Deep Time Drivers of Evolutionary Entities

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Declaration

I, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously been presented for an award at this, or any other, university.

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Abstract

Species are known to reflect evolutionary significant units (ESUs), however still deliberated is the potential existence and reality of higher units. The somewhat esoteric nature of naming higher taxa is not grounded in any evolutionary process, yet higher evolutionary significant units (HESUs) have been argued to be real, and patterns of shared processes likely drive the formation of distinct evolutionary entities in deep time. The veracity of this, however, remains unresolved. Here, I show that HESUs do exist within the mammalian clade Afrotheria, defined using a range of potential metrics. I constructed a phylogeny using fossil taxa, and applied it to investigate rates of diversification, and how these rates change with the presence or absence of extinct species. I used this phylogeny further when exploring the zoogeographic history of the clade, and for studying significant shifts in trait evolution, focusing on body mass and cranium morphology. Finally, I revisited diversification and searched for clusters of branching rates on the tree, and tested their stability in deep time. I found that shared histories of diversification, phenotype and zoogeography can all play a role in delineating HESUs. I further notice the important function of extinction as a macroevolutionary process that shapes many patterns within the clade, as well as the previously masked outcomes revealed when extinct taxa are included in analyses. My results here provide additional support to the reality of evolutionarily significant higher taxa and allow us to consider future areas of intriguing research into the comprehension of macroevolutionary dynamics.

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Chapter 1

General Thesis Introduction: Deep Time Drivers of Evolutionary Entities

1.1 Abstract

The concept of species as discernible, evolutionary distinct units is well established, yet whether such units exist above the species level continues to be debated. Although there are many definitions of species, the most widely accepted species concept is rooted in evolutionary processes. In contrast, higher, super-specific taxonomic ranks, originated by Linnaeus, appear in many instances to be ad hoc, lacking a consistent definition, and, importantly, have no obvious basis in any evolutionary process. However, higher evolutionary significant units (HESUs) appear to exist, suggesting that at least some higher taxa are not simply arbitrary constructs. This leads to the question; how should we define and quantify higher taxa? This inevitably invites the questioning of which processes lead to distinct HESUs. Here, I take the viewpoint that any meaningful definition of HESUs must emerge from a common set of evolutionary processes. In this thesis I examine the evidence for the evolutionary reality of higher taxa and consider how different approaches to studying macroevolution can lead to varying inferences of such clades, that could, in turn, be considered HESUs. In the sections that follow, I assess current definitions of higher taxa with particular focus on links between described taxonomic units and underlying evolutionary processes. I then explore how evolutionarily significant units should be defined. Finally, I outline the scope of this thesis in which I examine the deep time drivers of emergent HESUs in the mammalian clade Afrotheria.

1.2 Species Concepts and the Meaning of Higher Taxa

While it is widely agreed that species are real and meaningful biological units, the reality of taxa above the species level is far more controversial. The biological species concept (BSC) consolidated by Mayr defines species as clusters of natural populations of organisms that breed amongst themselves and that are reproductively isolated from other similar collectives (Mayr 1942, 1995; Coyne & Orr 2004; de Queiroz 2005). Thus, reproductive isolation is the key tenet for defining species and indeed the process of speciation. Unlike the Biblical ‘kinds’, this forces taxonomic relationships to be genetic, rather than morphological in nature. In contrast, definitions of taxa above the species level cannot rely on definitions based on reproductive isolation (Humphreys & Barraclough 2014; Simpson 1951). The challenge of defining higher taxa is more closely aligned with other species concepts, including the Darwinian, evolutionary and phylogenetic species concepts (Table 1; Stankowski & Ravinet 2021).

In contrast to Mayr’s thoughts, evolutionary species concepts (ESCs) use phylogeny and morphology to define species (Simpson 1961; Barraclough 2019). The ESCs define species as groups of organisms, descended from a common ancestor, indicated by the presence of apomorphies (derived traits), that can be considered indivisible quanta, existing as the smallest unit of taxonomy. The Darwinian species concept (DSC) uses phenotype to discern that a lineage, or fragment thereof, is a species, allowing paraphyletic populations to be considered species (Jolly 2014). Phylogenetic species concepts (PSCs) require species to be monophyletic and share similarities with ESCs (de Queiroz & Donoghue 1988; Nixon & Wheeler 1990). These concepts are explicitly pattern based, with species defined based on sets of characteristics, rather than being seen as the terminus of a biological process. This allows for further species to be realised, and avoids the self-evident hybridisation issue of the BSCs and other concepts that require reproductive isolation.

Higher taxa are frequently defined based on sets of apomorphies shared by clades, known as synapomorphies. Examples include feathers in Aves, chelonian shells and a greater number of thoracolumbar vertebrae present in afrotheres (Sánchez-Villagra *et al*. 2007). Broader employments of some species concepts, such as the ESCs, could reflect higher evolutionary entities.

Table 1. *Stankowski & Ravinet's definitions of a number of species concepts, procured and organised from their supplementary information (Stankowski & Ravinet 2021).*

Concept	Definition
Biological Species Concept I (BSCI) (Mayr 1942, 1995)	Species are a group of interbreeding natural populations that are reproductively isolated from other such groups.
Biological Species Concept II (BSCII) (Coyne & Orr 2004)	Species are groups of interbreeding natural populations that are substantially but not necessarily completely reproductively isolated from other such groups.
Cohesion Species Concept (CSC) (Tempelton 1985)	A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.
Darwinian Species Concept (DSC) (Jolly 2014)	A species is an evolutionary lineage, or lineage segment, that is phenotypically distinguishable from all other such units and is usefully distinguished in scientific discourse.
Ecological Species Concept (EcSC) (Van Valen 1976)	A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.
Evolutionary Genetic Species Concept (EgSC) (Birky *et al*. 2010)	Populations separated from each other by gaps that are significantly greater than $2N_e$ generations deep.
Evolutionary Species Concept I (EvSCI) (Simpson 1961)	A species is a single lineage of ancestral descendant populations or organisms, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.
Evolutionary Species Concept II (EvSCII) (Barraclough 2019)	An independently evolving group of organisms that is genetically and phenotypically distinct from other such groups.
Genealogical Species Concept (GgSC) (Baum & Donoghue 1995)	A species is a basal group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group, and that contains no exclusive group within it.
General Lineage Species Concept (GLSC) (de Queiroz 1998)	Species are segments of population-level evolutionary lineages.
Genetic Species Concept (GSC) (Baker & Bradley 2006)	A species is group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups.
Genotypic Cluster Species Concept (GCSC) (Mallet 1995)	A species is a distinguishable group of individuals that has few or no intermediates when in contact with other such clusters.
Phylogenetic Species Concept I (PSCI) (de Queiroz & Donoghue 1988)	A species is the smallest (exclusive) monophyletic group of common ancestry.
Phylogenetic Species Concept II (PSCII) (Nixon & Wheeler 1990)	A species is smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts).
Recognition Species Concept (RSC) (Paterson 1985)	Species are the most inclusive population of individual biparental organisms, which share a common fertilization system.
Unified Species Concept (USC) (de Queiroz 2007)	A species is a separately evolving metapopulation lineage.

Higher taxonomic ranks, being more ad hoc, are easier to name than define. Growing from the seven ranks of Linnaeus to contemporary rank prefixes such as ‘sub-’, ‘infra-’ and ‘parv-’, taxonomy has moved away from biologically **significant** ranks. Every clade could get a name and rank; by pruning the most ancestral lineage from the phylogenetic tree of a clade, a new clade is realised, which can then receive a new name and rank to distinguish it from the original, larger clade. This can also lead to very confusing names, but etymology is not at issue here. Consider human classification just within the apes as an example. *Homo sapiens* belongs to the subtribe Hominina in the tribe Hominini, in the subfamily Homininae, in the family Hominidae, in the superfamily Hominoidea. Hominina comprises *H. sapiens* and their closest now extinct australopith relatives. Hominini encompasses these and the lineage to *Pan* (chimpanzees), Homininae contains this and the gorilla tribe, Hominidae adds the orangutans to form the great apes and Hominiodea further includes the gibbon family Hylobatidae to round out the apes. This complex collection of ranks is useful for discerning relationships, but they are all almost certainly not significant in the grand scheme.

The PhyloCode is a set of rules that aim to classify irrespective of ranks, significantly, by naming clades on the basis of phylogenetics (de Queiroz & Cantino 2001). This is a continuation of ideas originated by Hennig in the early days of cladistics (Hennig 1966). Linnaean classification has changed over the centuries; although non-monophyly is still accepted, the modern taxonomist intends to adhere to having named ranks equalling clades. Under a scheme of phylogenetic nomenclature, monophyly is the sole, mandatory recourse. The three most frequently used ways to classify under phylogenetic taxonomy are the minimum clade, maximum clade and apomorphy based definitions. In these definitions, algebraic characters refer to specifiers, representing a species, specimen or apomorphy. A minimum clade based definition is the most recent common ancestor (MRCA) of A and B, and all descendants of that node, including the node itself. A maximum clade based definition is the first ancestor of A that is not also an ancestor of Z, and all descendants; this would be on the branch to A below, but not including, the MRCA node of A and Z. An apomorphy based definition is the earliest ancestor of A that possesses an inherited trait T, and all its descendants, even if that includes C which has lost trait T.

Criticisms have been levied against the PhyloCode. Lidén & Oxelman (1996) argue that Linnaean taxonomy already satisfies the requirements of phylogenetic classification, so a new system is not required. They also make a number of observations: that well established, traditional and convenient taxa could be forced to change their definitions, obviously so if they are non-monophyletic; that if a type taxon is found to lie outside its clade, the definition of that clade will now change to include more species, causing internal uncertainty; and that hierarchical ranks and binomial nomenclature would have to be discarded. Benton (2000, 2007) discusses that, in addition to these issues, the PhyloCode concept of stability is not true stability. The argument is that the PhyloCode has rigidity, but not flexibility and conservativeness. Linnaean taxonomy allows named taxa to subtly shift definitions as the world is better understood, with almost the entirety of the species within being conserved. The PhyloCode has names that are locked in, and if reclassification is needed to occur, the number of included lineages could expand rapidly beyond the intended clade that was attempted to be defined due to the 'infinitely elastic' property of the PhyloCode, where 'genera' could swell to be 'phyla', or 'phyla' collapse to be 'genera' (Benton 2000, 2007). One example mentioned by Benton (2007) is of the now discarded mammalian order Insectivora. If a phylogenetic nomenclature definition of the Lipotyphla included a tenrec and a hedgehog, the realisation of the Afrotheria would have inflated Lipotyphla to include almost every placental. Linnaean taxonomy allowed for the swift and painless sensible reclassification of the relevant clades, without any rules being broken or excepted. Benton further considers the bureaucracy, extra work load and confusion born from the compulsion of the PhyloCode to rewrite Linnaean taxonomy, as well as submitting that systematics over semantics should be the focus (Benton 2007). Responses to these criticisms are abundant, such as those by de Queiroz, one of the originators of the PhyloCode, who defends by clarifying that although traditional Linnaean taxonomy encourages naming clades only, the focus could be more on promoting 'nomenclatural explicitness, universality, and stability' at the expense of monophyly (de Queiroz 1997). Further to this, de Queiroz explains that internal clade relationships are not an issue for phylogenetics via referencing uncertain type taxa explicitly and that abolishing ranks is allowed, but not compulsory.

While the PhyloCode can be applied to any node in a phylogeny, it is not clear that these have any basis as distinct evolutionary units. Empirical studies have indicated that distinct evolutionary entities do exist above the species level. These entities are defined based on evolutionary processes, akin to a large scale application of the evolutionary species concepts, and are realised when, as with species, delimitation identifies some form of significantly different units. Defining species as evolutionary significant units, these entities of higher, super-specific taxa can be understood as higher evolutionary significant units (HESUs). This highlights the key question of how we define HESUs from any other clade.

Several issues exist with a purely phylogenetic approach to defining higher taxa. Firstly, apart from some rare geologically recently deceased examples (Puttick & Thomas 2015), genetic information of extinct species does not exist, so cladistic characteristic input is obligatory. Moreover, knowing where a split should be is challenging, so how do we consistently and logically identify HESUs? For example, consider the case of Sauropsida in which birds and crocodilians, the two extant clades of the Archosauria, diverged from one another at approximately the same time (c.240Mya, during the Triassic) as the Rhynchocephalia (tuatara) diverged from the Squamata (Gemmell *et al.* 2020). The Archosauria share a number of traits not shared by other reptiles, i.e. they no longer possess their Jacobson's organ, yet are clearly very distinct groups (Poncelet & Shimeld 2020). However, despite their morphological and ecological differences, under logical phylogenetic definitions, birds and crocodilians could belong to one group. In contrast, the tuatara is the last species of its order, a sister to the squamates within Lepidosauria, and is superficially similar to lizards. Looking on a tree alone, Archosauria and Lepidosauria are both large reptilian clades first appearing at similar times during the Triassic. The branching pattern of a phylogeny alone is not sufficient to identify higher taxa. This issue exists to varying extents across the tree of life on all scales. At a finer scale, for example, the pinnipeds (Park *et al*. 2024) raise a number of questions. Are all members unique enough to be considered one significant clade, or should they be split into eared or earless seals, or further still by separating the walrus from the other eared seals, as is the case with the current three Linnaean families?

The challenge is to identify delimiters which can both unify or separate clades where necessary. But how can we tell where an HESU begins? Under Linnaean taxonomy, Aves is distinct enough to be a class, but it exists within Reptilia, which is also a class. Moving further back and to broader groups, monophyletically Mammalia is a class that, along with Reptilia (and therefore Aves) exists within the class Amphibia, which in turn exists within the class Sarcopterygii (the bony fish). Having birds and bony fish being equal in rank is frustratingly paraphyletic. This equal rank nesting issue seems illogical in the context of phylogeny and in the quantification of HESUs. We should define ranks by data, not boxes, i.e. time-slicing or filling a number of species. Saying a rank can only possess *n* number of species before it is full is illogical, as is using arbitrary time, e.g. 5 million years for a species, 10 for a genus, 20 for a family, 40 for an order etc. If Aves and Sarcopterygii were both HESUs, they would have to be different ranks, implying ESUs might have more than two ranks, and that not all HESUs will be equal across all lineages. As nodes on the tree of life are imbalanced, multiple HESUs may be present in one lineage, where in the same period of time, fewer will exist on another (Alfaro *et al.* 2009).

As hinted at above, morphology can be informative in defining higher taxa, but as with genetics, has its own issues. Morphology is used in phylogenetic analyses so the majority of species throughout history that are extinct and are only represented by fossils can be included, as well as those extant species whose genomes have yet to be sufficiently sequenced or are only known by few specimens. The inclusion of morphology in phylogenetic research is also utilized to calibrate the dating of taxa and to verify realised molecular relationships (Wiens 2004). A prominent issue in defining higher taxa using traits is how to treat complex, multidimensional traits (Kemp 2016). For example, should whole units, such as a jaw, be treated as functional modules, or should modules be broken down further (e.g. treating individual teeth or even cusps individually as focal components)? Choices of evolutionary modules can lead to vastly different definitions of higher taxa.

A fundamental limitation of using trait data is convergent evolution. Moles are a particular and classic example of this. Taking a true mole (Talpidae), a golden mole (Chrysochloridae) and a marsupial mole (Notoryctidae) and placing them together, they could appear to be siblings from the same brood, but golden moles are more closely related to elephants, and marsupial moles to kangaroos, than they are to true moles (Springer *et al*. 2023). Taxonomists must be careful not to classify these three families into a clade alone. Viewing morphological data in the light of a genome-based phylogenetic scaffold should minimise the potential to be misled by convergent evolution. Convergence is at a particular risk of confusing relationships at a smaller scale. An issue could arise within Mustelidae, where otters have adapted to a semi-aquatic lifestyle, but weasels are more closely related to otters than they are to other mustelids that look like weasels (Law *et al*. 2018). Looking at fossils, it cannot be certain whether we are looking at an ancestor or a cousin. Is *Archaeopteryx* an extinct lineage or are modern birds their direct descendants (Witmer & Chiappe 2002; Clarke & Norell 2002)? We cannot truly know, but more questions are raised. Is *Archaeopteryx* one of the first birds or one of the last non-avian bird relatives? If *Archaeopteryx* marks the beginning of a new HESU, would it still be recognised as such if modern birds never evolved?

Other factors that can be included in a definition of higher taxa include behaviour, both social and individual, ecology and geography, but to define an HESU as opposed to a generic higher taxon, those traits with strong phylogenetic signal and/or with limited convergence should be of greatest use (Van Valen 1976; Kemp 2016; Humphreys and Barraclough 2014). Individuals of a certain species exist in similar ecological niches, occupying similar habitats and positions within food webs. Moving this up ranks and slightly broadening the scope of similarity could be an appropriate way to define higher taxa (Humphreys and Barraclough 2014). All canine species are remarkably similar in this regard, for example. As with most things, there are exceptions to the rule. Bears are generally omnivorous, but polar bears (*Ursus maritimus*) are almost exclusively carnivorous and giant pandas (*Ailuropoda melanoleuca*) famously survive almost entirely on bamboo. How specific or generic a definition of 'similar niche' is would affect any delimitation of HESUs. However, this is pattern based and would serve as no use to a definition of higher taxa rooted in processes.

Finally, geographical isolation can be considered (Park *et al*. 2024; Barraclough 2010; Humphreys & Barraclough 2014). Some taxa are defined because all species of their clade solely exist in one region. The region may prevent the organisms from leaving or be an ideal environment for them, forcing them to diversify in that region alone. Given enough time and sufficient rates of diversification, an isolated population can become a new species, and then a new higher taxon. Humphreys & Barraclough (2014) found that some traits that reflect niche favouritisms have lower variation within higher taxa than among them, and suggest geographic isolation as a justification of separate evolution found between Old and New World sisters, i.e. pigs and peccaries.

Defining higher taxa incorporates many facets of biology. Genetics is key to creating an accurate phylogeny to divide into higher taxa, that, due to the unbalanced reality of trees, will likely be at different Linnaean ranks across different lineages, and will likely see nesting of multiple HESUs into even higher, but not equivalent, ranks. Genetics alone cannot adequately define higher taxa. Morphology must also play a crucial part to highlight when and where higher taxa begin on a phylogeny. Beyond these, behavioural, ecological and geographical factors should also be considered in the definition and quantification of higher taxa. However, these ideas are based on describing a pattern of either ancestry or similarity. These approaches all rely on arbitrary cut-offs for HESUs and do not account for the processes that generate HESUs, so we need to consider the macroevolutionary processes that could generate distinct clade histories in terms of lineages and traits.

1.3 Macroevolutionary Routes to Higher Taxa

If higher taxa are distinct evolutionary units then they must emerge through shared macroevolutionary processes. For example, taxa within an HESU might share speciation rates or extinction rates (or both), or their phenotypes may have diverged around shared adaptive optima (e.g. G.G. Simpson's adaptive zones; Simpson 1944). Therefore, to understand the origins of higher taxa and to be able to define them we need to identify where on the tree of life groups of taxa share comparable histories of diversification (speciation and extinction) and phenotypic evolution. In the numerous papers on the subject by Barraclough, Humphreys and colleagues, processes that lead to significant higher entities are both simulated and tested empirically (Barraclough 2010; Fujisawa & Barraclough 2013; Humphreys & Barraclough 2014; Barraclough & Humphreys 2015; Humphreys *et al*. 2016). In this section I discuss recent models that explore routes to the origins of HESUs. These models emphasise the idea that taxa within an HESU share not only ancestry but also evolutionary fate.

Humphreys & Barraclough (2014) simulated speciation, extinction and dispersal of higher taxa. A clade was split into two sub-clades that experienced different conditions, representing common ancestry under different ecological or geographical conditions. High dispersal erodes any chance of higher taxa forming, and even at low levels, dispersal reduces divergence between sub-clades. The main indication was that lower dispersal correlates with higher phylogenetic clustering. Such clusters were shown being separated by markedly long branches in both the metacommunity modelling and real data analyses. Humphreys & Barraclough (2014) used the Generalised Mixed Yule Coalescent (GMYC) model on three large mammalian clades to search for clusters which represent HESUs. This likelihood model passes forward and backward along phylogenies and identifies where within-cluster branching rates are distinct from between-cluster branching to infer a change in evolutionary process and the possible phylogenetic positions of distinct evolutionary units above the species level.

Humphreys *et al*. (2016) explored clade dependence and independence, and constant and variable birth-death rates and their impact on HESU inference, specifically on the reliability of the GMYC model. A clade independent, constant rate model sees no change in rates over time or across lineages. An independent, variable rate model sees a change in rates at some point in time that affects all lineages equally. A clade dependent model would see variable rates occurring in different clades at different times, which would have no effect on other lineages. The null model of the GMYC is that no clusters exist, yet this was rejected by the constant rate modelling, implying illegitimate detectability of significant clusters. Using empirical data, the GMYC outperformed estimations of support derived from constant rate theory, allowing us to rule out constant rate simulations alone and focus our attention on variable rate models. The GMYC is not robust to high extinction models, and clade independent simulations insufficiently estimate real trees, both under constant rate conditions, and, of note, with unrealistically old root age estimates for simulated data under variable rate models. Further to this, the GMYC model is unable to distinguish between clade dependence and independence. The suggestions of the authors are to use the GMYC model for constant rate investigations in conjunction with simulations, and that the GMYC is weak alongside some variable rate independent models, with clade dependence currently being the most underexplored approach, yet will likely be of consequence in further studies of HESUs.

These models described above provide new insight into the reality of higher taxa and place particular emphasis on identifying evolutionary fates coupled with shared ancestry. Evolutionary fates are placed in the context of evolutionary history, similar selection pressures with shared phenotypic responses, and the role of geography, in generating evolutionary entities. Over the last quarter century significant advances in data availability, and perhaps more importantly, analytical methods, mean that assessing these macroevolutionary processes is a tractable problem. We are now able to robustly infer trends in diversification (Rabosky 2014; Rabosky *et al*. 2014; Mitchell *et al.* 2019), shifts in phenotypic processes (Bastide *et al*. 2018; Pagel *et al.* 2022), and biogeographic history (Matzke 2013).

One method to explore diversification is the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) created by Rabosky (2014). BAMM estimates speciation and extinction rates on trees of extant species. This method uses a reverse-jump Markov Chain Monte Carlo (RJ-MCMC) to travel and presumes a compound Poisson process explains the changes in branch rates. Rabosky (2014) implemented BAMM on the cetaceans and suggests little average speciation variation occurs across time, although this could be explained by a general low level slowing of speciation with a rapid burst followed by slowing within the dolphins, indicating that this clade may have a unique diversification history compared to other whales. In Mitchell *et al.* (2019), BAMM is expanded from its extant only limitation to include fossil taxa when evaluating diversification regimes. This FossilBAMM shows that analyses that include fossil data improve speciation, and more so extinction rate estimates, emphasising the importance of including extinct taxa in macroevolutionary investigations.

Phenotypic processes are studied by, among others, Pagel *et al.* (2022). They implement the Fabric model, which uses a RJ-MCMC to identify directional and evolvability shifts on phylogenetic trees. Directional shifts are substantial changes of the magnitude of a trait along a lineage, further than any anticipated changes from Brownian movement. Evolvability shifts appear when lineages considerably alter their ability to trek around trait space. Such models can also be utilised independently to explore trait evolution. The authors explored evolvability and directional shifts, as well as background walking, amongst the mammals. Notable findings were the directional size increase of the baleen whales and the shrinking of the sengis. A small clade of marsupials sees the largest evolvability intensification, and a smaller clade of rodents shows the furthermost contraction in evolvability. Their results indicate ‘watershed’ instances, where evolvability is significantly boosted, representing a trait dashing ahead.

Matzke (2013) created a new method for analysing biogeographic history called BioGeoBEARS, a shortening of Biogeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts. This method tests a number of different models to explore how biogeography varies on phylogenies. Park *et al*. (2024) use BioGeoBEARS to investigate pinniped zoogeographic history. They find that the ancestors of the walrus and the eared seals evolved in the North Pacific and the earless seals in the North Atlantic. Being able to visualise and track the geographic changes of taxa in deep time allows us to potentially make determinations about significant higher clades realised from geographic isolation.

1.4 Thesis Overview

1.4.1 The Afrotheria

The tractability of models for inferring distinct macroevolutionary regimes along different axes (diversification, traits, geography) means that we can potentially now identify robust HESUs. In this thesis I apply a range of diverse macroevolutionary approaches to address the question of HESUs in the mammalian clade Afrotheria.

The Afrotheria are a morphologically diverse clade of mammals currently classified into nine families: Elephantidae, Trichechidae, Dugongidae, Procaviidae, Orycteropodidae, Macroscelididae, Tenrecidae, Potamogalidae and Chrysochloridae. Across these nine families there are remarkable examples of ecological and morphological convergence with other mammal clades (Tabuce *et al.* 2008; Gheerbrant *et al.* 2016; Springer 2022). For example, the Elephantidae are large herbivores, convergent with rhinoceros and other true ungulates. Trichechidae (manatees) and Dugongidae are adapted to fully aquatic life, like cetaceans. Procaviidae (hyraxes) are small herbivores, akin to lagomorphs, rodents and small macropods. The sole member of Orycteropodidae (aardvark) is a medium-sized insectivore, like true anteaters and pangolins, and to a lesser extent, the numbat and short-beaked echidna. Macroscelididae (sengis) are small insectivores, similar to shrews, solenodons and shrew opossums. Tenrecidae are small omnivores, with a great deal of diversity; some appearing like opossums, hedgehogs, shrews or small rodents. Potamogalidae (otter shrews) resemble otters and Chrysochloridae (golden moles) are like both true and marsupial moles (Springer 2022; IUCN 2024).

As the name suggests, the Afrotheria are mainly distributed in Africa but with some lineages extending to other regions, most noticeably the aquatic sirenians (Springer 2022). Tenrecs are endemic to Madagascar, and are the only afrotherians found there. Additionally, there is a rich fossil record for Afrotheria that further extends both geographic distributions and morphological diversity, such as the once widely distributed extinct relatives of elephants. This exceptional diversity of morphological forms within Afrotheria, coupled with their fossil record and discrete geographic distribution, allows the clade to act as a miniature 'snapshot' of the mammalian tree of life and provides a basis for measuring the patterns and macroevolutionary dynamics of HESUs. In the chapters outlined below, I focus on related aspects of the evolution of Afrotheria to elucidate the reality of higher taxa.

Figure 1. *Images of some species of Afrotheria. (L-R) Top: African Bush Elephant, West Indian Manatee, Dugong. Middle: Rock Hyrax, Aardvark, Black and Rufous Sengi. Bottom: Lowland Streaked Tenrec, Giant Otter Shrew, Grant's Golden Mole. References: Loxodonta africana <fandom.com>, Trichechus manatus <treehugger.com>, Murray, Dugong dugon <fineartamerica.com>, Procavia capensis <fandom.com>, Retterath, Orycteropus afer <shutterstock.com>, Rhynchocyon petersi <upload.wikimedia.org>, Fenolio, Hemicentetes semispinosus <fineartamerica.com>, Potamogale velox <fandom.com>, Rathbun, Eremitalpa granti <afrotheria.net>.*

1.4.2 Chapter 2

In Chapter 2 I reconstruct the phylogeny of Afrotheria using a total evidence approach and use this to infer the diversification dynamics of the clade. In contrast to other recent studies, I aim to include as much fossil information as possible and for fossil data lacking character coding, I use taxonomically informed imputation to place fossils within the tree. This approach enables me to assess how the inclusion of fossil taxa influences inference of shifts in speciation and extinction rates and so reveals how fossils might shape our understanding of higher taxa. My results suggest that inferences of diversification regimes are strongly influenced by the inclusion of fossils, revealing previously unknown shifts in diversification rate, emphasising the role of extinction in shaping present day diversity, and showing that diversification based inference of higher taxa using extant trees is potentially problematic.

1.4.3 Chapter 3

In Chapter 3 I explore the zoogeographic history of Afrotheria, looking at present richness and phylogenetic β-diversity, as well as using BioGeoBEARS to visualise how zoogeographic patterns have differed across lineages and time. My results indicate that, with the exceptions of fully aquatic life and the isolation of Madagascar, no significant zoogeographic realms are realised within the Afrotheria. Extinction appears to be the main cause of present afrotherian diversity, with no true dispersal barriers forming for mainland lineages, implying zoogeography is not a useful metric in the delineation of HESUs within the Afrotheria.

1.4.4 Chapter 4

In Chapter 4 I use several models, starting with simple Brownian motion and progressing to those testing directional shifts and/or evolvability to explore phenotypic data, namely body mass and cranium morphology. The analyses of the models with the highest likelihood are then used to reflect on higher taxa within the Afrotheria. My results indicate that, for body mass, the surprising conclusion is that this greatly diverse clade is nothing more than the result of random walking, however, cranium analyses indicate evolvability shifts within a number of more recently diverged sub-clades, which further reinforces the realisation of evidentiarily defined higher taxa, and that, especially for species with no genetic information, morphological analyses are crucial to classification and the investigation of macroevolution.

1.4.5 Chapter 5

In Chapter 5 I use the Generalised Mixed Yule Coalescent model on phylogenies of the Afrotheria, including extinct species. My results suggest an estimated eleven diversification clusters in the present, mapping to between the Linnaean ranks of family and genus. These clusters can be considered HESUs. When both extant and extinct taxa are included, an average estimate of when these clusters begin to form within the clade is 35-36 million years ago. This validates that phylogenetically realised evolutionary entities can be uncovered, driven by diversification, and that Linnaean ranks do not necessarily reflect evolutionary significant higher taxa. To best understand our present, we must truly look in the past.

Chapter 2

Informing a Molecular and Morphological Phylogeny of Afrotheria

2.1 Abstract

Phylogenies provide the basis for elucidating macroevolutionary dynamics. As most lifeforms in history are now extinct, the inclusion of fossils in analyses is vital to truly understand these dynamics, yet most analyses presently undertaken are solely molecular, in part due to the difficulties involved in quantifying and incorporating morphological data in computational molecular approaches of phylogenetic synthesis. Here I generate a phylogeny of the clade Afrotheria, incorporating 635 extant and extinct species using a total-evidence molecular and morphological approach, which conforms to the current understanding of the clade's phylogenetic relationships. I further show that the illation of diversification in the clade is affected due to the use of fossil data. Patterns that were uncovered only when fossils were incorporated show that afrotheres diversification dynamics are volatile and the diversity of the group has been shaped most strongly by diminished extinction. The phylogenies and realised patterns from this study can be further used to better comprehend Afrotheria in a macroevolutionary sense.

2.2 Introduction

Ever since Darwin mused ‘I think’ and sketched out a tree, phylogenies have been a vital part of understanding evolutionary relationships (Darwin 1837). The discovery of more species and the rapid expansion of genomic data, as well as the advent of contemporary computational methods, have led to a more accurate and comprehensive understanding of evolutionary relationships across large parts of the tree of life (Jetz *et al.* 2012; Upham *et al.* 2019; Zurano *et al.* 2019). Phylogenies are important tools in topological, spatial and temporal analyses and form both the basis of modern taxonomy and our understanding of the patterns and processes that generate biological diversity.

Apropos, deductions of diversification have been noticeably untrustworthy when fossil taxa are lacking (Tarver & Donoghue 2011). A longstanding challenge has been incorporating both extant and extinct (fossil) taxa, necessary considering most lifeforms on Earth are now extinct. Indeed, the extended use of fossils in analyses is relatively novel and has been proven advantageous, for example, by revealing macroevolutionary dynamics in speciation and extinction rates that were not apparent with extant-only trees (Šmíd & Tolley 2019; Lloyd & Slater 2021). This suggests that the majority of diversification investigations to date, which are typically derived from genetic information alone, may be unreliable. This persists as a significant disparity between potential conclusions drawn from these analyses, as fossil data aids in dating and scaling trees, and this calibration of phylogenetic frameworks allows for macroevolutionary processes to be uncovered in deep time (Jetz *et al.* 2012; Upham *et al.* 2019; Šmíd & Tolley 2019; Lloyd & Slater 2021).

Importantly, recently developed tools (Rabosky 2014; Mitchell *et al.* 2019) for studying diversification dynamics are beginning to be applied to data sets of extant and extinct lineages, revealing new, and unexpected, insights into the accumulation of species diversity over time. For example, by using FossilBAMM, Lloyd & Slater (2021) highlight the essential roles of fossil data, their benefits over exclusively extant analyses and issues with morphological data in the diversification history of the Cetacea. One key role is on the comprehension of speciation and extinction regimes. Analyses that include fossil data can yield entirely different outcomes to exclusively molecular studies and uncover previously undetected patterns. Incorporating fossil information has been shown to ameliorate speciation, and particularly extinction inferences, to the point where tree topology and fossil ages combine to garner improved rate estimates over those from extant species alone (Lloyd & Slater 2021; Mitchell *et al.* 2019; Didier *et al.* 2017). These enhanced understandings can even lead to established hypotheses being altered, for example challenging the traditional view of a single, ancient colonization of Madagascar in lemurs (Gunnell *et al.* 2018). Louca & Pennell (2020) further argue that as a rule, purely extant analyses are solely beneficial for assuming speciation rates in the present, therefore investigations into extinction and speciation dynamics in deep time must include fossil data.

Here, I focus on the phylogeny and diversity dynamics of the Afrotheria, a morphologically varied clade of mammals. The Afrotheria are currently classified into nine families: Elephantidae, Trichechidae, Dugongidae, Procaviidae, Orycteropodidae, Macroscelididae, Tenrecidae, Potamogalidae and Chrysochloridae. Outstanding instances of ecological and morphological convergence with other mammal clades are found throughout these nine families (Tabuce *et al.* 2008; Gheerbrant *et al.* 2016). Elephantidae are large herbivores, convergent with rhinoceros and other true ungulates. Trichechidae (manatees) and Dugongidae are adapted to fully aquatic life, like cetaceans. Procaviidae (hyraxes) are small herbivores, akin to lagomorphs, rodents and small macropods. The sole member of Orycteropodidae (aardvark) is a medium-sized insectivore, like true anteaters and pangolins, and to a lesser extent, the numbat and short-beaked echidna. Macroscelididae (sengis) are small insectivores, similar to shrews, solenodons and shrew opossums. Tenrecidae are small omnivores, with a great deal of diversity; some appearing like opossums, hedgehogs, shrews or small rodents. Potamogalidae (otter shrews) resemble otters and Chrysochloridae (golden moles) are like both true and marsupial moles (IUCN 2024). Such a remarkable range of morphological variety within Afrotheria allows it to function as a miniature ‘snapshot’ of the mammalian class and act as a foundation for comprehending macroevolutionary dynamics.

Although phylogenies of Afrotheria exist, many just focus on small subsets of the clade (Carlen *et al*. 2017; Heritage *et al*. 2020) and those on a larger scale are incomplete (Seiffert 2007; Puttick & Thomas 2015). Carlen *et al.* (2017) solely explore the afrothere genus *Rhynchocyon* using only extant species information and support monophyly, while indicating *R. stuhlmanni* should be considered a species, not a subspecies of *R. cirnei*. Heritage *et al.* (2020) study a larger number of afrothere lineages and use a small number of fossil taxa for node calibration in the phylogenetic production, however many extant species are not included as the focus is on sengi subspecies.

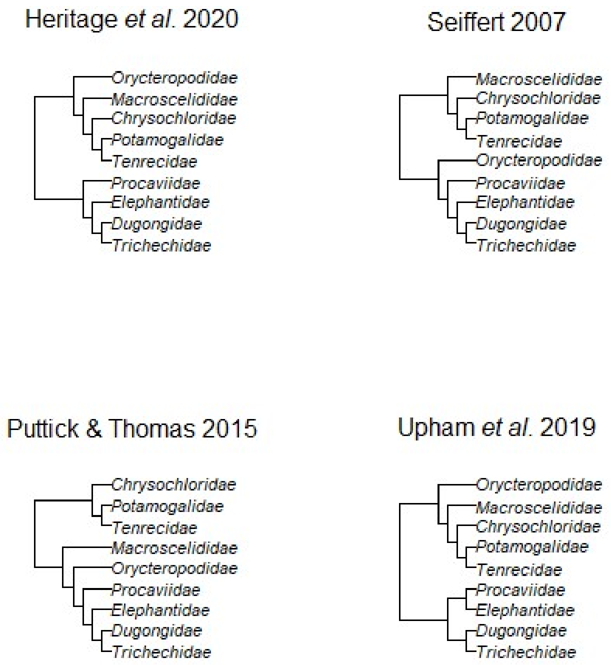

Heritage *et al.* 2020
Seiffert 2007
Puttick & Thomas 2015
Upham *et al.* 2019

Figure 1. *Phylogenetic relationships of extant Afrotheria inferred by previous studies.*

Their study introduces the new genus *Galegeeska*, represented by the sole species *G. revoilii*, and recognises all Macroscelididae genera to be monophyletic, except for *Elephantulus* due to the exclusion of two species from the investigation. Heritage *et al.* (2020) find with strong support the phylogenetic relationships shown in Figure 1. Advancements in phylogenetic synthesis, computational power and access to numbers of large genome sequences have occurred since the afrotherian study by Seiffert (2007) was undertaken. Although utilising a number of fossils in the morphological approach, only 16 extant afrothere species are included, out of over 80 recognised. Their study found different relationships to that of Heritage *et al.* (2020). Puttick & Thomas (2015) used molecular information for 77 extant and 9 recently extinct afrotherian species, as well as morphological information of 39 fossil afrotheres. This covers almost all extant members and provides good historical representation, but another different set of phylogenetic relationships were found. Tabuce *et al.* (2008) reviewed the then current understanding of Afrotheria. Although discussing many different possible taxonomies, they recognised a majority consensus phylogeny that is the same as that later realised by Heritage *et al.* (2020). The discrepancy between this common understanding of afrothere phylogenetic relationships and the other relationships found by Seiffert (2007) and Puttick & Thomas (2015) is obvious and calls for more research into realising an accurate, large scale phylogeny of Afrotheria. Upham *et al.* (2019) inferred a tree of the entirety of Mammalia using both molecular and morphological information, including fossil taxa. Their study found afrotheres have a relatively low speciation rate and realised another set of relationships. They did recognise Trichechidae and Dugongidae to be ‘zombie lineages’, where molecular divergence occurs more recently than the youngest ages that crown fossils infer, causing an indifference with existing understandings of fossil data. The relationship reported by Upham *et al.* (2019) was previously found by Kuntner *et al.* (2011), however they do note it as ‘contradicting many prior studies’ and to be ‘controversial’. Their analysis used 70% of extant afrothere species and was a purely molecular approach.

To best explore macroevolutionary dynamics, an accurate, complete phylogeny must be used. Here, I construct a new phylogeny of Afrotheria, incorporating as many extant and extinct taxa as possible. Specifically, I use a molecular and morphological total-evidence approach with a model-based and taxonomically informed methodology to infer potential positions for unsampled taxa to generate a large tree of >600 extinct and extant species. I then use the phylogeny to explore the diversification dynamics of Afrotheria and assess how our understanding of the contributions of speciation and extinction to diversity is strongly influenced by the inclusion/exclusion of fossil data.

2.3 Methods

2.3.1 Genetic Data

Sequences for 11 nuclear (ADORA3, APOB, APP, BDNF, BRCA1, GHR, IRBP, PNOC, RAG1, RAG2, VWF) and 13 mitochondrial (ATP6, ATP8, COI, COII, COIII, CytB, ND1, ND2, ND3, ND4, ND4L, ND5, ND6) genes across 79 extant and 6 extinct species of afrotherians (704 sequences in total) were collected from GenBank and added to the bioinformatics software platform Geneious Prime 2021.0.3. These genes were chosen as they are well sampled for many species and have been used in previous phylogenetic studies (see examples above). The 6 extinct species used were *Hydrodamalis gigas*, *Mammut americanum*, *Mammuthus columbi*, *M. exilis*, *M. primigenius* and *Palaeoloxodon antiquus*.

In Geneious Prime, individual genes were extracted from the multiplicates and each of the 24 collections of sequences were aligned using MAFFT v7.450 on default settings (Katoh *et al*. 2002; Katoh & Standley 2013). Initial trees were produced using RAxML v8 on default settings (Stamatakis 2014). These trees were used to identify potential errors in alignment, with exceptionally long branches indicating the possibility of alignment or data error. From this, errors were noticed in ND6 and RAG1. ND6 was fixed by reverse complementing the sequences. For RAG1, six sequences were identified as problematic. Specifically, *Heterohyrax brucei, Rhynchocyon petersi, Elephantulus rufescens, Amblysomus hottentotus, Macroscelides proboscideus* and *Elephas maximus* clustered together on single long branch. Based on previous studies, this is extremely unlikely to be correct. It was not possible to rectify the error by reverse complementing, so these 6 sequences were removed and the MAFFT alignments for these fixed genes were re-run, and new RAxML trees produced, showing no apparent errors.

Using Seqotron v1 the 24 MAFFT alignments were further checked for potential errors manually. Coding sequences were manually edited where necessary to ensure that all alignments were in the correct reading frame (Fourment & Holmes 2016). Using the Analyses of Phylogenetics and Evolution library (ape 5.3) (Paradis & Schliep 2019) in the statistical computing and graphics environment R (R Development Core Team 2020), the 24 Seqotron checked or edited MAFFT alignments were combined into a single, large alignment (26,538 base pairs) and a preliminary tree was generated in Geneious Prime using RAxML as a final check for clear alignment errors. PartitionFinder2 was then run on this concatenated alignment using linked branch lengths, the corrected Akaike Information Criterion (AICc) metric for model selection, and a greedy search scheme to consider the pre-defined BEAST collection of models (Lanfear *et al*. 2016; Lanfear *et al*. 2012; Guindon *et al*. 2010). From the 70 initial data sets; 23 protein-coding genes considered for each base pair position of the triplet code plus the non-coding APP, PartitionFinder2 recommended 51 partitions of the data (Table 1). PartitionFinder2 assigned one of 3 models as the best model for each subset; GTR, HKY or TRN (Tavaré 1986; Hasegawa *et al*. 1985; Tamura & Nei 1993), as well as SYM or K80, which are special instances of GTR and HKY respectively, where the base frequencies are equal (Zharkikh 1994; Kimura 1980). Furthermore, a gamma-distributed rate variation (G) and/or an estimated proportion of invariable sites (I) were also recommended for some subsets.

Table 1. *PartitionFinder2 Best Scheme showing the new subset designation, the best model, the number of sites and the original partition names.*

Subset	Best Model	Sites	Partition Names
1	GTR+G+X	603	IRBP_p2, ADORA3_p1
2	HKY+X	171	ADORA3_p2
3	GTR+G+X	763	PNOC_p3, IRBP_p3, ADORA3_p3
4	GTR+G+X	782	APOB_p1
5	GTR+G+X	782	APOB_p2
6	GTR+I+X	991	APOB_p3, RAG2_p3
7	GTR+G+X	862	APP
8	GTR+G+X	235	ATP6_p1
9	GTR+I+G+X	455	ND3_p2, ND4L_p2, ATP6_p2
10	TRN+I+G+X	463	ATP6_p3, COII_p3
11	TRN+G+X	70	ATP8_p1
12	HKY+G+X	70	ATP8_p2
13	HKY+I+G+X	70	ATP8_p3
14	GTR+G+X	1121	BDNF_p1, RAG1_p1
15	K80+I	264	BDNF_p2
16	GTR+G+X	264	BDNF_p3
17	GTR+G+X	1004	BRCA1_p1
18	GTR+G+X	1003	BRCA1_p2
19	GTR+G+X	1003	BRCA1_p3
20	GTR+I+G+X	517	COI_p1
21	GTR+I+G+X	779	COIII_p2, COI_p2
22	GTR+I+G+X	517	COI_p3
23	GTR+I+G+X	229	COII_p1
24	HKY+I+G+X	928	ND1_p2, COII_p2, CytB_p2
25	SYM+I+G	263	COIII_p1
26	TRN+I+G+X	262	COIII_p3
27	GTR+I+G+X	701	CytB_p1, ND1_p1
28	GTR+I+G+X	381	CytB_p3
29	GTR+G+X	568	GHR_p1, RAG2_p1
30	HKY+G+X	520	GHR_p2, PNOC_p2
31	TRN+G+X	359	GHR_p3
32	GTR+I+X	432	IRBP_p1
33	TRN+I+G+X	437	ND3_p3, ND1_p3
34	GTR+I+G+X	348	ND2_p1
35	GTR+I+G+X	956	ND2_p2, ND5_p2
36	GTR+G+X	348	ND2_p3
37	GTR+I+X	118	ND3_p1
38	GTR+I+G+X	1079	ND4_p1, ND5_p1
39	GTR+I+G+X	470	ND4_p2
40	GTR+I+G+X	1180	ND5_p3, ND4L_p3, ND4_p3
41	SYM+G	102	ND4L_p1

42	GTR+I+G+X	182	ND6_p1
43	HKY+G+X	182	ND6_p2
44	GTR+G+X	182	ND6_p3
45	GTR+G+X	161	PNOC_p1
46	HKY+I+G+X	857	RAG1_p2
47	TRN+G+X	857	RAG1_p3
48	HKY+I+X	209	RAG2_p2
49	TRN+G+X	480	VWF_p1
50	SYM+I+G	479	VWF_p2
51	HKY+G+X	479	VWF_p3

2.3.2 Morphological Data

A 395 character morphological matrix for 16 extant species which also have available genetic information and 39 fossil afrotherian species was acquired from previous studies; originally from Seiffert (2007), altered in Seiffert *et al*. (2012) and used by Puttick & Thomas (2015). The ages of the 39 fossil species were also collected from Puttick & Thomas (2015).

