevity thresholds. Analyses were performed with 62 calibrated nodes (Table 1) and four different combinations of evolutionary rate model (autocorrelated rates [AUTO], independent rates [IR]) and calibration type (hard bounded [HARD], soft bounded [SOFT]).

Clade	Analysis				Mean date from Meredith et al. (2011) ^A	Mean date from dos Reis et al. (2012) ^B
	AUTO, HARD	IR, HARD	AUTO, SOFT	IR, SOFT		
Placentalia	90.3 (88.2, 92.6)	92.8 (90.0, 95.9)	93.5 (91.1, 96.0)	91.3 (88.4, 94.6)	101.35	90.9
Afrotheria	75.2 (73.2, 77.8)	76.7 (73.8, 80.6)	77.4 (74.9, 80.3)	75.8 (71.7, 79.6)	80.89	71.3
Afroinsectivora	72.3 (70.2, 74.9)	73.5 (70.5, 77.4)	74.3 (71.9, 77.2)	72.7 (68.5, 76.4)	77.33	NA
Exafroplacentalia	87.5 (85.8, 89.5)	89.4 (86.9, 92.2)	90.7 (88.7, 92.8)	88.1 (85.5, 90.9)	99.38	90.2
Boreoeutheria	81.2 (79.9, 82.5)	82.6 (80.7, 84.7)	83.9 (82.4, 85.6)	81.5 (79.6, 83.8)	92.0	82.8
Laurasiatheria	75.0 (73.9, 76.1)	75.9 (74.0, 78.1)	77.1 (75.6, 78.7)	74.4 (72.2, 77.2)	84.56	75.3
Variamana	73.4 (72.3, 74.6)	74.0 (72.1, 76.2)	75.4 (73.8, 76.9)	72.5 (70.2, 75.4)	82.02	72.9
Fereuungulata	72.8 (71.6, 74.1)	73.4 (71.4, 75.7)	74.8 (73.2, 76.3)	72.0 (69.5, 74.9)	81.98	NA
Ostentoria	70.4 (69.0, 71.8)	70.3 (68.0, 72.7)	72.4 (70.6, 74.0)	68.9 (66.2, 71.9)	79.62	NA
Euarchontoglires	75.1 (74.3, 76.1)	76.1 (74.6, 77.7)	77.6 (76.3, 78.8)	75.8 (74.4, 77.6)	83.33	75.6
Primates	73.3 (72.3, 74.4)	74.4 (72.6, 76.3)	76.3 (74.9, 77.6)	74.2 (72.3, 76.1)	82.04	NA
Glires + Scandentia	74.7 (73.8, 75.6)	75.6 (74.1, 77.2)	77.0 (75.8, 78.3)	75.4 (73.9, 77.1)	82.78	NA
Glires	72.3 (71.5, 73.1)	73.1 (71.8, 74.6)	74.2 (73.0, 75.4)	73.1 (71.8, 74.7)	79.5	70.7

Abbreviations: NA, not reported or clade not applicable on dos Reis et al.'s (2012) tree.

^AMean dates based on table S6 of Meredith et al. (2011).

^BMean dates based on four analyses reported in table 1 of dos Reis et al. (2012).

Table 4

Table 4. Results of Templeton and winning-sites tests.

Trees	Length	Templeton p value	Winning-sites p value
Cretaceous taxa on placental stem (3 trees)	2293	1.00	1.00
Molecular scaffold (6 trees)	2319	0.0073* 0.0086* 0.0108* 0.0108* 0.0124* 0.0124*	0.0099* 0.0116* 0.0138* 0.0138* 0.0159* 0.0159*
Zalambdalestidae + Glires (6 trees)	2318	0.0461* 0.0473* 0.0499* 0.0509 0.0588 0.0633	0.0171* 0.0215* 0.0240* 0.0298* 0.0622 0.0690

Templeton and winning-sites test were performed to determine if there are statistically significant differences between different trees. Tests were performed with PAUP*. Trees with minimum branch lengths of zero were collapsed.

● = estimated divergence time between taxon 1 and taxon 2

☞ = fossil occurrence

■ = observed taxon range

■ = zombie lineage resulting from crown fossil(s) that are older than timetree estimate