# MACROEVOLUTION WITH FOSSIL AND LIVING TAXA

*by*

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# DECLARATION

I declare that this thesis has not been submitted as an exercise for a degree at this or any other University and it is, unless otherwise referenced, entirely my own work. I agree to deposit this thesis in the University's open access institutional repository or allow the library to do so on my behalf, subject to Irish Copyright Legislation and Trinity College Library conditions of use and acknowledgement.

Thomas Guillerme

## SUMMARY

Even if most of our current knowledge and tool-kits to study biodiversity focus on living species, the vast majority of the species that ever lived are long extinct. Therefore, to properly understand the drivers of biodiversity through time, it is crucial to combine data and methods from both living and fossil species in order to better assess macroevolutionary and macroecological patterns. My PhD focuses on ways to combine both living and fossil species into phylogenies and looks at how these phylogenies can be used for describing macroevolutionary patterns. I studied the use of both living and fossil species along two axes: firstly, the ability of modern phylogenetic methods to deal with molecular data for living species and morphological data for both living and fossil species; and secondly, the practicality of using such phylogenetic trees for more accurately describing patterns of diversification through time and space.

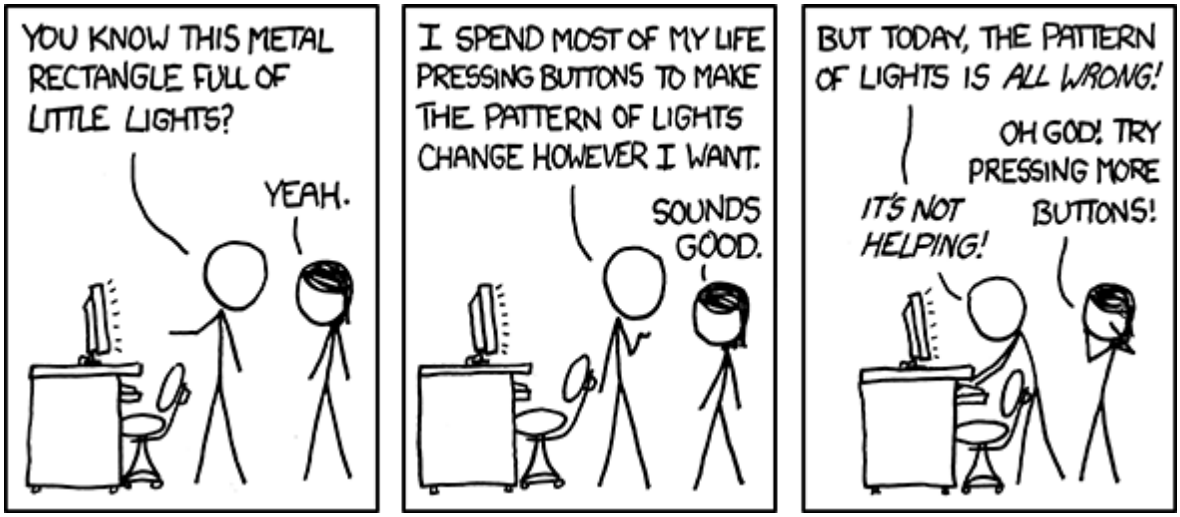
For the first part of this project, I ran extensive and thorough simulation analyses to test the effect of missing data on phylogenies topologies when using a combination of living and fossil data. I tested how multiple levels of missing data among living species, fossil species and the two combined affected our ability to recover the correct tree topology. I found that the amount of missing data among living species is the most crucial aspect for efficiently combining living and fossil species in the same phylogeny. Following these conclusions, I ran a thorough survey of the data available for living mammal species. I measured the amount of morphological data available within each mammalian order and tested whether this data was randomly distributed along the phylogeny or biased towards certain clades. The result of this analysis shows that although morphological data is scarce for living mammals, it is at least generally randomly distributed across the phylogeny.

For the second part of my PhD, I explored a way of using phylogenetic trees containing both living and fossil species to measure patterns of diversification among mammals through time. I measured changes in species richness as well as in morphological diversity (i.e. disparity) to describe mammalian diversification across the K-Pg boundary. I found that the K-Pg boundary had no significant effect on morphological diversification.

# ACKNOWLEDGEMENTS

Thanks folks!

# PREFACE



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CHAPTER 1

# INTRODUCTION

Today's amazing biodiversity represents only an overwhelmingly small fraction of the organisms that ever existed (Novacek and Wheeler, 1992; Raup, 1981). Even though it is widely accepted that the processes that shaped the patterns observed nowadays are influenced by evolutionary history (Fritz et al., 2013), most of the scientific endeavour in biology focus solely on living species. Ignoring this can lead to misinterpretation of macroevolutionary patterns and processes (Benton, 2015). For example, nowadays crocodilians constitute a species poor group (25 species; Uetz, 2010) with a low range of shapes and environments (marine or freshwater; Martin, 2008). Therefore when studying macroevolutionary patterns among all vertebrates, crocodilians will have a rather "marginal" effect. For example Wiens (2015) suggests that terrestriality is a driver of diversification among living vertebrates, a pattern essentially driven by Aves, Lepidosauria and Mammalia. However, crocodilians were much more diverse both in terms of species richness (244 species reported in Bronzati et al., 2015) or in terms shapes and environments (Stubbs et al., 2013). In the case of Wiens (2015), not including fossil species, conceal the true history of this clade, and thus, potentially biases the conclusions of the study.

Besides, including fossil species not only accounts for groups that were more diverse in the past, it also highly improves our descriptions of macroevolutionary patterns such as the timing of diversification events (e.g. significantly reducing node age confidence intervals; Ronquist et al., 2012a), the relationships among lineages (e.g. solving some controversial fossil placement; Dembo et al., 2015) or even gives a potential solution for understanding niche occupancy through time (e.g. Pearman et al., 2008). All this studies have led to a recent consensus among scientists that we need to combine both living and fossil species in macroevolutionary analysis (Jackson and Erwin, 2006; Quental and Marshall, 2010; Dietl and Flessa, 2011; Slater and Harmon, 2013; Fritz et al., 2013; Benton, 2015). Yet, in practice, only few studies have actively focused on combining them since the last three years (e.g. Ronquist et al., 2012a; Slater, 2013; Wood et al., 2013; Beck and Lee, 2014; Arcila et al., 2015; Dembo et al., 2015).

This scarcity is probably due to the fundamental differences between the two approaches to study macroevolution: using either living (neontological) or fossil (palaeontological) data.

The paleontological approachis based on cladistic data of the fossil record (i.e. discrete morphological observation). It relies on optimal criteria such as maximum parsimony (Hennig, 1966; Felsenstein, 2004) to resolve the relations among lineages and on stratigraphy to time such trees (Goloboff et al., 2008). This approach allows a direct interpretation of macroevolution in deep time and benefits from recent improvements both on data collection (e.g. 4541 characters in O'Leary et al., 2013, introducing the term "phenomics") and on dating method (e.g. the *cal3* method from Bapst, 2014). However, this approach does rarely takes into account full living diversity (e.g. only 38 out of 351 living primates for 119 fossil in Ni et al., 2013) and methods suffer from several biases (e.g. parsimony; Wright and Hillis, 2014).

Conversely, the neontological approach uses the vast amount of available molecular from living species and is based on probabilistic methods (e.g. Maximum Likelihood or Bayesian). This approach is based on evolutionary models that rely on the differences in DNA to resolve the relations among lineages and on some specific fossils' occurrence dates for timing the lineages divergence (i.e. the molecular clock; Zuckerkandl and Pauling, 1965). There has been enormous improvements of this approach in the last decade on both the evolutionary models (e.g. Bapst, 2013; Stadler and Yang, 2013; Heath et al., 2014) and on which fossils to use to calibrate the trees (Donoghue and Benton, 2007; Parham et al., 2012). However, this approach uses only the ages of certain fossils instead of the vast amount of informations available from the fossil record (e.g. species richness, traits, biogeography, etc).

## 1.1 PHYLOGENIES WITH LIVING AND FOSSIL TAXA

Nonetheless, the last three years have seen the development of the newly trending Total Evidence method (Ronquist et al., 2012a; Slater, 2013; Wood et al., 2013; Schrago et al., 2013; Beck and Lee, 2014; Arcila et al., 2015; Dembo et al., 2015). This methods allows to combine both molecular data from living taxa and morphological data from living and fossil taxa in the same phylogenetic matrices. It was first developed in the nineties (Eernisse and Kluge, 1993) but only recently successfully implemented in phylogenetic softwares (Ronquist et al., 2012b; Bouckaert et al.,

2014). By using both available neontological and palaeontological data, this methods allows to better study macroevolutionary patterns and processes. For example, it allowed great improvements on the estimation of divergence event (e.g. Ronquist et al., 2012a); evolutionary rates (e.g. Beck and Lee, 2014); topology (e.g. Dembo et al., 2015); traits evolution (e.g. Slater, 2013) or even speciation processes (e.g. Wood et al., 2013). There is, however, one drawback to this method: because it needs both molecular data for living taxa and morphological data for living and morphological taxa, it is susceptible to suffer from great amounts of missing data.

### 1.1.1 *Effects of missing data on topological inference using a Total Evidence approach*

As a first part of this PhD thesis, in the second chapter, I tackled the problem of missing data in Total Evidence matrices. I ran long term and thorough simulations to test how the topologies inferred from Total Evidence matrices were sensitive to missing morphological data. I removed morphological data from Total Evidence matrices via three parameters where data are potentially missing: (1) the number of living taxa with molecular data but no morphological data; (2) the amount of missing data in the fossil record and (3) the number of overall morphological characters in the matrix. I modified the level of data in the three parameters and in their combination and then inferred the phylogenies using both Maximum Likelihood and Bayesian approach. Finally, I compared how the missing data parameters and their interactions as well as the phylogenetic inference method influenced the ability of estimating the correct tree topology. I found that the number of living taxa with both morphological and molecular data are essential to recover accurate topologies. This study rose the question of how can we improve Total Evidence topologies and especially, how much morphological data are available for living taxa?

### 1.1.2 *Morphological data availability in living mammals*

Following this question, in the third chapter of this thesis, I monitored how many morphological data were available in the literature for living mammals. I downloaded all the recent available morphological matrices and counted the number of living mammals with available morphological data at three different taxonomic levels (species, genus and family) for each mammalian order. For each order with missing data, I measured if the data weren't biased toward some specific clades in

each order using phylogenetic structure methods (Webb et al., 2002). I found that a lot of living mammals have no morphological data at the species or the genus level but, that at least most of the available data was randomly distributed. These results highlight the importance of cladistics and collecting morphological data, even in the age of genomics, especially for combining living and fossil data in the same phylogenies.

## 1.2 TOTAL EVIDENCE PHYLOGENIES APPLICATIONS

The two previous chapters only focused on the technical and practical side of combining living and fossil taxa into phylogenies and underlined the importance of a good data overlap between living and fossil taxa. However, many studies have been able to use the Total Evidence method even with low overlap between living and fossil taxa by using strong topological constraints (Ronquist et al. 2012a; Schrago et al. 2013; Slater 2013; Beck and Lee 2014; but see Arcila et al. 2015; Dembo et al. 2015). This resulted in Total Evidence phylogenies were the topology are based on strong but valid *a priori* topologies (e.g. based on Meredith et al. 2011 for Slater 2013). The observable patterns in these phylogenies can then be used by biologists to test some hypothesis relating to macroevolutionary processes.

One example of pattern observed in phylogenies can be the shift of ecological dominant species through time due to drastic biotic or abiotic changes in the biosphere (e.g. mass extinctions). For example, Brachiopoda was a dominant shelled filter feeding clade during the Paleozoic (514 to 252 million years ago; Mya) but was replaced by Bivalvia at the end Permian extinction event (252 Mya) which is now the dominant group (Sepkoski 1981; Clapham et al. 2006 but see Payne et al. 2014). This type of replacement pattern has also been observed in other groups such as Formaninifera (Coxall et al., 2006), Ichtyosauria (Thorne et al., 2011) or Plesiosauria Benson and Druckenmiller 2014 and are often related to competition (Brusatte et al., 2008) or adaptive radiations (Losos, 2010). Another classical example is the “replacement” of the dominant non-avian dinosaurs by mammals after the infamous Cretaceous-Paleogene (K-Pg) extinction 66 Mya...