2.3.3 Initial Phylogenetic Construction

For the temporal analyses, the 6 extinct species with genetic data were considered extant, due to how geologically recently they became extinct; *P. antiquus* 30kya, *M. exilis* 13kya, *M. columbi* and *Mammut americanum* 11kya, *M. primigenius* 4kya and *H. gigas* by 1768. The 124 species phylogenies were then estimated using BEAUti and BEAST2, using a log normal relaxed clock and a fossilised birth death model (Bouckaert *et al*. 2019). This allows each branch to have its own clock rate and for all fossils to be included and used in the dating of nodes (Drummond *et al*. 2006; Heath *et al*. 2014).

2.3.4 Additional Phylogenetic Construction

Once completed, any nodes with >0.95 support were given monophyly constraints and a further 502 extinct and 9 extant species were added as constrained taxon sets before a second BEAST analysis was performed (Table S2.1). Many included species were from Sudamericungulata, a lineage of extinct South American mammals such as *Toxodon*, which were considered afrotherians by Avilla & Mothé (2021). These additional species positions were determined by previous studies, largely a taxonomic list on The Paleobiology Database (PBDB 2021). The 124 species phylogenies showed inconsistencies within Elephantidae relationships, so a solely Elephantidae BEAST run was performed, a small scale version of the first afrotherian analysis, with *T. manatus* as an outgroup (Figure 2). This rapidly reached a consistent representation of the relationships within

Elephantidae, and this was used as the basis for their positions in the second afrotherian analysis. The 635 species phylogenies were created using the same settings as the first run.

2.3.5 Diversification Analyses

BAMM and FossilBAMM were used for diversification analyses, as well as R and the BAMMtools R package (Rabosky 2014; Mitchell *et al.* 2019; Rabosky *et al*. 2014; R Development Core Team 2020). BAMM can only be applied to extant species and analyses were performed on both the 124 and 635 species phylogenies with all fossil species excluded. All BAMM and FossilBAMM (see below) analyses ran for 10^8 generations sampling every $2{\cdot}10^4$, expecting 5 rate shifts with certain time-mode variability for 4 Markov chains. The function setBAMMpriors in BAMMtools was used to estimate appropriate prior values. The initial λ and μ priors were 2.17726392008731 and the λ shift prior was 0.0215433922900307. The initial root speciation rate was 0.032, the initial root extinction rate was 0.005 and the initial shift parameter for the root process and the initial number of non-root processes were 0. Convergence was tested by plotting log likelihood against generations. FossilBAMM was used to analyse the phylogeny including all 635 species using the one-rate preservation model, and to run and be analysed, non-positive (0 length) branches were assigned a length equal to 1% of the minimum positive branch length. The following additional priors were used for FossilBAMM analyses: maximum extinction probability of 0.9999999, initial preservation rate of 0.1 and update rate preservation rate, update preservation rate scale and preservation rate prior of 1.

2.4 Results

2.4.1 Phylogenies

A maximum clade credibility (MCC) tree was taken from the first BEAST run (124 species) and except for Elephantidae irregularities noted above and shown in Figure 2, the phylogeny was consistent with other afrotherian trees, with most nodes having very good support (Tabuce *et al.* 2008). The MCC tree taken from the 635 species analysis (species with molecular and/or morphological data shown in Figure 3) was congruent with previous afrotherian phylogenies, largely because it was heavily influenced by a taxonomic fossil list and the monophyly constraints of almost the entire initial species phylogeny.

Figure 3, along with Figure S2.1, show Afrotheria branched into 2 lineages early on (74.74Mya, 95% HPD 82.05-71.99), a clade consisting of Orycteropodidae, Macroscelididae, Tenrecidae, Potamogalidae, Chrysochloridae and extinct relatives and a second clade of Elephantidae, Trichechidae, Dugongidae, Procaviidae and the Sudamericungulata and other extinct species.

Hyraxes and the Sudamericungulata diverged from proboscideans and sirenians 72.35Mya (74.98-67.06). Proboscideans and sirenians split 66.37Mya (70.73-61.41). Aardvarks branched from other members of their afrotherian lineage 72.6Mya (78.71-68.46), followed by sengis 68.88Mya (74.08-66.9). Golden moles then diverged from tenrecs and otter shrews 52.26Mya (58.71-47.88). *Chrysochloris*, *Elephantalus* and *Dendrohyrax* were found to be paraphyletic.

Deeper nodes throughout the tree are projected well below the oldest included taxa. The oldest extinct species in the tree are from around the K-Pg boundary (c.66Mya), yet the estimated root age exceeds this by ~10 million years. The inferred root age, and that of other deep splits in the tree, are consistent with other recent studies (Springer 2022).

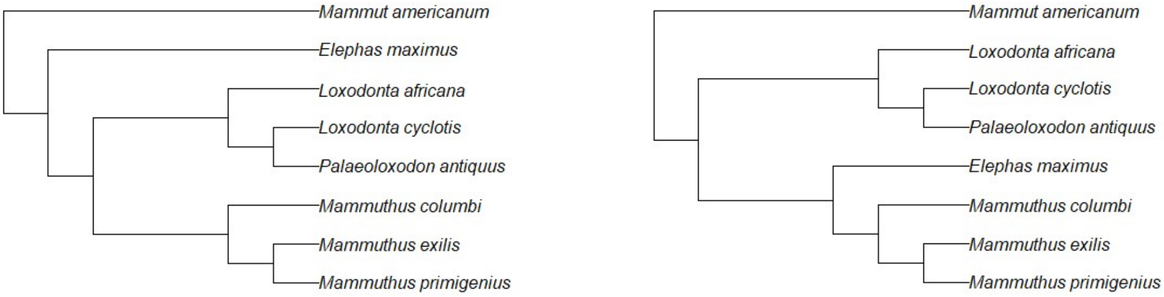


Figure 2. *Phylogenies that show the initial (L) and sole (R) Elephantidae relationships. Initial relationships are from the 124 species BEAST analysis. Sole relationships are from the Elephantidae only BEAST analysis.*

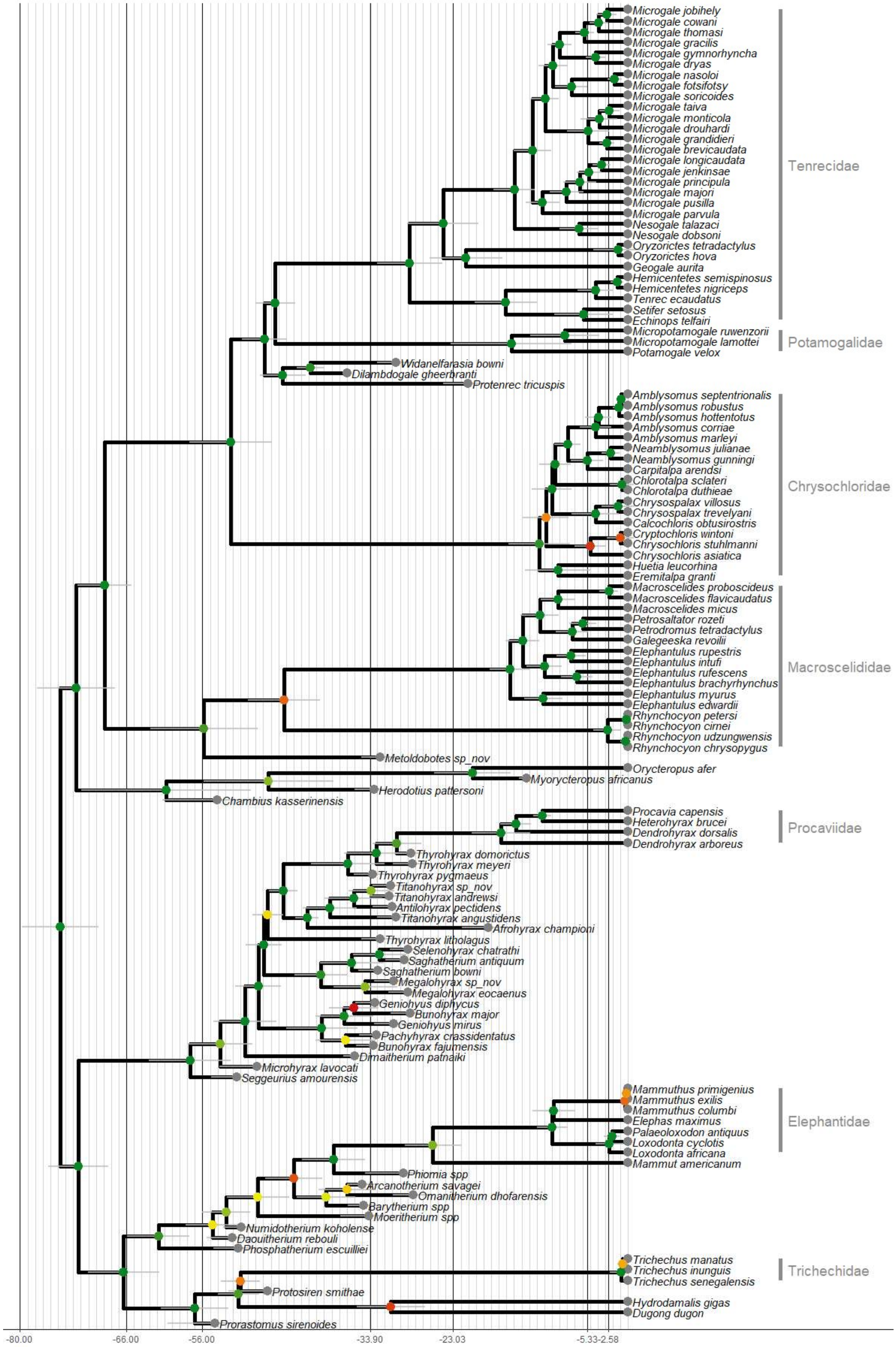

Microgale jobihely
Microgale cowani
Microgale thomasi
Microgale gracilis
Microgale gymnorhyncha
Microgale dryas
Microgale nasoloi
Microgale fotsifotsy
Microgale soricoides
Microgale taiva
Microgale monticola
Microgale drouhardi
Microgale grandidieri
Microgale brevicaudata
Microgale longicaudata
Microgale jenkinsae
Microgale principula
Microgale majori
Microgale pusilla
Microgale parvula
Nesogale talazaci
Nesogale dobsoni
Oryzorictes tetradactylus
Oryzorictes hova
Geogale aurita
Hemicentetes semispinosus
Hemicentetes nigriceps
Tenrec ecaudatus
Setifer setosus
Echinops telfairi
Micropotamogale ruwenzorii
Micropotamogale lamottei
Potamogale velox
Widanelfarasia bowni
Dilambdogale gheerbranti
Protenrec tricuspis
Tenrecidae
Potamogalidae
Amblysomus septentrionalis
Amblysomus robustus
Amblysomus hottentotus
Amblysomus corriae
Amblysomus marleyi
Neamblysomus julianae
Neamblysomus gunningi
Carpitalpa arendsi
Chlorotalpa sclateri
Chlorotalpa duthieae
Chrysospalax villosus
Chrysospalax trevelyani
Calcochloris obtusirostris
Cryptochloris wintoni
Chrysochloris stuhlmanni
Chrysochloris asiatica
Huetia leucorhina
Eremitalpa granti
Chrysochloridae
Macroscelides proboscideus
Macroscelides flavicaudatus
Macroscelides micus
Petrosaltator rozeti
Petrodromus tetradactylus
Galegeeska revoilii
Elephantulus rupestris
Elephantulus intufi
Elephantulus rufescens
Elephantulus brachyrhynchus
Elephantulus myurus
Elephantulus edwardii
Rhynchocyon petersi
Rhynchocyon cirnei
Rhynchocyon udzungwensis
Rhynchocyon chrysopygus
Macroscelididae
Metoldobotes sp_nov
Orycteropus afer
Myorycteropus africanus
Herodotius pattersoni
Chambius kasserinensis
Procavia capensis
Heterohyrax brucei
Dendrohyrax dorsalis
Dendrohyrax arboreus
Procaviidae
Thyrohyrax domorictus
Thyrohyrax meyeri
Thyrohyrax pygmaeus
Titanohyrax sp_nov
Titanohyrax andrewsi
Antilohyrax pectidens
Titanohyrax angustidens
Afrohyrax championi
Thyrohyrax litholagus
Selenohyrax chatrathi
Saghatherium antiquum
Saghatherium bowni
Megalohyrax sp_nov
Megalohyrax eocaenus
Geniohyus diphycus
Bunohyrax major
Geniohyus mirus
Pachyhyrax crassidentatus
Bunohyrax fajumensis
Dimaitherium patnaiki
Microhyrax lavocati
Seggeurius amourensis
Mammuthus primigenius
Mammuthus exilis
Mammuthus columbi
Elephas maximus
Palaeoloxodon antiquus
Loxodonta cyclotis
Loxodonta africana
Mammut americanum
Elephantidae
Phiomia spp
Arcanotherium savagei
Omanitherium dhofarensis
Barytherium spp
Moeritherium spp
Numidotherium koholense
Daouitherium rebouli
Phosphatherium escuilliei
Trichechus manatus
Trichechus inunguis
Trichechus senegalensis
Trichechidae
Protosiren smithae
Hydrodamalis gigas
Dugong dugon
Prorastomus sirenoides
-80.00
-66.00
-56.00
-33.90
-23.03
-5.33-2.58

***Figure 3.** A time calibrated phylogenetic tree of Afrotheria taken from the 635 species BEAST analysis (only species with molecular and/or morphological data shown). Horizontal grey bars represent the 95% highest posterior density (HPD) of each node. The coloured circles at each node represent the posterior probability support. Support values (0-100%) were divided into 4 equal sections along a colour gradient, with very poor (25%) support shown as red, poor (50%) support as orange, good (75%) support as yellow and very good (100%) as green. Each gridline represents 1 million years, with Epochs indicated by thin black vertical lines. From most distant to present, these are the end of the Late Cretaceous, Palaeocene, Eocene, Oligocene, Miocene, Pliocene and combined Pleistocene and Holocene. 7 Families are named, the other 2 only have one extant species: Dugongidae (Dugong dugon) and Orycteropodidae (Orycteropus afer).*

2.4.2 Diversification Analyses

Regular BAMM analyses do not allow the inclusion of extinct species, and the extant analysis of the 124 species tree implies that there is a high probability for zero significant shifts in diversification rate occurring (Figure 4a). Within extant afrotherian lineages, BAMM indicates that speciation rate very slightly increases over time, with the genus *Rhynchocyon* having a recent increased rate of speciation compared to the rest of the clade. However, this is negligible, as the entire lineage varies from just 0.085 to 0.11 speciation events per million years (EMy^{-1}); therefore further analyses are necessary to investigate the speciation, extinction and net diversification rates in more detail, and explore how analysing these rates with fossil species included impacts the results. Extant BAMM analyses of the pruned 635 species tree again show no rate shifts (Figure 4b) and a slight speciation increase over time, which is again negligible, with the whole lineage ranging between 0.14 to 0.17 speciation events per million years.

The FossilBAMM analyses differ substantially from those based on extant species alone. Figure 4c shows the distribution of the number of posterior rate shifts present, clearly indicating a strong signal in the data whereby the inferred number of posterior shifts greatly exceeds the prior. The inferred number of shifts ranges from 5 to 46, with a mean of 22.327. Figure 5 shows speciation rate ranged from 0.099 to 3.6 EMy^{-1}, extinction rate from 0.032 to 3.3 EMy^{-1} and net diversification rate from -0.22 to 0.3 EMy^{-1}. The lineage marked (**L**) is *Loxodonta* (including *Palaeoloxodon*) and shows a recent decrease in both speciation and extinction rates, and an increase in net diversification rate. Chrysochloridae (**C**), Macroscelididae (minus *Rhynchocyon*) (**M**) and Tenrecidae (**T**) show low speciation and extinction rates with high net diversification over the past ~40 million years. Over time, Figure 6 shows afrotherian speciation and extinction rates both follow a similar pattern to each other, increasing over the first ~10 million years from ~2 to just over 3 EMy^{-1}, followed by a gentle decrease to ~2.5 EMy^{-1} over the next ~25 million years. A plateau at ~2.5 EMy^{-1} holds for the next ~20 million years before a more rapid decrease over the last ~20 million years to ~0.5 EMy^{-1} at the present. The decline in both speciation and extinction could be a real biological signal or an artefact perhaps due to differential (reduced) sampling of fossil taxa closer to the present.

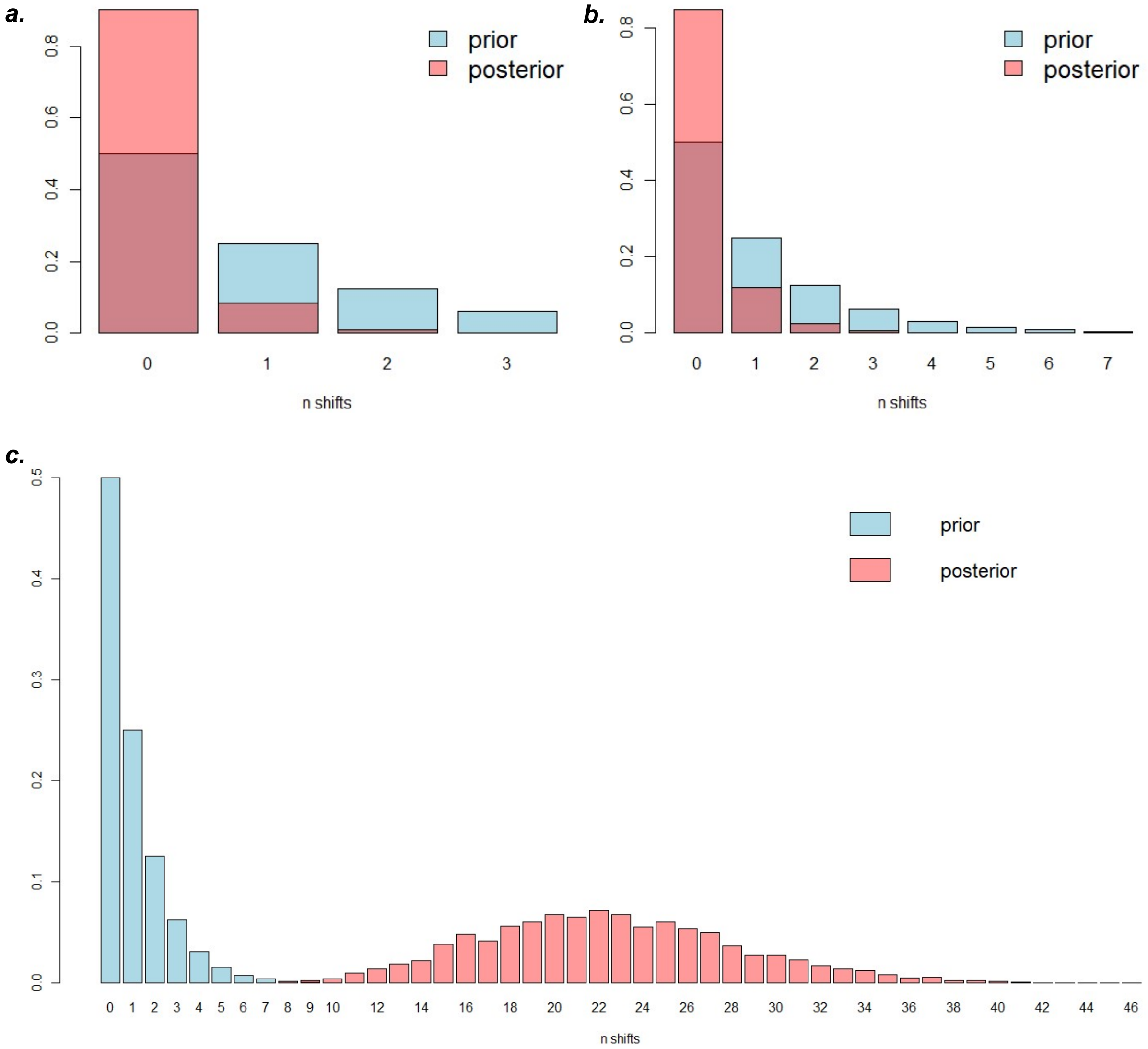


Figure 4. *Frequency distributions showing the probability of n-rate shifts occurring in (**a**) only the extant species from the 124 species phylogeny, (**b**) only the extant species from the 635 species phylogeny and (**c**) the full 635 species phylogeny.*

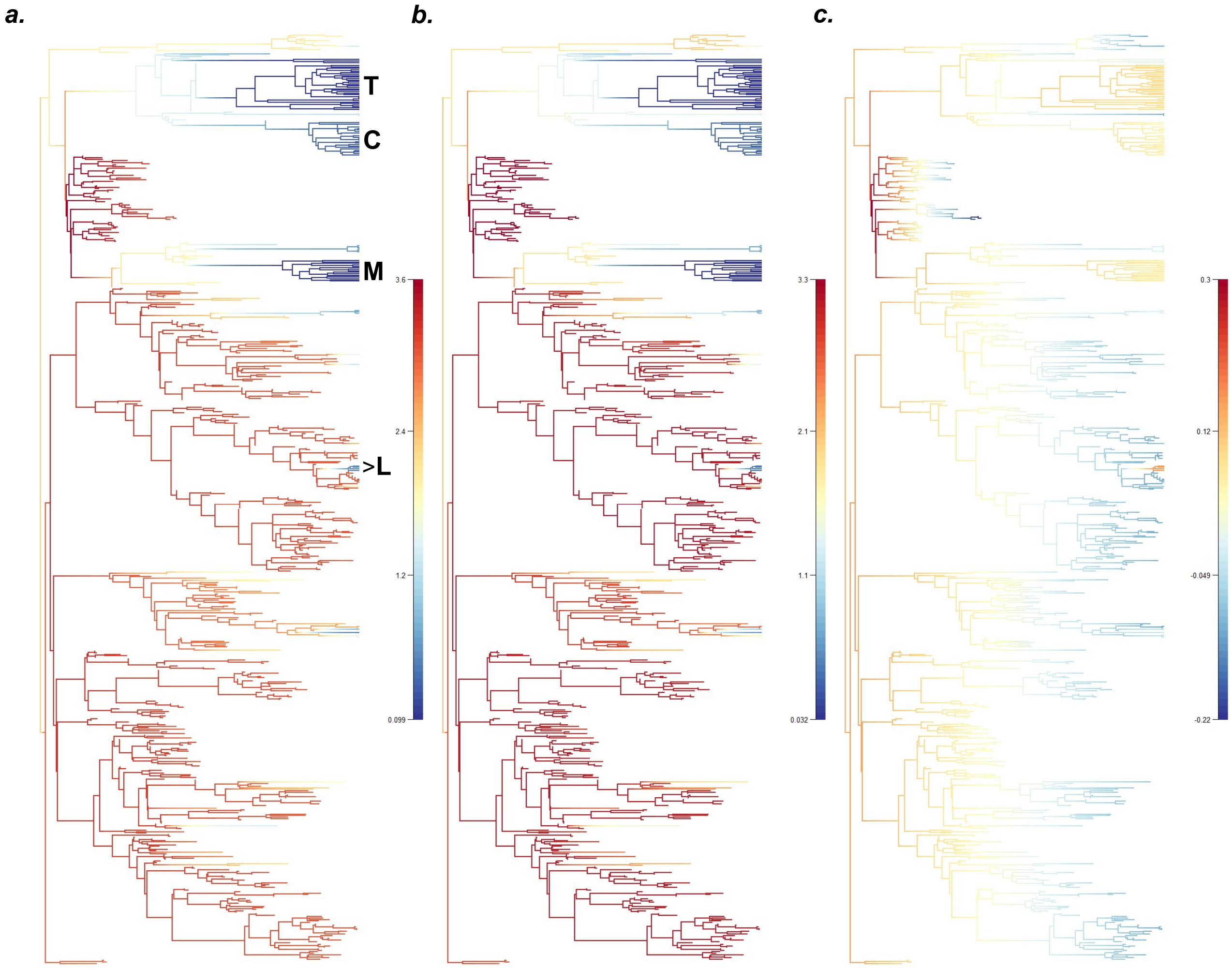


Figure 5. *Afrotherian phylogeny showing the inferred (**a**) speciation rate (speciation events per million years), (**b**) extinction rate and (**c**) net diversification. The lineages marked are (***L***) Loxodonta (including Palaeoloxodon), (***C***) Chrysochloridae, (***M***) Macroscelididae (minus Rhynchocyon) & (***T***) Tenrecidae.*

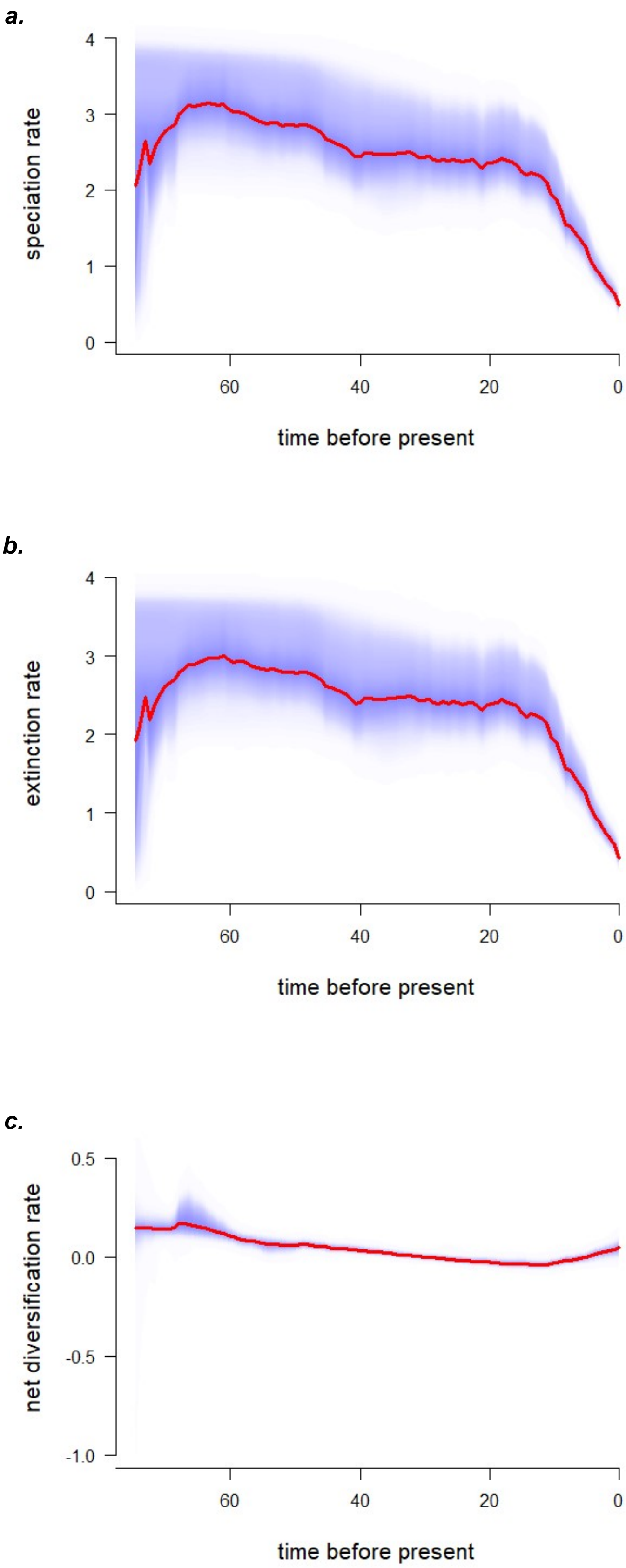


Figure 6. *Graphs that show, over time, the average (**a**) speciation rate (speciation events per million years), (**b**) extinction rate and (**c**) net diversification. All graphs taken from the FossilBAMM analyses.*

2.5 Discussion

Here I show that the inclusion of fossil taxa significantly alters inference of the diversification history of the Afrotheria. Analyses with FossilBAMM reveal shifts in both speciation and extinction rates that are not apparent when only extant taxa are analysed. This is in part due to the inability of a solely extant analysis to accurately determine rates of extinction, and therefore also net diversification (Louca & Pennell 2020). The extant only analyses here indicate zero rate shifts and show almost no change in speciation rate across lineages and through time. This is perhaps surprising because the remarkable morphological diversity among afrotherian families is suggestive of distinct diversification histories. However, the total species analyses clearly show significant variations in speciation rate and, along with the stronger extinction estimates, provide net changes of extant clades that were missed without the inclusion of fossil data.

Both speciation and extinction rates are inferred to decline through time towards the present and with relatively higher rates among extinct afrotherian lineages than among extant lineages. In addition, those extant clades that are more diverse (Tenrecidae + Potamogalidae, Chrysochloridae & Macroscelididae) have lower speciation and extinction rates and higher net diversification rates than the small or single-species lineages. When observing a taxon with many species, a logical assumption is that it is the product of rapid speciation, a supposition that could be biased by the speciation emphasis of solely extant analyses, however in extant afrotherians, these data imply it has actually been driven by decelerated extinction, resulting in much the same effect on net diversification. Extinction driven diversity like this has been found in other clades, such as within cetacean lineages (Lloyd & Slater 2021). These patterns were not observed in the extant only analyses and are only revealed due to the inclusion of fossil data. The critical presence of fossil data to uncover deep time diversification regimes found here and in other studies can lead to overturning our contemporary interpretations of deep time macroevolutionary dynamics.

Among extant afrotherians, the tenrec, otter shrew, golden mole and sengi lineages see decreases in speciation and extinction rates at their origins. The manatees do so after divergence from the dugong lineage and the elephants, hyraxes, dugong and aardvark all see these decreases close to the present. This could be due to the former lineages developing unique morphologies when compared to their close relatives near the time of divergence, and the other lineages, such as the elephants, being not too dissimilar from their recently extinct relatives. Further investigations into the ecology and morphology of afrothere lineages could elucidate the driving forces behind the diversification patterns identified here. Extant, diverse afrotherian clades are all comprised of small bodied species with striking convergence (tenrecs, otter shrews, golden moles & sengis) to other mammals. Their small size means they require less resources to survive, and convergence could indicate a beneficial body plan, both of which could reduce the risk of extinction. On the other hand, lineages with few species have very large bodies and, although still showing convergence to other mammals, do so at less of a degree than those small bodied species. Manatees are an example of this, when compared to other marine mammals.

The inference of macroevolutionary dynamics reported here are contingent on the accuracy of phylogenetic inference. The presence of Sudamericungulata is a novel addition to existing afrotherian phylogenies and analyses of the clade, as they were considered afrotherians by Avilla & Mothé (2021). Although first named in their study, members of the taxa had been suggested to belong to Afrotheria in previous investigations (Agnolin & Chimento 2011; Croft *et al*. 2020). There is some ambiguity in the realisation of these South American native ungulates as afrotherians. Welker *et al.* (2015) found one group of Sudamericungulata to form a clade with Litopterna as the closest relatives of Perissodactyla. If their study is true, this would reduce the accuracy of this study. More generally, the positions of a majority of fossil taxa included here are based on taxonomic constraints and the birth-death tree model so precise locations of rate shifts should be treated cautiously. Moreover, the fossil record is incomplete and even the large number of fossil taxa included here is likely to be an underestimate of the true palaeo-divesity of the Afrotheria. Despite these shortcomings, my results clearly show how excluding fossil taxa can lead to overlooking volatile diversification histories and the role of extinction in shaping diversity.

To conclude, the addition of reliable fossil taxa in phylogenetic and diversification analyses does affect any inferences made, probably beneficially, and reveals patterns hidden in solely extant analyses. Interesting diversification patterns have been detected within Afrotheria, specifically the clade has high volatility and is shaped by reduced extinction rates, not accelerated speciation. This is significant when considering the macroevolutionary dynamics of the clade, as it effects our understanding of how afrotherians evolved and the relationships of super-specific taxa within the clade. Additional studies should be undertaken to explore and better understand the patterns found here, their shaping forces, and their impacts on macroevolutionary elucidations.

Chapter 3

Exploring the Zoogeographic History of Afrotheria

3.1 Abstract

The diversity of life on Earth is often found grouped into geographic areas of communal taxonomy. Zoogeographic realms, formed by processes like dispersal and vicariance, could isolate taxa with shared ancestry and zoogeographic histories. These taxa could represent clades of evolutionary significance, and be considered one way to delineate higher evolutionary significant units (HESUs). However, the extent to which this is true is under-comprehended. Here, I show that the zoogeographic zones of the Afrotheria are mostly scattered, with no major patterns being found. Any barriers that do occur are weak, not containing unique taxa within them, and allowing large scale dispersal, the only exceptions being the sirenians and the tenrecs of Madagascar. Phylogeny over geography seems to shape any historical patterns in the distribution of the clade. My results indicate that, within the Afrotheria, HESUs are not expressed by mutual zoogeographic history. My analyses of the clade only considered extant species, so perhaps the inclusion of fossil taxa could garner different outcomes. If not, any explanation for the realisation of HESUs must come from a different perspective, such as by unique diversification or phenotypic history.

3.2 Introduction

Zoogeographic realms are global topographic regions demarcated by shared taxonomic groupings. In 1876, Alfred Russel Wallace presented his six identified mapped regions: Palaearctic, Ethiopian, Oriental, Australian, Neotropical and Nearctic, which have formed the bedrock of characterising faunal realms for a century and a half (Wallace 1876; Liu *et al*. 2023). Wallace had previously drawn a faunal barrier (Wallace's line) roughly SW-NE through the Makassar straight in Indonesia, to the east of Bali and Borneo and south east of Mindanao, which delineates a most striking faunal turnover from species more typical of Asia to species more typical of Australasia (Mayr 1944; White *et al*. 2021). More recently, the original realms of Wallace have been redesignated and updated, with greater knowledge and advancements in data processing, and pointedly, under the light of modern phylogenetics (Holt *et al*. 2013). Holt *et al*. (2013) recover 20 regions of evolutionary uniqueness from analysing over 21,000 tetrapod species. These regions are then grouped into 11 broader zoological realms that broadly follow the pattern of Wallace's regions.

Realms are observable, but what causes them to emerge? Vicariance and dispersal are both likely routes to the emergence of realms (Dupin *et al*. 2017; Sanmartín 2012). Vicariance would see a widespread ancestor undergoing allopatry, leaving a population in a now geographically isolated area that can become a new species. This could happen to many populations and over macroevolutionary timescales would lead to pockets of higher taxa that share a common ancestry (Sanmartín 2012). Dispersal would see a taxon evolve in one geographic area, then spread to others by crossing barriers that are difficult or less favourable to pass back across (White *et al*. 2021). Dispersal has been found as a major cause of biogeographic regionality formation in groups as varied as the avian class to the tomato family (White *et al*. 2021; Dupin *et al*. 2017). White *et al*. (2021) propose that for mammals and birds, Wallace's line formed due to taxa with high dispersal ability being limited by enduring water barriers. Dupin *et al*. (2017) found that within the tomato family Solanaceae, areas of biogeography were explained by dispersal over vicariance 6-fold.

Ficetola *et al*. (2017) discuss how barriers are not uniform, ranging from shallow to deep, and also consider climate and plate tectonics to be drivers of zoogeographic realms. Therefore, faunal assemblages are kept isolated inside realms by geological, physical, or climatic barriers (Ficetola *et al*. 2017; White *et al*. 2021). Geographic isolation is one proposed driver of higher evolutionary significant units (HESUs) above the species level (Barraclough 2010; Humphreys & Barraclough 2014). Dispersal, even at low levels, has been found to reduce speciation rates. Strong dispersal barriers could therefore form the basis of zoogeographic regions where shared historical diversification and dispersal processes among lineages within regions lead to the potential emergence of higher taxa (Humphreys & Barraclough 2014; Ficetola *et al*. 2017).

As a clade limited mostly to Africa, but with some species found in other regions, the Afrotheria have an interesting geographical distribution (Springer 2022). They are almost entirely constrained to sub-Saharan Africa, but with some wider dispersal, especially in the fossil record, and further, the switch from terrestrial to aquatic habitats occurs along some lineages; of note, the aquatic sirenians (Springer 2022; Tabuce *et al*. 2008). The dugong is found from the African coast, around the Indian Ocean and into the Pacific (IUCN 2024). Beyond Africa, manatees are found down the Atlantic coasts and inlets of North and South America, and up almost the entire Amazon river. Tenrecs are endemic to Madagascar, and are the only afrotherian lineage found there. Only the Asian elephant and rock hyrax are found terrestrially outside the continent, although the rock hyrax is also distributed across Africa (Springer 2022; IUCN 2024). Additionally, there is an abundant fossil record for Afrotheria that broadens geographic distributions, such as the once extensively spread extinct relatives of elephants, and the possible inclusion of some extinct South American native ungulates as afrotheres (Tabuce *et al*. 2008; Avilla & Mothé 2021).

Here, I explore the zoogeographic history of Afrotheria by mapping current distributions, patterns of turnover and transition zones. I investigate the existence of their zoogeographic realms using recent tools (Title *et al*. 2022; Maestri & Duarte 2020; Nakamura *et al*. 2024), then test historical zoogeographic signatures using BioGeoBEARS (Matzke 2013; Park *et al*. 2024), which employs a number of models to test how dispersal, extinction and a number of forms of speciation influence biogeographic patterns on phylogenies (Figure S3.1).

3.3 Methods

3.3.1 Zoogeographic Realms

Spatial data on species ranges of all mammals were procured from the IUCN Red List online resources (IUCN 2024). Using R, these data were filtered to just the Afrotheria, and included only their extant, native and resident or breeding ranges (R Development Core Team 2020). This resulted in 86 species. Multi-polygon sets were then combined so that each species was represented once and with their own unique total zone. Spatial data were processed using the packages ‘sf’, ‘sp’ and ‘terra’ (Pebesma & Bivand 2005, 2023; Pebesma 2018; Bivand *et al*. 2013; Hijmans 2024). EcoPhyloMapper (EPM, Title *et al*. 2022) was then used to create maps of species richness. For these analyses, species were classed as present in a hexagonal cell if at least 20% of the hexagon was covered by the species range, and small ranges (those where the entire range is contained within a cell) were retained. Hexagonal cells were used because they are recommended when calculating β-diversity (Title *et al*. 2022).

To test for distinct zoogeographic regions in the Afrotheria, I assessed phylogenetic β-diversity and the presence of transition zones between distinct afrotherian assemblages across space. For this analysis, the sirenians were too uniquely noisy in the data, indicating high turnover along the coasts where terrestrial afrotherians exist, so were removed for the mapping. In addition to the same EPM conditions, the phylogenetic β-diversity mapping used a radius of 101km (Title *et al.* 2022). This radius defines the distance of cells from the centroid of the focal cell over which β-diversity is calculated. For all phylogenetic analyses in this study, the phylogeny used was the MCC tree of Chapter 2, pruned to the necessary species, with trees handled using the package ‘ape’ (Paradis & Schliep 2019).

To identify evoregions, I used the R package ‘Herodotools’ (Maestri & Duarte 2020) and employed Ward clustering. Ward clustering was chosen because it yielded more stable and intuitive clusters. Evoregions are areas where most inhabitant species arise from a limited number of radiations, and here again the sirenians dominate the differentiation of zoogeographic patterns and quell terrestrial relationships, so were removed for the analyses. Herodotools relies on raster data so square cells, not hexagonal (which are polygons), were used (Title *et al.* 2022). Further data preparation was conducted using ‘PCPS’, ‘vegan’, ‘dplyr’ and ‘picante’ (Nakamura *et al.* 2024; Debastiani 2020; Oksanen *et al.* 2022; Wickham *et al.* 2023; Kembel *et al.* 2010).

3.3.2 Historical Zoogeographic Signatures

BioGeoBEARS tests a number of different models to explore how biogeography varies on phylogenies (Matzke 2013). The three models used here were DEC, DIVA and BayArea (Figure S3.1), all implemented in R (R Development Core Team 2020). All three models test for dispersal, extinction and narrow scale sympatry, and no time stratification was used. Further to this, DEC tests for subset sympatry and narrow vicariance, DIVA tests for narrow and widespread vicariance and BayArea tests for widespread sympatry (Matzke 2013, 2014). All models were fitted with and without the J parameter that tests for a founder-event speciation process (Matzke 2013, 2014). In these models, founder-event speciation occurs when a new lineage disperses to an unoccupied region at cladogenesis. The six models were compared to identify the model with the highest likelihood.

To perform analyses, BioGeoBEARS requires species to be assigned to one or more discrete geographic zones. Here, 88 extant species of Afrotheria were used, and divided into both 10 and 14 geographic zones (Table 1) to test zoogeographic patterns under differently defined regions. The zones were manually approximated from areas of repeated appearances across species from inspection of IUCN maps, and using these occurrences to determine regional borders. Unique areas were then defined for remaining species (IUCN 2024). The 10 zone analysis was also performed as a terrestrial only nine zone analysis by removing the four sirenians and the ‘Water’ zone. To allow the 14 zone model to run due to the large number of permutations, *Procavia capensis* was removed from the ‘Congo Basin’ zone. As continuous spatial data was being fitted to discrete zones, if a small minority of a species’ range existed in another region or other regions, I only assigned it to the region or regions that it mainly occurred in.

There are several differences in zone definitions between the 10 zone and 14 zone analyses (Table 1). Africa N (10A) lost the Atlas mountains, which became its own new zone, Atlas (14I). The rest of Africa N (10A) then merged with part of the 'Rest of Land' zone (10I) to become Africa N/Arabia (14A). The remaining part of 'Rest of Land' (10I) now became India/Asia SE (14J). Water (10J) became Africa W Water (14K), Americas E Water (14L), Amazon (14M) and Indian/Pacific Ocean (14N). All other zones remained the same.

In addition to my manually inferred regions, I also performed a distinct BioGeoBEARS analysis that used the evoregions inferred by Herodotools in order to provide an alternative perspective on afrotherian zoogeographic history. Herodotools inferred 13 regions (see Results). As these two species did not meet the filter criteria stated above for the geographic data, *Cryptochloris wintoni* and *Rhynchocyon stuhlmanni* were not included in the 13 zone BioGeoBEARS analyses of the evoregions. 11 terrestrial evoregions were used, with 2 further zones added for the manatees and dugong respectively.

Table 1. *Names of the 10 and 14 zones categorisations of manually inferred afrotherian assemblages.*

10	14
A: Africa N	A: Africa N/Arabia
B: Africa W	B: Africa W
C: Africa E	C: Africa E
D: Africa S	D: Africa S
E: Congo Basin	E: Congo Basin
F: Madagascar N	F: Madagascar N
G: Madagascar E	G: Madagascar E
H: Madagascar W	H: Madagascar W
I: Rest of Land	I: Atlas
J: Water	J: India/Asia SE
	K: Africa W Water
	L: Americas E Water
	M: Amazon
	N: Indian/Pacific Ocean

3.4 Results

3.4.1 Zoogeographic Realms

Identifying species richness (Figure 1) shows that afrotherians have their highest richness on eastern Madagascar, with moderate richness found throughout sub-Saharan Africa. Madagascan richness is solely driven by tenrecs, and there is low richness found outside Africa, comprising isolated (mainly sirenian) lineages. Identifying phylogenetic transition zones (Figure 2) shows the highest turnover in the south of western Africa, to the south and east of the Congo Basin and along the western coast of southern Africa. Moderate to high turnover is found along central to eastern Madagascar, along the southern border of the Sahara desert and in patches in southern Africa. Similarly, the evoregions inferred with Herodotools (Figures 3, S3.2) again shows patches that do not follow any easily interpreted geographic patterns, with the exception of Madagascar. Some regions had low affinity for all resident species, and were not used in the BioGeoBEARS analysis (regions B, E, N).

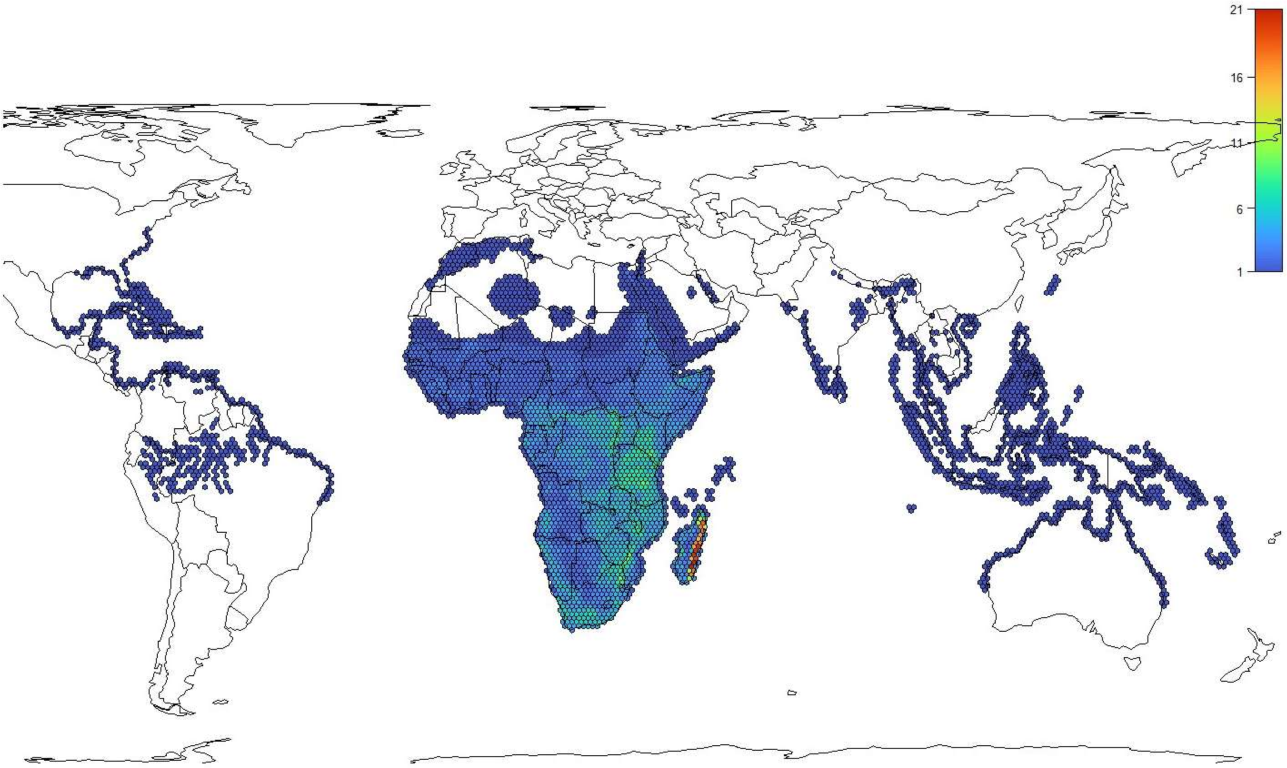


Figure 1. *Species richness of extant Afrotheria.*

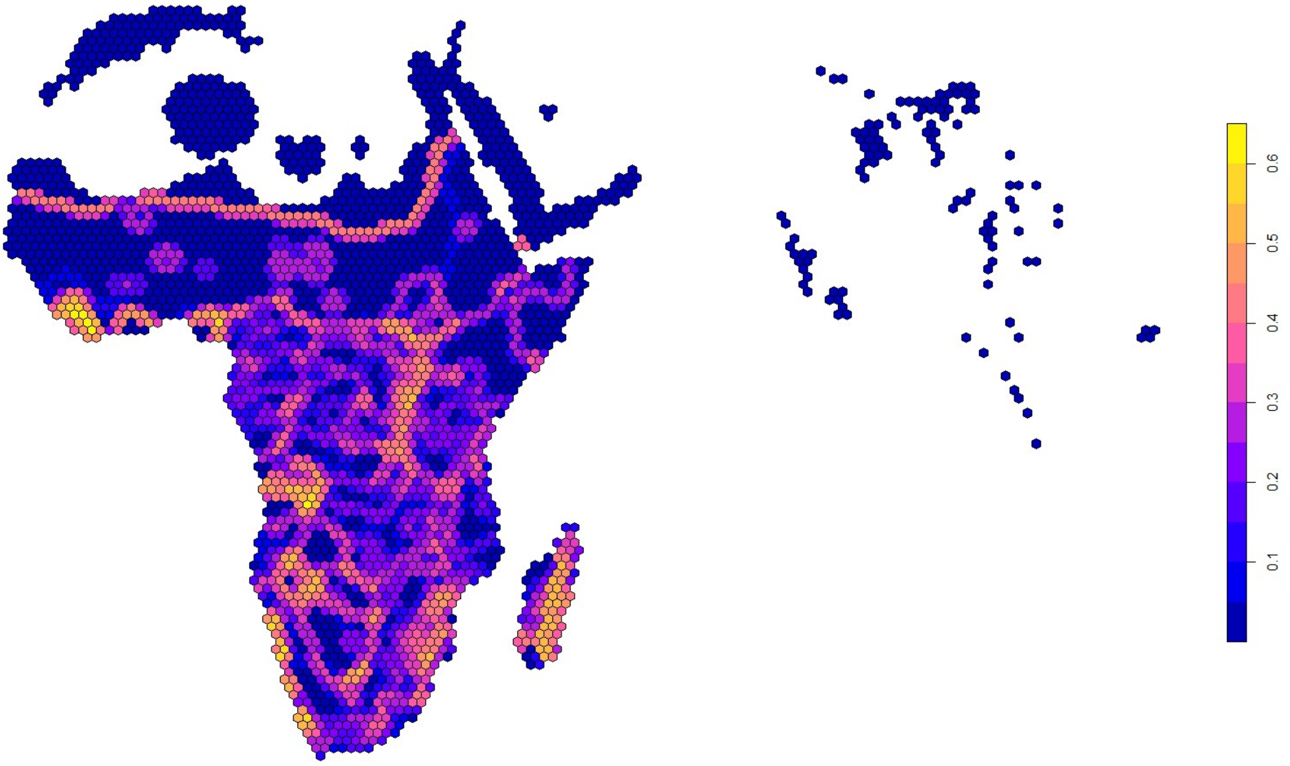


Figure 2. *Phylogenetic turnover of extant terrestrial Afrotheria. Scale from 0-1 reflects Sorensen dissimilarity for each cell.*

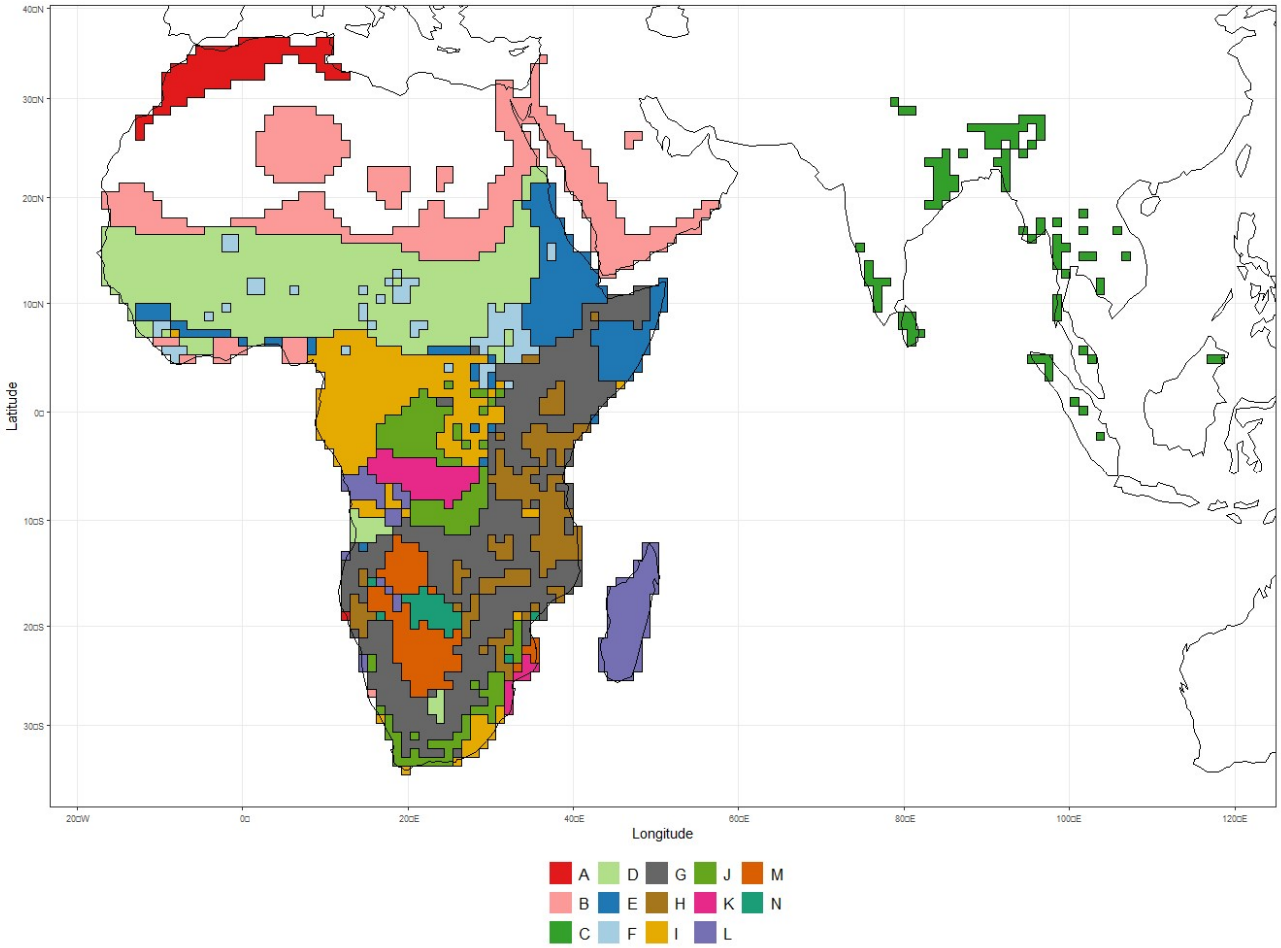


Figure 3. *The evoregions of extant terrestrial Afrotheria inferred by Herodotools.*

3.4.2 Historical Zoogeographic Signatures

The BayArea+J (i.e. with founder-event speciation) was the model with the highest likelihood for all analyses (Table 2). This implies that sympatry on all scales, as well as dispersal, extinction and founder-event speciation, all contributed to the shaping of afrotherian zoogeography. However, across the three manually inferred region analyses, the inferred parameters show that rates of extinction exceed rates of founder event speciation ~2.4-fold and exceed rates of dispersal ~17.9-fold (Table 2) implying that extinction is the strongest driver of observed zoogeography in Afrotheria. Alternatively, the evoregions BioGeoBEARS analysis sees reduced values of 0.79 times and 6.1 times respectively, suggesting that founder-event speciation has shaped the zoogeography of afrotheres slightly more than extinction has. Nevertheless, in all analyses, dispersal was found to be low.

Estimates of historical zoogeographic regions (Figure 4) have strong support for the last 30 million years and for lineages corresponding approximately to the Linnaean rank of family and below. Inferred ancestral regions (nodal pies in Figure 4) show strong confidence for one zone or a small collection of neighbouring zones, or present a second zone or zones that share considerable overlap with the first zone. The elephants and hyraxes are exceptions to this, with uncertainty in their ancestral ranges near the present. This is also true of the aardvark, likely due to it splitting from the other insectivorous afrotheres so long ago. Any estimates before 30 million years ago show considerable uncertainty, so should not be used to draw any conclusions about the larger scale, earlier distributions of the Afrotheria.

The 10 zone BioGeoBEARS analysis (Figure 4) suggest that Macroscelididae originated in south and east Africa, Chrysochloridae originated in south Africa, and Potamogalidae in the Congo Basin. Tenrecidae emigrated from Africa to east Madagascar, then spread across the island. In Macroscelididae, *Rhynchocyon* originated in east Africa, with the remaining clade of lineages originating in east and south Africa, with focus in the south. In Tenrecidae, hedgehog tenrecs stayed across Madagascar, whereas shrew tenrecs mainly diversified in the north and east of Madagascar.

The nine zone terrestrial only analysis suggests broadly the same patterns (Figure S3.3). The 14 zone analysis is also consistent, with Afrotheria originating in sub-Saharan Africa (Figure S3.4). The nodal pies show much stronger confidence in deep time on this analysis. The only distinct differences from other analyses are in the more complicated patterns for ‘water’ and that most recent ancestors of Procaviidae did not originate in the entirety of sub-Saharan Africa; they are not suggested to have partially originated in the Congo Basin, although this analysis did remove one species from the Congo Basin to allow it to run.

The 13 zone BioGeoBEARS analysis, based on the Herodotools evoregions (Figure 5) shows that the Linnaean families each considerably exist within their own geographic regions. This analysis shares the same approximate confidences and uncertainties as the analyses of manually inferred zones.

Table 2. *Results of the 6 BioGeoBEARS analyses for each set of zones (10, 9, 14, 13). Number of parameters (N), founder-event speciation (FES). 10 Zones: Africa (5), Madagascar (3), Rest of Land (1) and Water (1). 9 Zones: Africa (5), Madagascar (3), Rest of Land (1). 14 Zones: Africa (including Arabia) (6), Madagascar (3), India/SE Asia (1), Water (4). 13 Zones: Inferred from evoregions (Figure 3).*

10 Zones	Likelihood	N	Dispersal	Extinction	FES	AICc	AICc_wt
DEC	-277.6	2	0.0043	0.0018	-	559.3	6.40E-15
DEC+J	-274.7	3	0.0038	1.00E-12	0.0073	555.7	3.90E-14
DIVALIKE	-301	2	0.0057	0.0044	-	606	4.60E-25
DIVALIKE+J	-299.5	3	0.0049	0.0006	0.0067	605.4	6.40E-25
BAYAREALIKE	-269.1	2	0.0027	0.037	-	542.4	3.00E-11
BAYAREALIKE+J	-243.8	3	0.0013	0.023	0.0084	494	1

9 Zones	Likelihood	N	Dispersal	Extinction	FES	AICc	AICc_wt
DEC	-261.2	2	0.0052	0.0003	-	526.6	9.40E-13
DEC+J	-258.5	3	0.0047	1.00E-12	0.0078	523.4	4.70E-12
DIVALIKE	-282.6	2	0.0074	0.0061	-	569.3	4.80E-22
DIVALIKE+J	-281.8	3	0.0064	0.0028	0.0061	569.9	3.70E-22
BAYAREALIKE	-257.4	2	0.0035	0.037	-	518.9	4.30E-11
BAYAREALIKE+J	-232.4	3	0.0017	0.023	0.01	471.2	1

14 Zones	Likelihood	N	Dispersal	Extinction	FES	AICc	AICc_wt
DEC	-305	2	0.0034	0.0028	-	614.2	3.70E-19
DEC+J	-302.8	3	0.0029	0.0007	0.0053	611.8	1.30E-18
DIVALIKE	-327.5	2	0.0043	0.0034	-	659.1	6.80E-29
DIVALIKE+J	-326.4	3	0.0038	0.0014	0.0041	659	7.00E-29
BAYAREALIKE	-300.4	2	0.0021	0.036	-	604.9	4.00E-17
BAYAREALIKE+J	-261.5	3	0.0008	0.018	0.0079	529.4	1

13 Zones	Likelihood	N	Dispersal	Extinction	FES	AICc	AICc_wt
DEC	-207.4	2	0.0025	0.0031	-	419	0.0008
DEC+J	-201.8	3	0.0018	6.10E-10	0.0066	409.9	0.08
DIVALIKE	-215.7	2	0.0027	0.0004	-	435.6	2.10E-07
DIVALIKE+J	-213.4	3	0.0021	1.00E-12	0.0045	433.1	7.20E-07
BAYAREALIKE	-229.7	2	0.0024	0.032	-	463.6	1.80E-13
BAYAREALIKE+J	-199.4	3	0.0013	0.0079	0.01	405	0.92

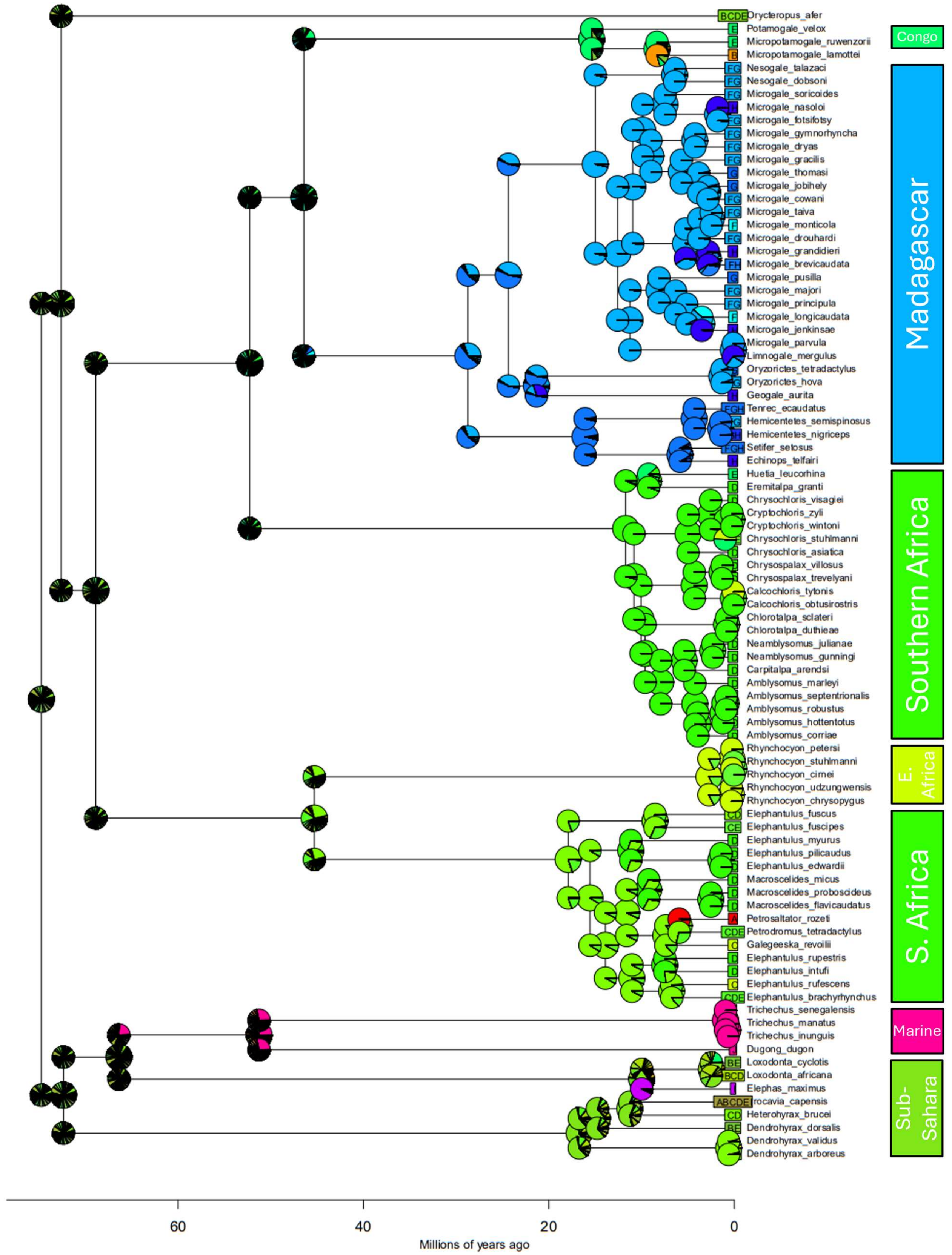


Figure 4. *A phylogeny that shows the zoogeographic history of extant Afrotheria from the BayArea+J 10 zone analysis. Letters refer to regions (Table 1). Note that there are a high number of possible area combinations, and the models indicate high levels of uncertainty in ancestral states. More similar colours indicate geographically adjacent regions. Broad region association is indicated by bars spanning clades.*

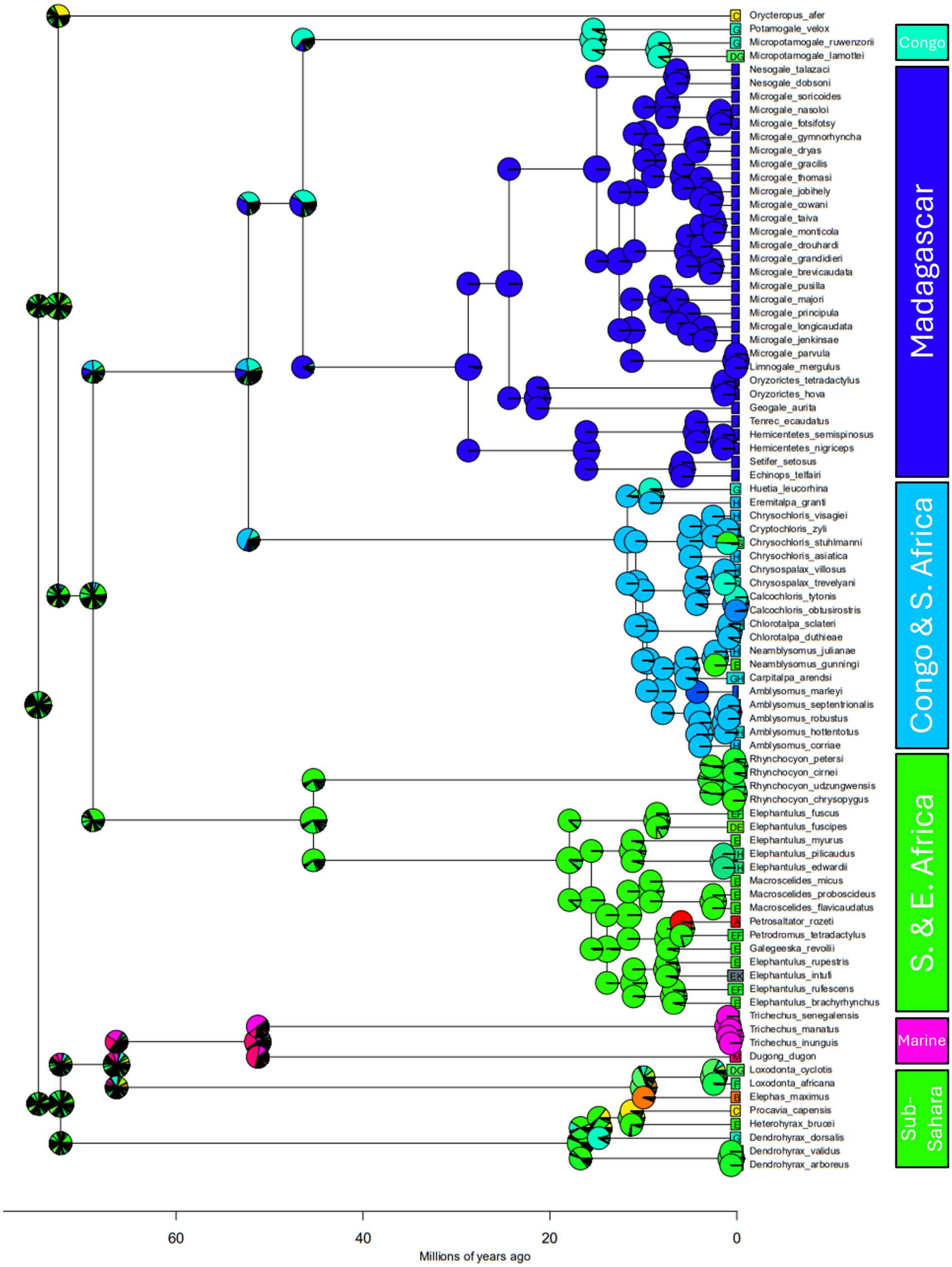


Figure 5. *A phylogeny that shows the zoogeographic history of extant Afrotheria from the BayArea+J 13 zone analysis derived from evoregions. Letters do not perfectly match Figure 3. With B,E,N removed, C in Figure 3 is B here, and so on accounting for those removed. L is the manatee's region and M is the dugong's. Note that there are a high number of possible area combinations, and the models indicate high levels of uncertainty in ancestral states. More similar colours indicate geographically adjacent regions. Broad region association is indicated by bars spanning clades.*

3.5 Discussion

Places with high faunal turnover can be considered boundary areas of flux between zones of phylogenetic and zoogeographic uniqueness. Here, a small number of areas are indicated, but the majority of afrotherian distribution is patchy, with no robust and distinct areas found, suggesting barriers to dispersal for Afrotheria are weak, at least across continental Africa. Madagascar appears to be a significantly unique area from all other land. Although significant changes in turnover appear across the island, there is not enough evidence to sub-divide it. The aquatic environments of the manatees and dugong are clearly distinct, not only from all other afrotheres, but also from each other.

The historical zoogeographic results indicate that when natural geography and richness are used to manually delineate zoogeographic zones, without any regard for phylogeny in their definitions, patterns are found on the phylogeny over time and lineages. The continental Potamogalidae are distinct from their closest relatives, the Malagasy Tenrecidae. The Chrysochloridae and Macroscelididae roughly follow their own geographic patterns also. Trichechidae and Dugongidae remain in their own separate areas. The genus *Rhynchocyon* has a slightly different geographic distribution than the remaining sengis, as do the hedgehog tenrecs from the shrew tenrecs, but these are both more subtle indications than definite patterns. Extinction over sympatry or dispersal appears to be the strongest driver of these patterns.

When phylogeny is included in definitions of zoogeographic zones (Maestri & Duarte 2020), the zones are geographically scattered, so are less based in geography and more driven by phylogeny. Some less well defined zones are found, implying diversity is driven by sympatry, followed by snap dispersal, and not by the presence of strong and persistent barriers to dispersal. Longer scale dispersal is again weak, as with the manually inferred regions, but extinction is reduced. Each Linnaean family adheres to its own approximate zoogeographic history, and zoogeographic barriers are subtle, not strong, implying that geography is not likely to have been a strong driver of HESUs within the Afrotheria.

Extinction is indicated here to have even higher rates than dispersal, implying that recent afrotherian distributions could be what remains of much more widely spread richness. This follows the idea of extinction driven patterns of macroevolution found in Chapter 2 with diversification rates, yet one limitation of these zoogeographic results is that they only come from analysing extant species. If fossil data were also included, different patterns of zoogeographic history might be realised.

The most obvious present day barrier to dispersal across Africa is the Sahara desert. Sub-Saharan species have difficulty moving into the large desert, and it isolates the Mediterranean Atlas mountains in the north west. The Congo Basin is surrounded by higher land, and contains within it tropical rainforest, which wraps around the south of western Africa. Smaller desert and dry steppe areas are found in the south of the continent. The rest of sub-Saharan Africa is made up of savannahs and dryer forests. Madagascar has a plateau that runs down almost the entire island, separating a sliver of tropical rainforest on the steep eastern slope from the larger savannah and steppe conditions on the majority of the island. Sudden transitions in climate and orography are features suggested by Ficetola *et al*. (2017) to make strong barriers, along with tectonics. Tectonics could explain the uniqueness of Madagascan species from their continental sisters, with Holt *et al*. (2013) further considering Madagascar to be a zoogeographic realm distinct from any of Wallace's regions, yet Ficetola *et al*. (2017) only deem tectonics to be strongly associated with deep phylogenetic splits. Saharo-Arabia and Guineo-Congo excise the remainder of Africa in the regionality work of Holt *et al*. (2013). These are areas with different climatic conditions compared to the remaining continent. Despite being observable, none of these barriers are strong. Change in seasonal temperature, the most significant driver of the isolation of the Congo Basin and west African rainforests, is found by Ficetola *et al*. (2017) to form the shallowest of zone boundaries. Afrotherians almost entirely avoid the Sahara desert, with virtually all continental species being found further south. A number of these species exist both in and out of the Congo Basin, suggesting that any differences in sub-Saharan Africa are not too detrimental to dispersal on a medium to large scale. On Madagascar, the central plateau does not fully disconnect the east of the island, allowing species to move around the north and south. Further, tenrecs enjoy such morphological diversity that it has allowed them to colonise the entire island.

Lester *et al*. (2007) found that, although sometimes important, dispersal is not a typical factor that influences range size, at least for marine taxa. This contradicts the perhaps logical reasoning that increasing dispersal ability increases range size, so we cannot assume that existing in a small range means that a species has limited dispersal ability. Within a large avian family, Claramunt *et al*. (2012) further consider the positive and negative affects dispersal has on speciation. Despite concluding that higher dispersal correlates with lower speciation, consistent with Humphreys & Barraclough (2014), Claramunt *et al*. (2012) postulate that this is the case in areas where isolation potential is low. When the chance of geographic isolation is high, higher dispersal might actually drive speciation instead of hindering it. Mayr's peripatry sees speciation by geographic isolation, and as he considered higher taxa to be formed by nothing more than speciation extrapolated, it is logical to assume that geographic isolation is a potential architect of higher taxa (Mayr 1982). Mayr originally conceptualised peripatric speciation from observing that the most peripherally isolated sub-group of a small taxon was often misclassified as a separate species, or even genus. *Drosophila* have been found to speciate as a result of island formation and consequential isolation in the Hawaiian islands, similar to the conjectures of Claramunt *et al*. (2012; Carson 1975; Mayr 1982). Therefore, in other clades, barrier intensity, possibly coupled with complementary variability of dispersal ability among taxa, could result in identifying geographically inferred HESUs, unlike here within the Afrotheria.

To summarise, the only clades that could be delimited by geographic significance here are the manatees, dugong and tenrecs. The sirenians occupy such a unique environment when compared to the remainder of the clade, and Madagascar forms a geographically isolated area for the tenrecs due to the significant dispersal barrier formed by the Mozambique Channel. Extinction is implied to be the most potent driver of zoogeographic patterns, with dispersal as the weakest by a considerable amount. These results contrast with previous studies which demonstrate dispersal as a significant driver of diversity over vicariance, yet concur with previous findings that even when dispersal is moderately low, speciation, and by extent the formation of HESUs, will not likely occur (White *et al*. 2021; Dupin *et al*. 2017; Claramunt *et al*. 2012; Humphreys & Barraclough 2014).

Chapter 4

Tempo and Mode of Phenotypic Divergence in Afrotherian Morphology

4.1 Abstract

Especially for species with no genetic information, morphological analyses are crucial to classification and the investigation of macroevolution. Simpsonian phenotypic macroevolution can be reflected by peaks on the adaptive landscape, where the alteration of phenotype rushes forward as populations change zones and potentially generate super-specific taxa that could bear evolutionary significance. How such higher evolutionary significant units (HESUs) arise from phenotypic divergence and the extent to which they correspond with Linnaean taxonomic ranks remains underexplored. Here, several models of heterogeneous trait evolution were used to explore phenotypic data, namely body mass and cranium morphology. The analyses of the best models were then used to reflect on higher taxa within the clade Afrotheria from a phenotypic perspective. For body mass, the surprising conclusion is that this greatly diverse clade cannot be distinguished from the random walk model, however, cranium analyses indicate evolvability shifts within a number of more recently diverged sub-clades. Specifically, the significant separations of the genus *Rhynchocyon* from the other sengis, as well as the hedgehog tenrecs from the shrew tenrecs, are suggested. My study therefore reinforces the realisation of evidentiarily defined higher taxa from a phenotypic perspective. The work provided here could form the basis for future analyses, particularly by including fossils in morphological analyses, as well as other parts of the anatomy beyond the cranium. Beyond this, expanding these analyses to higher clades, such as classes, would allow broader investigations into the reality and drivers of HESUs.

4.2 Introduction

In my previous chapters, I have discussed HESUs and explored the Afrotheria from the outlooks of phylogenetics, diversification and zoogeography. Here, I will explore HESUs within the Afrotheria from a phenotypic perspective. The adaptive landscape is a crucial allegory for conceptualising the processes that underpin evolution, and has been since the postulations of zoologists like Sewell Wright and G.G. Simpson in the 1930s and 40s (Wright 1932; Simpson 1944). For a biological population, allele frequencies, or their corresponding sets of genetic material or expressed traits, are compared with the average fitness of the population at a particular point. Peaks represent zones of optimal fitness, and the population is seen seeking these out amongst the landscape. At a macroevolutionary level, species might cluster around shared optima in the theoretical adaptive landscape and these clusters are often referred to as adaptive zones. Phenotypic ‘quantum leaps’, considerable surges in phenotype akin to Simpsonian mega-evolution, imply rapid evolution as species change adaptive zones (Cooney *et al*. 2017; Simpson 1944, 1953; Grossnickle *et al.* 2024). Simpson suggests three evolutionary tempos: bradytelic, horotelic and tachytelic (slow, medium and fast, Simpson 1944, 1953).

A long-standing debate in evolutionary theory is the argument of phyletic gradualism versus punctuated equilibrium (Eldredge & Gould 1972). Darwin’s original suggestion as to the manner of evolution effectively became phyletic gradualism, a protracted and somewhat unvarying process that leads to change (Darwin 1859). He was potentially biased as he had to make his revolutionary theory fly against the then held belief of continuous instant creation, so perhaps downplayed his ideas of non-uniform tempo (Eldredge 2006). Punctuated equilibrium suggests morphological stasis with sporadic and precipitous speciation (Eldredge & Gould 1972). Punctuated equilibrium can be considered a form or extension of phyletic gradualism. If phyletic gradualism is simply evolution at Simpson’s bradytelic pace, punctuated equilibrium is bradytely punctuated by tachytelic or horotelic phases. Further to this, quantum evolution is essentially punctuated equilibrium expanded to higher taxonomic echelons beyond the species level and with tempo pushed to the extremes, with horotely becoming impossible and reducing the entire process to a binary one. This is a particularly important deduction, as it allows evolutionary landscapes to network together the disparities between micro and macroevolution, and explains the lack of transitional organisms found in the fossil record, which should be found commonly as with distinct species if gradual change was solely true (Gould 1980; Cooney *et al*. 2017; Burin *et al.* 2023).

An approach to explore higher taxa is to undertake a phenotypic gambit, as morphology is exceedingly germane when conceptualising evolutionary landscapes (Slater & Friscia 2019; Burin *et al.* 2023). For example, Slater & Friscia (2019) explored body mass and dentition traits of the Carnivora. They found early bursts of trait diversification mapping to higher taxa, which dissipate towards the present as smaller groups diversify. These can be interpreted as instances of Simpson’s tachytely that then decrease in tempo. Sub-clades lose this signal and experience their own unique adaptive histories. Slater & Friscia suggest a hierarchy of adaptive radiation; a higher, general radiation with a second, lower, local level. Burin *et al.* (2023) explored the trait space of body length for both extant and fossil species of Cetacea. For extant species, they discovered the large variation of sizes, from small porpoises to extremely large rorquals, is represented by a markedly flat landscape. When fossil species were included, the landscape was flatter still. They noted some small, local optima, but no large scale processes drove cetacean body length. This contrasts with previous, extant only analyses of the clade. These examples highlight variation in the routes and realisation of potential evolutionary units that can be detected from phenotypic data.

The approaches to evaluate these macroevolutionary concepts have grown substantially in the last two decades. Most models are in some form extensions of the Brownian motion random walk model that has underpinned phylogenetic comparative methods since the pioneering work of Felsenstein (1985). Recently, complex models that test for directional and evolvability shifts in the focal trait have been developed (Pagel *et al.* 2022; Burin *et al.* 2023). Directional shifts are significant increases or decreases along a branch, beyond what would be expected of simple random walking. Evolvability shifts occur when lineages significantly change their adaptive potential, increasing or decreasing their capacity to explore trait space (Hansen *et al*. 2023; O'Meara *et al*. 2006; Venditti *et al*. 2011). Importantly, models that identify these shifts without prior hypotheses on their location, both independently and jointly, can be used to uncover phenotypic definitions of higher taxa (Venditti *et al*. 2011; Rabosky *et al*. 2013; Eastman *et al*. 2011; Elliot & Mooers 2014). While most of these models are focused on rate shifts (evolvability or rapid change on single branch), the recent Fabric model uses a reverse-jump Markov Chain Monte Carlo (RJ-MCMC) to identify both directional and evolvability shifts on phylogenetic trees (Pagel *et al.* 2022; Meade & Pagel 2022; Burin *et al.* 2023).

Despite being modest in species number and a geographically constrained lineage, Afrotheria are morphologically remarkably diverse. The nine families of Afrotheria (Elephantidae, Trichechidae (manatees), Dugongidae, Procaviidae (hyraxes), Orycteropodidae (aardvark), Macroscelididae (sengis), Tenrecidae, Potamogalidae (otter shrews) and Chrysochloridae (golden moles)) include species adapted to a fully aquatic life (sirenians), exceptionally large terrestrial herbivores (elephants), and numerous small insectivores (sengis, tenrecs and golden moles). The clade further includes a medium sized insectivore (aardvark), small herbivores (hyraxes), and the semi-aquatic otter shrews. This ecological diversity is coupled with enormous diversity of body size, shape and form, particularly in the skull. In just over 80 extant species, the clade is an ideal study system for testing Simpsonian models of phenotypic macroevolution and unpicking the role of phenotypic divergence in the emergence of HESUs.

The aims of this chapter are to assess the tempo and mode of divergence in afrotherian morphology, specifically their cranium shape and body mass, and to identify lineages with shifts in two types of macroevolutionary regime, by examining evolvability and directional shifts on the phylogeny of the clade, and to explore any shifts in the dynamics of trait evolution that might mark the emergence of HESUs.

4.3 Methods

4.3.1 Body Mass Data

Body mass values for 118 extant and extinct afrotheres (Table S4.1) were acquired mainly from Puttick & Thomas (2015), with additions from the EltonTraits database (Wilman *et al.* 2014) and *Rhynchocyon stuhlmanni* from the AnimalTraits database (Herberstein *et al.* 2022). These body mass values were then $\log_{10}$ transformed.

4.3.2 Cranium Data

Landmark data for 60 afrotherian species' skulls were acquired from Finlay & Cooper (2015) with additional data provided by Dr. Natalie Cooper (Natural History Museum). These data consisted of information from dorsal, lateral and ventral 2D images. In addition, 3D scans for *Dendrohyrax arboreus*, *Elephas maximus*, *Procavia capensis* and *Trichechus manatus* skulls were downloaded from MorphoSource and 2D images taken for each orientation. All images were landmarked following the position of the fixed landmarks from Finlay & Cooper (2015, see Figure S4.1) using tpsUtil32 and tpsdig264 (Rohlf 2015). I did not use the semilandmarks curves from Finlay and Cooper (2015). Their analyses were limited to tenrecs and golden moles and the additional complexity of including the extremely diverse crania of Afrotheria limits the points that can reliably be used as homologous landmarks.

Many species had more than one specimen, so the mean shape for each species was found by performing the Generalised Procrustes Analysis (GPA) and extracting the mean shape in the statistical computing and graphics environment R, using the packages 'Morpho', 'geomorph' and 'abind' (R Development Core Team 2020; Schlager 2017; Baken *et al.* 2021; Plate & Heiberger 2016). 'geomorph' was used to read the spatial data and 'abind' was used to bind landmark pairs and landmarks into a single object. 'Morpho' was then used to perform the GPA analyses. Now with just one shape for each species, the GPA was performed on all species. From the GPA analyses I identified the principal component axes (PCs) that cumulatively account for at least 80% of the total variation in skull shape for each of the three orientations. For all three orientations, this was the first four PCs. The PCs were used in subsequent analyses of morphological evolution.

4.3.3 Morphological Analyses

I assessed the evolution of body size and cranium shape using five different models implemented in BayesTraits V4 (Meade & Pagel 2022) that include the homogeneous Brownian motion model and variants of the heterogenous Fabric model. The models were Brownian motion, directional with no global trend, evolvability with no global trend and Fabric both with and without a global trend. All models were fitted using reversible jump Markov Chain Monte Carlo (RJ-MCMC) sampling in BayesTraits V4 (Meade & Pagel 2022). I used the MCC phylogenetic tree from Chapter 2, pruned to the 118 extant and extinct species with body mass data, or the 64 extant species with skull data, for each model. Each model was run for 20 million generations (one million generations burn in), sampling every 10,000. I used stepping stone sampling using 1,000 stones and 50,000 iterations per stone to calculate marginal likelihoods for model comparison. Each analysis was repeated with four independent runs and convergence was checked in Tracer (Rambaut *et al*. 2018). Model outputs were processed and summarised using the FabricPostProcessor (Meade & Pagel 2022) or the standalone variable rates post processor (Venditti *et al*. 2011).

4.4 Results

4.4.1 Trait variation

Body size is highly variable across the Afrotheria but highly clustered phylogenetically with close relatives tending to be more similar in size than more distant relatives (Figures 1 and S4.2). Elephants and sirenians are the largest bodied lineages, and the tenrecs, specifically the shrew tenrecs, are the smallest. Most extant afrotheres have a mass <1kg, with only the hyraxes, aardvark, sirenians and elephants exceeding this. *Rhynchocyon* are larger than other sengis, as are hedgehog tenrecs compared to shrew tenrecs.

The geometric morphometric analyses identify the major axes of cranial shape variation (Table 1). Figures 4 & 5 show the landmarks of the extremes for PC1 and PC2 respectively. For dorsal PC1, the scale of abstract skull shape runs from tenrec to elephant, with elephant being significantly more different than other afrotheres. PC2 runs from manatee to sengi, with manatee being the most extreme. For lateral PC1, the scale runs from manatee to a tenrec. Manatee, aardvark and the golden moles show the most difference from the mean shape. PC2 runs from dugong to elephant. Along with the elephant and a tenrec, the manatee and aardvark again show more difference. For ventral PC1, the scale runs from a tenrec to a golden mole. Golden moles, elephant and manatee show the most difference. PC2 runs from dugong to aardvark. These two, as well as a sengi, show the most difference.

Cranial morphology broadly aligns with afrotherian clades, although there is overlap, particularly on PCs 3 and 4 (Figure 2). This clustering is apparent when plotted on the phylogeny for PC1 in all orientations (Figure 3a, e, i), but is much less prevalent for PCs 2-4 (Figure 3). Note that these results are not a reflection of size because size is removed in the Procrustes analysis. For all orientations and PC values, the otter shrews and tenrecs group closely together, but the manatee and dugong always show distinct dissimilarity. Also, *Rhynchocyon* frequently differ from the remaining sengis. For PCs 1 and 2 in all orientations, golden moles never cluster with the tenrecs and otter shrews. Although showing some overlap, more so in PCs 3 and 4, sengis remain distinct from golden moles, tenrecs and otter shrews, which are their sister lineage.