### 1.2.1 *Cretaceous-Palaeogene extinction does not affect mammalian disparity*

In this fourth chapter, I studied the changes of morphological diversity (or disparity; Wills et al., 1994) through time using Total Evidence trees from Slater (2013) and

Beck and Lee (2014) to test whether the K-Pg extinction had an effect on mammal evolution. I propose a new approach to describe patterns of disparity through time base on the use of Total Evidence trees. This approach allows more precision in describing the changes through time as well as more freedom for choosing the underlining models of morphological evolution (e.g. punctuated or gradual; Hunt et al., 2015). Using this approach I found no evidence of changes in disparity in mammals around the K-Pg boundary, arguing that the extinction of non-avian dinosaurs had no direct effect on mammalian evolution.

This is just one example of the benefits of adding both living and fossil taxa in macroevolutionary studies. In the fifth chapter, I will discuss how the three previous chapters open new axis of research as well as the limitation of these studies. Finally I will present some concluding thoughts on the utility of combining data, methods and disciplines to better understand macroevlutionary patterns and processes.

CHAPTER 2

TOTAL EVIDENCE METHOD AND MISSING DATA

# Effects of missing data on topological inference using a Total Evidence approach [1]

[1] A similar version of this chapter is currently (2015/09/30) under review in Molecular Phylogenetics and Evolution. T.G. and N.C. designed the experiments; T.G. ran the analysis and interpreted the results; T.G. and N.C. wrote the manuscripts. *Specific acknowledgements*: thanks to Gavin Thomas, Frédéric Delsuc, Emmanuel Douzery, Trevor Hodkinson, Andrew Jackson, Nick Matzke, and April Wright for useful comments on our simulation protocol and manuscript. Thanks to Paddy Doyle, Graziano D'Innocenzo and Sean McGrath for assistance with the computer cluster. Thanks to the two anonymous reviewers for their useful and enthusiastic comments. *Data availability and reproducibility*: All the code used in this analysis is available on GitHub (goo.gl/4djNUf) with some information on how to use the various functions. Additionally all the simulated data is available on FigShare (dx.doi.org/10.6084/m9.figshare.1306861).

CHAPTER 3

MISSING DATA IN LIVING MAMMALS

# Assessment of cladistic data availability for living mammals [2]

## 3.1 SUMMARY

Analyses of living and fossil taxa are crucial for understanding changes in biodiversity through time. The Total Evidence method allows living and fossil taxa to be combined in phylogenies, by using molecular data for living taxa and morphological data for both living and fossil taxa. With this method, substantial overlap of morphological data among living and fossil taxa is crucial for accurately inferring topology. However, although molecular data for living species is widely available, scientists using and generating morphological data mainly focus on fossils. Therefore, there is a gap in our knowledge of neontological morphological data even in well-studied groups such as mammals.

We investigated the amount of morphological (cladistic) data available for living mammals and how this data was phylogenetically distributed across orders. 22 of 28 mammalian orders have <25% species with available morphological data; this has implications for the accurate placement of fossil taxa, although the issue is less pronounced at higher taxonomic levels. In most orders, species with available data are randomly distributed across the phylogeny, which may reduce the impact of the problem. We suggest that increased morphological data collection efforts for living taxa are needed to produce accurate Total Evidence phylogenies.

[2] A shorter version (2500 words) will be submitted under the same title to Biology Letters as an invited submission for a special issue on phylogenies with living and fossil species. This special issue is open to submission in December 2015. A pre-print is currently available at `http://dx.doi.org/10.1101/022970`. T.G. and N.C. designed the experiments; T.G. ran the analysis and interpreted the results; T.G. and N.C. wrote the manuscripts. *Specific acknowledgements*: thanks to David Bapst, Graeme Lloyd, Nick Matzke and April Wright. *Data availability and reproducibility*: all data and analysis code is available on GitHub (`https://github.com/TGuillerme/Missing_living_mammals`).

## 3.2 INTRODUCTION

There is an increasing consensus among evolutionary biologists that studying both living and fossil taxa is essential for fully understanding macroevolutionary patterns and processes (Slater and Harmon, 2013; Fritz et al., 2013; Wood et al., 2013). For example, including both living and fossil taxa in evolutionary studies can improve the accuracy of timing diversification events (e.g. Ronquist et al., 2012a), our understanding of relationships among lineages (e.g. Beck and Lee, 2014), and our ability to infer biogeographical patterns through time (e.g. Meseguer et al., 2015). To perform such analyses it is necessary to combine living and fossil taxa in phylogenetic trees. One increasingly popular method, the Total Evidence method (Eernisse and Kluge, 1993; Ronquist et al., 2012a), combines molecular data from living taxa and morphological data from both living and fossil taxa in a supermatrix (e.g. Pyron, 2011; Ronquist et al., 2012a; Schrago et al., 2013; Slater and Harmon, 2013; Beck and Lee, 2014; Meseguer et al., 2015), producing a phylogeny with living and fossil taxa at the tips. These phylogenies can be dated using methods such as tip-dating (Ronquist et al., 2012a; Wood et al., 2013) and incorporated into macroevolutionary studies (e.g. Ronquist et al., 2012a; Wood et al., 2013; Slater, 2013).

A downside of the Total Evidence method is that it requires a lot of data. One must collect molecular data for living taxa and morphological data for both living and fossil taxa; two types of data that require fairly different technical skills (e.g. molecular sequencing *vs.* anatomical description). Additionally, large chunks of this data can be difficult, or even impossible, to collect for every taxon present in the analysis. For example, fossils very rarely have molecular data and incomplete fossil preservation (e.g. soft *vs.* hard tissues) may restrict the amount of morphological data available (Sansom and Wills, 2013). Additionally, since the molecular phylogenetics revolution, it has become less common to collect morphological characters for living taxa when molecular data are available (e.g. in (Slater, 2013), only 13% of the 169 living taxa have coded morphological data). Unfortunately this missing data can lead to errors in phylogenetic inference; in fact, simulations show that the ability of the Total Evidence method to recover the correct phylogenetic topology decreases when there is a low overlap between morphological data in the living and fossil taxa (Guillerme and Cooper, In review), regardless the overall amount of morphological data available for the fossils (or the amount of molecular data available for the living species). The effect of missing data on topology is greatest when living taxa have

few morphological data. This is because (1) a fossil cannot branch in the correct clade if there is no overlapping morphological data in the clade; and (2) a fossil has a higher probability of branching within a clade with more morphological data available for living taxa, regardless of whether this is the correct clade or not (Guillerme and Cooper, In review).

The issues above highlight that it is crucial to have sufficient morphological data for living taxa in a clade before using a Total Evidence approach. However, it is unclear how much morphological data for living taxa is actually available (i.e. already coded from museum specimens and deposited in phylogenetic matrices accessible online), and how this data are distributed across clades. Intuitively, most people assume this kind of data has already been collected, but empirical data suggest otherwise (e.g. in (Ronquist et al., 2012a; Slater, 2013; Beck and Lee, 2014). To investigate this further, we assess the amount of available morphological data for living mammals to determine whether sufficient data exists to build reliable Total Evidence phylogenies in this group. We collected cladistic data (i.e. discrete morphological characters used in phylogenetics) from 286 phylogenetic matrices available online and measured the proportion of cladistic data available for each mammalian order. Additionally, because missing morphological data in living species can influence tree topology as described above, we determined whether the available cladistic data was phylogenetically overdispersed or clustered in the mammalian orders where data was missing. We find that available morphological data for living mammals is scarce but generally randomly distributed across phylogenies. We recommend that efforts be made to collect and share more cladistic data for living species to improve the accuracy of Total Evidence phylogenies.

## 3.3 MATERIALS AND METHODS

### 3.3.1 *Data collection and standardisation*

We downloaded all cladistic matrices containing any living and/or fossil mammal taxa from three major public databases (accessed 10th of June 2015): Morphobank (`http://www.morphobank.org/`) (O'Leary and Kaufman, 2011), Graeme Lloyd's website (`graemetlloyd.com/matrmamm.html`) and Ross Mounce's GitHub repository (`https://github.com/rossmounce/cladistic-data`). We also performed a systematic Google Scholar search (accessed 11th of June 2015) for matrices that were not uploaded to

these databases. We downloaded available matrices containing fossil and/or living mammal taxa from the three data bases using the following list of keywords:

`Mammalia; Monotremata; Marsupialia; Placentalia; Macroscelidea; Afrosoricida; Tubulidentata; Hyracoidea; Proboscidea; Sirenia; Pilosa; Cingulata; Scandentia; Dermoptera; Primates; Lagomorpha; Rodentia; Erinaceomorpha; Soricomorpha; Cetacea; Artiodactyla; Cetartiodactyla; Chiroptera; Perissodactyla; Pholidota; Carnivora; Didelphimorphia; Paucituberculata; Microbiotheria; Dasyuromorphia; Peramelemorphia; Notoryctemorphia; Diprotodontia`.

Note that some matrices have been downloaded from more than one database but that it is not an issue since we are interested in the total number of unique living OTUs and that if some where present in more than one matrix, they still only counted as one single OTU.

MORPHOBANK — We used the keywords listed above in the search menu of the Morphobank repository and downloaded the data associated with each project matching with the keywords.

GRAEME LLOYD — We downloaded all the matrices that were available with a direct download link in the mammal data section of Graeme Lloyd's website repository.

ROSS MOUNCE — We downloaded every 601 matrix from Ross Mounce's GitHub repository and then ran a shell script to select only the matrices that had any text element that match with one of the search terms. To make the matrix selection more thorough, we ignored the keywords case as well as the latin suffix (*ia*, *ata*, *ea*, and *a*).

GOOGLE SCHOLARS — To make sure we didn't miss any extra matrix that wasn't available on one of these repository, we ran a extra Google Scholar search. We downloaded the additional cladistic matrices from the 20 first search results matching with our selected keywords and with any of the 35 taxonomic levels (mammals Orders, Infraclasses and Class). We used the following key words:

*order* `("morphology" OR "morphological" OR "cladistic") AND characters matrix paleontology phylogeny`

were *order* was replaced by all the keywords listed above. For each 33 keywords, we selected the 20 first papers to match the Google search published since 2010

resulting in 660 papers. Among these papers, not all contained relevant data (discrete morphological characters AND mammalian data). We selected only the 20 first results per search term to avoid downloading articles that were to irrelevant. Among the 660 papers, only 50 contained a total of 425 extra living OTUs (Figure 3.1). Also we decided to select only the articles published since 2010 because nearly every one of the recent published matrix contains both a fraction of morphological characters and OTUs from previous studies. For example in primates the character *p7* coded first by Ross et al. (1998) is reused with the same living species in Seiffert et al. (2003), Marivaux et al. (2005), Seiffert et al. (2005), Bloch et al. (2007), Bloch et al. (2007), Kay et al. (2008), Silcox (2008), Seiffert et al. (2009), Tabuce et al. (2009), Boyer et al. (2010), Seiffert et al. (2010), Marivaux et al. (2013) and Ni et al. (2013).

We transformed all the non-nexus matrices (tnt, word, excel, jpeg) to nexus format manually. In total, we downloaded 286 matrices containing a total of 11010 operational taxonomic units (OTUs) of which 5228 were unique. In this study, we refer to OTUs rather than species since the entries in the downloaded matrices were not standardised and ranged from specific individual specimen names (i.e. the name of a collection item) to the family-level. Where possible, we considered OTUs at their lowest valid taxonomic level (i.e. species) but some OTUs were only valid at a higher taxonomic level (e.g. genus or family). Therefore for some orders, we sampled more genera than species (Table 3.1).

To select the lowest valid taxonomic level for each OTU, we standardised their taxonomy by correcting species names so they matched standard taxonomic nomenclature (e.g., *H. sapiens* was transformed to *Homo sapiens*). We designated as "living" all OTUs that were either present in the phylogeny of (Bininda-Emonds et al., 2007) or the taxonomy of (Wilson and Reeder, 2005), and designated as "fossil" all OTUs that were present in the Paleobiology database (`https://paleobiodb.org/`).

For OTUs that did not appear in these three sources, we first decomposed the name (i.e. *Homo sapiens* became *Homo* and *sapiens*) and tried to match the first element with a higher taxonomic level (genus or family). Any OTUs that still had no matches in the sources above were designated as non-applicable (NA; see Figure 3.2).

The number of characters in each matrix ranged from 6 to 4541. Matrices with few characters are problematic when comparing available data among matrices because (1) they have less chance of having characters that overlap with those of

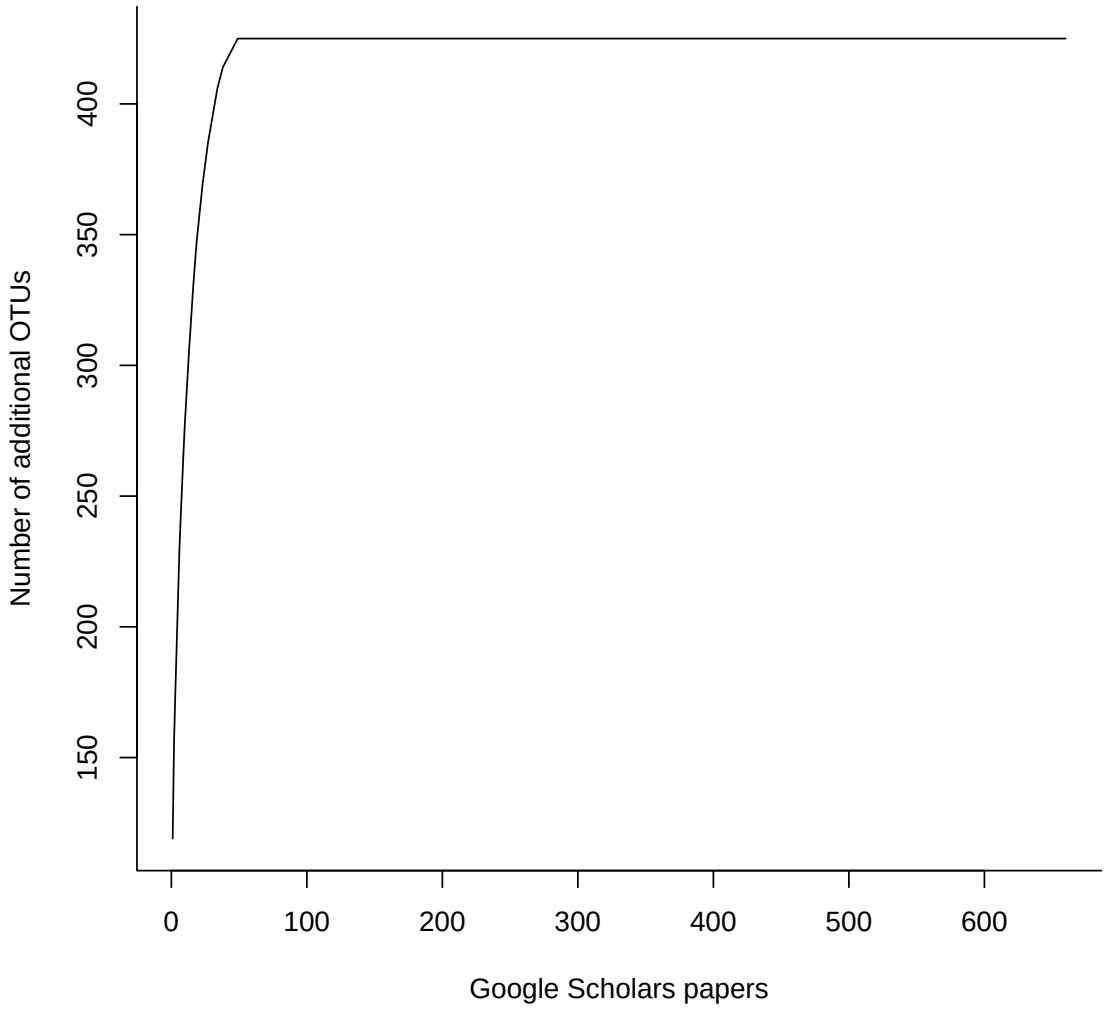


FIGURE 3.1: Google searches additional OTUs rarefaction curve. The x axis represent the number of google scholar matches (papers, books or abstracts) and the y axis represents the cumulative number of additional living OTUs per google scholar match.

other matrices (Wagner, 2000) and (2) they are more likely to contain a higher proportion of specific characters that are not-applicable across large clades (e.g. “antler ramifications” is a character that is only applicable to Cervidae not all mammals Brazeau, 2011). Therefore we selected only matrices containing >100 characters for each OTU. This threshold was chosen to correspond with the number of characters used in (Guillerme and Cooper, In review) and (Harrison and Larsson, 2015). Note that results of analyses with no character threshold are available in Supplementary Material. After removing all matrices with <100 characters, we retained 1074 unique living mammal OTUs from 126 matrices for our analyses.

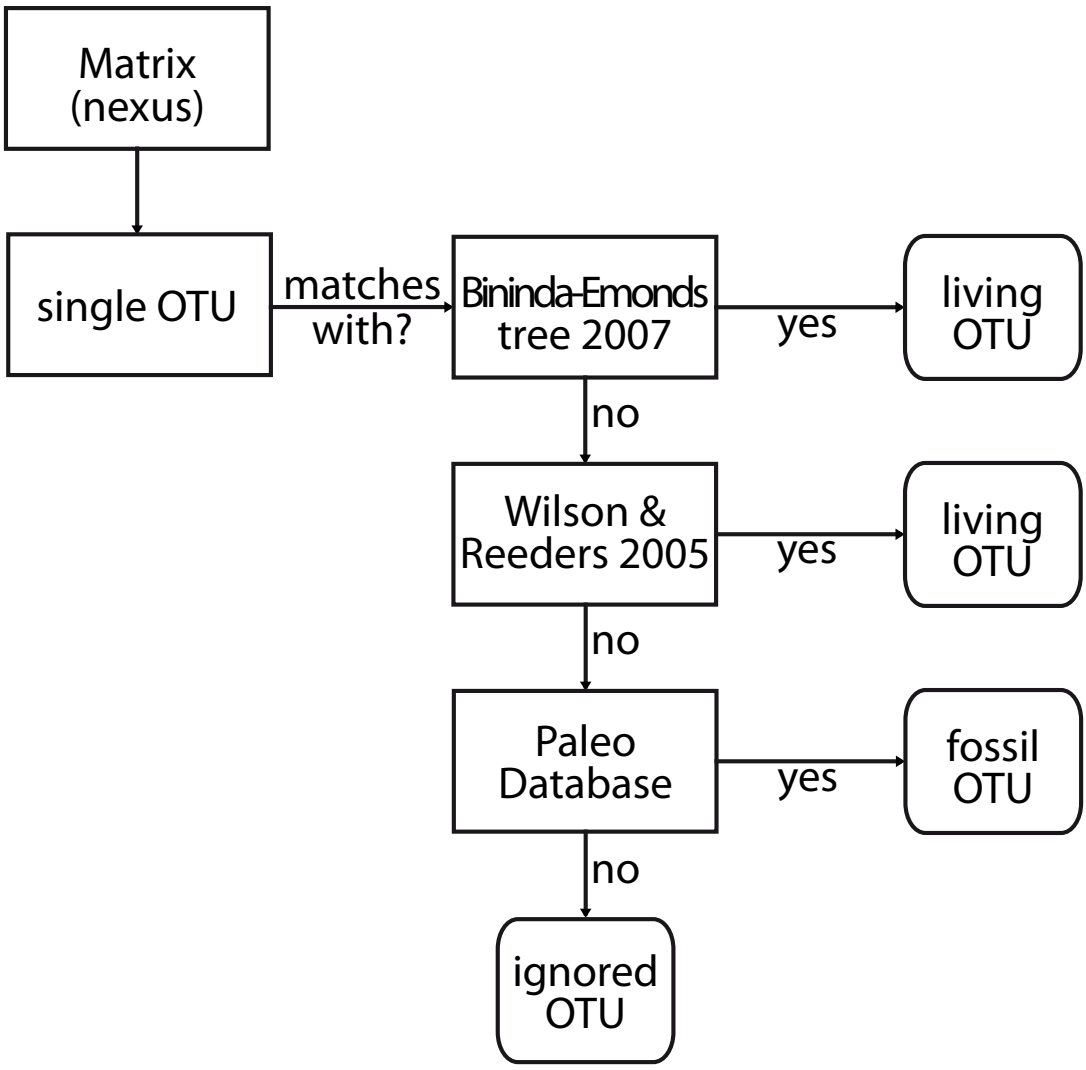


FIGURE 3.2: Taxonomic matching algorithm used in this study. For each matrix, each operational taxonomic units (OTU) is matched with the super tree from Bininda-Emonds 2007. If the OTU matches, then it is classified as living. Else it is matched with the Wilson & Reeders 2005 taxonomy list. If the OTU matches, then it is classified as living. Else it is matched with the Paleo Database list of mammals. If the OTU matches, then it is classified as fossil. Else it is ignored.

### 3.3.2 *Data availability and distribution*

To assess the availability of cladistic data for each mammalian order, we calculated the percentage of OTUs with cladistic data at three different taxonomic levels: family, genus and species. We consider orders with <25% of living taxa with cladistic data as having poor data coverage ("low" coverage), and orders with >75% of living taxa with cladistic data as having good data coverage (hereafter "high" coverage).

For orders with <100% cladistic data coverage at any taxonomic level, we investigated whether the available cladistic data was (i) randomly distributed, (ii) overdis-

persed or (iii) clustered, with respect to phylogeny, using two metrics from community phylogenetics: the Nearest Taxon Index (NTI; (Webb et al., 2002) and the Net Relatedness Index (NRI; (Webb et al., 2002). NTI is most sensitive to clustering or overdispersion near the tips, whereas NRI is more sensitive to clustering or overdispersion across the whole phylogeny (Cooper et al., 2008). Both metrics were calculated using the `picante` package in R (Kembel et al., 2010; R Core Team, 2015).

NTI (Webb et al., 2002) is based on mean nearest neighbour distance (MNND) and is calculated as follows:

$$NTI = -\left(\frac{\overline{MNND}_{obs} - \overline{MNND}_{n}}{\sigma(MNND_{n})}\right) \tag{3.1}$$

where $\overline{MNND}_{obs}$ is the observed mean distance between each of $n$ taxa with cladistic data and its nearest neighbour with cladistic data in the phylogeny, $\overline{MNND}_{n}$ is the mean of 1000 mean MNND between $n$ randomly drawn taxa, and $\sigma(MNND_{n})$ is the standard deviation of these 1000 random MNND values. NRI is similar but is based on mean phylogenetic distance (MPD) as follows:

$$NRI = -\left(\frac{\overline{MPD}_{obs} - \overline{MPD}_{n}}{\sigma(MPD_{n})}\right) \tag{3.2}$$

where $\overline{MPD}_{obs}$ is the observed mean phylogenetic distance of the tree containing only the $n$ taxa with cladistic data, $\overline{MPD}_{n}$ is the expected random MPD for $n$ taxa estimated by calculating the MPD from $n$ taxa randomly drawn from the phylogeny and repeated 1000 times, and $\sigma(MPD_{n})$ is the standard deviation of the 1000 random MPD values. Negative NTI and NRI values show that the focal taxa are more overdispersed across the phylogeny than expected by chance, and positive values reflect significant clustering.

We calculated NTI and NRI values for each mammalian order separately, at each different taxonomic level. For each analysis our focal taxa were those with available cladistic data at that taxonomic level and the phylogeny was the phylogeny of the order pruned from (Bininda-Emonds et al., 2007).

## 3.4 RESULTS

Across the 126 cladistic matrices we extracted, 22 out of 28 mammalian orders have low coverage (<25% of species with cladistic data) and six have high coverage (>75% of species with cladistic data) at the species-level. At the genus-level, three orders have low coverage and 12 have high coverage, and at the family-level, no orders have low coverage and 23 have high coverage (Table 3.1).