Table 1. *Percentage variance of each PC for each orientation.*

% Variance PC	D	L	V
PC1	47.49	38.98	44.62
PC2	18.1	18.86	18.13
PC3	13.74	14.91	14.13
PC4	11.45	8.27	9.46

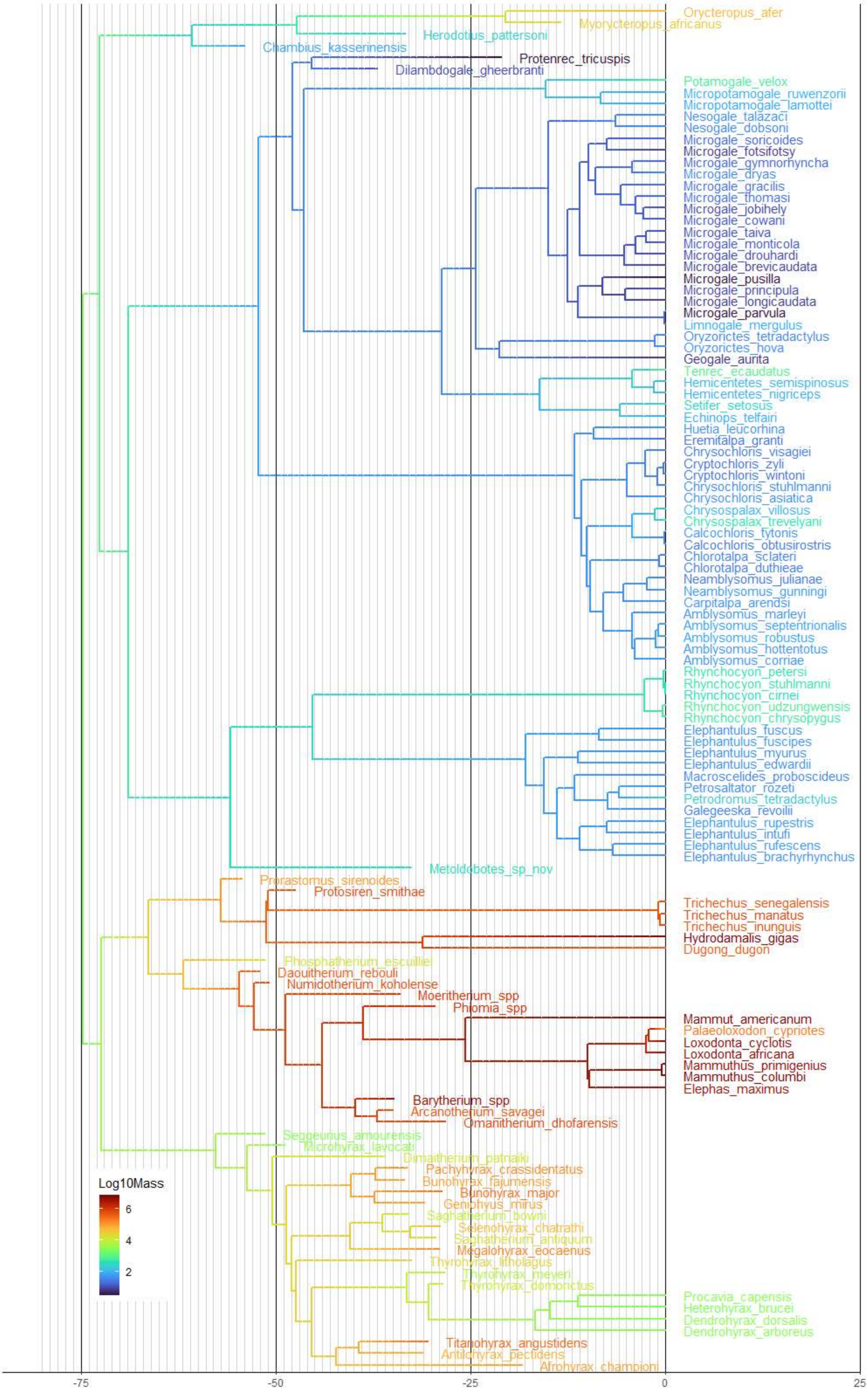


Figure 1. *Phylogeny of afrotherian body mass in* $\log_{10}$*(g). Tips are coloured according to* $\log_{10}$ *body mass and branches according to ancestral state estimation of* $\log_{10}$ *body mass under a Brownian motion model using the R package phytools (Revell 2012).*

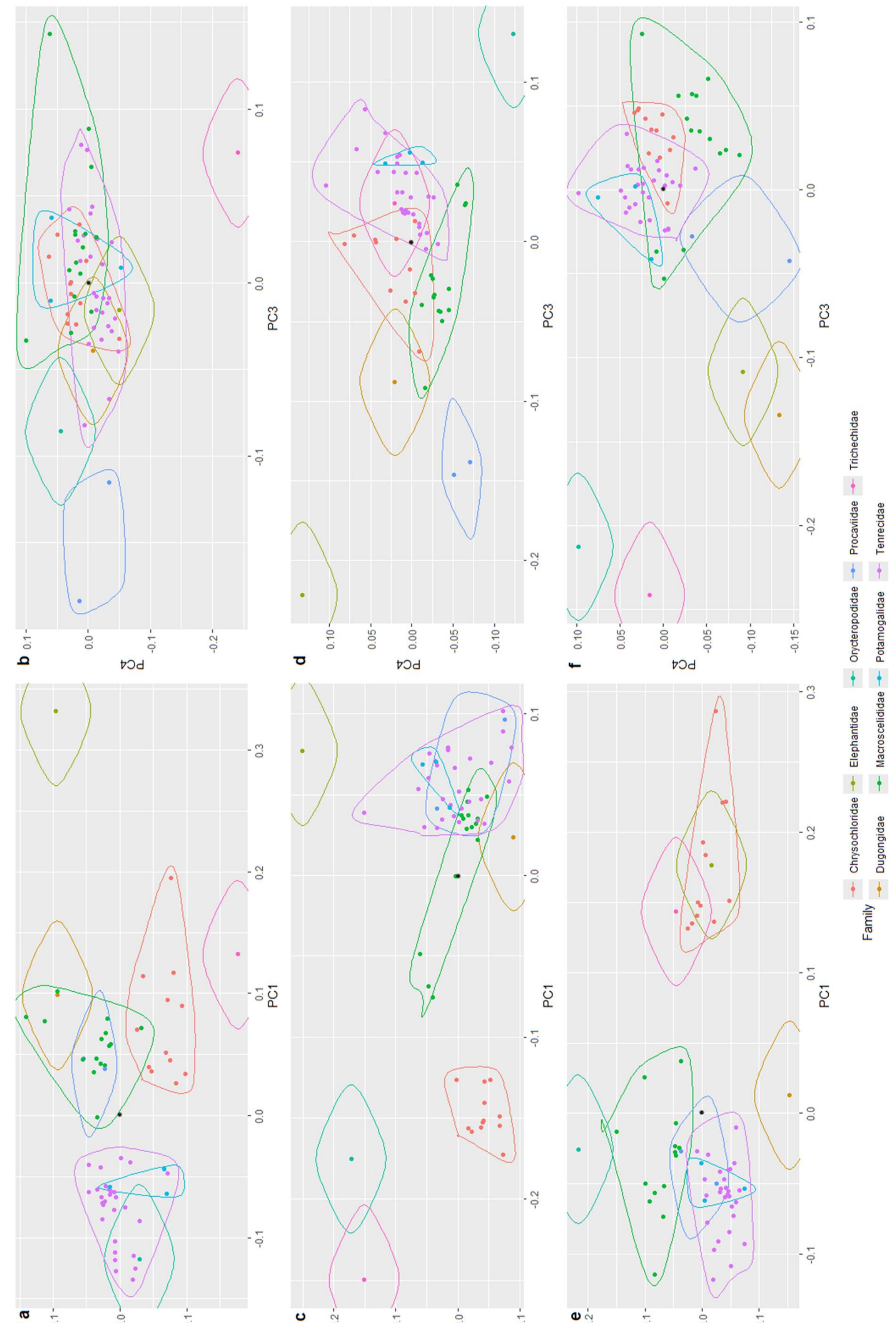


Figure 2. *Scatter plots of PC1 vs PC2 (a, c, e) and PC3 vs PC4 (b, d, f) for dorsal (a, b), lateral (c, d) and ventral (e, f) orientation. No. species per family: Chrysochloridae (12), Dugongidae (1), Elephantidae (1), Macroscelididae (15), Orycteropodidae (1), Potamogalidae (3), Procaviidae (2), Tenrecidae (28) and Trichechidae (1). Black dot is (0,0).*

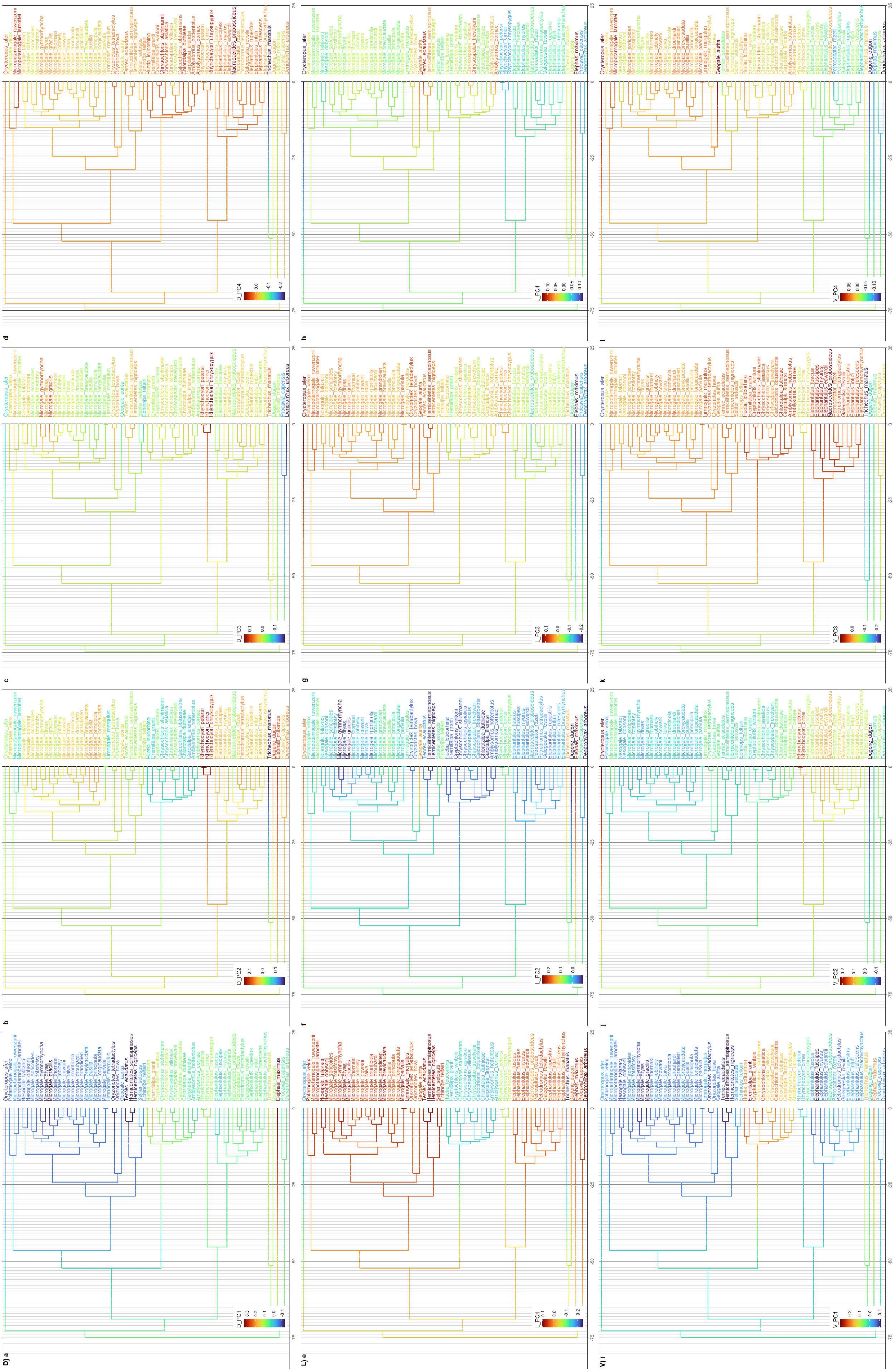
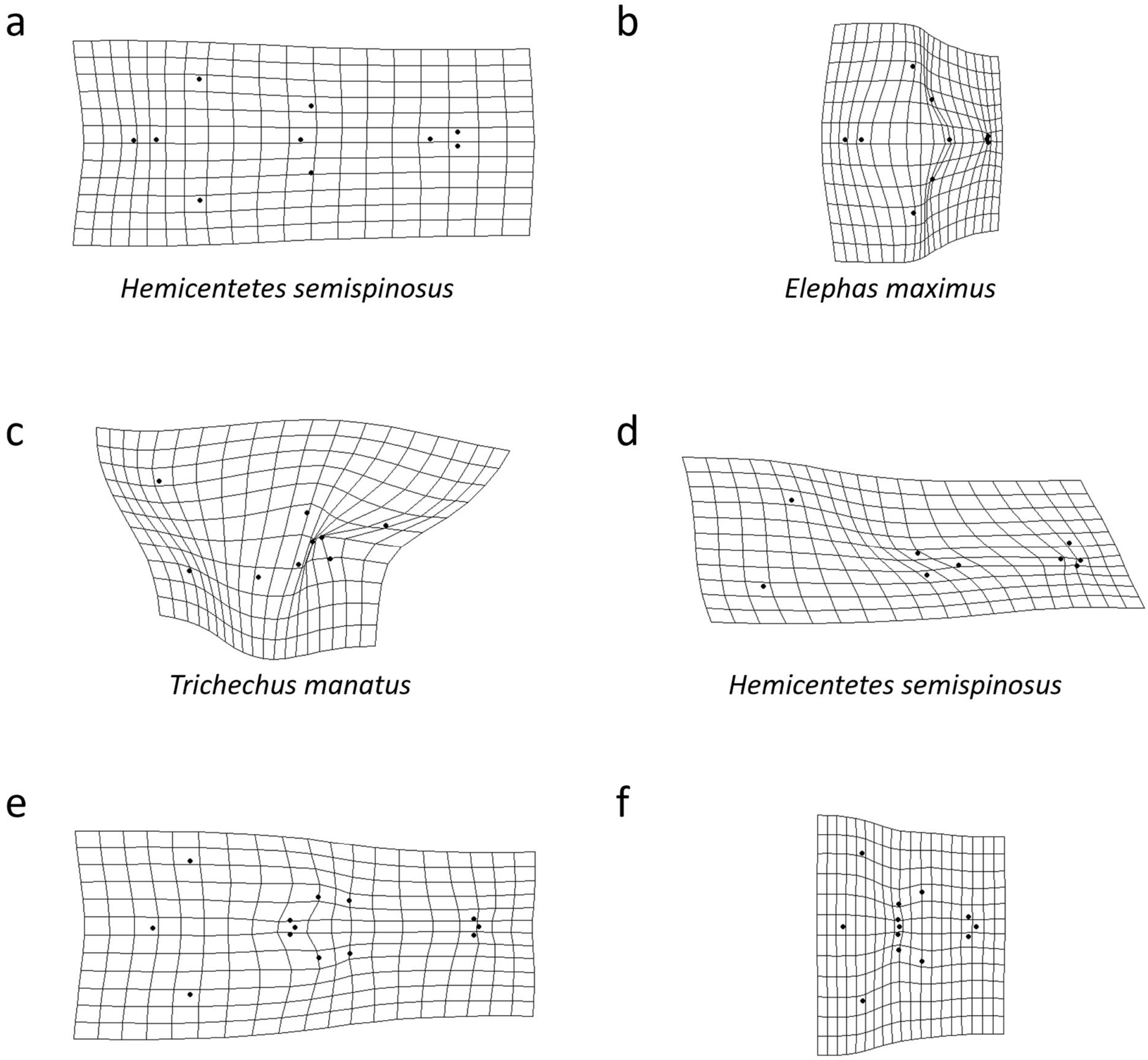

D) a
b
c
d
L) e
f
g
h
V) i
j
k
l
D_PC1
D_PC2
D_PC3
D_PC4
L_PC1
L_PC2
L_PC3
L_PC4
V_PC1
V_PC2
V_PC3
V_PC4
Orycteropus_afer
Elephas_maximus
Trichechus_manatus
Dugong_dugon
Dendrohyrax_arboreus
Procavia_capensis
-75
-50
-25
0
25

Figure 3. *Phylogenies of PC scores for each orientation. Panels a-d show inferred ancestral states for PCs1-4 respectively for the dorsal view landmarks. Panels e-h show the same for the lateral view and panels i-l show the ventral. Tips are coloured according to the PC scores and branches according to ancestral state estimation of PC scores under a Brownian motion model using the R package phytools (Revell 2012).*



Hemicentetes semispinosus

Elephas maximus

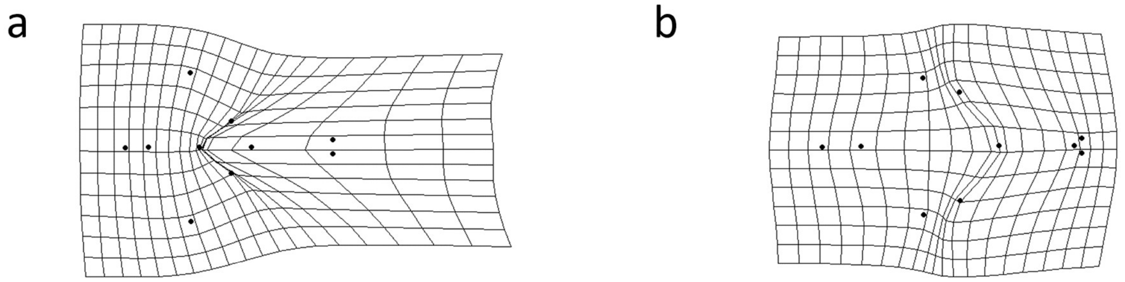
Trichechus manatus

Hemicentetes semispinosus

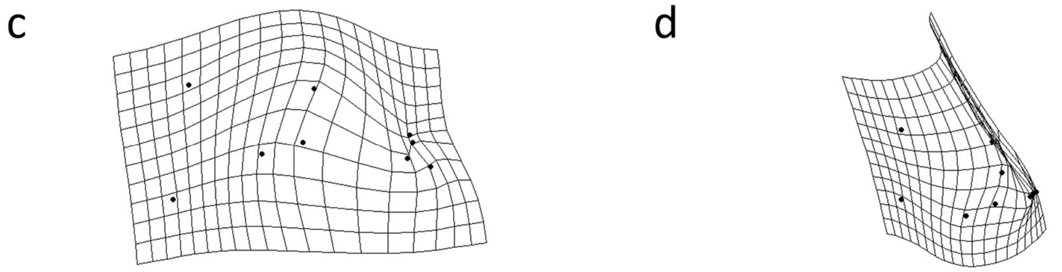
Hemicentetes semispinosus

Eremitalpa granti

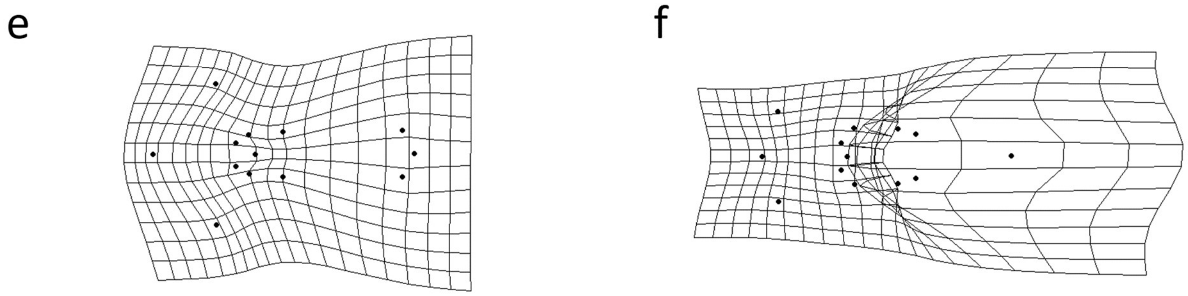
Figure 4. *Skull landmark relative warps of PC1 extremes for dorsal (a, b), lateral (c, d) and ventral (e, f) orientation.*



Trichechus manatus *Rhynchocyon cirnei*



Dugong dugon *Elephas maximus*



Dugong dugon *Orycteropus afer*

Figure 5. *Skull landmark relative warps of PC2 extremes for dorsal (a, b), lateral (c, d) and ventral (e, f) orientation.*

4.4.2 Models of trait evolution

4.4.2.1 Body mass evolution

The best fitting model for body mass was the Fabric model with no global trend (Table 2). The model fitted significantly better than either evolvability or directional evolution alone. The mean number of evolvability shifts was 8.78 and the mean number or directional shifts was 16.81. These results indicate that the evolution of afrotherian body size has involved rapid periods of divergence interspersed with directional shifts towards both smaller and larger size. However, the precise location of evolvability shifts is unclear with low posterior probabilities in all cases. Several directional shifts are strongly supported (posterior probabilities exceeding at least 65%). For example, *Palaeoloxodon cypriotes* showing a mean decrease of 18.7 times and *Limnogale mergulus* showing a mean increase of 15 times (Table 3, Figure 6).

Table 2. *The likelihood (highest in* ***bold****) of each model for each set of data and the mean number of estimated evolvability node shifts and directional branch shifts from the BayesTraits logs. PCS is all 4 together.*

	Brownian Motion	Directional Evolution	Evolvability	Fabric (Directional + Evolvability)	Fabric + Global Trend	Nodes (Evolvability)	Branches (Directional)
BS	-193.59	-118.05	-130.11	**-103.06**	-103.81	8.78	16.81
D_PC1	82.09	39.46	**85.59**	78.04	72.37	5.80	-
D_PC2	45.26	47.94	79.53	**86.75**	78.33	6.15	1.37
D_PC3	91.74	43.25	**92.49**	84.48	79.62	4.71	-
D_PC4	88.27	54.58	**91.99**	86.73	80.03	6.13	-
D_PCS	307.55	258.02	**365.78**	357.23	355.50	12.33	-
L_PC1	109.69	70.71	**113.99**	106.68	101.73	5.42	-
L_PC2	79.23	38.68	**85.97**	78.72	72.97	6.16	-
L_PC3	67.71	53.54	89.20	**91.91**	86.76	5.59	1.35
L_PC4	91.91	52.22	**100.23**	94.92	88.47	6.95	-
L_PCS	348.63	301.49	**410.10**	401.16	400.98	11.36	-
V_PC1	67.08	36.15	**74.55**	73.15	68.40	6.07	-
V_PC2	55.75	53.66	80.03	**89.20**	83.60	5.56	2.36
V_PC3	87.85	67.13	103.77	**105.84**	99.99	5.08	1.28
V_PC4	**103.96**	55.71	103.60	95.54	90.98	-	-
V_PCS	314.71	304.58	**392.36**	386.53	388.27	12.30	-

4.4.2.2 Cranium shape evolution

The best fitting model for skull shape depended on the orientation (dorsal, lateral, ventral) and the focal PC axes (Table 2), however the dominant model (10 of 15 traits) is evolvability suggesting that clades shift in the rate of evolution, rather than in the magnitude of the trait itself. The Fabric model receives the strongest support for four traits with the Brownian model favoured in a single case (Table 2). Where the Fabric model was the best fitting model, the number of directional shifts tended to be low (maximum 2.36, Table 2, Figure 7) whereas the number of evolvability shifts ranged from ~4-12 (Figure 8). Posterior support for shifts locations was variable and below I briefly highlight shifts occurring with 95%, 80%, or 65% posterior probability (Table 3, Figures 7 & 8).

The 95% posterior probability threshold identifies branches with the most strongly supported directional and evolvability shifts. Directional shifts are rare, but *L. mergulus* shows morphological skull directional change on multiple PC axes. Several PCs also indicate that *L. mergulus* and its sister *Microgale parvula* underwent significant increases in evolvability. Evolvability shifts for the shrew-like tenrecs are found twice, and once for the remaining tenrecs, otter shrews, non-*Rhynchocyon* sengis and the node of *Chrysochloris stuhlmanni* and *Cryptochloris wintoni*.

The 80% posterior probability threshold is more liberal and suggests several other shifts in evolvability (Table 3). These include non-*Rhynchocyon* sengis as well as various members of *Microgale*. *Elephantulus fuscipes* and *E. fuscus*, the most distantly related non-*Rhynchocyon* sengis, are sometimes shown to have distinct declines in evolvability. The *Chrysochloris stuhlmanni* and *Cryptochloris wintoni* node shows an evolvability increase in PC1 for the ventral view only. Similar evolvability shifts are also found with these two species along with all golden moles. The hedgehog tenrecs and otter shrews are found once.

The most liberal cut-off (65%) adds further, but more weakly supported evolvability shifts. For example, at this threshold, *Rhynchocyon* and the remaining sengis are often found to have independent downward shifts in evolvability. Many members of *Microgale* are again indicated often. Golden moles are found once as a whole and once as a majority, along with the *Chrysochloris stuhlmanni* and *Cryptochloris wintoni* node. All shrew-like tenrecs and the genus *Hemicentetes* are found once.

A number of times, either no significant shifts were found or the entire tree, except the root, was found to be significant. The latter was found when all four principal components were analysed together.

Table 3. *Shifts (directional (D) or evolvability (E)) at 3 percentage levels of occurrence. Below 95%, this casts a 'wider net' to present patterns with less confidence. PCS is all 4 together.*

Data	≥95%	≥80%	≥65%
BS	*Palaeoloxodon cypriotes* decrease is the only significant D shift (mean -1.27, 18.7x), no significant E shifts.	*Limnogale mergulus* increase (mean 1.18, 15x), no significant E shifts.	*Petrodromus tetradactylus* increase (mean 0.52, 3.35x) & *Chrysospalax trevelyani* increase (mean 0.54, 3.5x), *Calcochloris obtusirostris* decrease (mean -0.21 , 1.62x), no significant E shifts.
D_PC1	No significant E shift.	Non-*Rhynchocyon* sengis minus *Elephantulus fuscipes* & *E. fuscus* decrease.	All non-*Rhynchocyon* sengis decrease, *Chrysochloris stuhlmanni* & *Cryptochloris wintoni* E shift, mean scalar 2.2 increase, *Limnogale mergulus* & *Microgale parvula* E shift, mean scalar 1.4 increase, *M. cowani, M. jobihely* & *M. thomasi* decrease.
D_PC2	*Limnogale mergulus* only significant direction decrease (mean -0.08), no significant E shift.	-	-
D_PC3	No significant E shift.	-	-
D_PC4	No significant E shift.	*Limnogale mergulus* & *Microgale parvula* node shift, mean scalar 2.6 increase, small clade of *M. cowani, M. dryas, M. gracilis, M. gymnorhyncha, M. jobihely* & *M. thomasi* decrease.	*Limnogale mergulus*, *Microgale parvula, M. longicaudata, M. principula* & *M. pusilla* increase, rest of *Microgale* decrease.
D_PCS	Many significant E shifts – tenrecs, otter shrews, non-*Rhynchocyon* sengis and 0.58 decrease of *Chrysochloris stuhlmanni* & *Cryptochloris wintoni.*	Many significant E shifts – *Rhynchocyon* & golden moles decrease.	Many significant E shifts – every node except the root is significant.
L_PC1	Many significant E shifts – all shrew-like tenrecs.	Many significant E shifts – Non-*Rhynchocyon* sengis, all tenrecs & otter shrews.	Many significant E shifts – *Rhynchocyon* & golden moles decrease.

L_PC2	*Limnogale mergulus* & *Microgale parvula* node shift, mean scalar 3.17 increase.	Non-*Rhynchocyon* sengis decrease, small clade of *Limnogale mergulus*, *Microgale parvula, M. longicaudata, M. principula* & *M. pusilla* increase.	*Rhynchocyon* decrease, all shrew-like tenrecs, *Hemicentetes* and most golden moles.
L_PC3	No significant D or E shift.	-	-
L_PC4	*Limnogale mergulus* & *Microgale parvula* node shift, mean scalar 3.96 increase.	Non-*Rhynchocyon* sengis minus *Elephantulus fuscipes* & *E. fuscus* decrease, small clade of *M. cowani, M. gracilis, M. jobihely* & *M. thomasi* decrease.	Non-*Rhynchocyon* sengis decrease, *M. longicaudata, M. principula* increase, 8 other *Microgale* species decrease.
L_PCS	Many significant E shifts – every node except the root is significant.	-	-
V_PC1	*Limnogale mergulus* & *Microgale parvula* node shift, mean scalar 5.2 increase.	*Chrysochloris stuhlmanni* & *Cryptochloris wintoni* node shift, mean scalar 3.4 increase.	Most golden moles increase, *M. longicaudata, M. principula* & *M. pusilla* increase.
V_PC2	*Limnogale mergulus* only significant direction increase (mean 0.06), no significant E shift.	-	*Rhynchocyon cirnei* & *R. petersi increase* (mean 0.09), no significant E shift.
V_PC3	*Limnogale mergulus* only significant direction increase (mean 0.03), no significant E shift.	-	-
V_PC4	Average Brownian Variance $9.12 \cdot 10^{-5}$.	-	-
V_PCS	Many significant E shifts – every node except the root is significant.	-	-

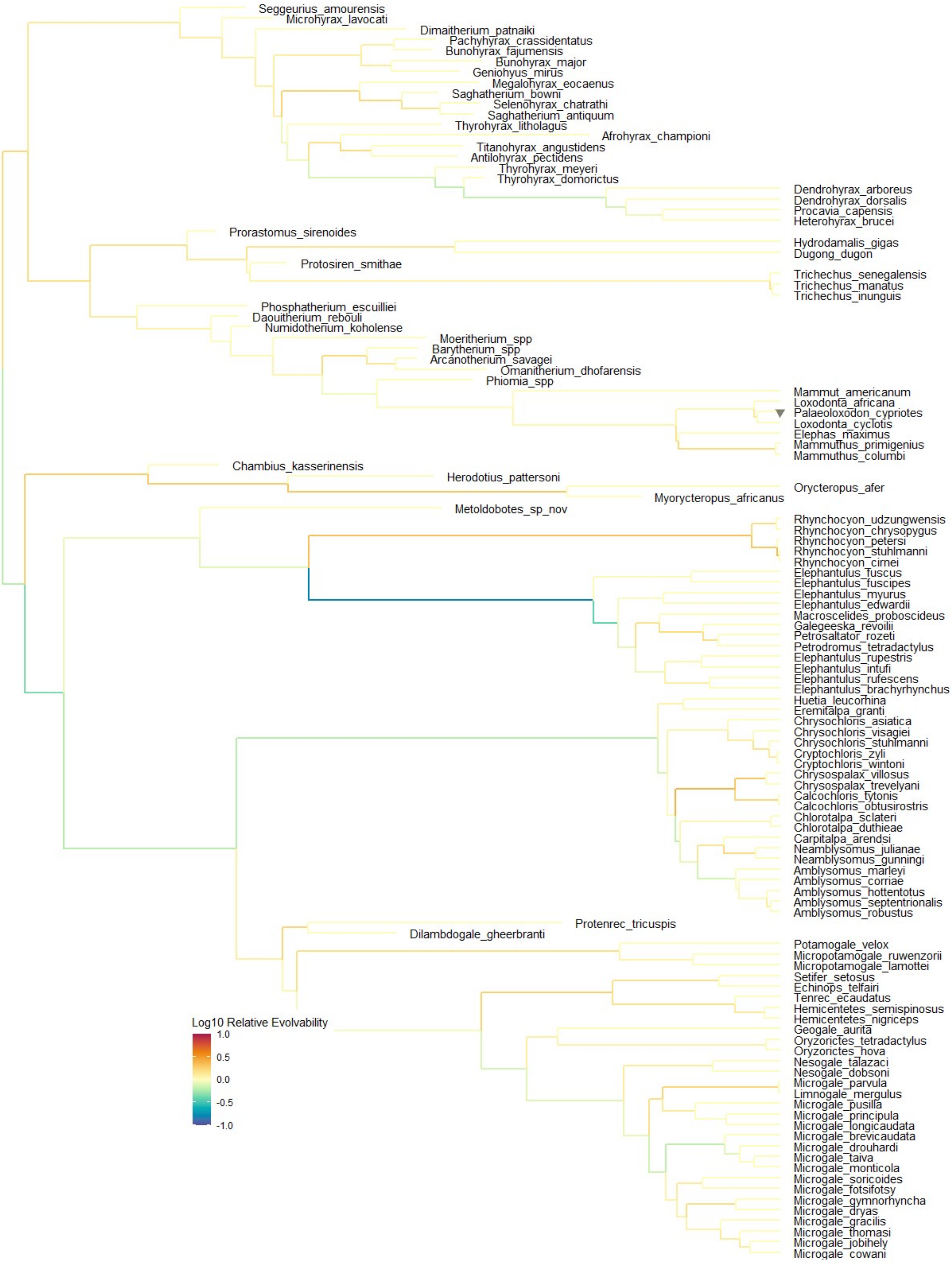


Figure 6. *Phylogeny of the Fabric model body mass results. Directional shift indicated by directional triangle.*

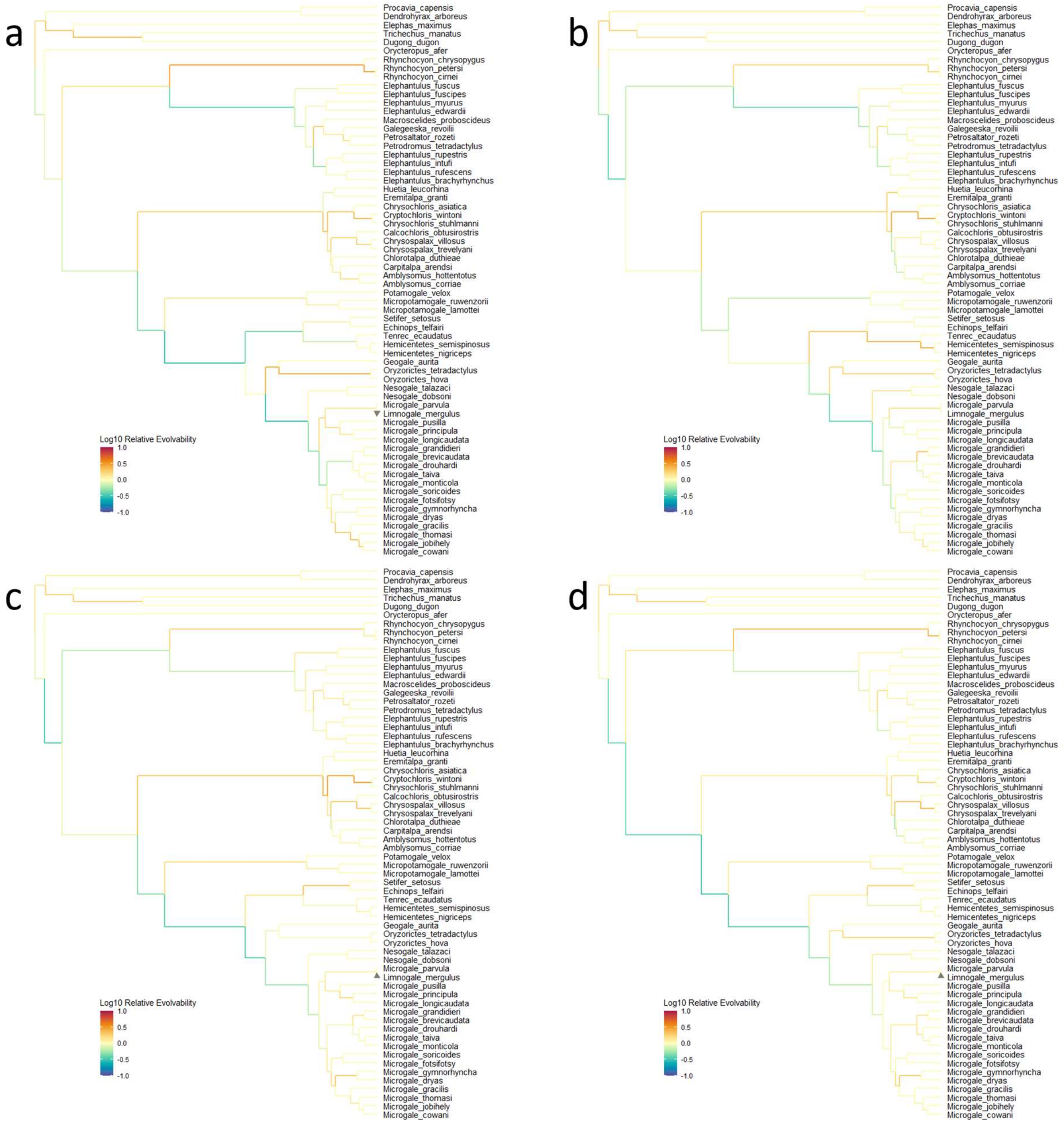


Figure 7. *Phylogenies of the Fabric model results for PCs. (a) D_PC2, (b) L_PC3, (c) V_PC2 and (d) V_PC3. Directional shifts indicated by directional triangles.*

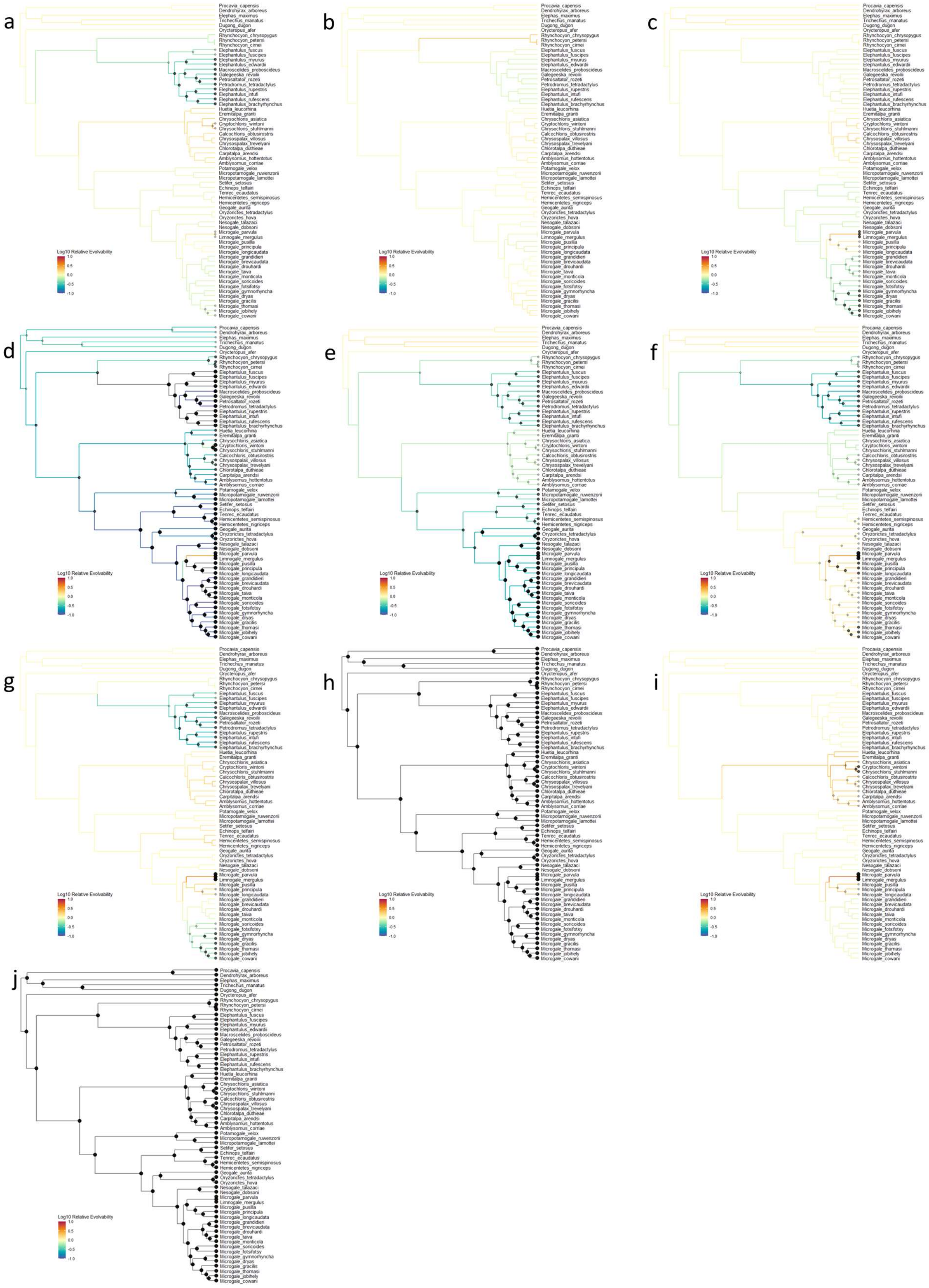
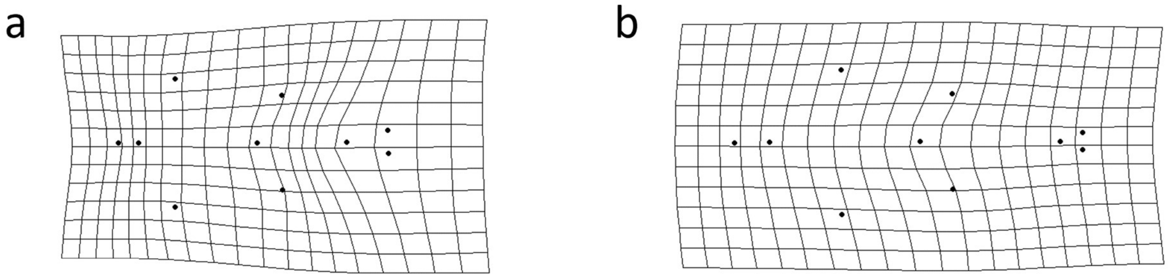
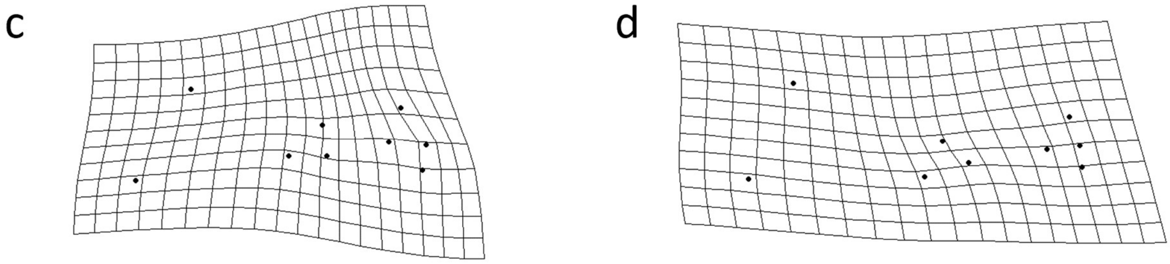


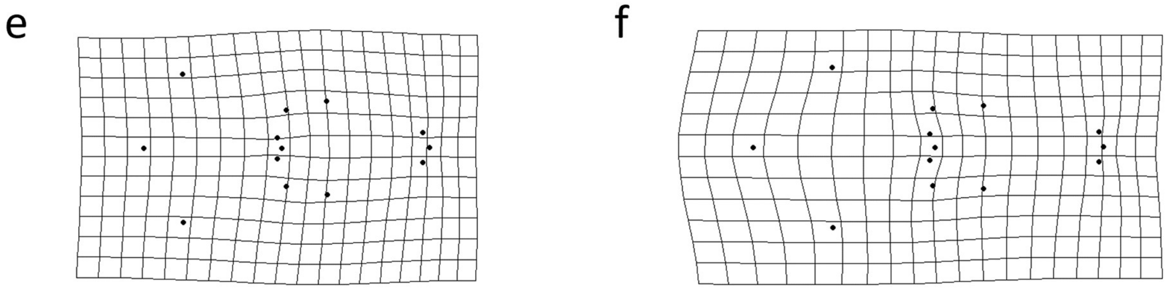
Figure 8. *Phylogenies of the evolvability model results for PCs. (a) D_PC1, (b) D_PC3, (c) D_PC4, (d) D_PCS, (e) L_PC1, (f) L_PC2, (g) L_PC4, (h) L_PCS, (i) V_PC1, (j) V_PCS. Evolvability shifts indicated by circles. Large black ≥95% occurrence. Medium dark grey ≥80% occurrence. Small light grey ≥65% occurrence.*



Limnogale mergulus *Microgale parvula*



Limnogale mergulus *Microgale parvula*



Limnogale mergulus *Microgale parvula*

Figure 9. *Relative warps of landmarks of Limnogale mergulus (a, c, e) and Microgale parvula (b, d, f) in dorsal (a, b), lateral (c, d) and ventral (e, f) orientation.*

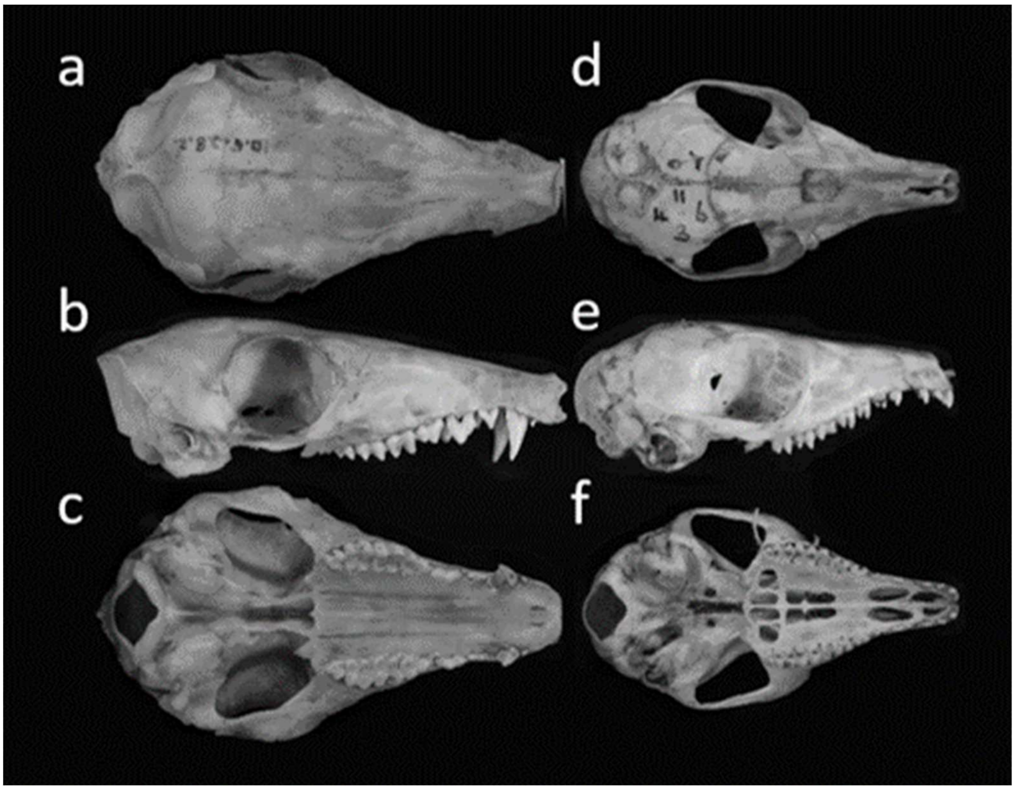


Figure 10. *Rhynchocyon chrysopygus (a-c) and Elephantulus brachyrhynchus (d-f) in dorsal (a, d), lateral (b, e) and ventral (c, f) orientation. All images adapted from Finlay and Cooper (2015).*

Figure 11. *Hemicentetes semispinosus (a-c) and Microgale jobihely (d-f) in dorsal (a, d), lateral (b, e) and ventral (c, f) orientation. All images adapted from Finlay and Cooper (2015).*

4.5 Discussion

My analyses reveal considerable heterogeneity in the evolution of afrotherian body size and cranium shape. While body size is notable for directional shifts, skull shape tends towards changes in evolvability. For body mass, the Fabric model indicated a decrease in directional change within the elephants. This shift reflects exceptional variation in elephant body size; *Palaeoloxodon cypriotes* weighs 0.2t, whereas other Elephantidae such as *Loxodonta cyclotis* weigh 4.75t. This is over an order of magnitude difference, with *P. cypriotes* at only just over 4% of the body mass of its closest relative. This is an example of insular dwarfism, specifically on Cyprus. Another directional change was detected nested within *Microgale*. *Limnogale mergulus* weighs 92g, and the paraphyletic *Microgale* ranges from *M. parvula* at 3.2g, which is the closest relative of *L. mergulus*, to *M. dryas* at 40g. *L. mergulus* is over twice as large as its largest close relative and almost 30 times the size of its closest relative. It is a semi-aquatic species among shrew-like tenrecs. The sengi *Petrodromus tetradactylus* weighs 198.3g and was indicated to have shifted directionally upwards. Its closest relative *Petrosaltator rozeti* weighs 45.3g and other close species range down to *Galegeeska revoilii* at 32.5g, so *P. tetradactylus* is almost 4.5 times the size of its closest and largest relative. *Chrysospalax* and *Calcochloris* are sister genera that both show directional changes within the Chrysochloridae. *Chrysospalax trevelyani* has a mass of 460g and *C. villosus* weighs 117.85g. *Calcochloris obtusirostris* weighs 26.3g and *C. tytonis* weighs 49.7g. The smallest and largest of this sub-clade are indicated to have shifted in opposite directions away from the mean. The mean mass is 163.46g, with the largest 2.8 times larger than the mean and almost 4 times larger than its closest relative and the smallest 6.2 times smaller than the mean and just over half the size of its closest relative.