TABLE 3.1: Number of taxa with available cladistic data for mammalian orders at three taxonomic levels. The left vertical bar represents "low" coverage (<25%); the right vertical bar represents "high" coverage (>75%). A negative Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) shows more phylogeneticaly dispersed taxa than expected by chance; a positive value shows more phylogeneticaly clustered taxa than expected by chance. Significant NRI or NTI values are highlighted in bold. *p <0.05; **p <0.01; ***p <0.001.

| Order | Taxonomic level | Proportion of taxa | Coverage | NRI | NTI |
|---|---|---|---|---|---|
| Afrosoricida | family | 2/2 | | | |
| Afrosoricida | genus | 17/17 | | | |
| **Afrosoricida** | **species** | **23/42** | | **1.89*** | 1.19 |
| Carnivora | family | 11/15 | | 0.43 | 1.68 |
| **Carnivora** | **genus** | **30/125** | | **4.14**** | **1.81*** |
| **Carnivora** | **species** | **42/283** | | **18.64**** | **3.02**** |
| Cetartiodactyla | family | 21/21 | | | |
| **Cetartiodactyla** | **genus** | **77/128** | | 0.87 | **1.77*** |
| **Cetartiodactyla** | **species** | **129/310** | | **2.72*** | 0.04 |
| Chiroptera | family | 13/18 | | 0.55 | 0.63 |
| **Chiroptera** | **genus** | **85/202** | | **16.91**** | **2.85**** |
| **Chiroptera** | **species** | **165/1053** | | **14.55**** | **3.44**** |
| Cingulata | family | 1/1 | | | |
| Cingulata | genus | 8/9 | | 1.49 | -1.63 |

| | | | | |
|---|---|---|---|---|
| Cingulata | species | 6/29 | 1.43 | 0.36 |
| Dasyuromorphia | family | 2/2 | | |
| Dasyuromorphia | genus | 7/22 | -1 | -1.45 |
| Dasyuromorphia | species | 8/64 | -1.15 | -0.62 |
| Dermoptera | family | 1/1 | | |
| Dermoptera | genus | 1/2 | | |
| Dermoptera | species | 1/2 | | |
| Didelphimorphia | family | 1/1 | | |
| Didelphimorphia | genus | 16/16 | | |
| Didelphimorphia | species | 40/84 | -0.94 | 0.36 |
| Diprotodontia | family | 9/11 | -0.8 | 0.56 |
| Diprotodontia | genus | 20/38 | -1.36 | -0.73 |
| Diprotodontia | species | 16/126 | -2.29 | -1.55 |
| Erinaceomorpha | family | 1/1 | | |
| Erinaceomorpha | genus | 10/10 | | |
| Erinaceomorpha | species | 21/22 | -1.1 | -0.3 |
| Hyracoidea | family | 1/1 | | |
| Hyracoidea | genus | 1/3 | | |
| Hyracoidea | species | 1/4 | | |
| Lagomorpha | family | 1/2 | | |
| Lagomorpha | genus | 1/12 | | |
| Lagomorpha | species | 1/86 | | |
| Macroscelidea | family | 1/1 | | |
| Macroscelidea | genus | 4/4 | | |

| | | | | |
|---|---|---|---|---|
| Macroscelidea | species | 5/15 | -0.98 | -1.38 |
| Microbiotheria | family | 1/1 | | |
| Microbiotheria | genus | 1/1 | | |
| Microbiotheria | species | 1/1 | | |
| Monotremata | family | 2/2 | | |
| Monotremata | genus | 2/3 | -0.71 | -0.71 |
| Monotremata | species | 2/4 | -1.01 | -1.03 |
| Notoryctemorphia | family | 1/1 | | |
| Notoryctemorphia | genus | 1/1 | | |
| Notoryctemorphia | species | 0/2 | | |
| Paucituberculata | family | 1/1 | | |
| Paucituberculata | genus | 2/3 | 0 | 0 |
| Paucituberculata | species | 2/5 | -0.64 | -0.65 |
| Peramelemorphia | family | 2/2 | | |
| Peramelemorphia | genus | 7/7 | | |
| Peramelemorphia | species | 16/18 | -0.09 | 1 |
| Perissodactyla | family | 3/3 | | |
| Perissodactyla | genus | 6/6 | | |
| Perissodactyla | species | 7/16 | 0.62 | -2.5 |
| Pholidota | family | 1/1 | | |
| Pholidota | genus | 1/1 | | |
| **Pholidota** | **species** | **3/8** | **2.64*** | **2.23*** |
| Pilosa | family | 3/5 | 0.94 | 0.93 |
| Pilosa | genus | 3/5 | -0.36 | -0.31 |

| | | | | |
|---|---|---|---|---|
| Pilosa | species | 3/29 | 0.33 | 0.79 |
| Primates | family | 15/15 | | |
| Primates | genus | 48/68 | -0.41 | -1.4 |
| Primates | species | 56/351 | -1.6 | -2.04 |
| Proboscidea | family | 1/1 | | |
| Proboscidea | genus | 1/2 | | |
| Proboscidea | species | 1/3 | | |
| Rodentia | family | 11/32 | -0.46 | -1.91 |
| Rodentia | genus | 21/450 | -2.11 | 0.3 |
| Rodentia | species | 15/2094 | -1.65 | -2.55 |
| Scandentia | family | 2/2 | | |
| Scandentia | genus | 2/5 | -0.77 | -0.76 |
| Scandentia | species | 2/20 | -1.79 | -1.99 |
| Sirenia | family | 2/2 | | |
| Sirenia | genus | 2/2 | | |
| Sirenia | species | 4/4 | | |
| Soricomorpha | family | 3/4 | -0.93 | -0.92 |
| **Soricomorpha** | **genus** | **19/43** | **6.98**** | **2.49*** |
| **Soricomorpha** | **species** | **19/392** | **13.19**** | **3.89**** |
| Tubulidentata | family | 1/1 | | |
| Tubulidentata | genus | 1/1 | | |
| Tubulidentata | species | 1/1 | | |

Among the mammalian orders containing OTUs with no available cladistic data, only six orders had significantly clustered data (Carnivora, Cetartiodactyla, Chi-

roptera and Soricomorpha at both species- and genus-level and Afrosoricida and Pholidota at the species-level only) and no order had significantly overdispersed data at any taxonomic level (Table 3.1).

Two contrasting results are shown in Figure 3.3 with randomly distributed OTUs with cladistic data in Primates (Figure 3.3A) and phylogenetically clustered OTUs with cladistic data in Carnivora (mainly Canidae; Figure 3.3B).

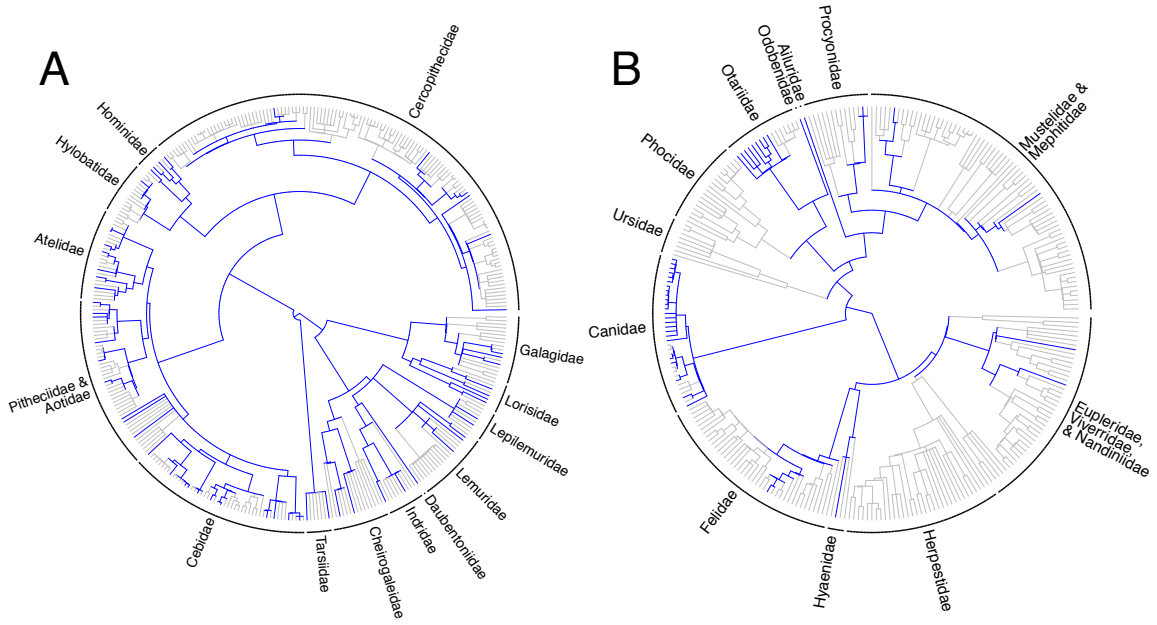


FIGURE 3.3: Phylogenetic distribution of species with available cladistic data across two mammalian orders (A: Primates; B: Carnivora). Edges are colored in grey when no cladistic data are available for a species and in blue when data are available.

## 3.5 DISCUSSION

Our results show that although phylogenetic relationships among living mammals are well-resolved (e.g. Bininda-Emonds et al., 2007; Meredith et al., 2011) , most of the data used to build these phylogenies is molecular, and very little cladistic data are available for living mammals compared to fossil mammals (e.g. O'Leary et al., 2013; Ni et al., 2013). This has implications for building Total Evidence phylogenies containing both living and fossil mammals, as without sufficient cladistic data for living species, fossil placements in these trees are very uncertain (Guillerme and Cooper, In review). Cladistic data coverage in living mammals varies across taxonomic levels and in its phylogenetic distribution. Higher taxonomic levels are always better sampled than lower ones and within these taxonomic levels, the available data are mostly randomly distributed across the phylogeny, apart from in six orders).

The number of living mammalian taxa with no available cladistic data was surprisingly high at the species-level: only six out of 28 orders have a high coverage of taxa with available cladistic data (and two of the 28 orders are monospecific!). This high coverage threshold of 75% of taxa with available cladistic data represents the minimum amount of data required before missing data has a significant effect on the topology of Total Evidence trees (Guillerme and Cooper, In review). Beyond this threshold, there is considerable displacement of wildcard taxa (*sensu* Kearney, 2002) and decreases in clade conservation (Guillerme and Cooper, In review). Therefore we expect a high probability of topological artefacts for the placement of fossil taxa at the species-level in most mammalian orders. However, data coverage seems to be less of an issue at higher taxonomic levels (i.e. genus- and family-level). This point is important from a practical point of view because of the slight discrepancy between the neontological and palaeontological concept of species. While neontological species are described using morphology, genetic distance, spatial distribution and even behaviour, palaeontological species can be based only on morphological, spatial and temporal data (e.g. Ni et al., 2013). Because of this, most palaeontological studies are using the genus as their smallest OTU (e.g. Ni et al., 2013; O'Leary et al., 2013). Thus data availability at the genus-level in living mammals should be our primary concern when aiming to build phylogenies of living and fossil taxa.

When only a few species with cladistic data are available, the ideal scenario is for them to be phylogenetically overdispersed (i.e. that there is data for at least every sub-clade) to maximize the possibilities of a fossil branching from the right clade. The second best scenario is that species with cladistic data are randomly distributed across the phylogeny. In this scenario we expect no special bias in the placement of the fossil (Guillerme and Cooper, In review), it is therefore encouraging that for most orders, species with cladistic data were randomly distributed across the phylogeny of each order. The worst case scenario for fossil placement is that species with cladistic data are phylogenetically clustered. In this situation we expect two major biases to occur: first, the fossil will not be able to branch within a clade containing no data, and second, the fossil will have a higher probability, at random, of branching within the clade containing most of the available data. This means that fossils with uncertain phylogenetic affinities (*incertae sedis* will have a higher probability of branching within the most sampled clade just by chance). Our results suggest that this may be an issue, at the genus-level, in Carnivora, Cetartiodactyla,

Chiroptera and Soricomorpha. For example, a Carnivora fossil will be unable to branch in the Herpestidae that has no species with cladistic data, and will also have more chance to branch, randomly, within the Canidae clade than any other clade in Carnivora (Figure 3.3B). Thus, in Total Evidence trees, placements of some carnivoran fossils should considered with caution. In this study, we treated all cladistic matrices as equal in a similar way to molecular matrices. For example, if matrix A contained 100 characters for taxa X and Y, and matrix B contained 50 different characters for taxa X and Z, we assumed that both matrices can be combined in a supermatrix containing 150 independent characters for taxon X, 100 for taxon Y and 50 for taxon Z. Unfortunately, cladistic data cannot always be treated in this way because some characters may overlap. For example, if matrix A has a character coding for the shape of a particular morphological feature and matrix B has a character coding for the presence of this same morphological feature and a second character coding for its shape, then these three characters are non-independent compound characters (Brazeau, 2011). However, in reasonably sized matrices (>100 characters; Guillerme and Cooper, In review; Harrison and Larsson, 2015) it is more likely that a number of characters are consistently conserved among the different matrices and thus easily combinable. For example, within the Primate cladistic literature, the character *p7* - the size of the $4^{th}$ lower premolar paraconid - has been used consistently for >15 years (e.g. Ross et al., 1998; Marivaux et al., 2005; Ni et al., 2013) and can therefore be combined among the matrices. A conservative approach to avoid compound characters would be to select only the most recent matrix for each group, but this would result in the loss of a lot of data.