Despite the sheer and extreme changes in afrotherian body size, covering 6 orders of magnitude from 3 gram tenrecs to 5 tonne elephants, and the extinct Steller's sea cow at ~7 tonnes, these body mass analyses show only a handful of significant directional shifts and no changes in evolvability within the Afrotheria. From this study, body size, at least when considered alone, is not informative for delimiting HESUs within Afrotheria, but it could be useful in other clades.

For cranium shape, most shifts are in evolvability rather than direction. The branch leading to *Limnogale mergulus* however is frequently indicated with high occurrence to have undertaken shifts in both direction, and, at the node along with *Microgale parvula*, evolvability. Their landmarks are shown in Figure 9. Non-*Rhynchocyon* sengis and most or all shrew-like tenrecs, mostly formed from *Microgale*, are both clades that often show evolvability shifts, with their closest relatives, the remainders of Macroscelididae and Tenrecidae respectively, following less frequently, or specifically with less than 65% occurrence. The difference between *Rhynchocyon* and other Macroscelididae species can be explained by Figure 10. The *Rhynchocyon* skull is wider at the tip of the snout, and has smaller eye sockets set farther back in the skull. The side profile of the upper jaw sees it curve straighter, and have longer teeth. The difference between shrew tenrecs and hedgehog tenrecs can be explained by Figure 11. The *Hemicentetes* skull, a hedgehog tenrec, is longer and narrower than the *Microgale* skull. Laterally, at the base, the *Microgale* skull is rounder. Other, less frequently found patterns are *Chrysochloris stuhlmanni* and *Cryptochloris wintoni* shifting different to the other golden moles, *Elephantulus fuscipes* and *E. fuscus* shifting different to the other non-*Rhynchocyon* sengis and the otter shrews being separate from the tenrecs. *C. wintoni* appears much more squat lengthwise than its relatives. *E. fuscipes* has a slightly longer snout compared to other non-*Rhynchocyon* sengis. Otter shrew skulls have many differences between those of both shrew and hedgehog tenrecs.

Tenrecs might be expected to be highly evolvable, as they have adaptively radiated to fill numerous vacant niches on Madagascar, yet Finlay & Cooper (2015) suggest that the intra-clade morphological variation of the tenrecs is no different than the intra-clade diversity of the golden moles. Cooney *et al*. (2017) found that the adaptive radiations of younger sub-clades in Aves show limited divergence compared to major shifts within the phenotype of higher taxa, suggesting that intra-clade diversity is low and inter-clade diversity is high. It could therefore be understood that HESUs may show reduced variations in morphology internally, but will be significantly different to sister taxa. These findings could argue against the splitting of Macroscelididae and Tenrecidae into sub-clades that reflect HESUs.

In Chapter 2, my diversification analyses found differences between rates of speciation, extinction and net diversification between *Rhynchocyon* and the remaining Macroscelididae species, with *Rhynchocyon* having higher speciation and extinction rates, and a lower net diversification rate than the other sengis. This finding of giant sengis and all other sengis to be significantly unique both in terms of diversification history and phenotype is strong evidence that they do represent HESUs. In my previous chapters, the tenrecs have not shown any significant internal differences, but here are morphologically suggested to exist as two sub-clades. The other 7 families, however, appear, both from these cranium and body mass data, to have occurred from random walking, and cannot be defined as HESUs from these phenotypic data, despite some suggestions being made by diversification and zoogeography, and the separate clustering of most families from their sister lineages in Figure 2.

Limnogale being so often found to have undergone both directional and evolvability shifts could potentially indicate the beginning of what could in countless generations time become a new HESU. The sole species of *Limnogale* is the semi-aquatic web-footed tenrec, presenting convergently similar to otters and the more closely related otter shrews, although its closest relatives are the shrew-like tenrecs. Before being found to nest phylogenetically within the paraphyletic *Microgale*, *Limnogale* was often found classified with the otter shrews (Asher & Hofreiter 2006; Salton & Szalay 2004).

Pagel *et al.* (2022) find so called ‘watershed’ moments of enhanced evolvability throughout the mammalian tree, where evolutionary potential is significantly amplified, indicating a race forward in the characteristic. The results here are evidence that morphological factors can define HESUs; although body mass did not, cranium morphology did strongly indicate four clades to often experience within clade shifting in evolvability compared to the background afrotherian Brownian rate or that of their closest relatives. This is consistent with the idea that HESUs should represent lineages with distinct shared evolutionary histories. When considered in conjunction with the diversification and zoogeographic analyses, these phenotypic data add further evidence to the realisation of some afrotherian HESUs.

Chapter 5

Phylogenetic Realisation of Super-specific Evolutionary Significant Units in Afrotheria

5.1 Abstract

Linnaean ranks do not necessarily reflect evolutionary significant higher taxa. Linnaean taxonomy usually defines by phenotypes, but real taxa reflect diversification processes. A phylogenetic exploration of diversification, a key process in the genesis of distinct entities, could elucidate significance at a super-specific level. Using the Generalised Mixed Yule Coalescent (GMYC) model on phylogenies of the clade Afrotheria, including extinct species, an estimated 11 diversification clusters are found in the present, mapping to between the Linnaean ranks of family and genus. These clusters can be considered higher evolutionary significant units (HESUs). When both extant and extinct taxa are included, an average estimate of when these clusters begin to form within the clade is 35-36 million years ago. This validates that phylogenetically realised evolutionary entities can be uncovered, driven by diversification.

5.2 Introduction

All species are classified into many hierarchical taxonomic ranks, but adequately defining these ranks is challenging. Realising evolutionary significant entities on the tree of life, instead of Linnaean higher taxa, as well as the processes that drive and shape them is important to our understanding of macroevolution. Although species are easy to define, naming higher taxa is arguably simpler than discerning them. Empirical evidence indicates that higher taxa could represent higher evolutionary significant units (HESUs), defined using patterns of characteristics, akin to the phylogenetic species concept (Barraclough 2010; Humphreys & Barraclough 2014; Humphreys *et al.* 2016; Nixon & Wheeler 1990). This allows super-specific classification to no longer be ad-hoc, and instead be based upon evolutionary force. The degree to which named higher taxa adequately represent HESUs is currently unknown, and more significantly, the drivers of such evolutionary entities remain underexplored. Understanding this degree of representation and the generators of HESUs is crucial to explaining and comprehending the diversity of our planet, both in the present and throughout time.

Multiple approaches to identifying the existence of HESUs exist. In Chapter 2, I examined variation in diversification rates as a possible means to identify HESUs. In Chapter 3, I examined geographic isolation (Barraclough 2010; Humphreys & Barraclough 2014) and in Chapter 4 I explored trait evolution (Humphreys & Barraclough 2014). Several traits that map to ecological niches were found by Humphreys & Barraclough (2014) to have lower within-cluster variation compared to among clusters, and the authors suggest geographic isolation as a rationalisation of unrelated evolution found between Old and New World sisters, i.e. pigs and peccaries. Trait evolution was further explored by Humphreys & Barraclough (2014) when they found large ratios while comparing inter and intra cluster values of a number of morphological and ecological traits across four mammalian orders. These distinct processes show a level of interconnectedness, for example, even a small amount of dispersal will slightly reduce geographic isolation but can heavily inhibit speciation, producing an air of disarray when factors overlap (Humphreys & Barraclough 2014; Claramunt *et al*. 2012; Suárez *et al.* 2022).

An alternative to this suite of approaches is the Generalised Mixed Yule Coalescent (GMYC) model, that delimits clusters of branching rates on a tree, making it a potential way to uncover and measure HESUs phylogenetically (Pons *et al.* 2006; Humphreys & Barraclough 2014; Humphreys *et al.* 2016). The GMYC is a likelihood approach that combines the forward through time birth process of the Yule model with coalescent theory, which combines two states into their common ancestor until a single state is reached at the phylogenetic root. The model initially expects that all lineages belong to one group and the threshold times uncovered indicate the estimated temporal locations where diversification within significant sub-units begins to occur. The GMYC model functions solely on ultra-metric trees, which at first glance makes it appear that we are limited to drawing conclusions singularly from the present, however, to explore deep time, time-slices could be taken by moving the line of the 'present' into the past.

Here, again focusing on the Afrotheria, and using the phylogeny inferred earlier in my work as a template, I aim to delimit HESUs within Afrotheria under the macroevolutionary criterion of diversification, using the GMYC model to phylogenetically infer HESUs (Pons *et al.* 2006). I further test the stability of HESUs throughout time when fossil taxa are included. As noted throughout the thesis, Afrotheria provides a good clade for inferring HESUs because it has well established, unique Linnaean ranks, with a large diversity, and previous chapters of my work have implied various regimes that possibly represent HESUs. The Afrotheria are currently classified into 9 families: Elephantidae, Trichechidae (manatees), Dugongidae, Procaviidae (hyraxes), Orycteropodidae (aardvark), Macroscelididae (sengis), Tenrecidae, Potamogalidae (otter shrews) and Chrysochloridae (golden moles).

Further to the existence of HESUs, the question of their stability is significant. HESUs are typically ascertained from extant taxa, with selection positively affecting those areas of an adaptive landscape with high fitness, leading to evolutionary units being formed (Cooney et al. 2017; Simpson 1944, 1953). Alternatively, extinction could passively decimate areas of a tree, leaving taxa down a now isolated lineage, like birds remaining as the final refuge of the dinosaurs. HESUs might therefore be defined by extinction history rather than adaptation. Extinction driven diversity has been found earlier in my thesis within the Afrotheria and by Lloyd & Slater (2021) in Cetacea, and if we include extinct taxa in an investigation, it is possible to yield different results than from extant alone (Gunnell *et al*. 2018). In actual fact, the absence of fossils, especially in solely extant diversification analyses, can be misleading, and could misinfer significant higher taxa by missing or adding ostensible diversification rate shifts (Lloyd & Slater 2021; Šmíd & Tolley 2019). Beyond using different taxa, if we moved the 'temporal goalposts', would the same HESUs still appear? Is an HESU only significant because it has had millions of years to diversify, or would it be significant as soon as its MRCA diverged? The analyses in this chapter aim to cast new light on the temporal stability of HESUs by taking snapshots through time with now extinct taxa treated as contemporary tips.

5.3 Methods

All analyses are derived from the distribution of 10,001 phylogenetic trees from the extant+extinct tree inference described in Chapter 2. The tree includes a total of 635 species (88 extant, 547 extinct). The distribution of trees were read into the statistical computing and graphics environment R using the Analyses of Phylogenetics and Evolution package (ape 5.3) (R Development Core Team 2020; Paradis & Schliep 2019). The last 5000 trees were used for any subsequent analysis to ensure that all were drawn from a well-mixed, post-burnin distribution. 100 trees were then randomly sampled from this distribution. These 100 random trees form the basis of all subsequent GMYC analyses.

5.3.1 Analyses of Extant Taxa

The Species Limits by Threshold Statistics (splits) package by Ezard *et al.* (2021) was used to perform the GMYC analyses to infer HESUs (Pons *et al.* 2006). The GMYC model can identify either one or multiple branching rate changes on a tree, depending on the model used (single/multiple threshold GMYC model). The GMYC model is only suitable for ultra-metric trees (i.e. trees where all tips are extant at the focal point in time) and my initial analyses focused on currently extant taxa. Therefore, all extinct tips were dropped from the 100 trees using ape. The single and multiple threshold GMYC models were then applied to all 100 trees in the random distribution sequentially. The most likely position(s) of thresholds for HESUs were recorded. Note that I focus on the single threshold model because the multiple threshold model has been shown to be unstable (Fujisawa & Barraclough 2013).

To examine how GMYC-defined HESUs vary through time based on presently extant species alone, analyses were conducted in sequential 5 million year time-slices from the present to 70 Mya. The trees were time-sliced at 5 million year intervals using the package paleotree (Bapst 2012). In the time-sliced trees, any lineages that crossed the time interval were considered as “extant” for that time window. This leaves tips that cross the time-slice but do not stop there, i.e. the trees were not ultrametric. Excess branch length at the tips was removed using phytools (Revell 2012) ensuring that all trees were ultrametric. The single and multiple threshold GMYC model analyses were performed on each time-slice and each tree in the 100 tree distribution.

5.3.2 Analyses Including Extinct Taxa

The approach described above was also applied to the full tree including both extant and extinct taxa. Any lineages that did not reach the focal time-slice threshold were considered extinct for that time-slice and dropped from the tree. A key difference between the extant-only and extant+extinct analyses is that the number of lineages included inevitably declines as we move from the present to the past in analyses of extant lineages, but diversity can both increase and decrease when incorporating fossil data. Also, very recent extinctions are often counted as extant here.

5.4 Results and Discussion

5.4.1 Analyses of Extant Taxa

Focusing in the present, the GMYC single threshold model indicates that HESUs do exist within the Afrotheria. Extant Afrotheria cover 6 orders, 9 families and 35 genera, and the single threshold analyses indicate 11 (confidence interval 10-13) significant diversification entities, with a threshold time of 22.09 million years ago, and considering 7 of 9 Linnaean families to be entities (Figure 1, Table 1a). The families Procaviidae, Elephantidae, Dugongidae, Trichechidae, Chrysochloridae, Potamogalidae and Orycteropodidae represent such entities, with Macroscelididae and Tenrecidae being further divided (Figure 1). The genus *Rhynchocyon* is shown to be its own cluster, with the rest of Macroscelididae forming another monophyletic cluster. Members of *Rhynchocyon* are an order of magnitude larger than the rest of their family (Puttick & Thomas 2015), and have been suggested to be split from other sengis in two of my previous chapters. Within Tenrecidae, the genera *Hemicentetes*, *Echinops*, *Setifer* and *Tenrec* (subfamily Tenrecinae) form one cluster, and the remaining species form another. These four genera all possess spines, thus a prominent convergence with hedgehogs, whereas the other genera are more shrew like. This split was also inferred by my phenotypic cranium analyses. Potamogalidae being distinct from Tenrecidae is further evidence for the otter shrews to be considered their own family, as realised by Everson *et al.* (2016) and all my previous data chapters, as some still consider them to be classically part of Tenrecidae. Tenrecs are terrestrial and endemic to Madagascar, whereas otter shrews are semi-aquatic and found in sub-Saharan Africa, as well as obviously being convergently lutrine.

This is all concordant with findings in other taxa (Carnivora, Euungulata, Lagomorpha) that, at least for mammals, HESUs fall somewhere between the family and genus levels (Humphreys & Barraclough 2014). Generally speaking, for extant taxa, the GMYC produces HESUs that are consistent with named higher taxa. One sengi HESU represents a named subfamily (Macroscelidinae), as does one tenrec HESU (Tenrecinae). The other tenrec HESU is comprised of two named subfamilies, one containing only a single species, that my phylogenies found to nest inside the other. As *Rhynchocyon* is the only extant genus in the sengi subfamily to which it belongs, these analyses are unable to determine whether it is the genus or the subfamily that represents the HESU.

For the extant lineages under the single threshold model, the number of entities, and the timing threshold for identifying the presence of such entities, appears to be stable over the last 10 million years. My analyses for the present, 5 and 10 million years ago show significance, always with 11 entities, and a mean estimate of the branching threshold is 22.54 million years ago (Table 1a). As we move back in time, the number of entities declines, but are no longer significant with time-slices older than 10 million years (Figures 2, S5.1 & S5.2, Table 1a). In contrast to the single threshold model, the multiple threshold model does not indicate any present day HESUs (Table 1a), yet shows HESUs in the recent past. For the present, this is illogical, as once an entity arises, it cannot vanish, even through extinction. Its significance on macroevolutionary history remains for all time, and if even a single species of an entity remains, then the entity still exists. For the null hypothesis to be rejected 5 million years ago and accepted in the present, all but a single entity, which represents all extant afrotherians, must have become extinct within the last 5 million years. This is an example of the temperamental nature of the multiple threshold analyses, with Fujisawa & Barraclough (2013) advising to be cautious when using it, and that the single threshold approach outperforms the multiple. The single threshold operates under the assumption that all between-group diversification takes place before all within-group branching. The multiple threshold model relaxes this constraint and uses an iterative split and fuse heuristic procedure on standing groups, but has been found to over-split and diminish confidence. The multiple threshold results found here are not currently reliable, but, as suggested by Fujisawa & Barraclough (2013), an enhanced delimitation algorithm could let the multiple threshold GMYC model become a valuable tool for future analyses, as multiple thresholds likely exist. Therefore, this investigation will focus solely on the results of the single threshold analyses, which are reliable, and disregard the multiple threshold when coming to any conclusions of macroevolutionary dynamics.

5.4.2 Analyses Including Extinct Taxa

The inclusion of extinct taxa reveals a more complex pattern in the identification of evolutionary entities. For the single threshold analyses of all lineages, in the present, a mean of 12 (rather than 11 in the extant only analysis) entities are indicated, with a confidence interval of between 6-17, and an indication that 25.93 million years ago is when one would expect to see within-cluster branching beginning to occur (Table 1b, Figure S5.3). For the MCC tree, the same 11 entities as the extant analyses are found, with two exceptions (Figure S5.3). The tenrecs are split into four, and the extinct Steller's sea cow is considered an extant entity separate from the dugong. The multiple threshold analyses for all taxa again show no significance in the present (Table 1b).

When including extinct taxa, trends through time differ. As noted above, the extant lineages in time only show significance between the present and 10 million years ago, with the branching threshold ranging from 22.09 to 22.79 million years ago. In contrast, in the analyses through time for the single threshold analyses of all lineages, only those time-slices between the present and 20 million years ago show any significant diversification clusters (Figure 3, Table 1b). The estimated point in time where the branching threshold occurs ranges between 25.93 and 43.04 million years ago. For 25-70 million years ago, the null hypothesis of no within-cluster branching is favoured by the GMYC model. These analyses include what would have been extinct species at each time-slice due to the variations in the 100 trees.

Moving backwards through time, the number of entities fluctuates up and down, unlike the decrease in the extant lineages (Figure 3). When considering all significant time-slices, the mean branching threshold is 35.66 million years ago (Table 1b). Different trees produce different results, hence taking an average of 100 trees. Figures 4 & 5, and S5.5 & S5.6, show the difference between the MCC tree estimating only a few clusters, to a random tree (7289) finding many. These figures, along with S5.3, S5.4 & S5.7, show an example of the clusters found for all lineages over the significant time-slices. The entities found also change. In the present, the MCC tree splits the tenrecs into four, but 5 million years ago, they are kept as a single entity.

The multiple threshold analyses show significance between 5-25 million years ago, indicating that the null hypothesis should be accepted in the present and for the time-slices 30-70 million years ago. However, as noted above, the results of the multiple threshold analysis should be treated with caution.

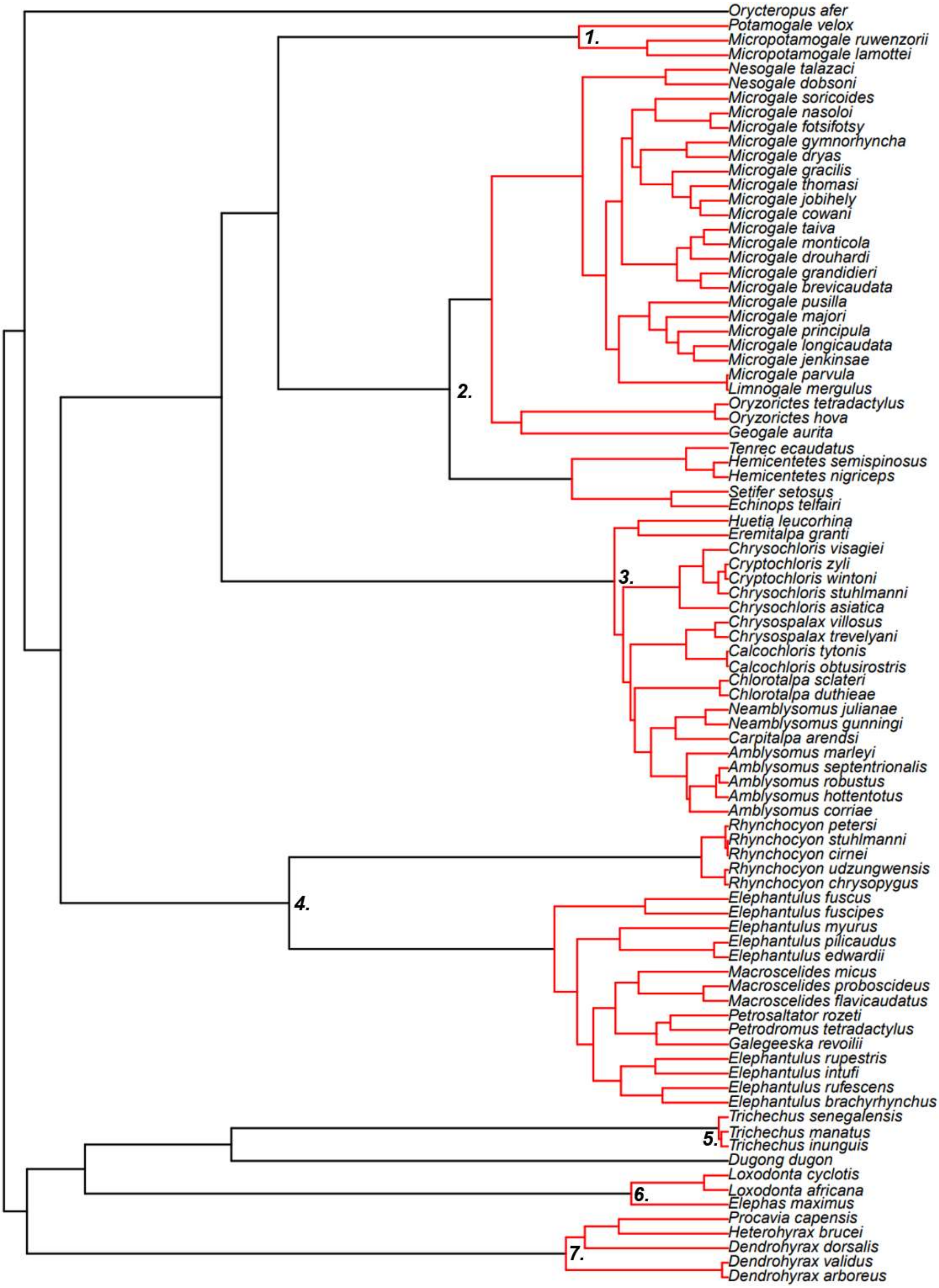


Figure 1. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for extant afrotherian lineages in the present. The black-to-red colour transition indicates the beginning of a new cluster. The genera Dugong and Orycteropus are not highlighted red as they only contain a single species. Families:* ***1.*** *Potamogalidae* ***2.*** *Tenrecidae* ***3.*** *Chrysochloridae* ***4.*** *Macroscelididae* ***5.*** *Trichechidae* ***6.*** *Elephantidae* ***7.*** *Procaviidae.*

Table 1. *GMYC single (ST) and multiple (MT) threshold mean results of 100 randomly sampled trees from those generated in Chapter 2 for (**a**) extant and (**b**) all afrotherian lineages at various time-slices. Age and threshold (Th) times in million years. Entities rounded and show confidence interval. LR (0) indicates the null likelihood ratio and p-value significance indicated as *** <0.001, ** <0.01 and * <0.05.*

a. Extant		ST			MT				
Age	LR (0)	LR	Entities	Threshold	LR	Entities	Th (µ)	Th (min)	Th (max)
0	12.01	18.73***	11 (10-13)	22.09	5.77	59 (42-74)	6.67	1.22	13.95
5	-33.65	18.75***	11 (8-13)	22.79	8.61*	30 (27-35)	12.29	6.79	19.38
10	-42.05	19.52***	11 (7-13)	22.74	18.76***	16 (15-19)	19.81	13.43	27.43
15	-35.05	8.67	10 (6-13)	25.07	9.05	11 (8-11)	26.57	21.69	31.46
20	-29.21	4.5	9 (3-11)	32.39	4.38	9 (4-9)	35.98	25.26	46.7
25	-25.91	3.02	6 (2-9)	51.8	3.73	8 (3-9)	41.33	29.47	53.19
30	-23.88	2.02	3 (1-9)	69.69	2.38	8 (1-8)	48.43	46.89	49.98
35	-22.82	1.7	3 (1-9)	69.14	2.23	8 (1-8)	49.03	47.34	50.71
40	-21.65	2.68	6 (1-9)	56.7	2.51	8 (2-8)	49.87	48.29	51.46
45	-18.25	3.03	5 (2-7)	60.04	3.82	6 (3-6)	62.2	58.04	66.36
50	-15.59	3.26	5 (2-6)	60.11	3.66	5 (2-5)	63.04	58.48	67.61
55	-12.81	2.2	3 (1-5)	69.87	2.94	5 (2-5)	70.1	69.15	71.06
60	-11.04	1.2	2 (1-5)	74.03	2.21	4 (2-5)	72	71.68	72.33
65	-8.99	1.28	3 (1-5)	73.38	1.88	4 (1-4)	72.22	71.73	72.71
70	-5.34	1.68	2 (1-3)	73.73	2.06	4 (2-4)	73.63	72.89	74.37

b. All		ST			MT				
Age	LR (0)	LR	Entities	Threshold	LR	Entities	Th (µ)	Th (min)	Th (max)
0	21.89	14.19**	12 (6-17)	25.93	4.14	69 (32-79)	5.8	1.23	12.05
5	-29.38	16.63***	14 (8-23)	33.5	12.05**	41 (40-47)	14.46	7.4	24.54
10	-22.16	13.51**	15 (5-27)	43.04	11.37**	45 (42-53)	18.81	12.22	27.34
15	-38.68	14.21**	19 (10-31)	38.64	14.58**	42 (40-48)	24.63	16.82	34.98
20	-41.56	10.79*	28 (17-41)	37.18	12.39**	45 (41-51)	29.97	22.78	39.53
25	-39.17	7.92	29 (14-47)	43.83	10.01*	46 (38-52)	34.05	27.52	42.3
30	-31.16	5.49	36 (11-56)	45.93	7.29	49 (37-56)	38.92	32.3	47.39
35	-16.32	4.43	22 (9-55)	57.34	4.87	46 (22-58)	43.93	37.37	50.85
40	-6.08	4.19	26 (8-59)	59.14	5.57	48 (29-59)	46.93	41.85	52.73
45	7.37	4.3	25 (8-60)	62.04	5.98	51 (29-61)	50.33	46.52	55.48
50	-1.64	3.86	22 (5-47)	62.52	5.27	41 (23-48)	54.93	51.59	58.76
55	-4.76	3.53	19 (6-38)	64.58	4.04	32 (12-37)	59.35	56.73	62.25
60	3.95	3.35	12 (4-32)	69.49	2.57	33 (6-35)	63.37	61.49	65.37
65	0.16	2.95	8 (2-21)	70.6	2.53	17 (3-19)	67.11	66.01	68.23
70	-5.29	2.49	3 (1-6)	73.4	2.7	5 (2-6)	72.39	71.67	73.12

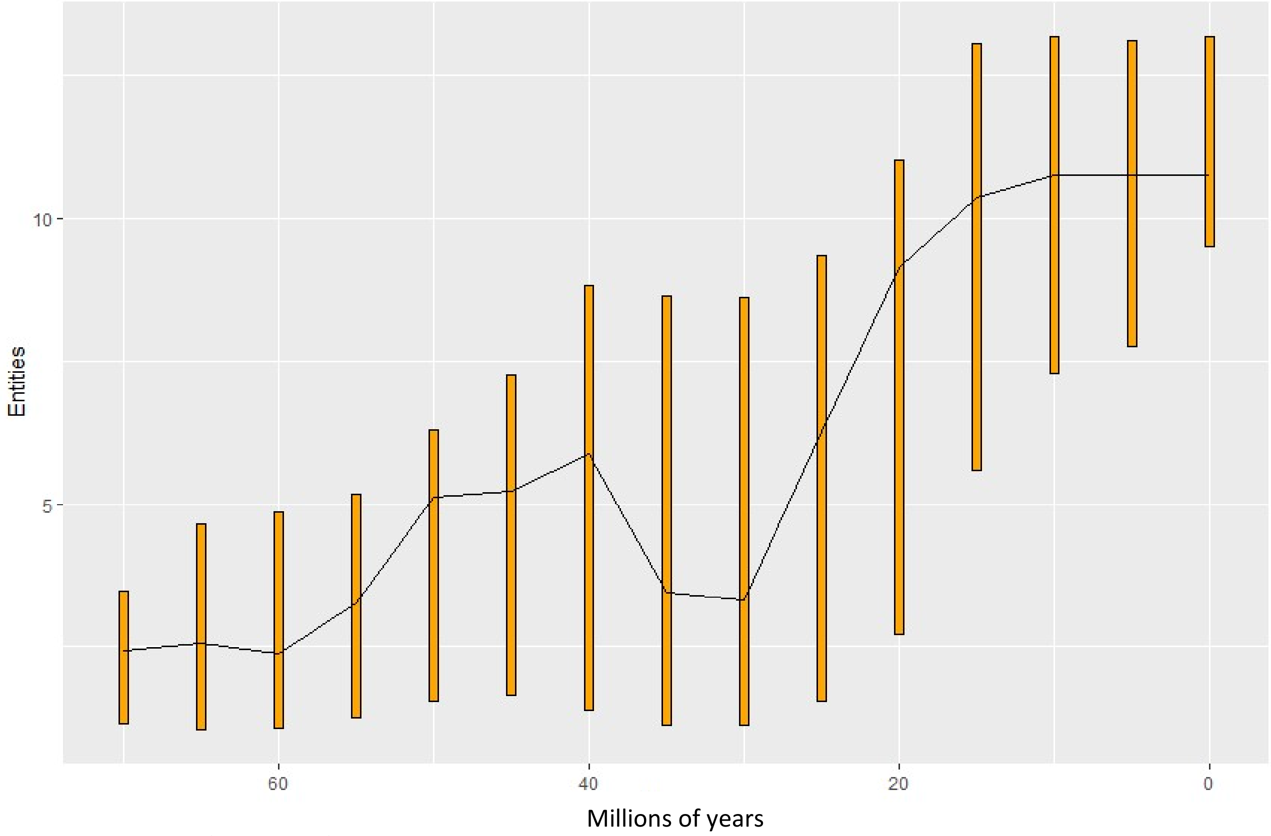


Figure 2. *Mean (black line) entities for 100 trees of extant only lineages in time. Orange bars represent the range of mean minimum to mean maximum entities. Only 0-10 million years ago are significant.*

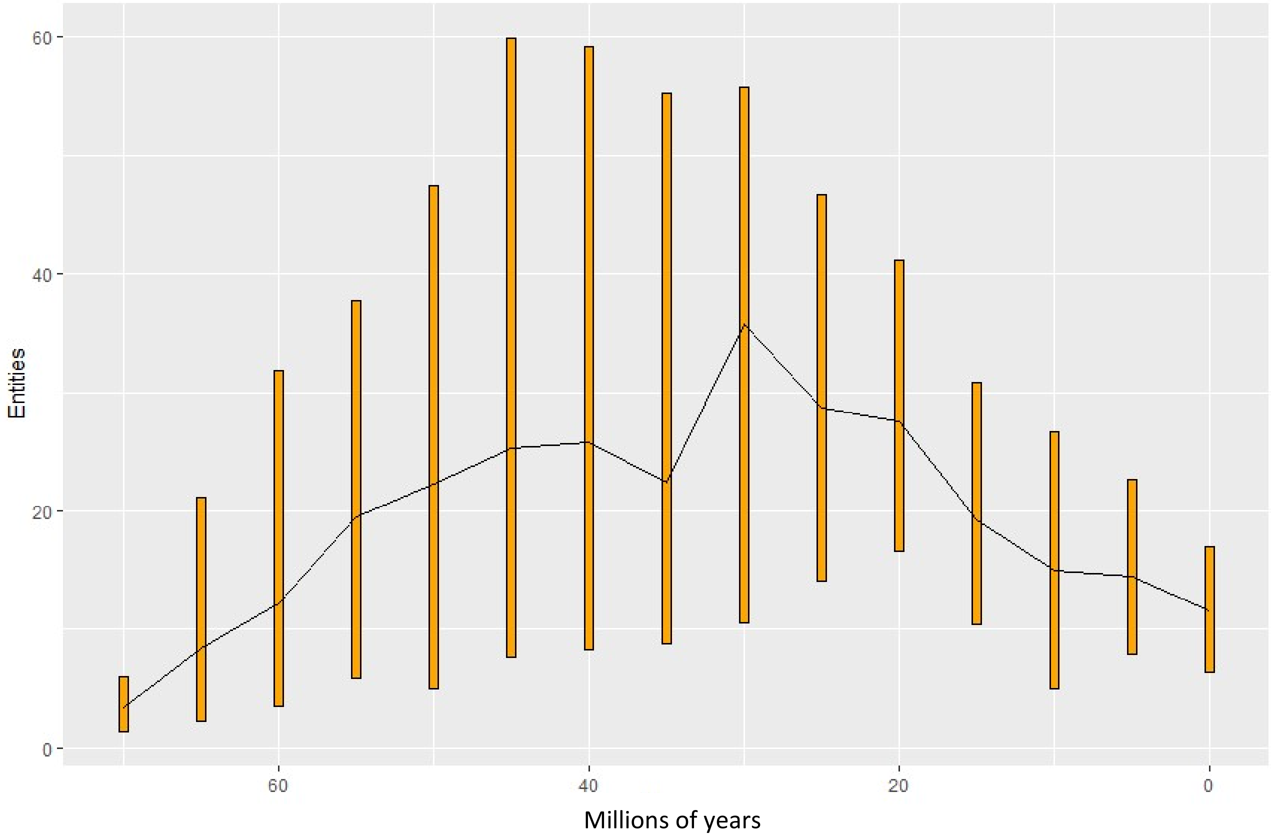


Figure 3. *Mean (black line) entities for 100 trees of all (extant+extinct) lineages in time. Orange bars represent the range of mean minimum to mean maximum entities. Only 0-20 million years ago are significant.*

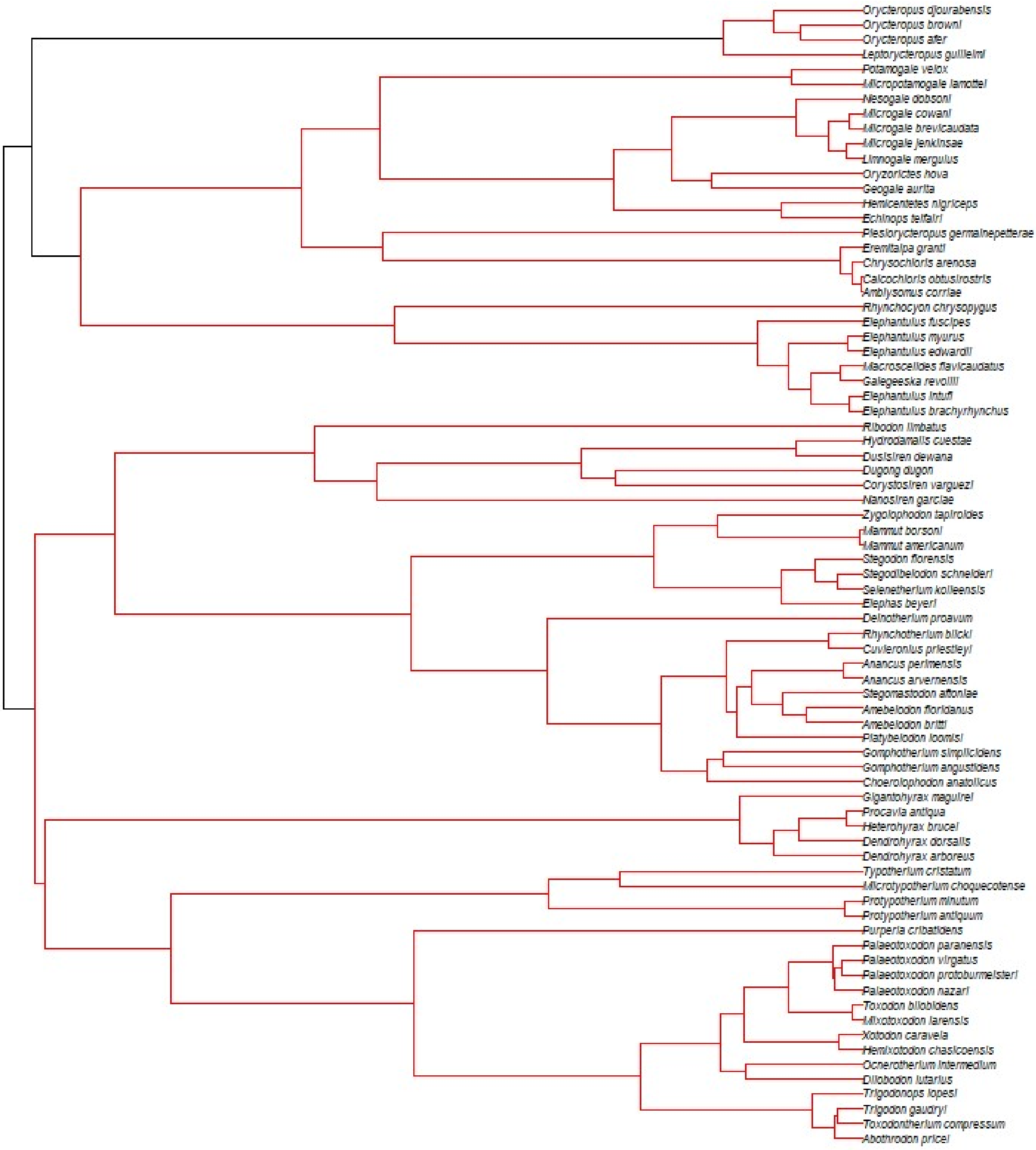


Figure 4. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for all afrotherian lineages 10 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

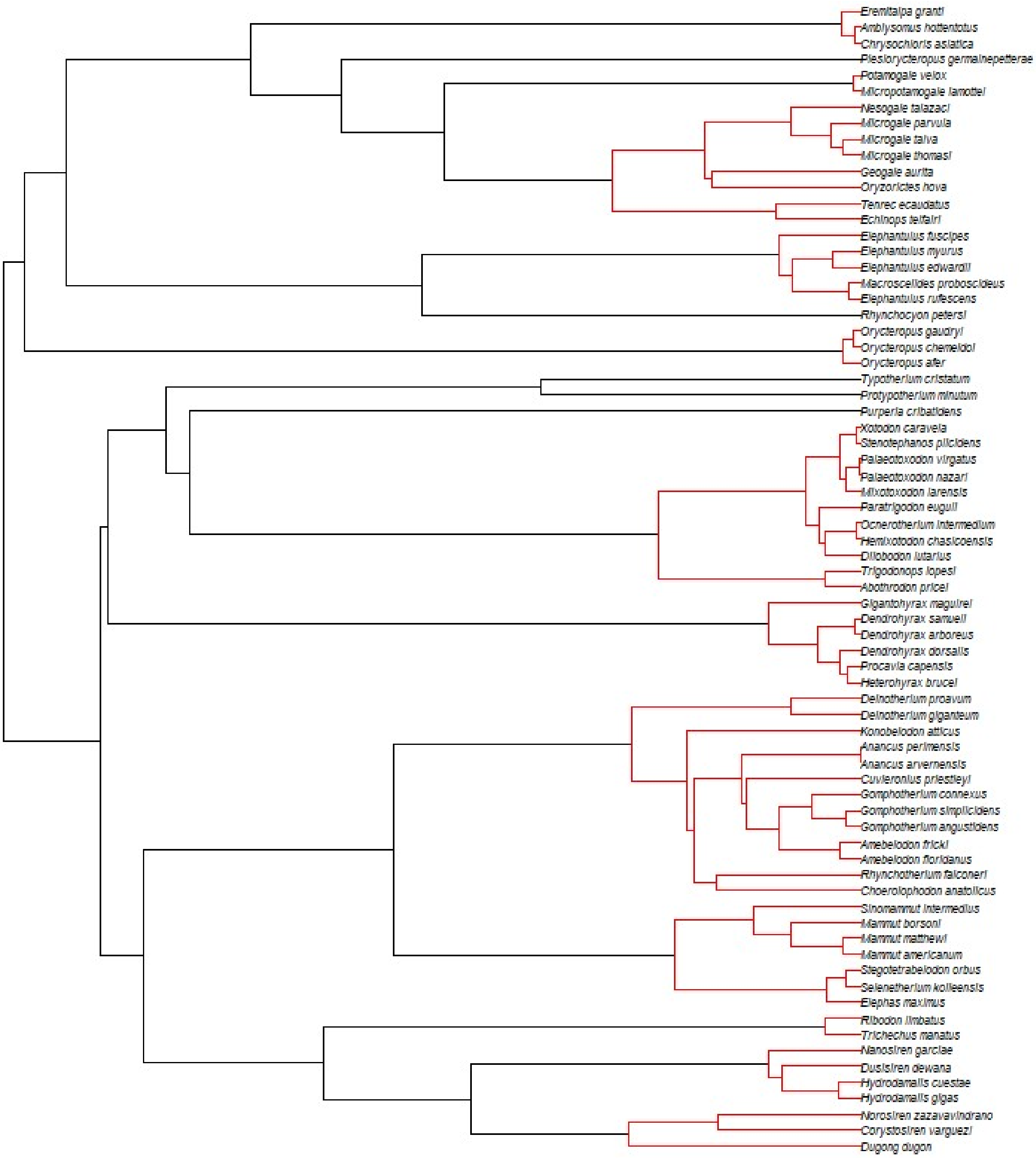


Figure 5. *A phylogeny of the GMYC single threshold results of tree 7289 from Chapter 2 for all afrotherian lineages 10 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon petersi represents all Rhynchocyon, as they had not evolved yet.*

5.5 Conclusions

My analysis of extant lineages suggest that 11 HESUs within Afrotheria are expected to be seen 22-23 million years ago. These map from the Linnaean ranks of family to genus. While these clades can be considered higher evolutionary significant units, and demonstrate that a phylogenetic approach to elucidating higher taxa is beneficial, there is variation between the results of solely extant and all species analyses. Notably, the estimation of the branching threshold shows how the present is just a snapshot of time. With extinct lineages included, the threshold for identifying entities moves back to 35-36 million years ago on average. Including extinct lineages therefore extends the time scale over which HESUs are supported. Another key difference between extant-only and extant+extinct analyses is that with fossil taxa included, the number of entities increases. The fossil analyses reveal entirely extinct clades as HESUs, for example the gomphotheres, extinct elephant relatives. The 11 extant HESUs are kept, on the whole, throughout the temporal total taxa analyses, although the tenrecs present some uncertainty. The stability of the 11 HESUs regardless of the inclusion of extinct taxa suggest that these are robust, however, the additional HESUs that only emerge with time-slicing are a clear reminder that we must travel back and include those species lost to time to glean a complete picture of macroevolutionary dynamics.

Chapter 6

General Thesis Discussion: Deep Time Drivers of Evolutionary Entities

6.1 Chapter Findings

The overall objectives of this thesis were to reveal the degree of relationship between HESUs and named higher taxa with the Afrotheria, and elucidate how such units can be realised and what processes form them in deep time. In this section, I will recap on the main results of each data chapter.

In Chapter 2, my aims were to create an accurate phylogeny of Afrotheria, incorporating extant and extinct species, then to test how incorporating fossil data in diversification analyses influences the inference of shifts in speciation and extinction rates. I found that including fossil taxa in analyses greatly influences the inference of macroevolutionary processes. Practically no variations in diversification rates are found in the solely extant analyses of Afrotheria, but including the extinct species reveals that numerous rate shifts have occurred over a significant scale, and that some larger clades share unique rates when compared to their sister lineages. Diversity of the Afrotheria appears to be driven by reduced extinction, not increased speciation, an observation made in other clades by other studies (i.e. Cetacea, Lloyd & Slater 2021). Lineages with high speciation rates have high extinction rates, and those with low speciation rates have low extinction rates, suggesting that the nature of afrotherian diversification history is volatile. The more diverse clades have lower speciation and extinction rates, and higher net diversification rates, than the smaller lineages, and see the reduction in speciation and extinction rates at their origins, while the less numerous lineages see a reduction much closer to the present. These larger clades further share significantly smaller body sizes and much more striking convergence to other mammalian lineages when compared to the clades with only a few extant species. Lineages that share diversification histories different to their sisters could be identified as higher evolutionary significant units (HESUs).

In Chapter 3, my aims were to investigate the existence of afrotherian zoogeographic realms and to test historical zoogeographic signatures and the patterns that influence them. I found that zoogeographic realms are a poor metric for classifying higher taxa within the Afrotheria. Only the sirenians and tenrecs exist in unique enough areas to be considered distinct, while all other taxa see a much patchier distribution. Dispersal barriers on Africa are clearly weak, and where there is dispersal, speciation is usually very low (Claramunt *et al.* 2012; Humphreys & Barraclough 2014). When regions are manually inferred from natural geography and richness, irrespective of phylogenetics, some moderately noticeable patterns of shared zoogeographic history are found on the phylogeny of Afrotheria, although the sirenians and tenrecs have the only strong patterns.

Extinction is found to be the most powerful driver of afrotherian zoogeography, by a significant margin. When geography and phylogenetics are used to delineate regions, phylogenetic relationships heavily influence the realisation of regions, overpowering the geography, with Linnaean families following their own regions. Sympatry with near instant dispersal is the main driver of these patterns, with extinction as a close second, and dispersal again being very weak. Overall, it is likely that the current zoogeography of afrotheres is the result of extinction reducing a more widely spread distribution, and only those clades with exceptionally strong dispersal barriers could reflect HESUs.

In Chapter 4, my aims were to assess the tempo and mode of divergence in afrotherian morphology, identify lineages with shifts in diversification and/or evolvability, and to see whether any such shifts might mark the emergence of HESUs. I found that the Afrotheria possess extensive heterogeneity in body size and cranium shape evolution. Only a few species show significant directional shifts in body mass, so it must be concluded that the afrotheres' trek through trait space has been overall consistent with a model of Brownian motion. Cranium morphology, on the other hand, sees a number of evolvability shifts on higher nodes. *Rhynchocyon* shifts differently to other sengis, and the hedgehog tenrecs shift differently to the shrew tenrecs. Several other lineages occasionally show shifts, but not as often as these clades. *Limnogale mergulus* (and its sister *Microgale parvula*) is often found to behave differently to the remaining paraphyletic *Microgale*, potentially indicating the genesis of a future HESU. Whereas most afrotheres can explain their varied body size and cranium shape through simply randomly walking, the four clades of *Rhynchocyon*, the remaining sengis, the hedgehog tenrecs and the shrew tenrecs show significant shifts in cranium evolvability and could be considered HESUs.

In Chapter 5, my aims were to phylogenetically infer HESUs by delimiting clusters of diversification rates and to test the stability of HESUs throughout time and when extinct species are included. I found that when analysing only extant lineages through time, different patterns emerge than when extinct taxa are included. An average estimate of the threshold where branching rate clusters are expected to begin is pushed back from the extant only estimate of ~22-23 million years to ~35-36 million years by the presence of fossil taxa. Branching diversification rate clusters could reflect HESUs (Humphreys & Barraclough 2014), and in the present, 11 are found, mapping to 7 of 9 Linnaean families, with Macroscelididae and Tenrecidae being sub-divided into the *Rhynchocyon* and the remaining sengis, and the hedgehog tenrecs and the shrew tenrecs, respectively. These same clusters are also found when looking in the past of both extant only and extant+extinct lineages, with a number of now lost extinct HESUs also being indicated. An exception to this is Tenrecidae, which in the fossil analyses is sometimes grouped as one or further split into more than two clades.

6.2 Are HESUs found within Afrotheria?

My analyses suggest that HESUs do exist within Afrotheria, and extinction is often found to be a driving force for macroevolutionary patterns in deep time (Lloyd & Slater 2021). In Chapters 2 & 3, extinction was found to be the strongest driver of afrotherian diversity, both phylogenetically and zoogeographically. The eroding effect of extinction may be more relevant to defining HESUs than adaptation. A small leap forward of a new trait could be misinterpreted to the rest of a clade if all closely related species are made extinct. If the most basal lineage of a large HESU and a more newly evolved species within it are later made the only survivors of extinction, might they be split into two HESUs? If the answer is yes, then is this what has happened to the realisation of current and past HESUs? Consider bears. The panda diverged from other bears at approximately the same time as the walrus diverged from the eared seals, yet all bears are one family, and the walrus exists in its own family. If the only bears to survive were the panda and the polar bear, their differences in diversification, morphology, geography and even diet could render them as significantly unique if we did not know what the ‘average bear’ was. All bears fall into a rough normal distribution in these traits, with these two species near the opposite extremes. If just these two were known, due to extinction, they would form a bimodal distribution with two peaks, potentially realising them as two HESUs.

In all four data chapters, Potamogalidae (otter shrews) and Tenrecidae (tenrecs) are considered to be distinct. Tenrecidae have higher net diversification and are geographically isolated from the continental Potamogalidae, solely existing on Madagascar, the only realised terrestrial zoogeographic region of the Afrotheria. My morphological analyses suggest that, based on skull shape, Tenrecidae are split into sub-clades, causing Potamogalidae to be realised as an HESU due to the monophyletic nature of HESUs, a split further suggested by the GMYC analyses as these groups form different branching rate clusters. The traditional taxonomy, still used very recently, of otter shrews as ‘otter shrew tenrecs’ (i.e. Finlay & Cooper 2015) should therefore be disregarded, with the otter shrews confidently advocated as an HESU, more in line with Everson *et al.* (2016).

In three chapters, all but zoogeographically, *Rhynchocyon* are found to be distinct from the other Macroscelididae. The genus has higher rates of speciation and extinction, and lower net diversification, than its sister sub-clade. Phenotypically, members of each sub-clade see evolvability shifts in cranium morphology occur differently than to the other, and they each form their own branching rate clusters. Being found as unique entities thrice within my data analyses suggests that they could be recognised as HESUs.

Some clades were found twice in my chapters to be unique. Trichechidae and Dugongidae are found to be lineages distinct from each other by the zoogeography and branching rate cluster analyses. The dugong is found in the Indian and Pacific oceans, and the manatees are found in the

Atlantic and up several large riverways. Hedgehog tenrecs are found to be distinct from shrew tenrecs by the morphological and GMYC analyses, although there is an air of uncertainty with their diversification rates. All Tenrecidae lineages are found to share very similar rates in Chapter 2, but the temporal displacement analyses of Chapter 5 sometimes either group or further split the family. Chrysochloridae share their own rates of diversification different to the tenrecs and otter shrews, and are found to be their own cluster in the GMYC analyses.

Overall, my results suggest that, for HESUs within the Afrotheria, some units are found that generally reflect named Linnaean families. Macroscelididae is not strongly associated with being a potential HESU, with the two sengi subfamilies (Rhynchocyoninae & Macroscelidinae) being evidenced here to be HESUs, as opposed to the whole family. On my phylogeny, sub-divisions of Macroscelidinae were found to be non-monophyletic, and no further splitting was suggested by any chapter. Tenrecidae sometimes has evidence to be a potential HESU, with geography and Chapter 2 diversification analyses indicating that tenrecs are one significant group. However, as mentioned above, there is some evidence for them to be split (i.e. morphological), although some of this evidence is uncertain (i.e. GMYC diversification analyses). Of the three tenrec subfamilies, one (Oryzorictinae) was found to be paraphyletic. Geogalinae, containing a single species, was found to follow the patterns of a combined clade when added to Oryzorictinae. Sometimes (i.e. the GMYC analyses), *Oryzorictes*, found in my work to be a sister to Geogalinae, and not as a sister to the clade of *Microgale, Limnogale* and *Nesogale*, was split from these other lineages, and adding Tenrecinae, realised four clusters. The two golden mole subfamilies were not recognised as monophyletic in my phylogeny, and no splitting of any kind was found within the family. Discrepancies between my realised intra-family relationships and current classifications could explain why monophyletic HESUs were not found when larger families have named super-generic taxa.

6.3 Future

My results have shown an important role for extinction in determining how we interpret macroevolutionary patterns. Extinction and fossils influence our understanding of HESUs by unmasking patterns hidden by extant and speciation only analyses of evolutionary processes. Extinction modelling could be an intriguing future endeavour in the realisation of HESUs and other macroevolutionary studies, as could empirical analyses into the effects of extinction on higher taxa and their shaping processes (Lloyd & Slater 2021; Humphreys & Barraclough 2014). Relatedly, not all of my analyses used extinct taxa, but those that did found very different outcomes than any solely extant investigations. Exploring zoogeographic and phenotypic histories using fossil data may reveal patterns not uncovered here (Louca & Pennell 2020). As birth-death time trees are calculated, simplistically, from speciation and extinction rates, and the sampling probability of a species being found in the tree, there are an infinite number of permutations of speciation and extinction rate for any given net diversification rate (Louca & Pennell 2020). If the extinction and sampling probability are known, then there will only be one solution for the speciation rate. Including fossil data allows us to better approximate these values, thus heavily limiting the number of potential solutions of likely diversification histories, meaning interpretations of macroevolutionary concepts, including HESUs, should be much better. Further, it is practically impossible for every extinct species to be known, but including more fossil taxa will likely better represent the true history of a clade. Additional challenges may exist, such as by contemplating whether preserved fossils are a biased subset of all species that have lived, as the fossil record has many biases towards certain environmental conditions and forms of organisms being required for fossilisation.

Exploring other clades that possess different conditions to the Afrotheria, such as in terms of geographic uniqueness, morphological variation or diversification history, may find other processes that shape HESUs. Exploring different sized clades, i.e. a class or classes, could prove interesting. In a study of all mammals, or indeed all tetrapods, would the same HESUs found here within the Afrotheria still be found? What about even higher ESUs? If a Level 1 ESU is equal to a species, and a Level 2 ESU (HESU) approximately echoes a family, what does a Level 3 ESU represent? Do they even exist, and if so, what about levels beyond, until Earth's entire biohistory forms a single ESU? Alfaro *et al*. (2009) find distinct diversification histories of a number of clades deep within the tree of vertebrate life. HESUs might be found at higher taxonomic ranks in one clade compared to another, as HESUs are realised when they differ from their sisters, showing change that is significantly slower or faster than average.

Chiroptera likely have limited morphological diversity, yet have a cosmopolitan distribution. Morphology would likely be less useful in differentiating them, but how does one allocate zoogeographic boundaries for a taxon that can fly? Exploring how diversification, morphology and geography lead to HESUs being realised in the bats could be a very different enterprise than here within Afrotheria. Serpentes again show reduced morphological diversity, and are again cosmopolitan, with the exception of more polar regions and a handful of temperate islands, with some lineages adapted to aquatic existence. Zoogeography might play a larger role in finding HESUs within the snakes. Marsupials are very diverse, with many lineages found on Australia and nearby islands, and further distribution to the Americas. Although geography may play a role here, morphology may be more important when finding HESUs within. Diversification rate clusters are likely one of the best ways to delimit HESUs, but considering other evidence, such as morphology and geography, could reinforce patterns left ambiguous by phylogenetic only identification. To allow all of life to be searched for realised HESUs, some common, formal definition of what an HESU is and how they are to be detected is needed.

6.4 Conclusion

To summarise the common patterns of, and conclude my thesis, extinction is suggested to be a significant deep time driver of evolutionary entities within the Afrotheria. The otter shrews, along with giant sengis and the remaining sengis, are strongly supported to be realised as HESUs. The manatees, dugong and golden moles, and potentially the hedgehog tenrecs and shrew tenrecs, also show support in being considered HESUs. Due to monophyly, the aardvark, hyraxes and elephants must also each be realised as HESUs, as found by the branching rate cluster analyses throughout time. The evidence does indicate that HESUs do exist within the Afrotheria, mapping to or just below the Linnaean rank of family. Future analyses, concerning the impact of extinction, and exploring other clades beyond Afrotheria, could uncover even deeper insights into the elucidations of macroevolutionary dynamics.

Appendix

Table S2.1. *List of species added from the Paleobiology Database, with age ranges and references.*

Name	Age	Reference
Abdounodus hamdii	61.6-59.2	Gheerbrant *et al.* 2001
Abothrodon pricei	11.62-0.0117	Paula Couto 1956
Acamana ambiguus	42-36	Simpson *et al.* 1962
Acoelodus oppositus	55.8-48	Ameghino 1897
Acoelodus proclivus	41.3-38	Ameghino 1902
Acoelodus terminalis	55.8-48	Ameghino 1902
Adapisorex gaudryi	59.2-56	Lemoine 1883
Adunator abditus	61.7-56.8	Secord 2008
Adunator fredericki	63.3-61.7	Winterfeld 1982
Adunator ladae	63.3-56.8	Winterfeld 1982
Adunator martinezi	63.3-61.7	Winterfeld 1982
Adunator meizon	61.7-56.8	Secord 2008
Adunator minutus	61.7-55.8	Krishtalka 1976
Afrochoerodon kisumuensis	16.9-11.62	Picford 2001
Afrohypselodontus grandis	41.3-38	Senut & Pickford 2021
Afrohypselodontus minus	41.3-38	Senut & Pickford 2021
Afromastodon coppensi	23.03-11.608	Pickford 2003
Albertogaudrya carahuasensis	48.6-37.2	Carbajal *et al.* 1977
Albertogaudrya robusta	48-42	Roth 1904
Albertogaudrya unica	55.8-48	Ameghino 1901
Aletodon conardae	61.7-56.8	Winterfeld 1982
Aletodon gunnelli	58.7-55.8	Gingerich 1977
Aletodon quadravus	61.7-56.8	Gingerich 1983
Allalmeia atalaensis	42-36	Rusconi 1946
Amebelodon britti	13.6-4.9	Lambert 1990
Amebelodon floridanus	10.3-5.333	Shoshani & Tassy 1996
Amebelodon fricki	13.6-4.9	Barbour 1927
Amebelodon grandincisivus	9.7-8.7	Tassy 1999
Amphilemur eocaenicus	47.8-41.3	Heller 1935
Anancus arvernensis	7.246-0.126	Hautier *et al.* 2009
Anancus defloccatus	2.588-0.0117	Hay 1926
Anancus kenyensis	11.608-3.6	MacInnes 1942
Anancus lehmanni	11.608-5.333	Konidaris & Roussiakis 2019
Anancus orarius	2.588-0.0117	Hay 1926
Anancus perimensis	11.608-5.333	Falconer & Cautley 1847
Anayatherium ekecoa	29-21	Shockey 2005
Anayatherium fortis	29-21	Shockey 2005
Ancylocoelus frequens	29-21	Ameghino 1894
Anisosiren pannonica	47.8-41.3	Kordos 1979
Anomotherium langewieschei	33.9-23.03	Siegfried 1965
Antarctodon sobrali	47.8-38	Bond *et al.* 2011
Antepithecus brachystephanus	55.8-38	Ameghino 1901
Antepithecus innexus	41.3-38	Ameghino 1904
Antofagastia turneri	48-42	García López & Babot 2015
Aphanobelodon zhaoi	15.97-13.82	Wang *et al.* 2017

Apheliscus chydaeus	55.8-48.6	Gingerich 1994
Apheliscus insidiosus	55.8-48.6	Cope 1875
Apheliscus nitidus	61.7-55.8	Simpson 1937
Apheliscus wapitiensis	55.8-48.6	Rose 1981
Archaeophylus patrius	29-21	Ameghino 1897
Archaeopithecus rogeri	57-37.2	Ameghino 1897
Archaeoplus incipiens	23.03-15.97	Ameghino 1898
Arenagale calcareus	41.3-38	Pickford 2015
Argyrohippus boulei	21-17.5	Ameghino 1902
Argyrohyrax proavus	29-21	Ameghino 1897
Arsinoitherium giganteum	28.1-23.03	Sanders *et al.* 2004
Arsinoitherium zitteli	33.9-23.03	Beadnell 1902
Asmodeus osborni	29-21	Ameghino 1894
Astraponotus assymmetrus	41.3-38	Simpson 1967
Astraponotus dicksoni	48-42	Simpson 1967
Astraponotus dilatatus	48-42	Simpson 1967
Astraponotus holdichi	48-42	Simpson 1967
Astraponotus thompsoni	48-42	Simpson 1967
Astrapothericulus iheringi	20.44-15.97	Ameghino 1902
Astrapotherium guillei	15.97-13.82	Kramarz *et al.* 2019
Astrapotherium magnum	17.5-16.3	Ameghino 1889
Astrapotherium ruderarium	21-17.5	Kramarz & Bond 2010
Baguatherium jaureguii	33.9-28.4	Salas *et al.* 2006
Barytherium grave	38-28.1	Andrews 1901
Berrulestes pellouini	59.2-56	Hooker & Russell 2012
Berrulestes phelizoni	59.2-56	Hooker & Russell 2012
Berrulestes poirieri	59.2-56	Hooker & Russell 2012
Bharatisiren indica	28.1-23.03	Bajpai *et al.* 2006
Bharatisiren kachchhensis	23.03-20.44	Bajpai & Domning 1997
Blancotherium buckneri	13.6-10.3	May 2019
Boreastylops lumbrerensis	47.8-38	Vucetich 1980
Brachyhyrax aequatorialis	20.44-15.97	Pickford 2004
Brachyhyrax oligocenus	28.4-20.44	Rasmussen & Gutierrez 2009
Brachystephanus postremus	42-36	Simpson *et al.* 1962
Caenophilus tripartitus	11.8-10	Ameghino 1904
Callistosiren boriquensis	28.1-23.03	Velez-Juarbe & Domning 2015
Campanorco inauguralis	48.6-37.2	Bond *et al.* 1984
Caribosiren turneri	28.4-23.03	Reinhart 1959
Carodnia feruglioi	66-61.6	Simpson 1935
Carodnia inexpectans	55.8-48.6	Antoine *et al.* 2015
Carodnia vieirai	58.7-48.6	Paula Couto 1952
Carolozittelia tapiroides	56-38	Ameghino 1901
Chilgatherium harrisi	28.1-23.03	Sanders *et al.* 2004
Choerolophodon anatolicus	9.7-8.7	Ozansoy 1965
Choerolophodon chioticus	15.97-11.608	Tobien 1980
Choerolophodon pentelici	11.608-5.333	Geraads *et al.* 2005
Chrysochloris arenosa	5.333-3.6	Asher & Avery 2010
Chrysochloris bronneri	5.333-3.6	Asher & Avery 2010
Cingulodon magioncaldai	66-61.6	De Bast & Smith 2017

Cochilius fumensis	29-21	Simpson 1932
Colbertia falui	41.3-38	Fernández *et al.* 2021
Colbertia lumbrerense	47.8-38	Bond 1981
Colbertia magellanica	58.7-48.6	Paula Couto 1952
Colombitherium tolimense	37.2-33.9	Hoffstetter 1970
Colpodon distinctus	21-17.5	Ameghino 1902
Comahuetherium coccaorum	21-17.5	Kramarz & Bond 2011
Coquenia bondi	41.3-38	Deraco *et al.* 2008
Coresodon scalpridens	29-21	Ameghino 1894
Corystosiren varguezi	10.3-3.6	Domning 1990
Crenatosiren olseni	33.9-23.03	Domning 1991
Crivadiatherium iliescui	48.6-37.2	Radulesco & Sudre 1985
Crivadiatherium mackennai	48.6-37.2	Radulesco *et al.* 1976
Culebratherium alemani	23.03-15.97	Velez-Juarbe & Wood 2019
Cuvieronius priestleyi	1.8-0.3	Madden 1983
Cuvieronius tropicus	2.588-0.0117	Osborn 1936
Damarachloris primaevus	47.8-41.3	Pickford 2019
Deinotherium bozasi	11.608-0.781	Arambourg 1934
Deinotherium giganteum	13.82-3.6	Kaup 1829
Deinotherium indicum	11.62-7.246	Falconer 1845
Deinotherium proavum	11.608-5.333	Iliopoulos *et al.* 2014
Dendrohyrax samueli	11.608-5.333	Pickford 2005
Diamantochloris inconcessus	47.8-41.3	Pickford 2015
Dilobodon lutarius	9-6.8	Ameghino 1886
Dioplotherium allisoni	20.44-4.9	Domning 1989
Dipavali petri	59.2-56	Van Valen 1978
Dolichostylodon saltensis	41.3-38	García López & Powell 2009
Domningia sodhae	23.03-20.44	Thewissen & Bajpai 2009
Dorraletes diminutivus	61.7-56.8	Gingerich 1983
Dusisiren dewana	11.62-7.246	Takahashi *et al.* 1986
Dusisiren jordani	11.62-3.6	Domning 1978
Dusisiren reinharti	15.97-11.62	Domning 1978
Edvardotrouessartia sola	56-41.3	Ameghino 1901
Elephas beyeri	2.588-0.0117	von Koenigwald 1956
Elephas melitensis	2.588-0.0117	Falconer 1868
Elephas nawataensis	11.62-2.588	Tassy 2003
Eoastrapostylops riolorense	58.7-55.8	Soria & Powell 1981
Eomorphippus obscurus	36-29	Ameghino 1901
Eorhynchocyon rupestris	41.3-38	Senut & Pickford 2021
Eosiren abeli	47.8-41.3	Sickenberg 1934
Eosiren imenti	33.9-28.1	Domning *et al.* 1994
Eosiren libyca	38-33.9	Andrews 1902
Eosiren stromeri	38-33.9	Domning 1994
Eotheroides aegyptiacum	47.8-41.3	Palmer 1899
Eotheroides babiae	47.8-41.3	Bajpai *et al.* 2006
Eotheroides clavigerum	38-33.9	Zalmout & Gingerich 2012
Eotheroides lambondrano	48.6-37.2	Samonds & Zalmout 2009
Eotheroides sandersi	38-33.9	Zalmout & Gingerich 2012
Eotheroides waghapadarensis	47.8-41.3	Das & Basu 1994

Eotmantsoius perseverans	48.6-33.9	Simons *et al.* 1991
Eritherium azzouzorum	59.2-56	Gheerbrant 2009
Eritreum melakeghebrekristosi	33.9-23.03	Shoshani *et al.* 2006
Etayoa bacatensis	61.7-55.8	Villarroel 1987
Eurybelodon shoshanii	23.03-5.333	Lambert 2016
Eurystephanodon cattanii	48-42	Roth 1904
Geniohyus magnus	33.9-28.1	Matsumoto 1926
Gesneropithex peyeri	56-33.9	Hürzeler 1946
Gigantohyrax maguirei	3.6-2.588	Kitching 1965
Gigarton louisi	59.2-56	Hooker & Russell 2012
Gigarton meyeri	59.2-56	Hooker & Russell 2012
Gigarton sigogneauae	59.2-56	Hooker & Russell 2012
Gingerichia geoteretes	61.7-56.8	Zack *et al.* 2005
Gomphotherium angustidens	16.9-5.333	Burmeister 1837
Gomphotherium connexus	11.608-5.333	Hopwood 1935
Gomphotherium gratum	2.588-0.0117	Hay 1916
Gomphotherium productum	15.97-13.6	Tobien 1972
Gomphotherium shensiensis	13.82-11.62	Chang & Zhai 1978
Gomphotherium simplicidens	10.3-4.9	Tobien 1972
Gomphotherium wimani	11.608-5.333	Hopwood 1935
Granastrapotherium snorki	15.97-11.608	Johnson & Madden 1997
Griphodon peruvianus	48.6-37.2	Anthony 1924
Guilielmoscottia plicifera	48-42	Ameghino 1901
Haplaletes andakupensis	66-63.3	Van Valen 1978
Haplaletes disceptatrix	63.3-56.8	Simpson 1935
Haplaletes pelicatus	61.7-56.8	Gazin 1956
Haplomylus bozemanensis	55.8-50.3	Robinson & Williams 1997
Haplomylus scottianus	55.8-48.6	Gingerich 1994
Haplomylus simpsoni	61.7-55.8	Rose 1981
Haplomylus speirianus	55.8-50.3	Matthew 1915
Haplomylus zalmouti	55.8-48.6	Gingerich & Smith 2006
Hemixotodon chasicoensis	10-9	Cabrera & Kraglievich 1931
Henricofilholia lustrata	29-21	Ameghino 1901
Henricofilholia vucetichia	33.9-28.1	Ribeiro *et al.* 2010
Henricosbornia ampla	47.8-41.3	Simpson 1948
Henricosbornia lophodonta	56-38	Ameghino 1901
Henricosbornia minuta	55.8-37.2	Simpson 1948
Heterohyrax auricampensis	11.1-9.7	Rasmussen *et al.* 1996
Heterolophodon ampliatus	48-42	Roth 1904
Hilarcotherium castanedaii	13.8-11.8	Vallejo-Pareja *et al.* 2015
Hilarcotherium miyou	20.44-13.82	Carrillo *et al.* 2018
Homalodotherium cunninghami	17.5-16.3	Flower 1884
Homalostylops atavus	58.7-48.6	Paula Couto 1954
Homalostylops parvus	47.8-41.3	Simpson 1948
Huilatherium pluripicatum	13.8-11.8	Villarroel & Guerrero Diaz 1985
Hydrodamalis cuestae	11.62-2.588	Domning 1978
Hylomysoides qiensis	55.8-48.6	Tong & Wang 2006
Hypsamasia seni	47.8-41.3	Maas *et al.* 1998
Ignigena minisculus	55.8-48	Hitz *et al.* 2006

Indosiren javanensis	12.7-11.608	Domning 1996
Indosiren koeningswaldi	23.03-15.97	Sahni & Mishra 1975
Interatherium robustum	17.5-16.3	Ameghino 1891
Italosiren bellunensis	23.03-20.44	Voss *et al.* 2017
Johnbell hatcheri	36-28.4	Hitz et al. 2006
Kaupitherium bronni	33.9-28.1	Voss & Hampe 2017
Kaupitherium gruelli	33.9-28.1	Voss & Hampe 2017
Khamsaconus bulbosus	56-47.8	Sudre *et al.* 1993
Kibenikhoria get	57-55.8	Simpson 1935
Kilgai moolakharzani	55.8-48.6	Malkani 2019
Konobelodon atticus	11.608-5.333	Konidaris *et al.* 2014
Kutchisiren cylindrica	23.03-15.97	Bajpai *et al.* 2010
Leontinia gaudryi	33.9-21	Ameghino 1894
Leptorycteropus guilielmi	11.62-2.588	Patterson 1975
Liarthrus copei	29-21	Ameghino 1894
Litocherus lacunatus	63.3-56.8	Gingerich 1983
Litocherus notissimus	61.7-56.8	Gingerich 1983
Litocherus zygeus	61.7-56.8	Gingerich 1983
Litomylus dissentaneus	63.3-56.8	Simpson 1935
Litomylus ishami	61.7-56.8	Gazin 1956
Litomylus orthronepius	66-63.3	Johnston & Fox 1984
Losodokodon losodokius	28.4-20.44	Rasmussen & Gutierrez 2009
Louisina marci	59.2-56	Hooker & Russell 2012
Louisina mirabilis	59.2-56	Russell 1964
Lunania zhoui	48.6-37.2	Huang 2002
Macrocranion germonpreae	55.8-48.6	Smith 1997
Macrocranion junnei	55.8-48.6	Smith *et al.* 2002
Macrocranion nitens	59.2-47.8	Krishtalka 1976
Macrocranion vandebroeki	56-47.8	Smith *et al.* 2002
Maddenia lapidaria	33.9-28.1	Kramarz & Bond 2009
Mammut borsoni	8.7-2.588	Lacombat *et al.* 2008
Mammut cosoensis	4.9-1.8	Shoshani & Tassy 1996
Mammut floridanum	11.608-0.0117	Hay 1902
Mammut furlongi	23.03-5.333	Shotwell & Russell 1963
Mammut matthewi	13.82-1.8	Shoshani & Tassy 1996
Mammut pacificus	2.588-0.012	Dooley *et al.* 2019
Mammut raki	4.9-1.8	Tedford 1981
Mammuthus chosaricus	0.781-0.126	Dubrovo 1966
Mammuthus creticus	2.588-0.126	Bate 1907
Mammuthus hayi	1.8-0.3	Barbour 1915
Mammuthus lamarmorae	3.6-0.0117	Major 1883
Mammuthus meridionalis	3.2-0.126	Nesti 1825
Mammuthus trogontherii	2.588-0.126	Pohlig 1885
Martinmiguelia fernandezi	41.3-38	Bond & López 1995
Maxschlosseria consumata	47.8-41.3	Simpson 1967
Maxschlosseria expansa	55.8-48	Simpson 1967
Maxschlosseria minima	55.8-41.3	Simpson 1967
Maxschlosseria minuta	47.8-38	Simpson 1967
Maxschlosseria praeterita	47.8-38	Ameghino 1901

Maxschlosseria rusticula	47.8-41.3	Simpson 1967
Maxschlosseria septa	47.8-38	Simpson 1967
Megalohyrax gevini	56-37.2	Sudre 1979
Megalohyrax minor	33.9-28.1	Andrews 1904
Mendozahippus fierensis	29-21	Cerdeño & Vera 2010
Meroehyrax kyongoi	28.4-20.44	Rasmussen & Gutierrez 2009
Metaxytherium albifontanum	28.1-23.03	Velez-Juarbe & Domning 2014
Metaxytherium aquitaniae	23.03-20.44	Pilleri 1987
Metaxytherium arctodites	15.97-13.82	Aranda-Manteca *et al.* 1994
Metaxytherium crataegense	28.1-13.6	Aranda-Manteca *et al.* 1994
Metaxytherium krahuletzi	20.44-13.82	Deperet 1895
Metaxytherium lovisati	20.44-13.82	Capellini 1886
Metaxytherium medium	16.9-11.608	Hooijer 1952
Metaxytherium serresii	20.44-3.6	Trouessart 1898
Metaxytherium subapenninum	23.03-3.2	Pilleri 1988
Microtypotherium choquecotense	20.44-5.333	Villarroel 1974
Miocochilius anomopodus	13.8-11.8	Stirton 1953
Miocochilius federicoi	13.8-11.8	Croft 2007
Miodugong brevicranius	15.97-13.82	Deraniyagala 1969
Miosiren canhami	23.03-5.333	Sickenberg 1934
Miosiren kocki	20.44-15.97	Dollo 1889
Mixotoxodon larensis	3.6-0.0117	Van Frank 1957
Moeritherium chehbeurameuri	41.3-33.9	Delmer *et al.* 2006
Moeritherium gracile	38-28.1	Andrews 1902
Moeritherium lyonsi	38-28.1	Andrews 1901
Moeritherium trigodon	41.3-28.1	Sanders *et al.* 2010
Monshyus praevius	66-61.6	Sudre & Russell 1982
Moqueguahippus glycisma	29-21	Shockey *et al.* 2006
Morrillia barbouri	1.8-0.3	Shoshani & Tassy 1996
Myohyrax oswaldi	23.03-11.608	Andrews 1914
Namachloris arenatans	41.3-38	Pickford 2015
Namagale grandis	41.3-38	Pickford 2015
Namahyrax corvus	47.8-41.3	Pickford *et al.* 2008
Namasengi mockeae	41.3-38	Senut & Pickford 2021
Nanosiren garciae	10.3-3.6	Domning & Aguilera 2008
Nanosiren sanchezi	11.62-7.246	Domning & Aguilera 2008
Nementchatherium rathbuni	48.6-33.9	Tabuce *et al.* 2012
Nementchatherium senarhense	41.3-33.9	Tabuce *et al.* 2001
Neomatronella gassoni	56-47.8	Hooker 2010
Neomatronella luciannae	56-47.8	Russell *et al.* 1975
Neotrigodon utoquineae	11.62-7.246	Spillman 1949
Norosiren zazavavindrano	11.62-7.246	Samonds *et al.* 2019
Notiomastodon platensis	11.608-0.0117	Ferreti 2008
Notoetayoa gargantuai	66-61.6	Gelfo *et al.* 2008
Notohippus toxodontoides	17.5-16.3	Ameghino 1890
Notopithecus adapinus	55.8-38	Ameghino 1897
Notopithecus amplidens	48-42	Simpson 1967
Notostylops appressus	47.8-38	Simpson 1948
Notostylops aspectans	47.8-38	Ameghino 1902

Notostylops brachycephalus	55.8-48	Ameghino 1904
Notostylops murinus	55.8-48	Ameghino 1897
Notostylops pendens	55.8-38	Simpson 1948
Notostylops pigafettai	55.8-48	Simpson 1948
Ocepeia daouiensis	61.6-59.2	Gheerbrant *et al.* 2001
Ocepeia grandis	61.6-59.2	Gheerbrant *et al.* 2014
Ocnerotherium intermedium	10-3.6	Pascual 1954
Oldfieldthomasia anfractuosa	41.3-38	Ameghino 1901
Oldfieldthomasia debilitata	55.8-48	Simpson 1967
Oldfieldthomasia parvidens	41.3-38	Ameghino 1901
Oldfieldthomasia transversa	41.3-38	Ameghino 1901
Orome deepi	56-47.8	Bauzá *et al.* 2019
Orthogeniops ameghinoi	33.9-28.4	Ameghino 1902
Orycteropus browni	11.608-5.333	Colbert 1933
Orycteropus chemeldoi	23.03-5.333	Pickford 1975
Orycteropus djourabensis	5.333-0.0117	Lehmann *et al.* 2004
Orycteropus gaudryi	13.82-5.333	Forsyth Major 1888
Orycteropus mauritanicus	11.608-5.333	Arambourg 1954
Orycteropus minutus	23.03-11.608	Pickford 1975
Orycteropus pilgrimi	11.608-5.333	Colbert 1933
Orycteropus pottieri	11.608-8.7	Ozansoy 1965
Othnielmarshia curvicrista	47.8-38	Simpson 1948
Othnielmarshia lacunifera	56-38	Ameghino 1901
Othnielmarshia reflexa	47.8-38	Simpson 1948
Otronia muehlbergi	48-42	Roth 1901
Paginula parca	47.8-38	Ameghino 1901
Palaeoamasia kansui	56-37.2	Ozansoy 1966
Palaeomastodon beadnelli	33.9-28.1	Andrews 1901
Palaeomastodon minor	33.9-28.1	Andrews 1904
Palaeomastodon parvus	33.9-28.1	Andrews 1905
Palaeomastodon wintoni	33.9-28.1	Andrews 1905
Palaeotoxodon nazari	10-9	Cabrera & Kraglievich 1931
Palaeotoxodon paranensis	9-6.8	Laurillard 1842
Palaeotoxodon protoburmeisteri	9-6.8	Ameghino 1887
Palaeotoxodon virgatus	9-6.8	Ameghino 1886
Palyeidodon obtusum	21-11.62	Roth 1898
Pampahippus arenalesi	47.8-38	Bond & López 1993
Pampahippus secundus	47.8-38	Deraco & García-López 2016
Paralitherium tarkanyense	38-33.9	Kordos 1977
Parapliohyrax ngororaensis	13.82-11.62	Pickford & Fisher 1987
Parastrapotherium crassum	48.6-15.97	Ameghino 1902
Parastrapotherium holmbergi	29-21	Ameghino 1894
Parastrapotherium martiale	29-21	Ameghino 1901
Parastrapotherium symmetrum	21-17.5	Kramarz & Bond 2010
Parastrapotherium voghti	29-21	Kramarz & Bond 2008
Paratrigodon euguii	10-9	Cabrera & Kraglievich 1931
Pascualihippus boliviensis	29-21	Shockey 1997
Patagonhippus canterensis	33.9-28.1	López *et al.* 2010
Patagonhippus dukei	33.9-28.1	López *et al.* 2010

Patriarchus palmidens	17.5-16.3	Ameghino 1889
Peripantostylops minutus	47.8-41.3	Ameghino 1904
Periphragnis cristatus	48-42	Roth 1904
Periphragnis exauctus	48-38	Simpson 1967
Periphragnis palmeri	48-42	Simpson 1967
Periphragnis vicentei	33.9-28.4	Bradham *et al.* 2015
Perutherium altiplanense	59.2-47.8	Grambast *et al.* 1967
Pezosiren portelli	47.8-41.3	Domning 2001
Phiomia major	28.1-23.03	Sanders *et al.* 2004
Phiomia serridens	33.9-28.1	Andrews & Beadnell 1902
Pisanodon nazari	10-6.8	Cabrera & Kraglievich 1931
Platybelodon barnumbrowni	13.6-10.3	Barbour 1932
Platybelodon danovi	13.65-12.75	Borrissiak 1928
Platybelodon grangeri	13.82-11.62	Osborn 1929
Platybelodon loomisi	10.3-5.333	Barbour 1932
Plesiorycteropus germainepetterae	0.126-0	MacPhee 1994
Plesiorycteropus madagascariensis	0.126-0	Filhol 1895
Posnanskytherium desaguaderoi	6.8-3	Liendo Lazarte 1943
Posnanskytherium inchasense	4-3	Anaya & MacFadden 1995
Primelephas korotorensis	11.608-3.6	Mackaye *et al.* 2008
Priscosiren atlantica	28.1-23.03	Velez-Juarbe & Domning 2014
Proadinotherium muensteri	21-17.5	Ameghino 1902
Proadinotherium saltoni	29-21	Shockey & Anaya 2008
Procavia antiqua	7.246-0.0117	Broom 1934
Procavia pliocenica	5.333-3.6	Pickford 2005
Prochrysochloris miocaenicus	23.03-11.608	Butler & Hopwood 1957
Prodeinotherium bavaricum	16.9-11.1	Shoshani & Tassy 1996
Prodeinotherium hobleyi	20.44-11.62	Shoshani & Tassy 1996
Prodeinotherium orlovii	23.03-15.97	Sahni & Tripathi 1957
Prodeinotherium pentapotamiae	20-11.62	Shoshani & Tassy 1996
Progaleopithecus fissurellatus	29-21	Ameghino 1904
Progaleopithecus tournoueri	29-21	Ameghino 1904
Progomphotherium maraisi	23.03-11.608	Pickford 2003
Prohalicore dubaleni	20.44-15.97	Flot 1887
Prohyrax hendeyi	23.03-11.608	Pickford 1994
Prohyrax tertiarius	20.44-15.97	Stromer 1922
Prolouisina atavella	61.6-59.2	Hooker & Russell 2012
Promyohyrax namibiensis	41.3-38	Senut & Pickford 2021
Propyrotherium saxeum	48-42	Ameghino 1901
Protanancus macinnesi	13.82-11.62	Arambourg 1945
Protosiren eothene	47.8-41.3	Zalmout *et al.* 2003
Protosiren sattaensis	41.3-38	Gingerich *et al.* 1995
Prototherium ausetanum	41.3-38	Balaguer & Alba 2016
Prototherium intermedium	37.2-33.9	Bizzotto 1983
Prototherium veronense	38-23.03	Sickenberg 1934
Prototrigodon rothi	16.3-15.5	Kraglievich 1930
Protypotherium antiquum	11.62-6.8	Ameghino 1882
Protypotherium attenuatum	20.44-13.82	Ameghino 1887
Protypotherium australe	17.5-15.5	Ameghino 1894

Protypotherium bifidens	16.3-10	Vera *et al.* 2018
Protypotherium colloncurensis	16.3-7.246	Vera *et al.* 2017
Protypotherium concepcionensis	13.82-11.62	Solórzano *et al.* 2019
Protypotherium endiadys	16.3-7.246	Vera *et al.* 2017
Protypotherium minutum	10-6.8	Cabrera & Kraglievich 1931
Protypotherium praerutilum	17.5-16.3	Ameghino 1887
Protypotherium sinclairi	21-17.5	Kramarz *et al.* 2015
Pseudopachyrucos foliiformis	48-42	Ameghino 1901
Punapithecus minor	48-42	López & Bond 1995
Purperia cribatidens	11.62-7.246	Paula Couto 1981
Pyrotherium macfaddeni	29-21	Shockey & Anaya-Daza 2004
Pyrotherium romerii	29-21	Ameghino 1888
Pyrotherium sorondoi	29-21	Ameghino 1894
Qatranilestes oligocaenus	33.9-28.1	Seiffert 2010
Qilulestes schieboutae	55.8-48.6	Tong & Wang 2006
Rhynchippus brasiliensis	29-21	Soria & Alvarenga 1989
Rhynchippus equinus	56-21	Ameghino 1897
Rhynchippus pumilus	33.9-21	Ameghino 1897
Rhynchotherium blicki	23.03-4.9	Webb & Tessman 1968
Rhynchotherium falconeri	10.3-1.8	Osborn 1923
Ribodon limbatus	11.62-7.246	Ameghino 1883
Rosendo pascuali	36-28.4	Wyss et al. 2018
Rukwalorax jinokitana	28.4-23.03	Stevens *et al.* 2009
Rupestrohyrax palustris	41.3-38	Pickford 2015
Rytiodus heali	11.62-7.246	Domning 2011
Saghatherium humarum	33.9-28.1	Rasmussen & Simons 1988
Saghatherium magnum	33.9-28.1	Andrews 1904
Saghatherium majus	33.9-28.1	Andrews 1906
Saghatherium minus	33.9-28.1	Andrews & Beadnell 1902
Saloumia gorodiskii	47.8-41.3	Tabuce *et al.* 2020
Satshatemnus bonapartei	58.7-55.8	Soria 1989
Scaglia kraglievichorum	47.8-41.3	Simpson 1957
Scarrittia barranquensis	33.9-21	Ribeiro *et al.* 2010
Scarrittia canquelensis	29-21	Simpson 1934
Scarrittia robusta	29-21	Ubilla *et al.* 1994
Selenetherium kolleensis	5.333-3.6	Mackaye *et al.* 2005
Simpsonotus major	66-59.2	Pascual *et al.* 1978
Simpsonotus praecursor	66-59.2	Pascual *et al.* 1978
Sinomammut intermedius	11.1-0.781	Mothé *et al.* 2016
Sinomastodon bumiajuensis	2.588-0.781	van den Bergh 1999
Sirenavus hungaricus	47.8-41.3	Kretzoi 1941
Sperrgale minutus	41.3-38	Pickford 2015
Stegodibelodon schneideri	5.333-3.6	Coppens 1972
Stegodon florensis	2.588-0.126	van den Bergh 1999
Stegodon kaisensis	11.608-3.6	Hopwood 1939
Stegodon luzonensis	2.588-0.0117	von Koenigwald 1956
Stegodon sompoensis	3.6-0.781	Hooijer 1964
Stegodon sondaari	2.588-0.781	van den Bergh 1999
Stegodon sumbaensis	2.588-0.0117	Sartono 1979