Despite the absence of good cladistic data coverage for living mammals, the Total Evidence methods still seems to be the most promising way of combining living and fossil data for macroevolutionary analyses. Following the recommendations in (Guillerme and Cooper, In review), we need to code cladistic characters for as many living species possible. Fortunately, data for living mammals is usually readily available in natural history collections, therefore, we propose that an increased effort be put into coding morphological characters from living species, possibly by engaging in collaborative data collection projects through web portals such as *MorphoBank* (O'Leary and Kaufman, 2011). Such an effort would be valuable not only to phylogeneticists, but also to any researcher focusing understanding macroevolutionary patterns and processes.

CHAPTER 4

# SPATIO-TEMPORAL DISPARITY IN MAMMALS AT THE K-PG BOUNDARY

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> "The most erroneous stories are those we think we know best - and therefore never scrutinize or question."
>
> S.J. Gould

## Cretaceous-Palaeogene extinction does not affect mammalian disparity [3]

[3] A similar version of this chapter will be submitted to Evolution soon. T.G. and N.C. designed the experiments; T.G. ran the analysis and interpreted the results; T.G. and N.C. wrote the manuscripts. *Specific acknowledgements*: thanks to Graeme Lloyd, Andrew Jackson, Gavin Thomas and Sive Finlay. *Data availability and reproducibility*: Data will be available on Dryad or Figshare. Code for reproducing the analysis is available on GitHub (`https://github.com/TGuillerme/SpatioTemporal_Disparity`).

CHAPTER 5

# DISCUSSION

## 5.1 THE FUTURE OF THE TOTAL EVIDENCE METHOD

Combined with tip-dating is super interesting but we need more data. To do so we can use plateforms such as morphobank and foster collaboration on big projects. Also we can make all the data available blablabla.

However, there are some limitations: Maybe tip-dating isn't that good? Compared to the nice recent node dating models... (Arcila) Also the Mk model is really crude and overly simplistic.

One way to improve could be a REAL total evidence dating using also trait data, biogeography, etc... In reality, all this parameters have an influence of lineages history and should technically be taken into account. But data problem is likely to increase, an needs models need to be improved as well. And in the end, how many parameters do we want?

## 5.2 DIVERSITY IS MULTIDIMENSIONAL

Diversity is often just seen as the sheer number of species. However, the processes that led to this pattern is fundamentaly intangled with all the other aspects of diversity. For example, specious rich groups have also so traits, etc... It is important to disentangle. But other dimensions as well: Ecological, life history, etc. We need to take into account more of these "disparity" patterns to really understand what happened. Especially when combining living and fossil, species richness is a really poor indicator of diversity.

However, this is more complex, species diversity is easy to interprate (many populations isolations through time) but disparity is a bit harder. What IS disparity? What metric to use? How to express the changes etc... Also, all these metrics are just using proxies.

But The statistician George Box wrote "essentially, all models are wrong, but some are useful" (Box and Draper, 1987). This is still really promising and can be

improved first by underestanding how all this works in a theoretical way (building the models). And only then apply it to observed patterns.

## 5.3 WHAT IS THE REAL EFFECT OF COMBINING?

Maybe only important when groups have actually a complex history? Old clades might have no living descendants and the question is therefore N/A Recent subclades maybe not have changed much in diversity so adding fossils might not change much. But we never know! Example of the giant lemur (recently extinct).

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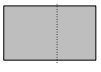
APPENDIX A

SUPPLEMENTARY DATA TO CHAPTER 3

# Assessment of cladistic data availability for living mammals

The following section contains supplementary results to the chapter “Assessment of cladistic data availability for living mammals”: the available data structure using the NTI and the PD metric; the proportion of available data and the data structure for all the matrices (including the matrices with less than 100 characters); and phylogenetical representation of the data availability per order (excluding Primates and Carnivora, present in the main body).

TABLE A.1: Number of taxa with available cladistic data for mammalian orders at three taxonomic levels (without any character threshold; results from the 286 matrices). The coverage represents the proportion of taxa with available morphological data. The left vertical bar represents 25% of available data (“low” coverage if <25%); The right vertical bar represents 75% of available data (“high” coverage if >75%). When the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI) are negative, taxa are more phylogenetically dispersed than expected by chance; when NRI or NTI are positive, taxa are more phylogenetically clustered by expected by chance. Significant NRI or NTI are highlighted in bold. *p <0.05; **p <0.01; ***p <0.001.

| Order | Taxonomic level | Proportion of taxa | Coverage | NRI | NTI |
|---|---|---|---|---|---|
| Afrosoricida | family | 2/2 |  | | |
| Afrosoricida | genus | 17/17 |  | | |
| Afrosoricida | species | 23/42 |  | 1.75 | 1.08 |
| Carnivora | family | 14/15 |  | 0.63 | 0.6 |
| **Carnivora** | **genus** | **54/125** |  | **4.81**** | **1.78*** |

| | | | | |
|---|---|---|---|---|
| **Carnivora** | **species** | **76/283** | **7.66**** | **0.85** |
| Cetartiodactyla | family | 21/21 | | |
| Cetartiodactyla | genus | 100/128 | 0.85 | 0.94 |
| **Cetartiodactyla** | **species** | **171/310** | **1.92*** | **-0.46** |
| Chiroptera | family | 15/18 | -0.28 | 0.56 |
| **Chiroptera** | **genus** | **93/202** | **13.47**** | **1.1** |
| **Chiroptera** | **species** | **215/1053** | **8.82**** | **1.22** |
| Cingulata | family | 1/1 | | |
| Cingulata | genus | 8/9 | 1.51 | -1.57 |
| **Cingulata** | **species** | **9/29** | **1.9*** | **0.11** |
| Dasyuromorphia | family | 2/2 | | |
| Dasyuromorphia | genus | 8/22 | -0.75 | -1.07 |
| Dasyuromorphia | species | 9/64 | -0.88 | -0.34 |
| Dermoptera | family | 1/1 | | |
| Dermoptera | genus | 1/2 | | |
| Dermoptera | species | 1/2 | | |
| Didelphimorphia | family | 1/1 | | |
| Didelphimorphia | genus | 16/16 | | |
| Didelphimorphia | species | 42/84 | -1.65 | 0.2 |
| Diprotodontia | family | 11/11 | | |
| Diprotodontia | genus | 25/38 | -1.13 | -1.31 |
| Diprotodontia | species | 31/126 | 0.48 | -1.77 |
| Erinaceomorpha | family | 1/1 | | |
| Erinaceomorpha | genus | 10/10 | | |

| | | | | |
|---|---|---|---|---|
| Erinaceomorpha | species | 21/22 | -1.07 | -0.2 |
| Hyracoidea | family | 1/1 | | |
| Hyracoidea | genus | 1/3 | | |
| Hyracoidea | species | 1/4 | | |
| Lagomorpha | family | 2/2 | | |
| Lagomorpha | genus | 5/12 | -1.06 | -0.95 |
| Lagomorpha | species | 12/86 | -0.62 | -1.88 |
| Macroscelidea | family | 1/1 | | |
| Macroscelidea | genus | 4/4 | | |
| Macroscelidea | species | 12/15 | -1.3 | -1.06 |
| Microbiotheria | family | 1/1 | | |
| Microbiotheria | genus | 1/1 | | |
| Microbiotheria | species | 1/1 | | |
| Monotremata | family | 2/2 | | |
| Monotremata | genus | 2/3 | -0.72 | -0.69 |
| Monotremata | species | 2/4 | -0.97 | -0.97 |
| Notoryctemorphia | family | 1/1 | | |
| Notoryctemorphia | genus | 1/1 | | |
| Notoryctemorphia | species | 0/2 | | |
| Paucituberculata | family | 1/1 | | |
| Paucituberculata | genus | 3/3 | | |
| Paucituberculata | species | 5/5 | | |
| Peramelemorphia | family | 2/2 | | |
| Peramelemorphia | genus | 7/7 | | |

| | | | | |
|---|---|---|---|---|
| Peramelemorphia | species | 16/18 | -0.13 | 0.97 |
| Perissodactyla | family | 3/3 | | |
| Perissodactyla | genus | 6/6 | | |
| Perissodactyla | species | 10/16 | -0.07 | -2.63 |
| Pholidota | family | 1/1 | | |
| Pholidota | genus | 1/1 | | |
| Pholidota | species | 4/8 | 1.18 | 0.94 |
| Pilosa | family | 4/5 | 1.87 | 2 |
| Pilosa | genus | 4/5 | -0.96 | 0.36 |
| **Pilosa** | **species** | **5/29** | **1.28** | **2.38*** |
| Primates | family | 15/15 | | |
| Primates | genus | 48/68 | -0.35 | -1.33 |
| Primates | species | 64/351 | -0.67 | -1.27 |
| Proboscidea | family | 1/1 | | |
| Proboscidea | genus | 2/2 | | |
| Proboscidea | species | 2/3 | -0.69 | -0.69 |
| Rodentia | family | 18/32 | 0.66 | -0.98 |
| Rodentia | genus | 82/450 | -1.66 | 1.55 |
| **Rodentia** | **species** | **90/2094** | **2.76*** | **2.34*** |
| Scandentia | family | 2/2 | | |
| Scandentia | genus | 2/5 | -0.74 | -0.74 |
| Scandentia | species | 3/20 | -1.88 | -0.84 |
| Sirenia | family | 2/2 | | |
| Sirenia | genus | 2/2 | | |

| | | | | | |
|---|---|---|---|---|---|
| Sirenia | species | 4/4 |  | | |
| Soricomorpha | family | 3/4 |  | -0.98 | -0.99 |
| **Soricomorpha** | **genus** | **19/43** |  | **7.11**** | **2.59**** |
| **Soricomorpha** | **species** | **21/392** |  | **10.65**** | **3.56**** |
| Tubulidentata | family | 1/1 |  | | |
| Tubulidentata | genus | 1/1 |  | | |
| Tubulidentata | species | 1/1 |  | | |

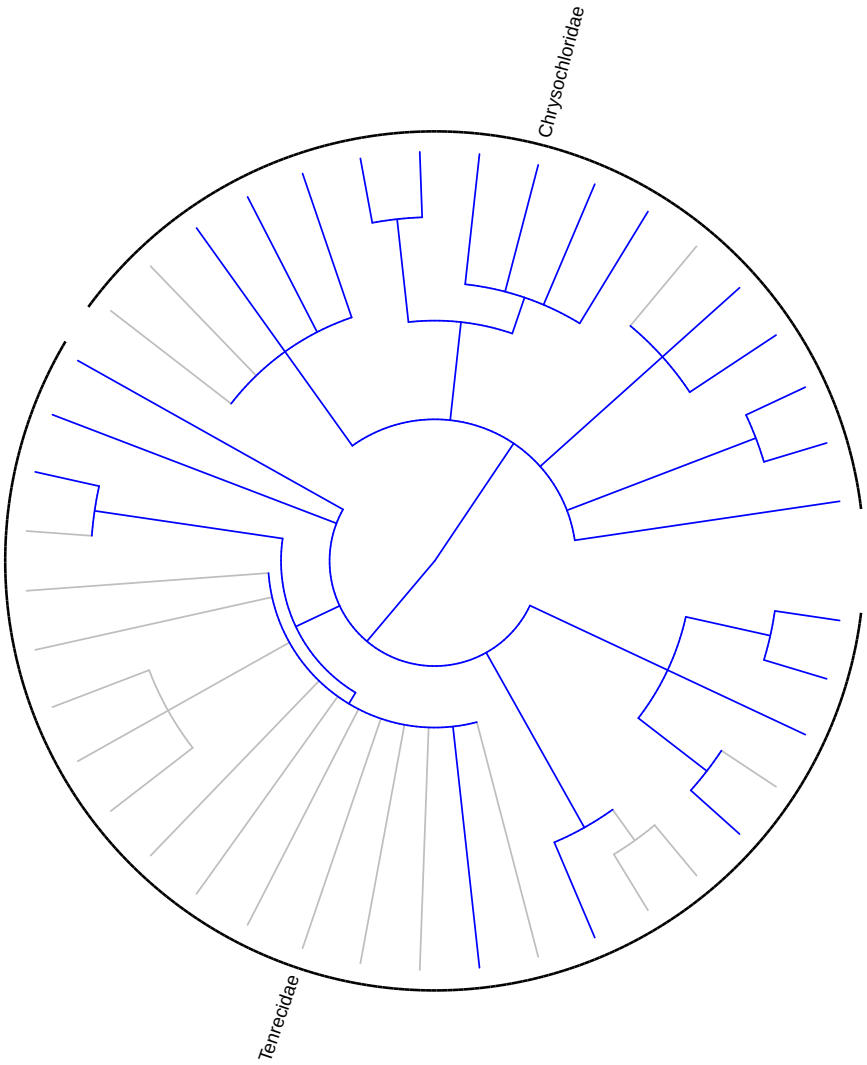



FIGURE A.1: Distribution of available morphological data across Afrosoricida. Edges are colored in grey when no morphological data is available or in blue when data is available.

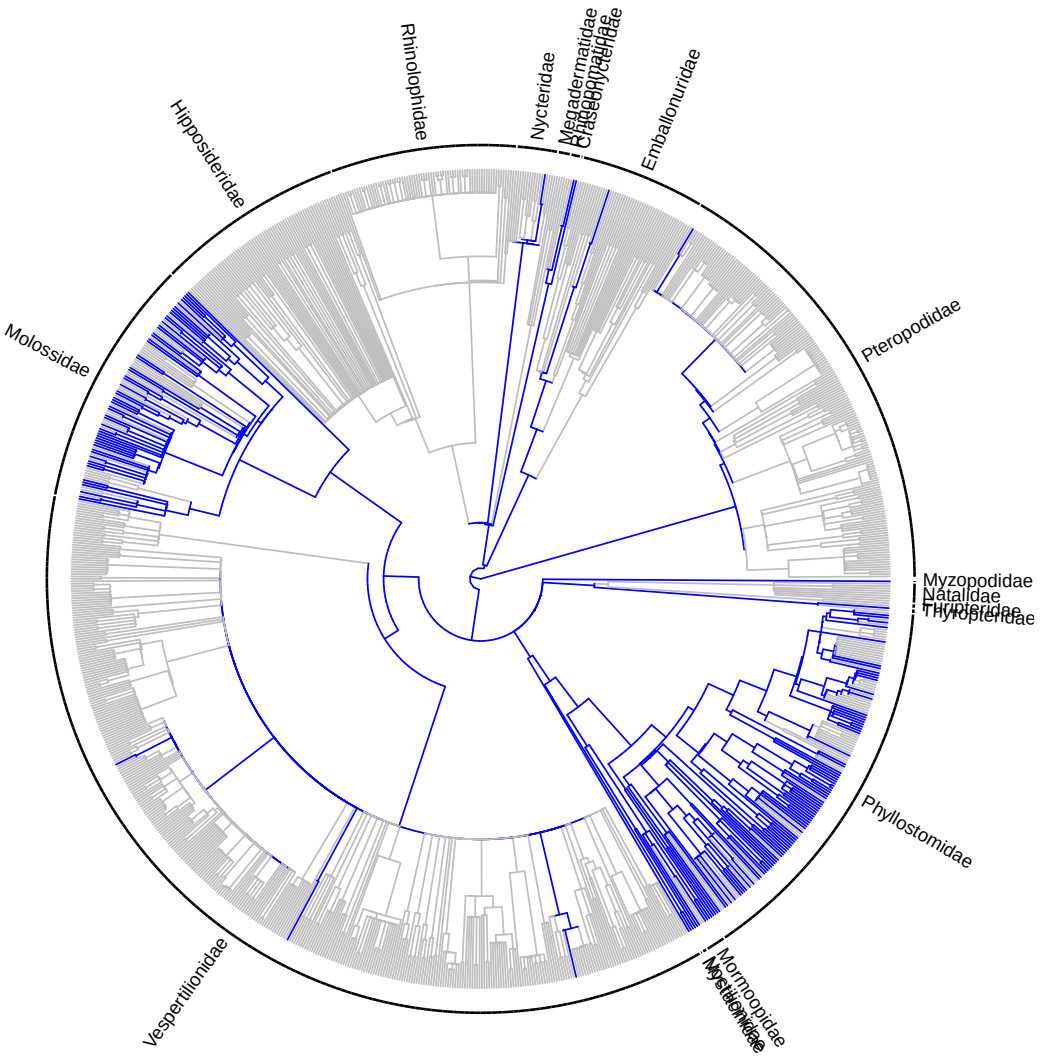



FIGURE A.2: Distribution of available morphological data across Chiroptera. Edges are colored in grey when no morphological data is available or in blue when data is available.

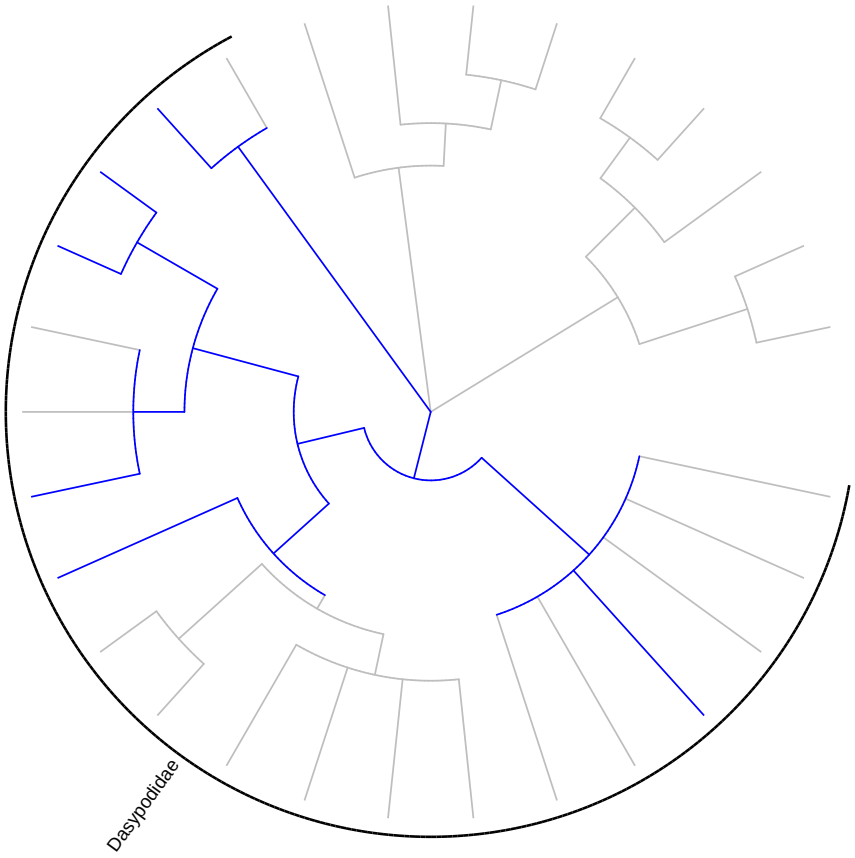



FIGURE A.3: Distribution of available morphological data across Cingulata. Edges are colored in grey when no morphological data is available or in blue when data is available.

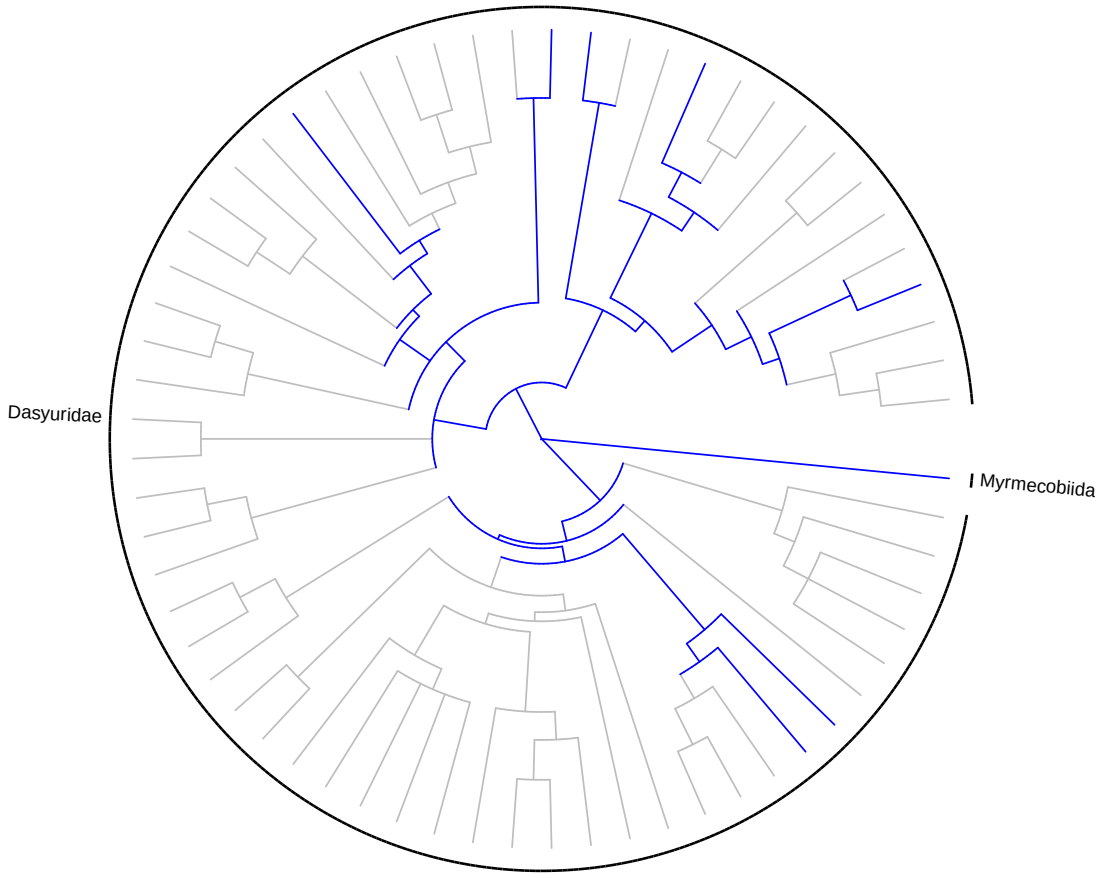



FIGURE A.4: Distribution of available morphological data across Dasyuromorphia. Edges are colored in grey when no morphological data is available or in blue when data is available.