Stegodon yuanmouensis	2.588-0.0117	You *et al.* 1978
Stegolophodon iravaticus	15.97-0.781	Sein 2020
Stegomastodon aftoniae	2.588-0.126	Osborn 1924
Stegomastodon mirificus	4.9-0.3	Pohlig 1912
Stegosiren macei	33.9-28.1	Domning & Beatty 2019
Stegotetrabelodon orbus	11.608-5.333	Maglio 1970
Stegotetrabelodon syrticus	13.82-5.333	Petrocchi 1941
Stenotephanos plicidens	9-6.8	Ameghino 1885
Stylolophus major	56-47.8	Gheerbrant *et al.* 2020
Stylolophus minor	56-47.8	Gheerbrant *et al.* 2018
Suniodon catamarcensis	48-42	López 1995
Taubatherium major	29-21	Soria & Alvarenga 1989
Taubatherium paulacoutoi	29-21	Soria & Alvarenga 1989
Teratopithecus elpidophoros	56-41.3	López *et al.* 2020
Termastherium flacoensis	33.9-28.4	Wyss *et al.* 2018
Tetragonostylops apthomasi	47.8-41.3	Paula Couto 1963
Tetralophodon longirostris	13.82-5.333	Falconer 1857
Thryptodon brailloni	59.2-56	Hooker & Russell 2012
Thyrohyrax kenyaensis	28.4-20.44	Rasmussen & Gutierrez 2009
Thyrohyrax libycus	33.9-28.4	Coster *et al.* 2015
Thyrohyrax microdon	23.03-20.44	Rasmussen & Gutierrez 2009
Titanohyrax mongereaui	56-41.3	Sudre 1979
Titanohyrax tantulus	56-41.3	Court & Hartenberger 1992
Titanohyrax ultimus	33.9-28.1	Matsumoto 1922
Toxodon bilobidens	0.781-0.012	Ameghino 1887
Toxodon gezi	0.781-0.012	Ameghino 1917
Toxodon gracilis	0.781-0.0117	Gervais & Ameghino 1880
Toxodon paranensis	11.62-7.246	Ameghino 1883
Toxodon platensis	9-0.0117	Owen 1837
Toxodontherium compressum	9-6.8	Ameghino 1883
Toxodontherium reverendum	9-6.8	Ameghino 1889
Trachytherus alloxus	29-21	Billet *et al.* 2008
Trachytherus ramirezi	29-21	Shockey *et al.* 2016
Trachytherus subandinus	29-21	Villarroel 1994
Transpithecus obtentus	41.3-38	Ameghino 1901
Trigodon gaudryi	6.8-4	Ameghino 1887
Trigodonops lopesi	11.62-0.0117	Roxo 1821
Trigonolophodon elegans	48-28.4	Roth 1904
Trigonolophodon inflatus	48-42	Roth 1904
Trigonostylops wortmani	47.8-38	Ameghino 1897
Tsamnichoria cabrerai	48-42	Simpson 1936
Typotherium cristatum	3.6-0.781	Serres 1857
Ultrapithecus rutilans	41.3-38	Ameghino 1901
Uruguaytherium beaulieui	29-21	Kraglievich 1928
Utemylus latomius	61.7-56.8	Gingerich 1983
Utemylus serior	61.7-56.8	Zack *et al.* 2005
Walbeckodon girardi	59.2-56	Hooker & Russell 2012
Walbeckodon krumbiegeli	61.6-59.2	Hooker & Russell 2012
Xenastrapotherium aequatorialis	23.03-20.44	Johnson & Madden 1997

Xenastrapotherium chaparralensis	23.03-15.97	Johnson & Madden 1997
Xenastrapotherium christi	17.5-16.3	Kraglievich 1928
Xenastrapotherium kraglievichi	13.8-11.8	Cabrera 1929
Xenosiren yucateca	10.3-4.9	Domning 1989
Xenostephanus chiottii	42-36	Simpson *et al.* 1962
Xotodon caravela	7.246-3.6	Armella *et al.* 2018
Xotodon doellojuradoi	9-6.8	Frenguelli 1920
Xotodon foricurvatus	9-6.8	Ameghino 1885
Xotodon maimarensis	6.8-4	Bonini *et al.* 2017
Zionodon satanus	46.2-40.4	Dunn & Rasmussen 2009
Zionodon walshi	46.2-40.4	Dunn & Rasmussen 2009
Zygolophodon aegyptensis	16.9-15.97	Sanders & Miller 2002
Zygolophodon morotoensis	23.03-11.608	Pickford 2003
Zygolophodon tapiroides	12.7-3.6	Madden 1980
Zygolophodon turicensis	15.97-7.246	Shoshani & Tassy 2005

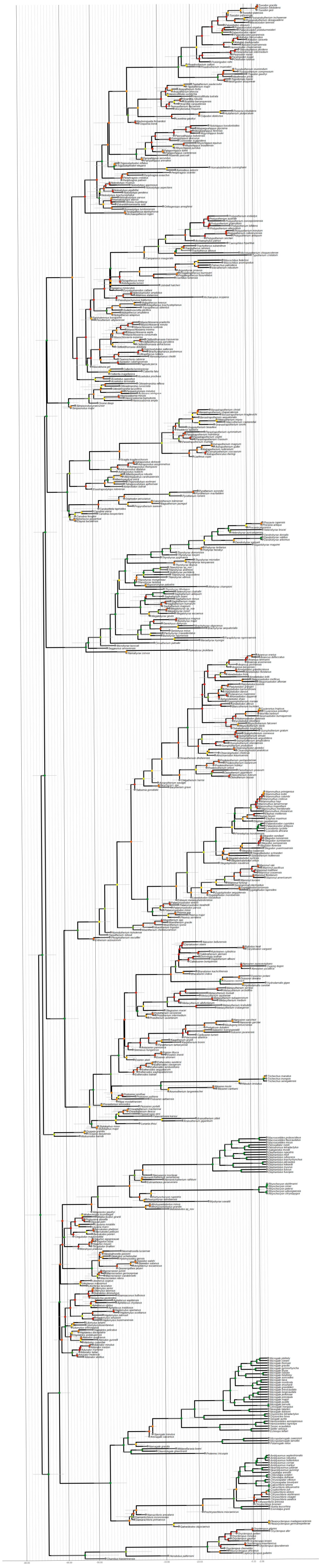
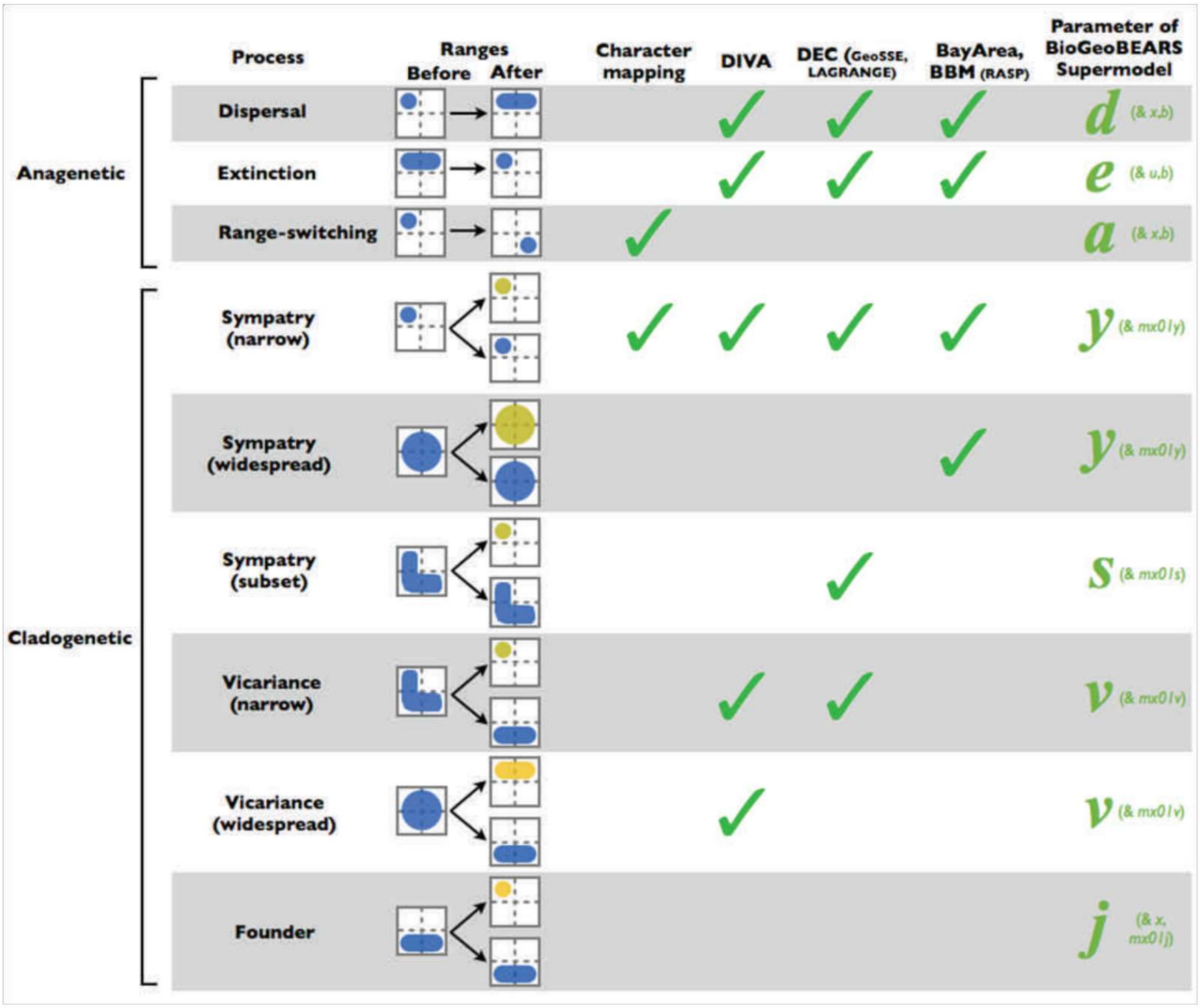

Amblysomus corriae
Amblysomus marleyi
Neamblysomus julianae
Neamblysomus gunningi
Carpitalpa arendsi
Chlorotalpa sclateri
Chlorotalpa duthieae
Chrysospalax villosus
Chrysospalax trevelyani
Calcochloris tytonis
Calcochloris obtusirostris
Cryptochloris zyli
Cryptochloris wintoni
Chrysochloris stuhlmanni
Chrysochloris visagiei
Chrysochloris asiatica
Chrysochloris arenosa
Chrysochloris bronneri
Huetia leucorhina
Eremitalpa granti
Namachloris arenatans
Diamantochloris inconcessus
Damarachloris primaevus
Prochrysochloris miocaenicus
Plesiorycteropus madagascariensis
Plesiorycteropus germainepetterae
Qatranilestes oligocaenus
Orycteropus pilgrimi
Orycteropus afer
Orycteropus pottieri
Orycteropus minutus
Orycteropus gaudryi
Orycteropus browni
Orycteropus mauritanicus
Orycteropus djourabensis
Orycteropus chemeldoi
Myorycteropus africanus
Leptorycteropus guilielmi
Herodotius pattersoni
Chambius kasserinensis
-80.00
-66.00
-56.00
-33.90
-23.03
-5.33
-2.58

Figure S2.1. *A time calibrated phylogenetic tree of Afrotheria. Horizontal grey bars represent the 95% highest posterior density (HPD) of each node. The coloured circles at each node represent the posterior probability support. Support values (0-100%) were divided into 4 equal sections along a colour gradient, with very poor (25%) support shown as red, poor (50%) support as orange, good (75%) support as yellow and very good (100%) as green. Each gridline represents 1 million years, with Epochs indicated by thin black vertical lines. From most distant to present, these are the end of the Late Cretaceous, Palaeocene, Eocene, Oligocene, Miocene, Pliocene and combined Pleistocene and Holocene.*



	Process	Character mapping	DIVA	DEC (GeoSSE, LAGRANGE)	BayArea, BBM (RASP)	Parameter of BioGeoBEARS Supermodel
Anagenetic	Dispersal		✓	✓	✓	*d* (& x,b)
	Extinction		✓	✓	✓	*e* (& u,b)
	Range-switching	✓				*a* (& x,b)
Cladogenetic	Sympatry (narrow)	✓	✓	✓	✓	*y* (& mx01y)
	Sympatry (widespread)				✓	*y* (& mx01y)
	Sympatry (subset)			✓		*s* (& mx01s)
	Vicariance (narrow)		✓	✓		*v* (& mx01v)
	Vicariance (widespread)		✓			*v* (& mx01v)
	Founder					*j* (& x, mx01j)

Figure S3.1. *Matzke 2013 Figure 1. The processes assumed by different historical biogeographic methods. Each of these processes is controlled by the specified parameter(s) in the BioGeoBEARS supermodel, allowing them to be turned on or off, or estimated from the data. The ranges indicate a world with 4 zones.*

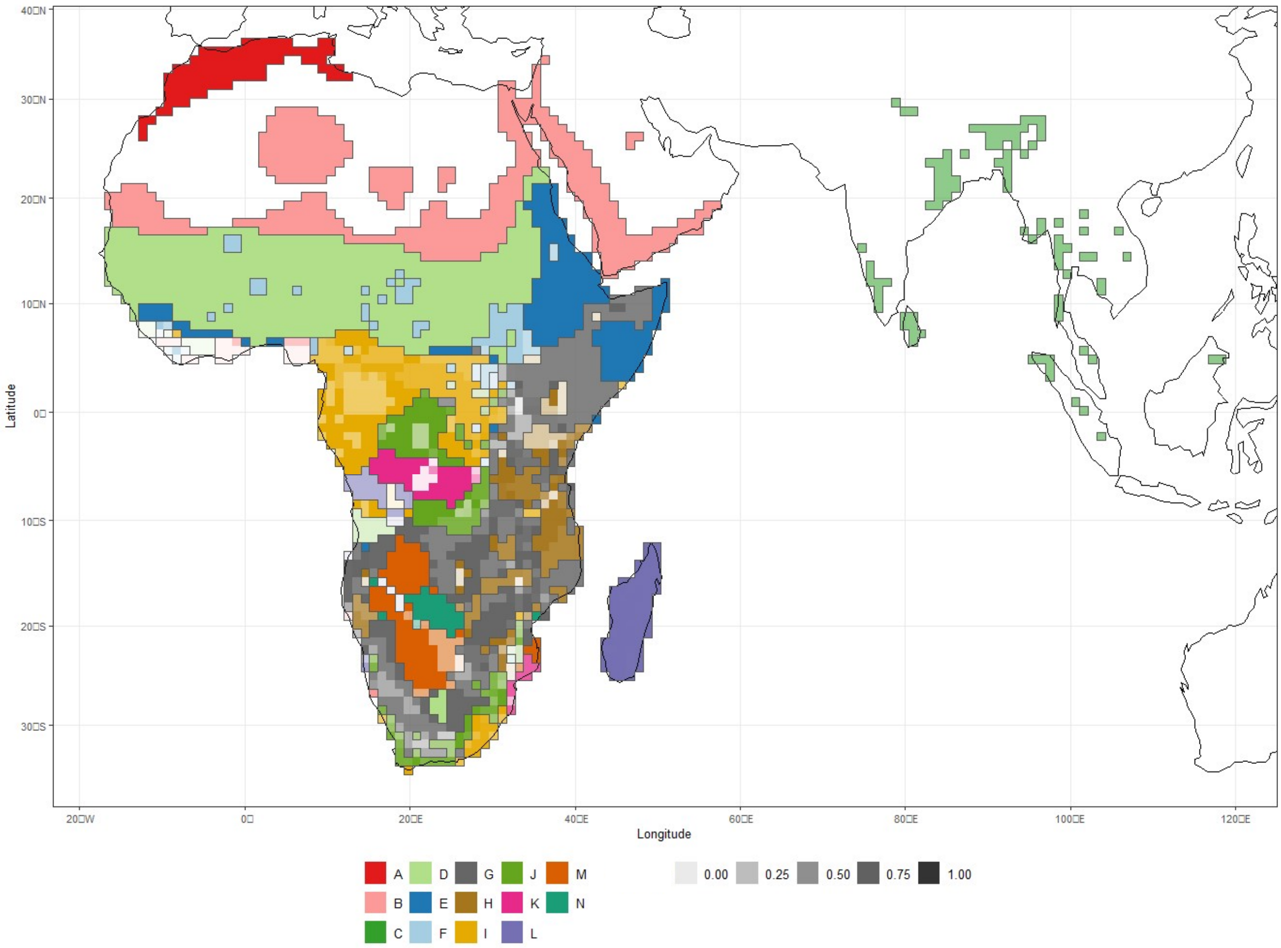


Figure S3.2. *The evoregions of extant terrestrial Afrotheria, with affiliation intensity.*

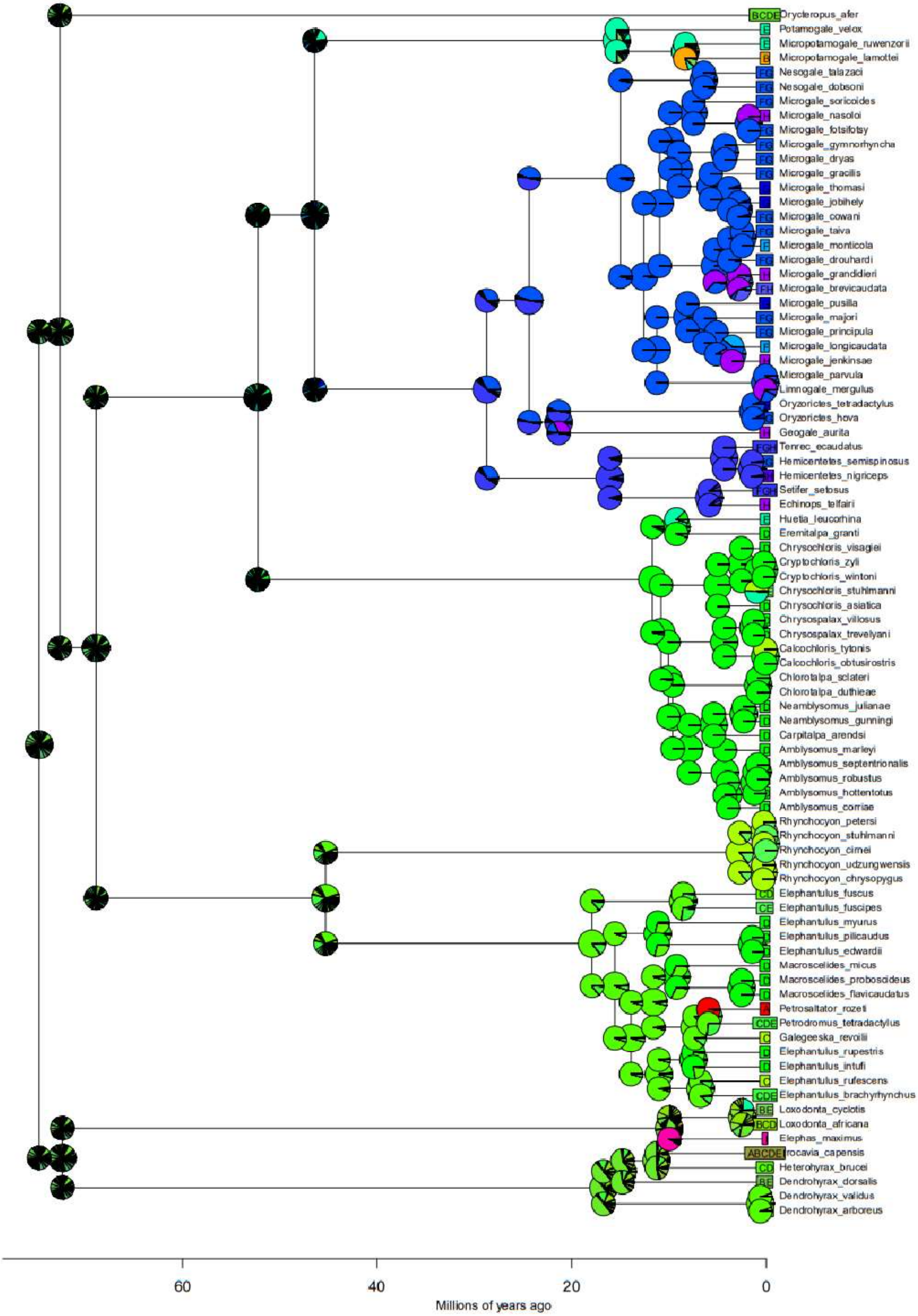


Figure S3.3. *A phylogeny that shows the zoogeographic history of extant Afrotheria from the BayArea+J 9 zone analysis. Letters refer to regions (Table 1).*

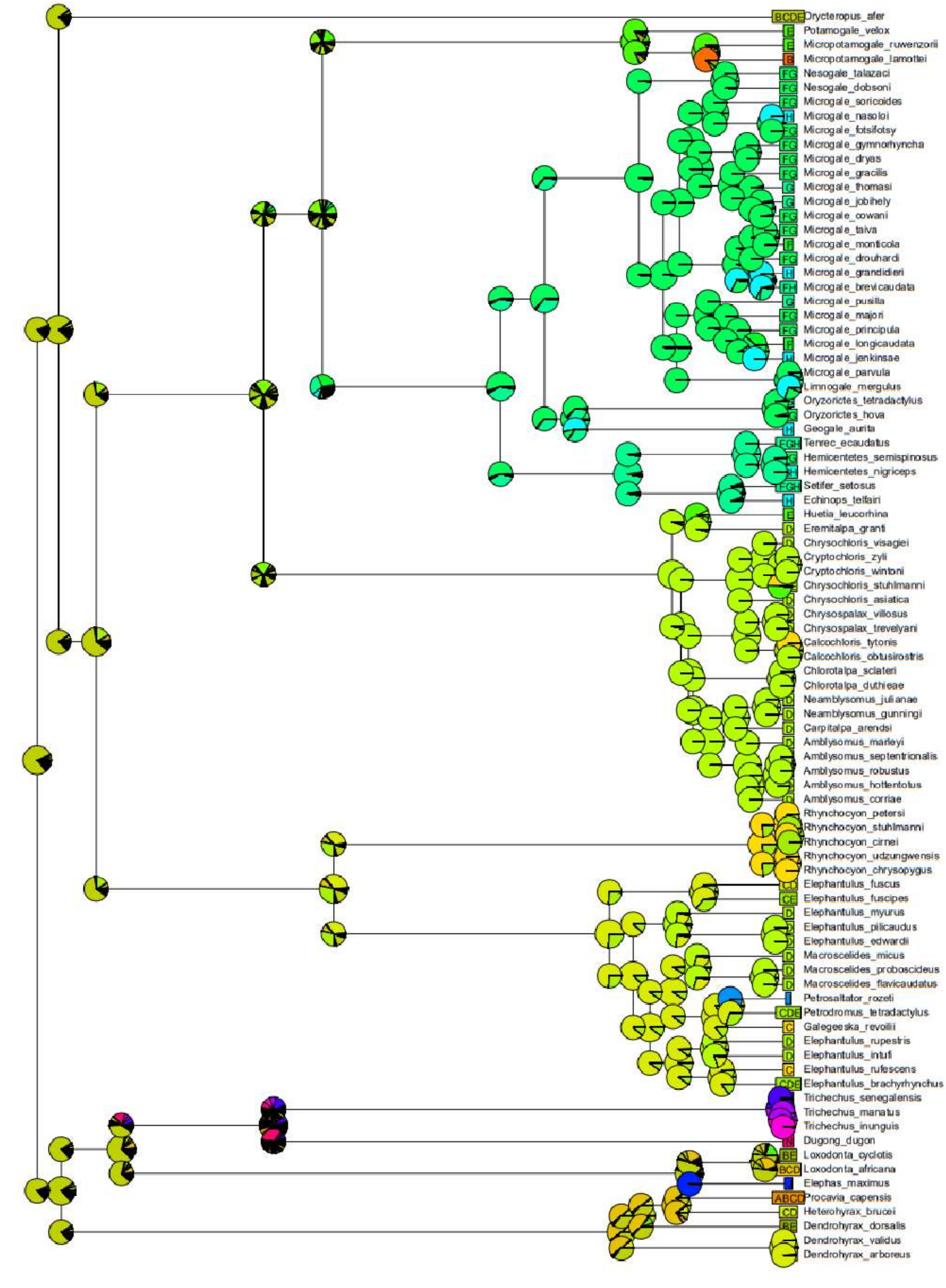


Figure S3.4. *A phylogeny that shows the zoogeographic history of extant Afrotheria from the BayArea+J 14 zone analysis. Letters refer to regions (Table 1).*

***Table S4.1.** Afrotherian body mass in grams (g).*

Species	Mass (g)
Afrohyrax championi	82300
Amblysomus corriae	51.5
Amblysomus hottentotus	53.5
Amblysomus marleyi	52.6
Amblysomus robustus	76
Amblysomus septentrionalis	69
Antilohyrax pectidens	55884.4097
Arcanotherium savagei	396016.4
Barytherium spp	4000000
Bunohyrax fajumensis	82300
Bunohyrax major	232200
Calcochloris obtusirostris	26.3
Calcochloris tytonis	49.7
Carpitalpa arendsi	51.5
Chambius kasserinensis	71.2
Chlorotalpa duthieae	29.5
Chlorotalpa sclateri	34.45
Chrysochloris asiatica	49
Chrysochloris stuhlmanni	42
Chrysochloris visagiei	30
Chrysospalax trevelyani	460
Chrysospalax villosus	117.85
Cryptochloris wintoni	25
Cryptochloris zyli	25
Daouitherium rebouli	364000
Dendrohyrax arboreus	2949.99
Dendrohyrax dorsalis	3175
Dilambdogale gheerbranti	10.8
Dimaitherium patnaiki	14373.7
Dugong dugon	410000
Echinops telfairi	87.5
Elephantulus brachyrhynchus	45.3
Elephantulus edwardii	49.25
Elephantulus fuscipes	57
Elephantulus fuscus	45.5
Elephantulus intufi	45.8
Elephantulus myurus	45.1
Elephantulus rufescens	57.3
Elephantulus rupestris	61.5
Elephas maximus	3320691
Eremitalpa granti	23
Galegeeska revoilii	32.5
Geniohyus mirus	83109.6
Geogale aurita	6.69
Hemicentetes nigriceps	102.99
Hemicentetes semispinosus	116
Herodotius pattersoni	244.4
Heterohyrax brucei	2402
Huetia leucorhina	49.7
Hydrodamalis gigas	6738250
Limnogale mergulus	92
Loxodonta africana	4640000
Loxodonta cyclotis	4750000.01
Macroscelides proboscideus	38.2
Mammut americanum	6016667
Mammuthus columbi	6630000
Mammuthus primigenius	4282889
Megalohyrax eocaenus	155400
Metoldobotes sp nov	375.4
Microgale brevicaudata	8.9
Microgale cowani	13.8
Microgale drouhardi	10.5
Microgale dryas	40
Microgale fotsifotsy	7.7
Microgale gracilis	23.3
Microgale gymnorhyncha	18.2
Microgale jobihely	10
Microgale longicaudata	8.08
Microgale monticola	13.9
Microgale parvula	3.2
Microgale principula	10.2
Microgale pusilla	3.5
Microgale soricoides	18.7
Microgale taiva	11.8
Microgale thomasi	22.9
Microhyrax lavocati	3400
Micropotamogale lamottei	78
Micropotamogale ruwenzorii	98.5
Moeritherium spp	1000000
Myorycteropus africanus	28792.5
Neamblysomus gunningi	59.6
Neamblysomus julianae	28
Nesogale dobsoni	38
Nesogale talazaci	48.2
Numidotherium koholense	558000
Omanitherium dhofarensis	624744.3
Orycteropus afer	52350
Oryzorictes hova	44.2
Oryzorictes tetradactylus	36
Pachyhyrax crassidentatus	134200

Species	Mass (g)
Palaeoloxodon cypriotes	200000
Petrodromus tetradactylus	198.3
Petrosaltator rozeti	45.3
Phiomia spp	1080958
Phosphatherium escuilliei	15000
Potamogale velox	656
Procavia capensis	3020
Prorastomus sirenoides	98155.5
Protenrec tricuspis	3.14
Protosiren smithae	542000
Rhynchocyon chrysopygus	534.8
Rhynchocyon cirnei	352
Rhynchocyon petersi	471
Rhynchocyon stuhlmanni	490
Rhynchocyon udzungwensis	710
Saghatherium antiquum	16826.7
Saghatherium bowni	9200
Seggeurius amourensis	2932
Selenohyrax chatrathi	45900
Setifer setosus	273
Tenrec ecaudatus	852
Thyrohyrax domorictus	10900
Thyrohyrax litholagus	22200
Thyrohyrax meyeri	6500
Titanohyrax angustidens	262700
Trichechus inunguis	480000
Trichechus manatus	689185
Trichechus senegalensis	454000

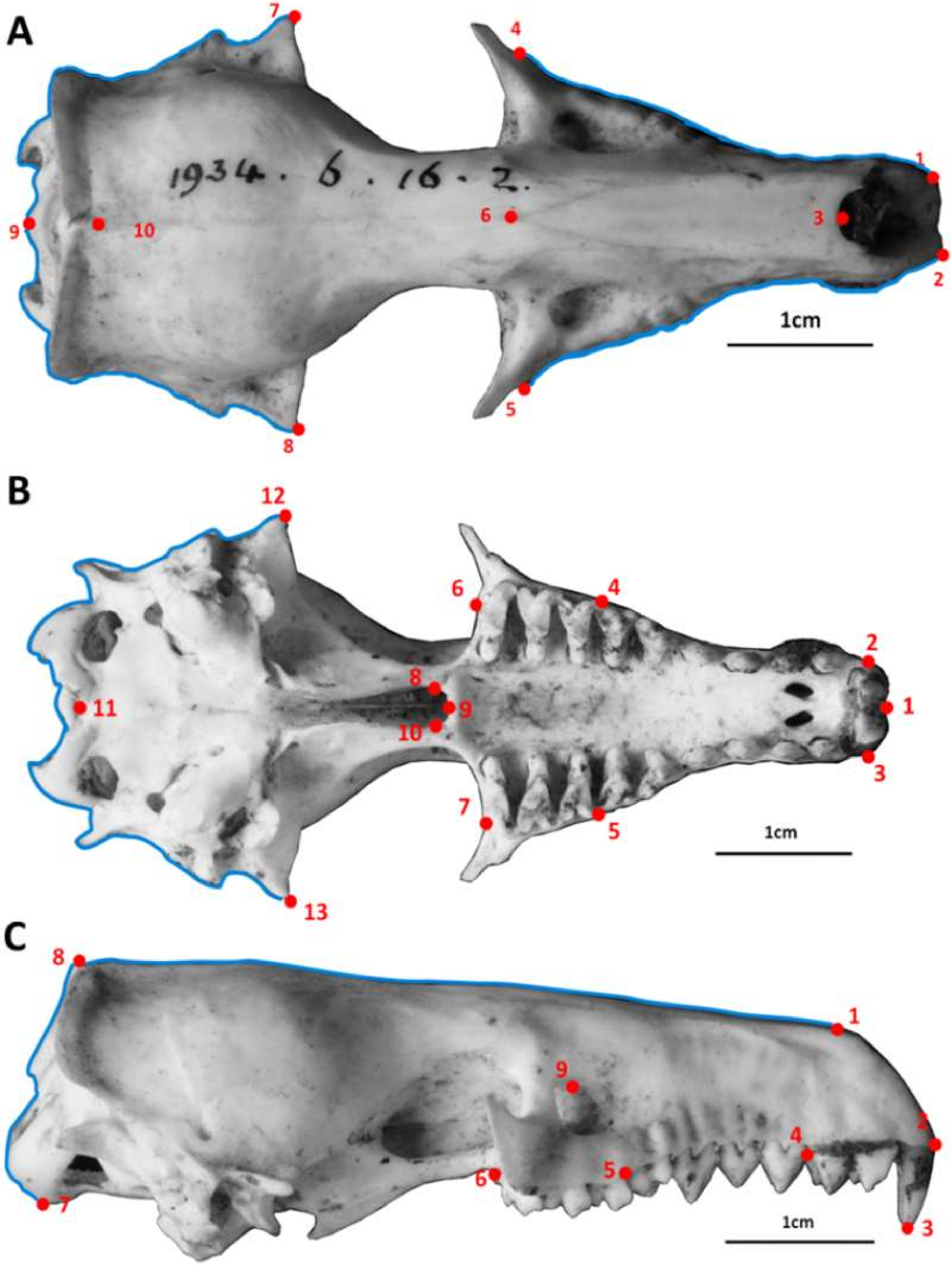


Figure S4.1. *Finlay & Cooper 2015 Figure 2. Their description reads: Figure 2 Skulls: dorsal, ventral and lateral landmarks. Landmarks (numbered points) and curves (outlines) for the skulls in dorsal (A),ventral (B) and lateral (C) view. See the Supplemental Information for detailed landmark descriptions. The skulls are an example of a Potamogale velox (otter shrew tenrec), museum accession number BMNH 1934.6.16.2.*

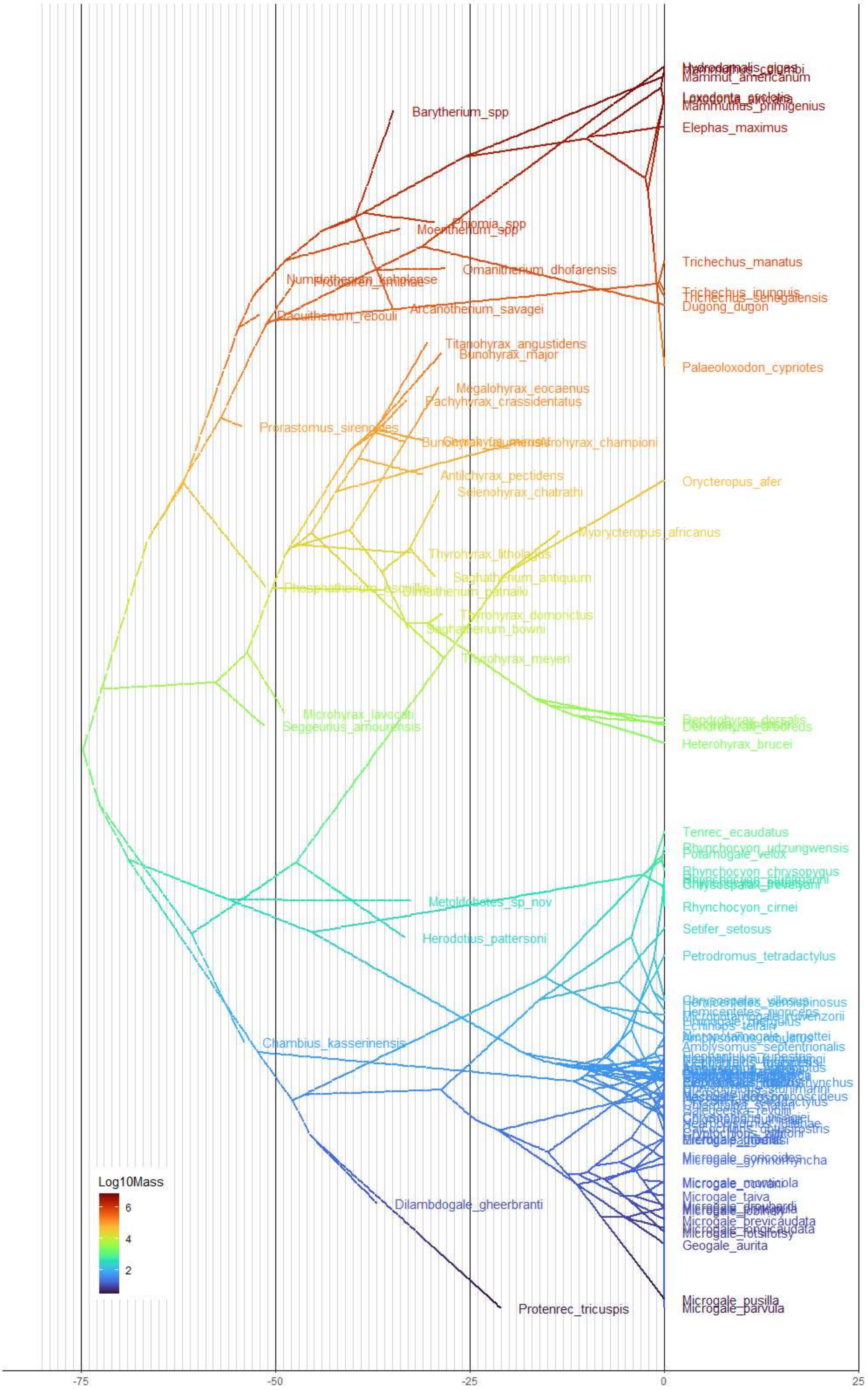


Figure S4.2. *Phylogeny of afrotherian body mass in $\log_{10}$(g) with mass on the y-axis.*

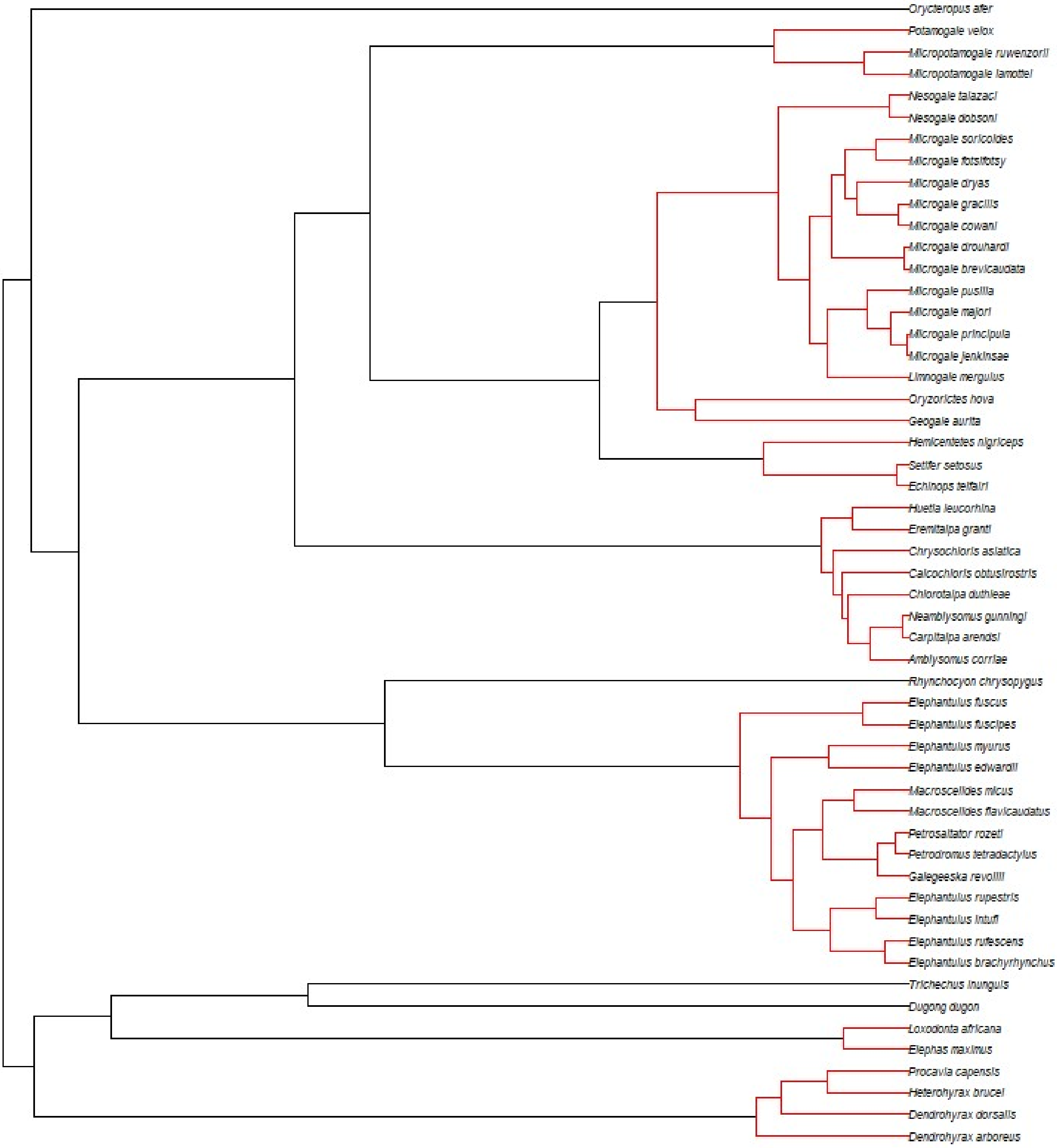


Figure S5.1. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for extant afrotherian lineages 5 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

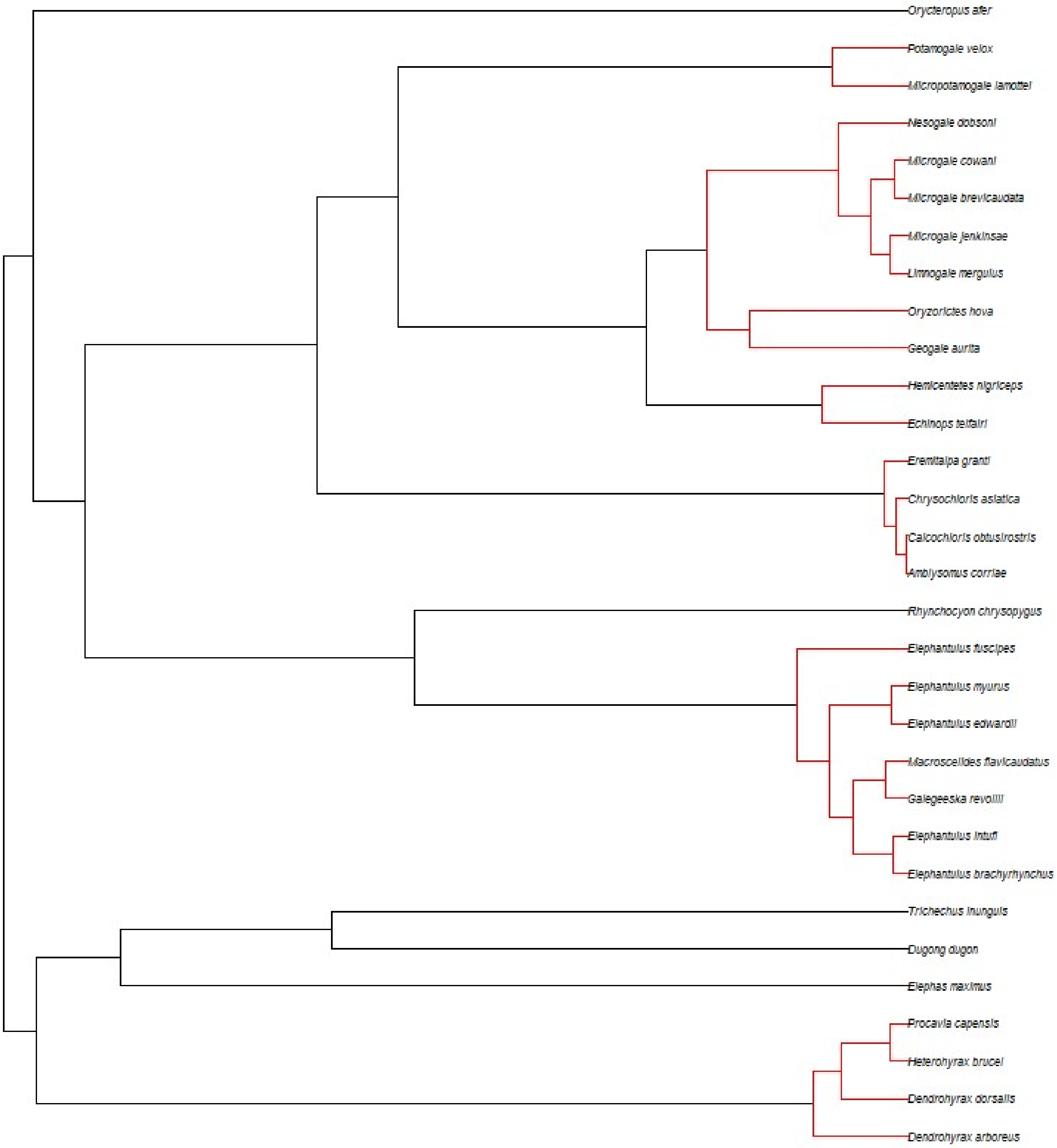


Figure S5.2. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for extant afrotherian lineages 10 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