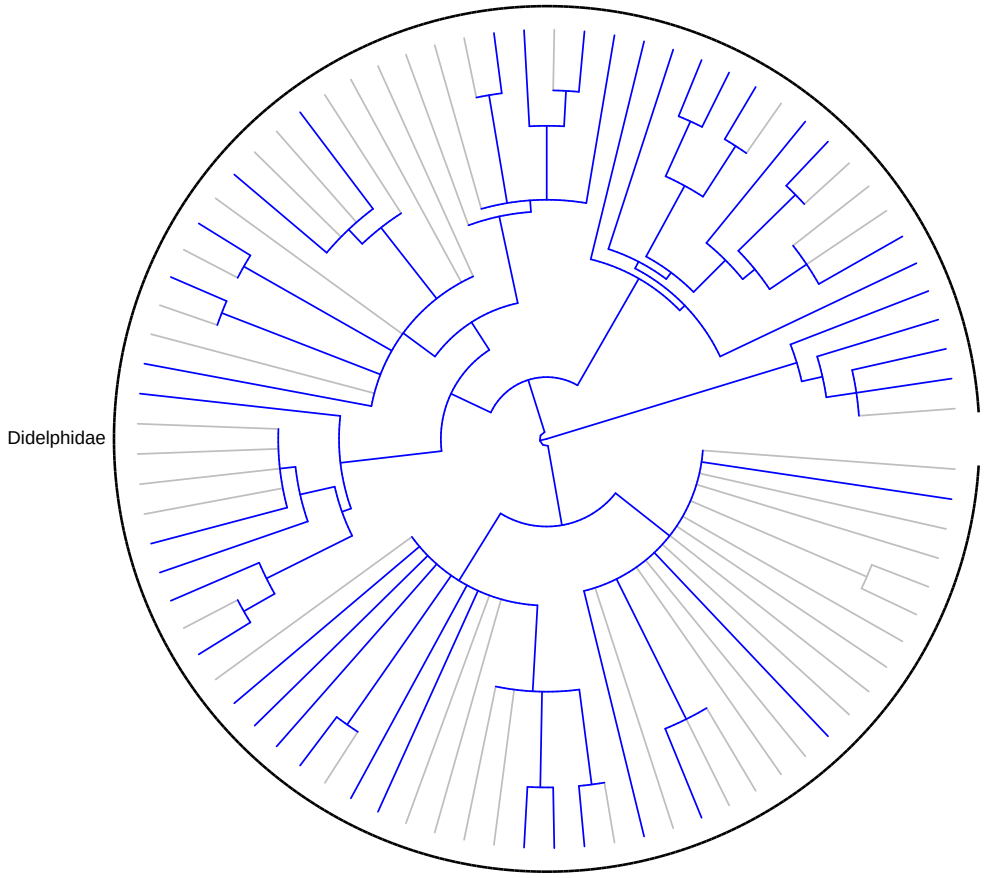



FIGURE A.5: Distribution of available morphological data across Didelphimorphia. Edges are colored in grey when no morphological data is available or in blue when data is available.

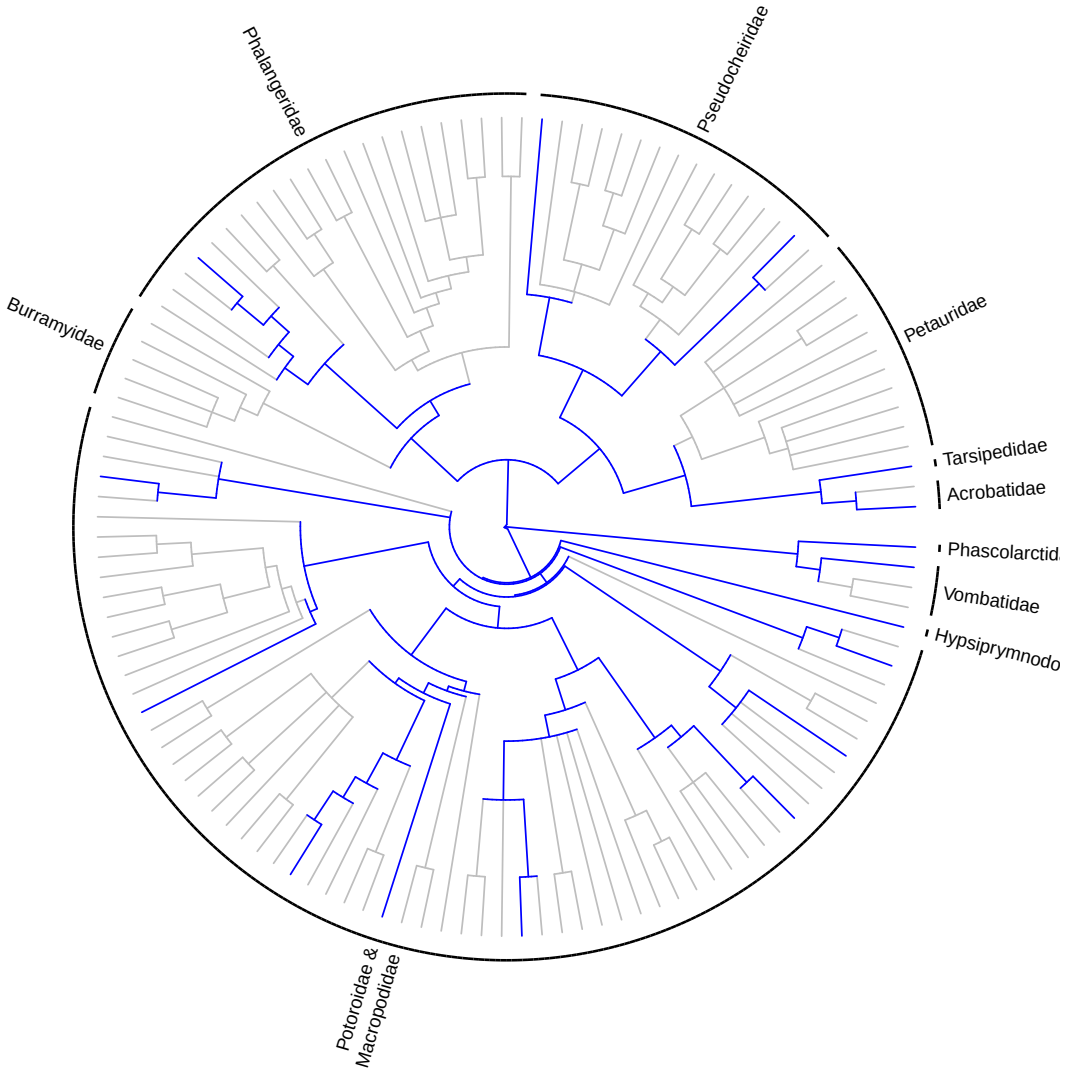



FIGURE A.6: Distribution of available morphological data across Diprotodontia. Edges are colored in grey when no morphological data is available or in blue when data is available.

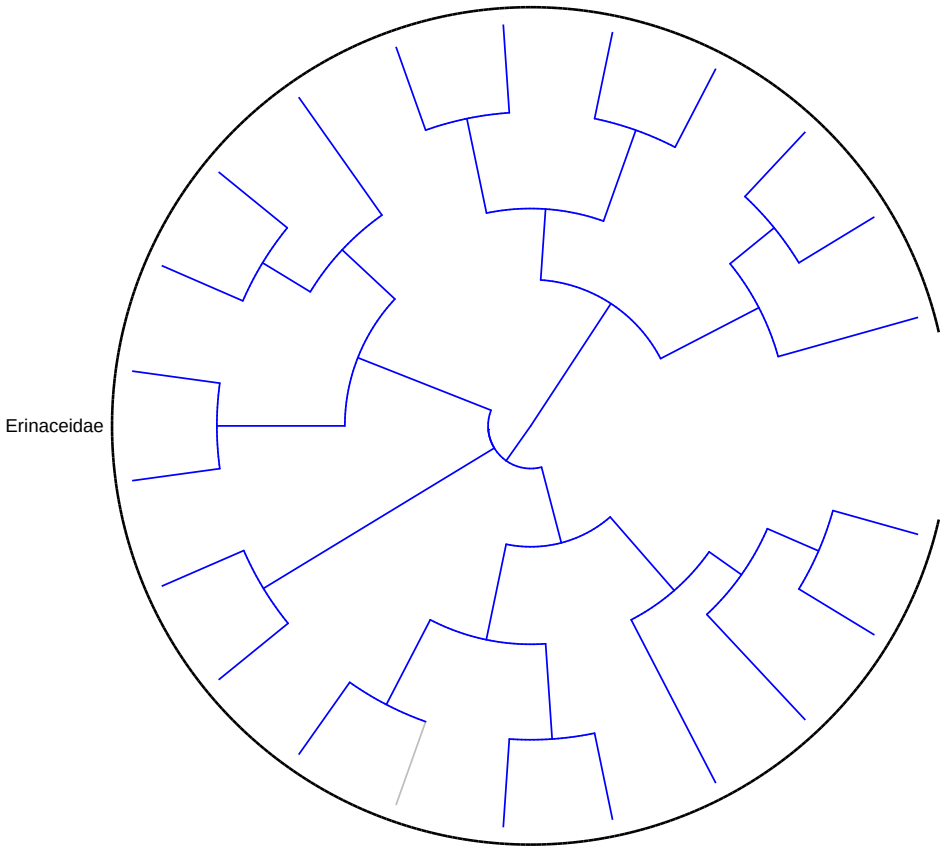



FIGURE A.7: Distribution of available morphological data across Erinaceomorpha. Edges are colored in grey when no morphological data is available or in blue when data is available.

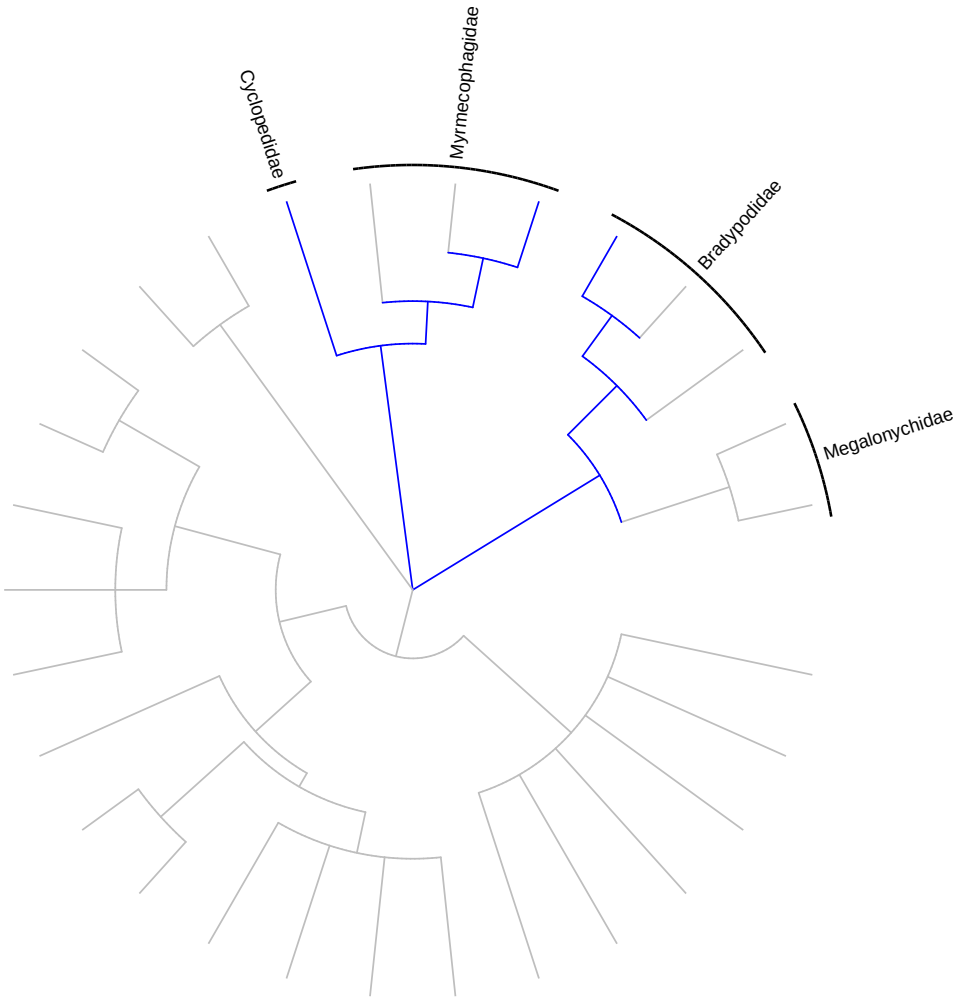



FIGURE A.8: Distribution of available morphological data across Pilosa. Edges are colored in grey when no morphological data is available or in blue when data is available.

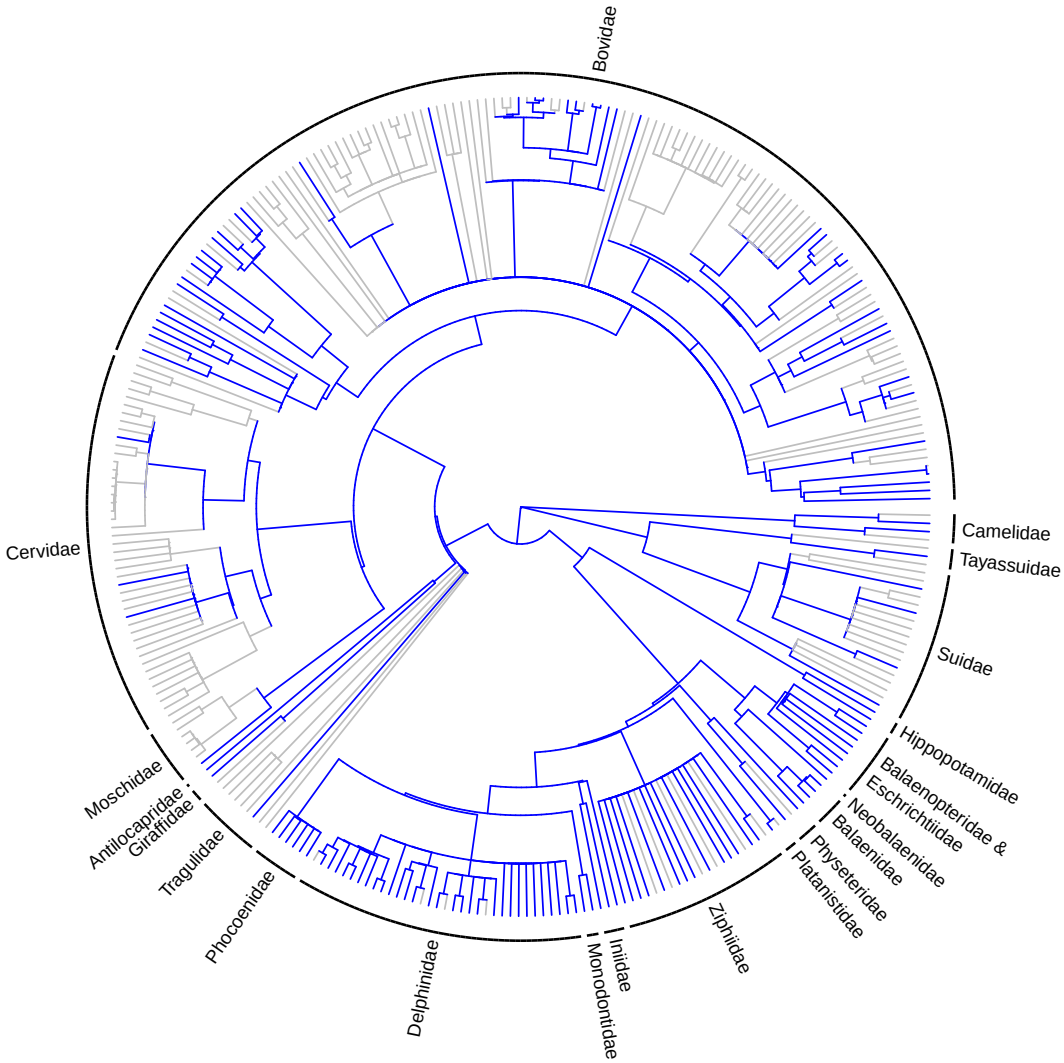



FIGURE A.9: Distribution of available morphological data across Cetartiodactyla. Edges are colored in grey when no morphological data is available or in blue when data is available.

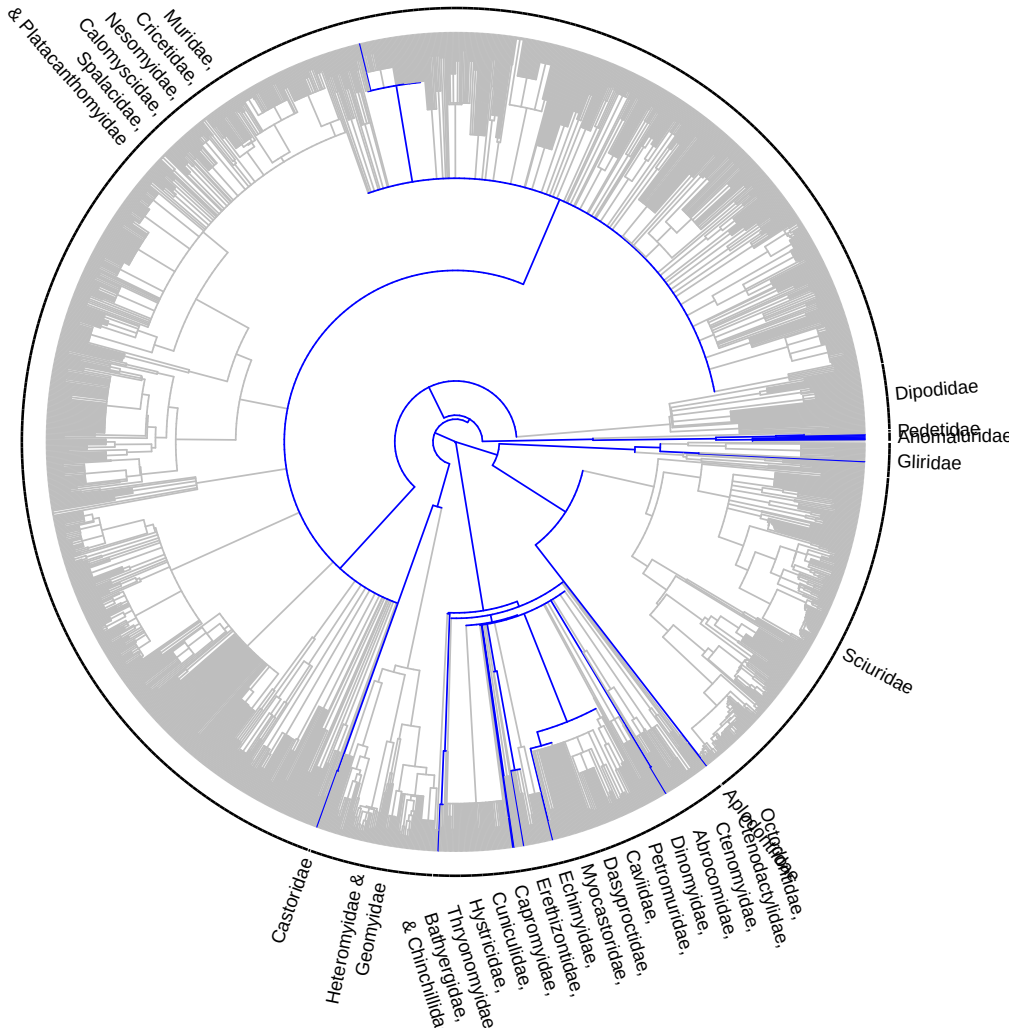



FIGURE A.10: Distribution of available morphological data across Rodentia. Edges are colored in grey when no morphological data is available or in blue when data is available.

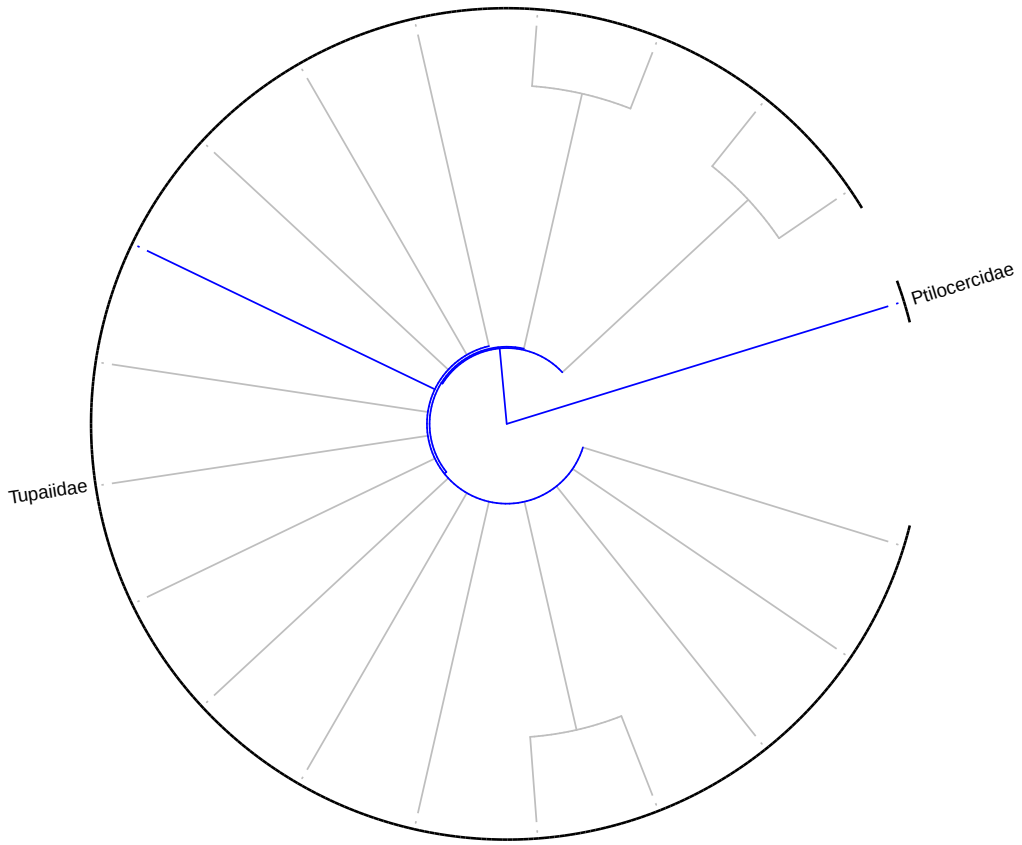



FIGURE A.11: Distribution of available morphological data across Scandentia. Edges are colored in grey when no morphological data is available or in blue when data is available.

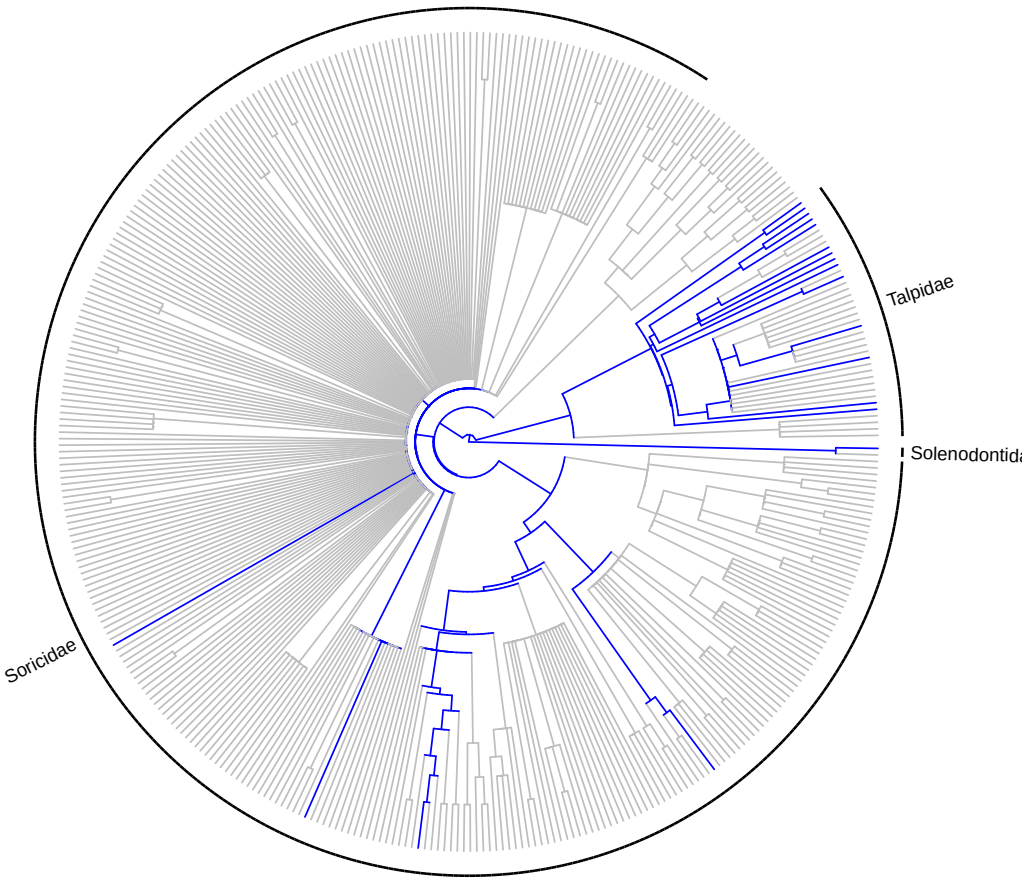



FIGURE A.12: Distribution of available morphological data across Soricomorpha. Edges are colored in grey when no morphological data is available or in blue when data is available.