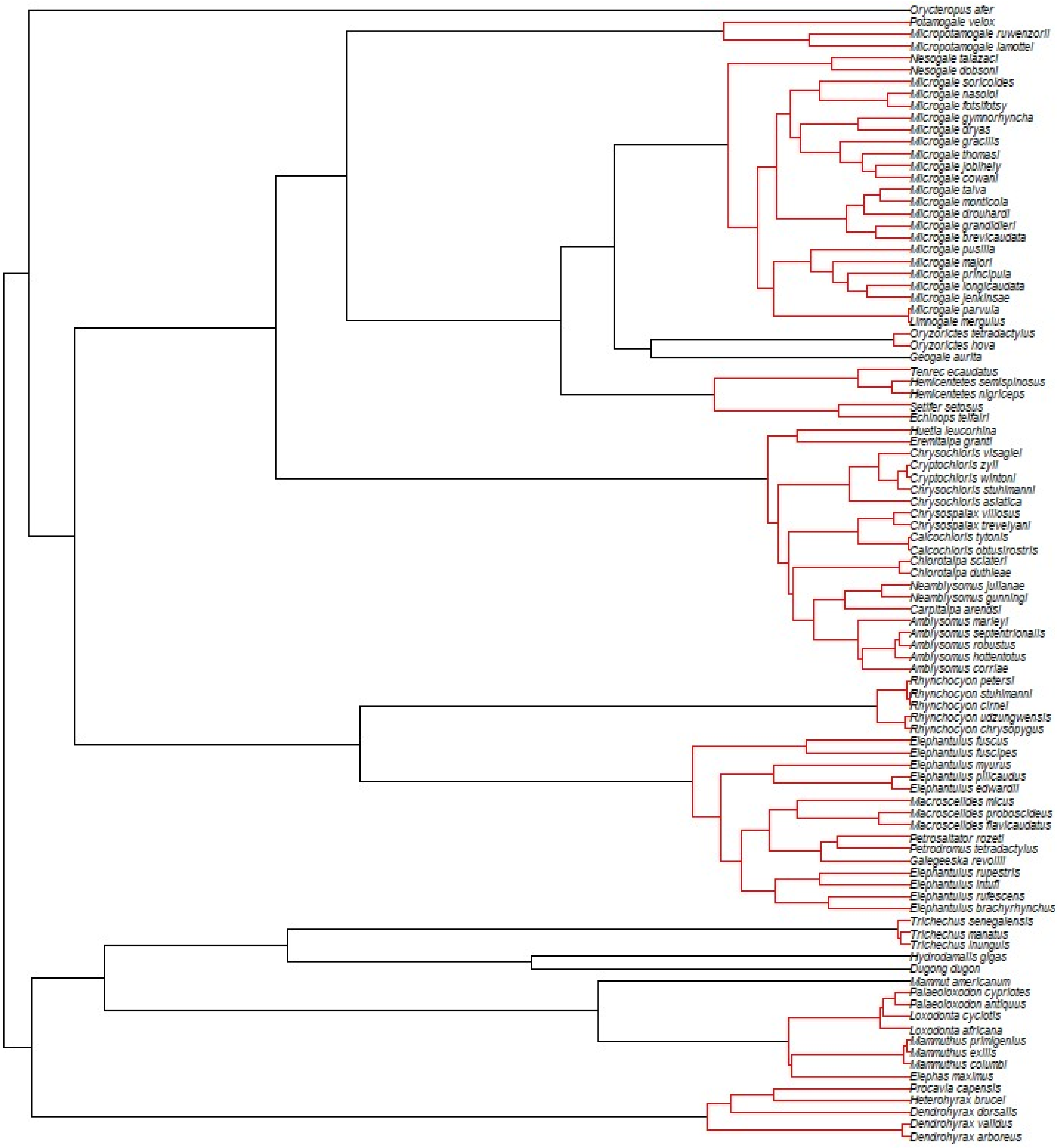


Figure S5.3. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for all afrotherian lineages in the present. The black-to-red colour transition indicates the beginning of a new cluster. Note some recently extinct species are present (i.e. Hydrodamalis gigas).*

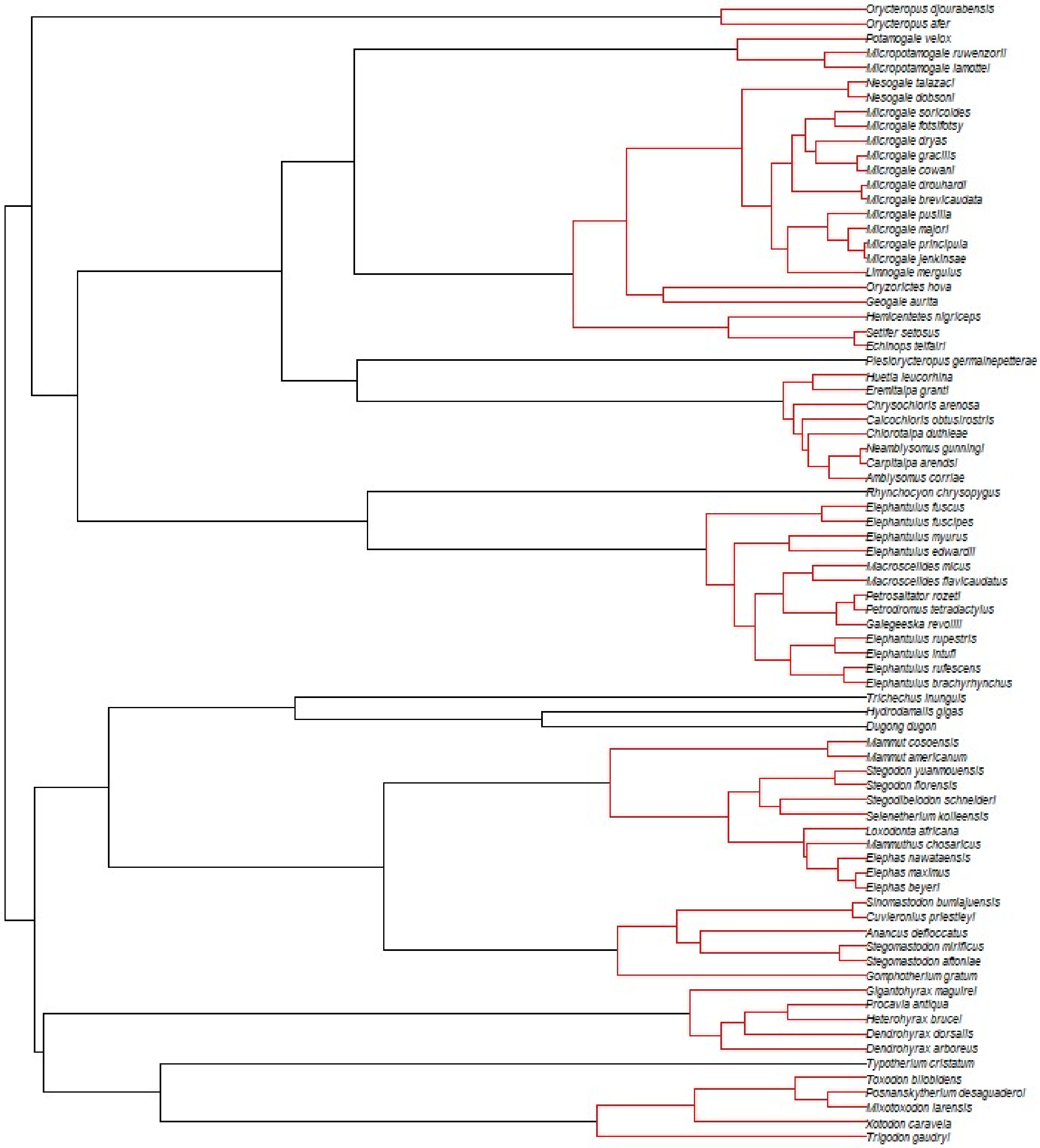


Figure S5.4. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for all afrotherian lineages 5 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

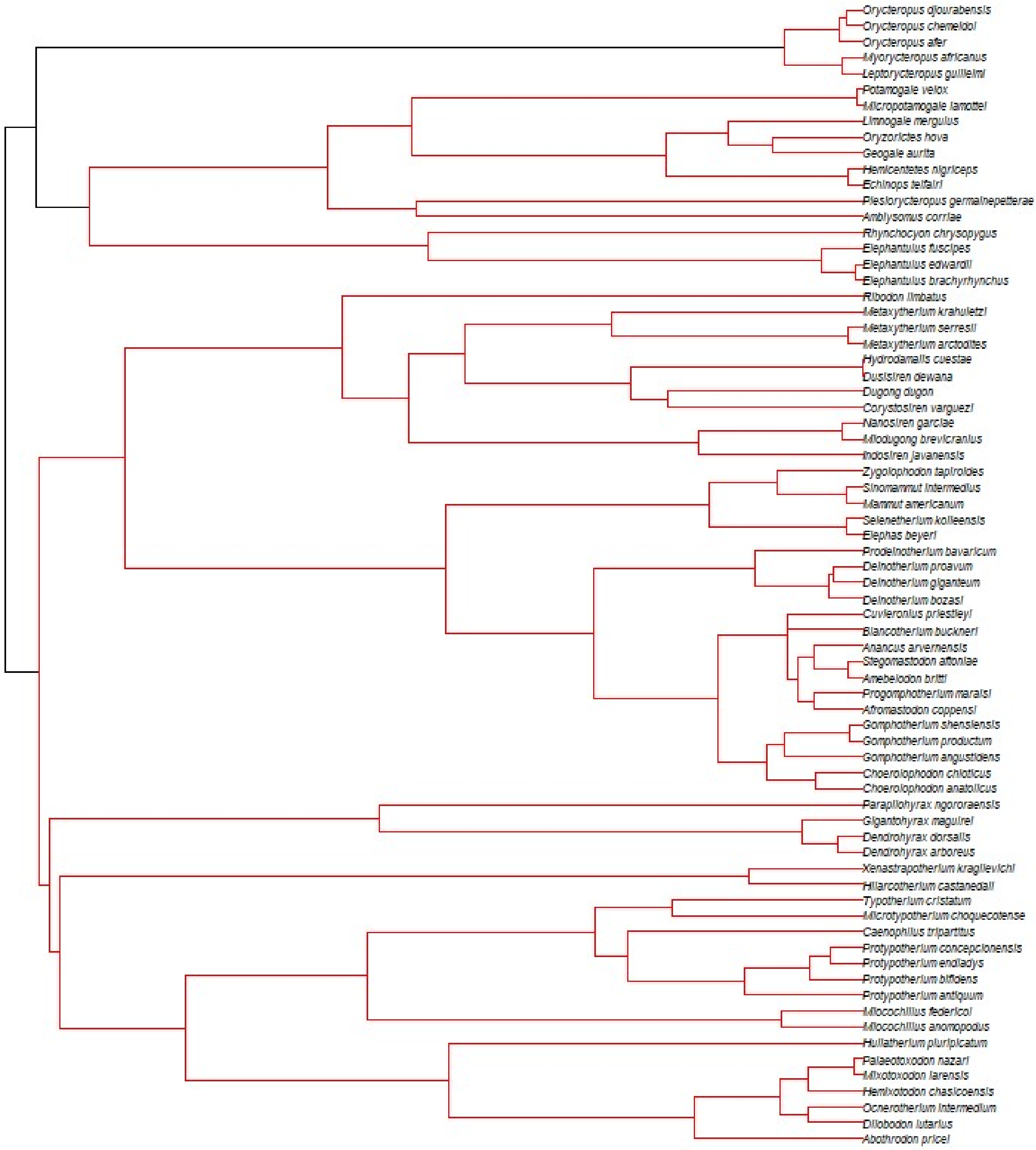


Figure S5.5. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for all afrotherian lineages 15 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

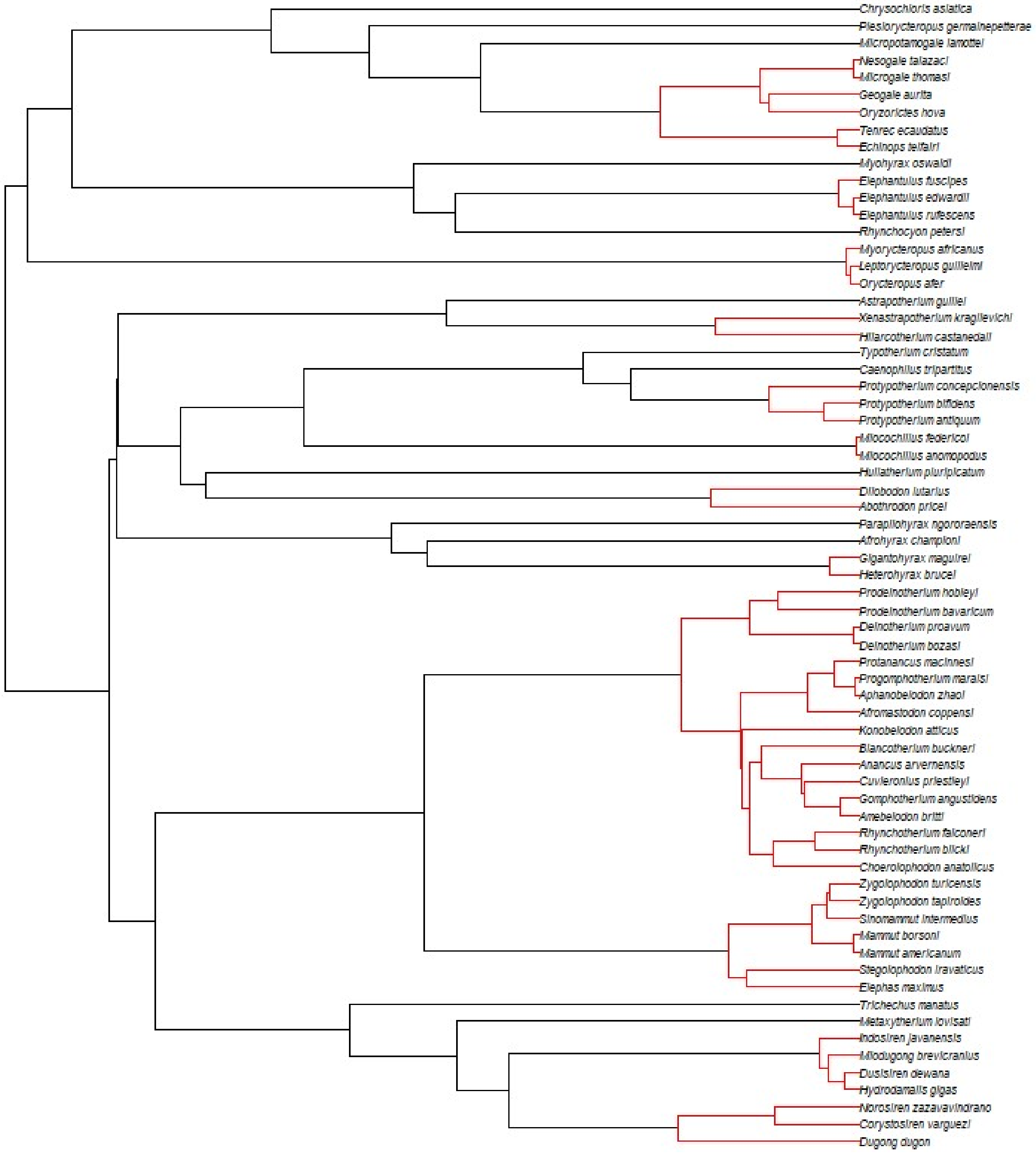


Figure S5.6. *A phylogeny of the GMYC single threshold results of tree 7289 from Chapter 2 for all afrotherian lineages 15 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon petersi represents all Rhynchocyon, as they had not evolved yet.*

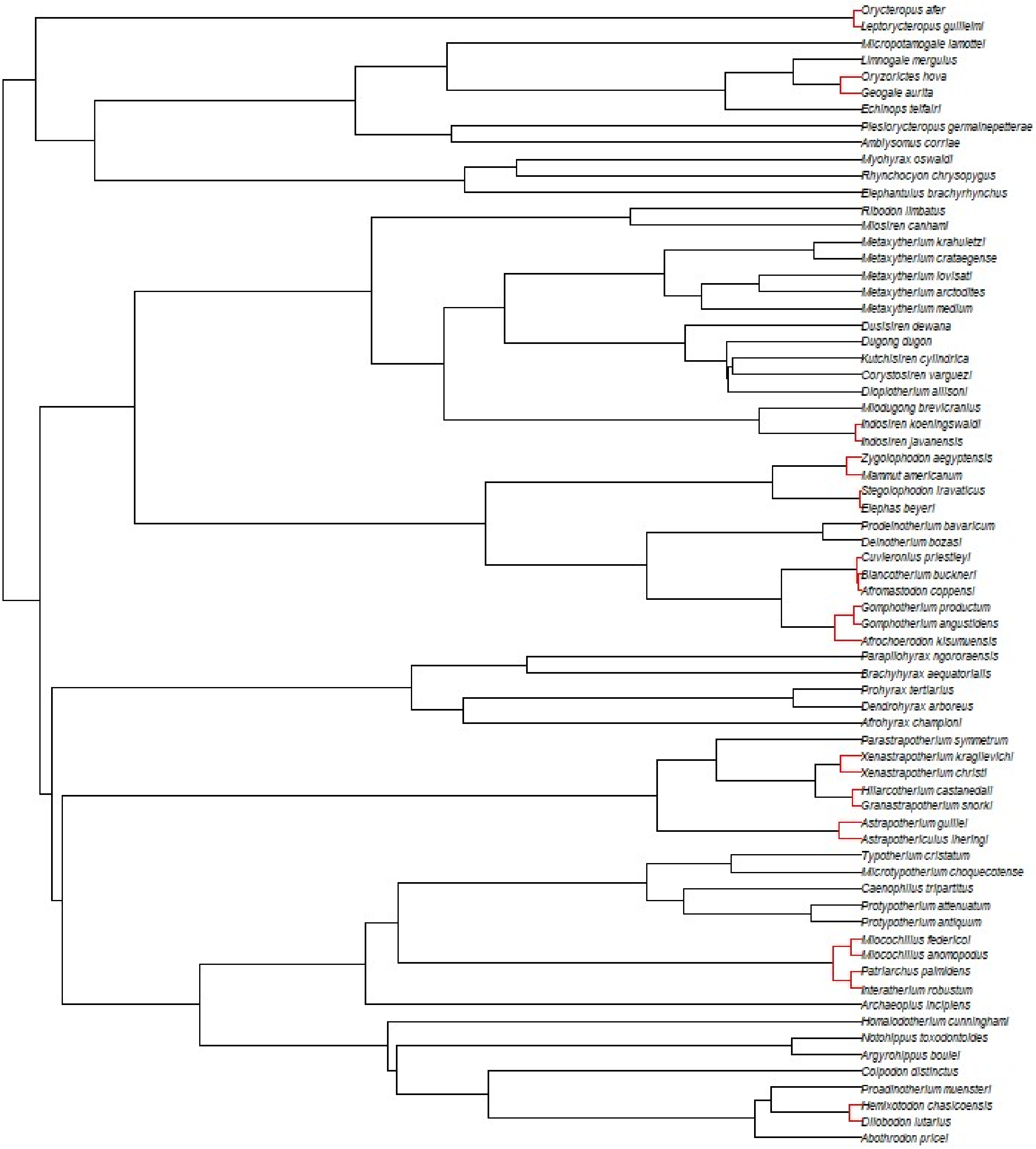


Figure S5.7. *A phylogeny of the GMYC single threshold results of the MCC tree from Chapter 2 for all afrotherian lineages 20 million years ago. The black-to-red colour transition indicates the beginning of a new cluster. Lineages that will have future species are given the tip label of one of these species; for example Rhynchocyon chrysopygus represents all Rhynchocyon, as they had not evolved yet.*

References

Agnolin, F.L. & Chimento, N.R. (2011) Afrotherian affinities for endemic South American “ungulates”. *Mamm. Biol.* **76** 101-8

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G. & Harmon, L.J. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences, USA*. **106** 13410-4

Asher, R.J. & Hofreiter, M. (2006) Tenrec Phylogeny and the Noninvasive Extraction of Nuclear DNA. *Syst. Biol.* **55**(2) 181-94

Avilla, L.S & Mothé, D. (2021) Out of Africa: A New Afrotheria Lineage Rises From Extinct South American Mammals. *Front. Ecol. Evol.*

Baken, E.K., Collyer, M.L., Kaliontzopoulou, A. & Adams, D.C. (2021) geomorph v4.0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution.* **12** 2355-63

Baker, R.J. & Bradley, R.D. (2006) Speciation in mammals and the genetic species concept. *J. Mammal*. **87** 643-62

Bapst, D.W. (2012) paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods Ecol. Evol*. **3** 803-7 doi: 10.1111/j.2041-210X.2012.00223.x

Barraclough, T.G. & Humphreys, A.M. (2015) The evolutionary reality of species and higher taxa in plants: a survey of post-modern opinion and evidence. *New Phytologist*. **207** 291-6

Barraclough, T.G. (2010) Evolving entities towards a unified framework for understanding diversity at the species and higher levels. *Phil. Trans. R. Soc. B.* **365** 1801-13

Barraclough, T.G. (2019) *The Evolutionary Biology of Species*. Oxford University Press

Bastide, P., Ané, C., Robin, S. & Mariadassou, M. (2018) Inference of Adaptive Shifts for Multivariate Correlated Traits. *Systematic Biology*. **67**(4) 662-80

Baum, D.A. & Donoghue, M.J. (1995) Choosing among alternative "phylogenetic" species concepts. *Syst. Bot*. 560-73

Benton, M.J. (2000) Stems, nodes, crown clades, and rank−free lists: is Linnaeus dead? *Biological Reviews*. **75** 633-48

Benton, M.J. (2007) The Phylocode: Beating a dead horse? *Acta Palaeontologica Polonica*. **52**(3) 651-5

Birky Jr, C.W., Adams, J., Gemmel, M. & Perry, J. (2010) Using population genetic theory and DNA sequences for species detection and identification in asexual organisms. *PLoS One*. **5** e10609

Bivand, R., Pebesma, E. & Gomez-Rubio, V. (2013) *Applied spatial data analysis with R, Second edition*. Springer, NY

Bouckaert, B., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, R., Siveroni, I., Suchard, M.A., Wu, C-H., Xie, D., Zhang, C., Stadler, T. & Drummond, A.J. (2019) BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*. **15**(4)

Burin, G., Park, T., James, T.D., Slater, G.J. & Cooper, N. (2023) The dynamic adaptive landscape of cetacean body size. *Current Biology*. **33** 1-8

Carlen, E.J., Rathbun, G.B., Olson, L.E., Sabuni, C.A., Stanley, W.T. & Dumbacher, J.P. (2017) Reconstructing the molecular phylogeny of giant sengis (Macroscelidea; Macroscelididae; *Rhynchocyon*). *Molecular Phylogenetics and Evolution*. **113** 150-60

Carson, H.L. (1975) The genetics of speciation at the diploid level. *Amer. Natur*. **109** 83-92

Claramunt, S., Derryberry, E.P., Remsen Jr, J.V. & Brumfield, R.T. (2012) High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc Biol Sci*. **279** 1567-74

Clarke, J.A. & Norell, M.A. (2002) The Morphology and Phylogenetic Position of Apsaravis ukhaana from the Late Cretaceous of Mongolia. *American Museum Novitates*. **3387** 1-46

Cooney, C.R., Bright, J.A., Capp, E.J.R., Chira, A.M., Hughes, E.C., Moody, C.J.A., Nouri, L.O., Varley, Z.K. & Thomas, G.H. (2017) Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*. **542** 344-7

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates Sunderland, MA

Croft, D.A., Gelfo, J.N. & López, G.M. (2020) Splendid Innovation: The Extinct South American Native Ungulates. *Annu. Rev. Earth Planet. Sci*. **48**(11) 1-32

Darwin, C. (1837) *Notebook B: (Transmutation of species)*

Darwin, C. (1859) *On the Origin of Species*. John Murray

de Queiroz, K. & Cantino, P.D. (2001). Phylogenetic nomenclature and the PhyloCode. *Bull. Zool. Nom*. **58** 254-71

de Queiroz, K. & Donoghue, M.J. (1988) Phylogenetic systematics and the species problem. *Cladistics*. **4** 317-38

de Queiroz, K. (1997) Misunderstandings about the phylogenetic approach to biological nomenclature: a reply to Lidén and Oxelman. *Zool. Scr*. **26** 67-70

de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation. in Howard, D.J. & Berlocher, S.H. eds. *Endless forms: species and speciation*. Oxford University Press 57-75

de Queiroz, K. (2005) Ernst Mayr and the modern concept of species. *PNAS*. **102** 6600-7

de Queiroz, K. (2007) Species concepts and species delimitation. *Syst. Biol*. **56** 879-86

Debastiani, V.J. (2020) PCPS: Principal Coordinates of Phylogenetic Structure. R package version 1.0.7. <https://CRAN.R-project.org/package=PCPS>

Didier, G., Fau, M. & Laurin, M. (2017) Likelihood of tree topologies with fossils and diversification rate estimation. *Syst. Biol.* **66** 964-87

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed Phylogenetics and Dating with Confidence. *PloS Biol.* **4**(5)

Dupin, J., Matzke, N.J., Särkinen, T., Knapp, S., Olmstead, R.G., Bohs, L. & Smith, S.D. (2017) Bayesian estimation of the global biogeographical history of the Solanaceae. *Journal of Biogeography*. **44**(4) 887-99

Eastman, J.M., Alfaro, M.E., Joyce, P., Hipp, A.L. & Harmon, L.J. (2011) A Novel Comparative Method for Identifying Shifts in the Rate of Character Evolution on Trees. *Evolution*. **65** 3578-89

Eldredge, N. & Gould, S.J. (1972) *Punctuated equilibria: an alternative to phyletic gradualism*. In T.J.M. Schopf, ed., Models in Paleobiology. San Francisco: Freeman Cooper. 82-115

Eldredge, N. (2006) *Confessions of a Darwinist*. The Virginia Quarterly Review **82** 32-53

Elliot, M.G. & Mooers, A.Ø. (2014) Inferring ancestral states without assuming neutrality or gradualism using a stable model of continuous character evolution. *BMC Evol. Biol*. **14**(226)

Everson, K.M., Soarimalala, V., Goodman, S.M. & Olson, L.E. (2016) Multiple Loci and Complete Taxonomic Sampling Resolve the Phylogeny and Biogeographic History of Tenrecs (Mammalia: Tenrecidae) and Reveal Higher Speciation Rates in Madagascar's Humid Forests. *Syst. Biol.* **65**(5) 890-909

Ezard, T., Fujisawa, T. & Barraclough, T. (2021) splits: SPecies' LImits by Threshold Statistics. R package version 1.0-20/r56 <https://R-Forge.R-project.org/projects/splits/>

Felsenstein, J. (1985) Phylogenies and the Comparative Method. *The American Naturalist*. **125**(1) 1-15

Ficetola, G., Mazel, F. & Thuiller, W. (2017) Global determinants of zoogeographical boundaries. *Nat. Ecol. Evol*. **1**

Finlay, S. & Cooper, N. (2015) Morphological diversity in tenrecs (Afrosoricida, Tenrecidae): comparing tenrec skull diversity to their closest relatives. *PeerJ*. 3:e927 doi: 10.7717/peerj.927

Fourment, M. & Holmes, E.C. (2016) Seqotron: a user-friendly sequence editor for Mac OS X. *BMC Research Notes*. **9**(106)

Fujisawa, T. & Barraclough, T.G. (2013) Delimiting Species Using Single-Locus Data and the Generalized Mixed Yule Coalescent Approach: A Revised Method and Evaluation on Simulated Data Sets. *Syst. Biol.* **62**(5) 707-24

Gemmell, N.J., Rutherford, K., Prost, S., Tollis, M., Winter, D., Macey, J.R., Adelson, D.L., Suh, A., Bertozzi, T., Grau, J.H., Organ, C., Gardner, P.P., Muffato, M., Patricio, M., Billis, K., Martin, F.J., Flicek, P., Petersen, B., Kang, L., Michalak, P., Buckley, T.R., Wilson, M., Cheng, Y., Miller, H., Schott, R.K., Jordan, M.D., Newcomb, R.D., Arroyo, J., Valenzuela, N., Hore, T.A., Renart, J., Peona, V., Peart, C.R., Warmuth, V.M., Zeng, L., Kortschak, R.D., Raison, J.M., Velásquez Zapata, V., Wu, Z., Santesmasses, D., Mariotti, M., Guigó, R., Rupp, S.M., Twort, V.G., Dussex, N., Taylor, H., Abe, H., Bond, D.M., Paterson, J.M., Mulcahy, D.G., Gonzalez, V.L., Barbieri, C.G., DeMeo, D.P., Pabinger, S., Van Stijn, T., Clarke, S., Ryder, O., Edwards, S.V., Salzberg, S.L., Anderson, L., Nelson, N., Stone, C. & Ngatiwai Trust Board (2020) The tuatara genome reveals ancient features of amniote evolution. *Nature*. **584** 403-9

Gheerbrant, E., Filippo, A. & Schmitt, A. (2016) Convergence of afrotherian and Laurasiatherian Ungulate-Like Mammals: First Morphological Evidence from the Paleocene of Morocco. *PLoS ONE* **11**(7)

Gould, S.J. (1980) *G. G. Simpson, Paleontology and the Modern Synthesis*. In E. Mayr and W. B. Provine, eds., The Evolutionary Synthesis. Cambridge MA: Harvard University Press. 153-72

Grossnickle, D.M., Sadier, A., Patterson, E., Cortés-Viruet, N.N., Jiménez-Rivera, S.M., Sears, K.E. & Santana, S.E. (2024) The hierarchical radiation of phyllostomid bats as revealed by adaptive molar morphology. *Current Biology*. **34**(6) 1284-94

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*. **59**(3) 307-21

Gunnell, G.F., Boyer, D.M., Friscia, A.R., Heritage, S., Manthi, F.K., Miller, E.R., Sallam, H.M., Simmons, N.B., Stevens, N.J. & Seiffert, E.R. (2018) Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's aye-aye. *Nat Commun*. **9**(3193)

Hansen, T.F., Houle, D., Pavlicev, M. & Pélabon, C. (2023) *Evolvability: A Unifying Concept in Evolutionary Biology?* Massachusetts Institute of Technology

Hasegawa, M., Kishino, H. & Yano, T. (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*. **22** 160-74

Heath, T.A., Huelsenbeck, J.P. & Stadler, T. (2014) The fossilized birth–death process for coherent calibration of divergence-time estimates. *PNAS*. **111**(29)

Hennig, W. (1966) *Phylogenetic systematics*. tr. Davis, D.D. & Zangerl, R. Urbana, IL: Univ. of Illinois Press

Herberstein, M.E., McLean, D.J., Lowe, E., Wolff, J.O., Khan, M.K., Smith, K., Allen, A.P., Bulbert, M., Buzatto, B.A., Eldridge, M.D.B., Falster, D., Fernandez Winzer, L., Griffith, S.C., Madin, J.S., Narendra, A., Westoby, M., Whiting, M.J., Wright, I.J & Carthey, A.J.R. (2022) AnimalTraits - a curated animal trait database for body mass, metabolic rate and brain size*. Sci Data*. **9** 265

Heritage, S., Rayaleh, H., Awaleh, D.G. & Rathbun, G.B. (2020) New records of a lost species and a geographic range expansion for sengis in the Horn of Africa. *PeerJ.* 8:e9652 https://doi.org/10.7717/peerj.9652

Hijmans, R. (2024) terra: Spatial Data Analysis. R package version 1.7-71. <https://CRAN.R-project.org/package=terra>

Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013) An update of Wallace's zoogeographic regions of the world. *Science*. **339** 74-8

Humphreys, A.M. & Barraclough, T.G. (2014) The evolutionary reality of higher taxa in mammals. *Proc. R. Soc. B.* **281**

Humphreys, A.M., Rydin, C., Jønsson, K.A., Alsop, D., Callender-Crowe, L.M & Barraclough, T.G. (2016) Detecting evolutionarily significant units above the species level using the generalised mixed Yule coalescent method. *Methods in Ecology and Evolution.* **7** 1366-75 doi: 10.1111/2041-210X.12603

IUCN (2021) The International Union for Conservation of Nature (IUCN) Red List of Threatened Species. <https://www.iucnredlist.org>

IUCN (2024) The International Union for Conservation of Nature (IUCN) Red List of Threatened Species. <https://www.iucnredlist.org>

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*. **491** 444-8

Jolly, C.J. (2014) A Darwinian species definition and its implications. *Evol. Anthropol*. **23** 36-38

Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*. **30**(4) 772-80

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*. **30**(14) 3059-66

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*. **26** 1463-4

Kemp, T.S. (2016) *The Origin of Higher Taxa*. Oxford University Press, Oxford

Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* **16**(2) 111-20

Kuntner, M., May-Collado, L.J. & Agnarsson, I. (2011) Phylogeny and conservation priorities of afrotherian mammals (Afrotheria, Mammalia). *Zoologica Scripta* **40** 1-15

Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution.* **29**(6) 1695-1701

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2016) PartitionFinder 2: new methods for selecting partitioned models of evolution formolecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*. DOI: dx.doi.org/10.1093/molbev/msw260

Law, C.J., Slater, G.J. & Mehta, R.S. (2018) Lineage Diversity and Size Disparity in Musteloidea: Testing Patterns of Adaptive Radiation Using Molecular and Fossil-Based Methods. *Systematic Biology*. **67**(1) 127–44

Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*. **10** 745-58

Lidén, M. & Oxelman, B. (1996) Do we need phylogenetic taxonomy? *Zool. Scr*. **25** 183-5

Liu, Y., Xu, X., Dimitrov, D., Pellissier, L., Borregaard, M.K., Shrestha, N., Su, X., Luo, A., Zimmermann, N.E., Rahbek, C. & Wang, Z. (2023) An updated floristic map of the world. *Nature Communications*. **14**

Lloyd, G.T. & Slater, G.J. (2021) A Total-Group Phylogenetic Metatree for Cetacea and the Importance of Fossil Data in Diversification Analyses. *Syst. Biol.*

Louca, S. & Pennell, M.W. (2020) Extant timetrees are consistent with a myriad of diversification histories. *Nature*. **580** 502-5

Maestri, R. & Duarte, L. (2020) Evoregions: Mapping shifts in phylogenetic turnover across biogeographic regions. *Methods Ecol. Evol*. **11** 1652-62

Mallet, J. (1995) A Species definition for the modern synthesis. *Trends Ecol. Evol*. **10** 294-9

Matzke, N.J. (2013) Probabilistic Historical Biogeography: New Models for Founder-Event Speciation, Imperfect Detection, and Fossils Allow Improved Accuracy and Model-Testing. *Frontiers of Biogeography*. **5**(4), 242-8

Matzke, N.J. (2014) Model Selection in Historical Biogeography Reveals that Founder-event Speciation is a Crucial Process in Island Clades. *Systematic Biology*. **63**(6) 951-70

Mayr, E. (1942) *Systematics and the Origin of Species.* Columbia Univ. Press, New York

Mayr, E. (1944) Wallace's Line in the Light of Recent Zoogeographic Studies. *Q. Rev. Biol*. **19**

Mayr, E. (1982) Speciation and Macroevolution. *Evolution*. **36**(6) 1119-32

Mayr, E. (1995) Species, classification, and evolution. in Arai, R., Kato, M. & Doi Y. eds. *Biodiversity and Evolution*. National Science Museum Foundation, Tokyo 3-12

Meade, A. & Pagel, M. (2022) BayesTraits. University of Reading. <http://www.evolution.reading.ac.uk/BayesTraitsV4.0.0/BayesTraitsV4.0.0.html>

Mitchell, J.S., Etienne, R.S. & Rabosky, D.L. (2019) Inferring Diversification Rate Variation From Phylogenies With Fossils. *Systematic Biology*. **68**(1) 1-18

Nakamura, G., Rodrigues, A.V., Luza, A.L., Maestri, R., Debastiani, V. & Duarte, L. (2024) Herodotools: An R package to integrate macroevolution, biogeography and community ecology. *Journal of Biogeography*. **51**(4) 533-43

Nixon, K.C. & Wheeler, Q.D. (1990) An Amplification of the Phylogenetic Species Concept. *Cladistics*. **6** 211-23

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C. & Weedon, J. (2022) vegan: Community Ecology Package. R package version 2.6-4. <https://CRAN.R-project.org/package=vegan>

O'Meara, B.C., Ané, C., Sanderson, M.J. & Wainwright, P.C. (2006) Testing for Different Rates of Continuous Trait Evolution Using Likelihood. *Evolution*. **60** 922-33

Pagel, M., O'Donovan, C. & Meade, A. (2022) General statistical model shows that macroevolutionary patterns and processes are consistent with Darwinian gradualism. *Nature Communications*. **13** 1113

Paradis, E. & Schliep, K. (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*. **35** 526-8

Park, T., Burin, G., Lazo-Cancino, D., Rees, J.P.G., Rule, J.P., Slater, G.J. & Cooper, N. (2024) Charting the course of pinniped evolution: insights from molecular phylogeny and fossil record integration. *Evolution*.

Paterson, H.E.H. (1985) The Recognition Concept of Species. in Vrba, E. ed. *Species and Speciation*. Transvaal Museum Monograph No. 4. Pretoria 21-9

Pebesma, E. & Bivand, R. (2005) Classes and methods for spatial data in R. *R News*. **5**(2) 9-13 <https://CRAN.R-project.org/doc/Rnews/>

Pebesma, E. & Bivand, R. (2023) *Spatial Data Science: With Applications in R*. Chapman and Hall, CRC. https://doi.org/10.1201/9780429459016

Pebesma, E. (2018) Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*. **10**(1) 439-46 https://doi.org/10.32614/RJ-2018-009

Plate, T. & Heiberger, R. (2016) abind: Combine Multidimensional Arrays. R package version 1.4-5. <CRAN.R-project.org/package=abind>

Poncelet, G. & Shimeld, S.M. (2020) The evolutionary origins of the vertebrate olfactory system. *Open Biol*. **10**

Puttick, M.N. & Thomas, G.H. (2015) Fossils and living taxa agree on patterns of body mass evolution: a case study with Afrotheria. *Proc. R. Soc. B*. **282**

R Development Core Team (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Rabosky, D.L. (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PloS One*. **9**

Rabosky, D.L., Grundler, M.C., Anderson, C.J., Title, P.O., Shi, J.J., Brown, J.W., Huang, H. & Larson., J.G. (2014) BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*. **5** 701-7

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J. & Alfaro, M.E. (2013) Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*. **4**(1958)

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology.* syy032. doi:10.1093/sysbio/syy032

Revell, L. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution.* **3** 217-23. doi:10.1111/j.2041-210X.2011.00169.x

Rohlf, F.J. (2015) The tps series of software. *Hystrix, It. J. Mamm.*

Salton, J.A. & Szalay, F.S. (2004) The Tarsal Complex of Afro-Malagasy Tenrecoidea: A Search for Phylogenetically Meaningful Characteristics. *Journal of Mammalian Evolution*. **11**(2) 73-104

Sánchez-Villagra, M.R., Narita, Y. & Kuratani, S. (2007) Thoracolumbar vertebral number: The first skeletal synapomorphy for afrotherian mammals. *Systematics and Biodiversity*. **5**(1) 1-7

Sanmartín, I. (2012) Historical Biogeography: Evolution in Time and Space. *Evo. Edu. Outreach*. **5** 555-68

Schlager, S. (2017) Morpho and Rvcg – Shape Analysis in R. *Statistical Shape and Deformation Analysis.* 217-56

Seiffert, E.R. (2007) A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evol. Biol*. **7**(224)

Seiffert, E.R., Nasir, S., Al-Harthy, A., Groenke, J.R., Kraatz, B.P., Stevens, N.J. & Al-Sayigh, A.R. (2012) Diversity in the later Paleogene proboscidean radiation: a small barytheriid from the Oligocene of Dhofar Governorate, Sultanate of Oman. *Naturwissenschaften*. **99**(2) 133-41

Simpson, G.G. (1944) *Tempo and mode in evolution*. Columbia University Press

Simpson, G.G. (1951) The Species Concept. *Evolution*. **5**(4) 285-98

Simpson, G.G. (1953) *Major Features of Evolution*. Columbia University Press

Simpson, G.G. (1961) *Principles of Animal Taxonomy*. Columbia University Press

Šmíd, J. & Tolley, K.A. (2019) Calibrating the tree of vipers under the fossilized birth-death model. *Sci Rep*. **9**(5510)

Springer, M.S. (2022) Afrotheria. *Current Biology*. **32** 205-10

Springer, M.S., Emerling, C.A. & Gatesy, J. (2023) Three Blind Moles: Molecular Evolutionary Insights on the Tempo and Mode of Convergent Eye Degeneration in *Notoryctes typhlops* (Southern Marsupial Mole) and Two Chrysochlorids (Golden Moles). *Genes (Basel)*. **14**(11)

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*. **30**(9) 1312-3

Stankowski, S. & Ravinet, M. (2021) Quantifying the use of species concepts. *Current Biology*. **31**(9) 428-9

Suárez, D., Arribas, P., Jiménez-García, E. & Emerson, B.C. (2022) Dispersal ability and its consequences for population genetic differentiation and diversification. *Proc. R. Soc. B*. **289**(1975)

Tabuce, R., Asher, R.J. & Lehmann, T. (2008) afrotherian mammals: a review of current data. *Mammalia*. **72** 2-14

Tamura, K. & Nei, M. (1993) Estimation of the Number of Nucleotide Substitutions in the Control Region of Mitochondrial DNA in Humans and Chimpanzees. *Mol. Biol. Evol*. **10**(3) 512-26

Tarver, J.E. & Donoghue, P.C.J. (2011) The Trouble with Topology: Phylogenies without Fossils Provide a Revisionist Perspective of Evolutionary History in Topological Analyses of Diversity. *Systematic Biology*. **60**(5) 700-12

Tavaré, S. (1986) Some Probabilistic and Statistical Problems in the Analysis of DNA Sequences. *Lectures on Mathematics in the Life Sciences*. **17** 57-86

Templeton, A.R. (1989) The meaning of species and speciation: a genetic perspective, in Otte, D. & Endler, J.A. eds. *Speciation and its Consequences*. Sunderland, Mass., USA, Sinauer Associates 3-27

The Paleobiology Database (PBDB) (2021) <https://paleobiodb.org>

Title, P.O., Swiderski, D.L. & Zelditch, M.L. (2022) EcoPhyloMapper: An r package for integrating geographical ranges, phylogeny and morphology. *Methods in Ecology and Evolution*. **13** 1912-22

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019) Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol*. **17**(12)

Van Valen, L. (1976) Ecological Species, Multispecies, and Oaks. *Taxon*. **25** 233-9

Venditti, C., Meade, A. & Pagel, M. (2011) Multiple routes to mammalian diversity. *Nature.* **479** 393-6

Wallace, A.R. (1876) *The Geographical Distribution of Animals*. Cambridge Univ. Press, Cambridge

Welker, F., Collins, M.J., Thomas, J.A., Wadsley, M., Brace, S., Cappellini, C., Turvey, S.T., Reguero, M., Gelfo, J.N., Kramarz, A., Burger, J., Thomas-Oates, J., Ashford, D.A., Ashton, P.D., Rowsell, K., Porter, D.M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J.V., Kiley, P., Elliott, J.A., Kelstrup, C.D., Mullin, V., Hofreiter, M., Willerslev, E., Hublin, J-J., Orlando, L., Barnes, I. & MacPhee, R.D.E. (2015) Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. *Nature*. **522** 81-4

White, A.E., Dey, K.K., Stephens, M. & Price, T.D. (2021) Dispersal syndromes drive the formation of biogeographical regions, illustrated by the case of Wallace's Line. *Global Ecol. Biogeogr*. **30** 685-96

Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023) dplyr: A Grammar of Data Manipulation. R package version 1.1.4. <https://CRAN.R-project.org/package=dplyr>

Wiens, J.J. (2004) The Role of Morphological Data in Phylogeny Reconstruction. *Syst. Biol*. **53**(4) 653-61

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*. **95**(7) 2027

Witmer, L. & Chiappe, L. (2002) *Mesozoic Birds: Above the Heads of Dinosaurs*. Berkeley: University of California Press

Wright, S. (1932) *The roles of mutation, inbreeding, crossbreeding, and selection in evolution*. Proceedings of the Sixth International Congress on Genetics. **1** 356-66

Zharkikh, A. (1994) Estimation of evolutionary distances between nucleotide sequences. *J. Mol. Evol.* **39** 315-29

Zurano, J.P., Magalhães, F.M., Asato, A.E., Silva, G., Bidau, C.J., Mesquita, D.O. & Costa, G.C. (2019) Cetartiodactyla: Updating a time-calibrated molecular phylogeny. *Molecular Phylogenetics and Evolution*. **133** 256-62