

Assessment of cladistic data availability for living mammals

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Abstract

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.

Key words: Total Evidence method, phylogenetic clustering, morphological matrix, extinct, topology

INTRODUCTION

There is an increasing consensus among biologists that studying both living and fossil taxa is essential for fully understanding macroevolutionary patterns and processes [1, 2]. To perform such analyses it is necessary to combine living and fossil taxa in phylogenetic trees. One increasingly popular method, the Total Evidence method [3, 4], combines molecular data from living taxa and morphological data from both living and fossil taxa in a supermatrix (e.g. [5, 4, 6, 1, 7]), producing a phylogeny with living and fossil taxa at the tips. A downside of this method is that it requires molecular data for living taxa and morphological data for both living and fossil taxa. Chunks of this data can be difficult, or impossible, to collect for every taxon in the analysis. For example, fossils rarely have molecular data and incomplete fossil preservation may restrict the amount of morphological data available. Additionally, it has become less common to collect morphological characters for living taxa when molecular data is available (e.g. in [8], only 13% of living taxa have coded morphological data). Unfortunately this missing data can lead to errors in phylogenetic inference. Simulations show that the ability of the Total Evidence method to recover the correct topology decreases when there is little overlap between morphological data in living and fossil taxa, and that the effect of missing data on topology is greatest when living taxa have few morphological data [9]. This is because (1) fossils cannot branch in the correct clade if it contains no morphological data for living taxa; and (2) fossils have a higher probability of branching within clades with more morphological data for

living taxa, regardless of whether this is the correct clade [9].

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 is distributed across clades. Intuitively, most people assume this kind of data has already been collected, but empirical data suggest otherwise (e.g. in [4, 8, 7]). 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 also determine whether the available cladistic data is phylogenetically overdispersed or clustered across mammalian orders.

MATERIALS AND METHODS

Data collection and standardisation

We downloaded all cladistic matrices containing any living and/or fossil mammal taxa from three major public databases: MorphoBank (<http://www.morphobank.org/> [10]), 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 for matrices that were not uploaded to these databases (see Supplementary Materials Section 1 for a detailed description of the

search procedure). In total, we downloaded 286 matrices containing 5228 unique operational taxonomic units (OTUs). We used OTUs rather than species since entries in the matrices ranged from species to families, and standardised the taxonomy as described in Supplementary Materials (section 1). We designated as “living” all OTUs that were either present in the phylogeny of [11] or the taxonomy of [12].

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 other matrices [13] 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 [14]). Therefore we selected only matrices containing >100 characters for each OTU. This threshold was chosen to correspond with the number of characters used in [9] and [15]. Results of analyses with no threshold are available in Supplementary Material. After removing matrices with <100 characters, we retained 1074 unique living mammal OTUs from 126 matrices.

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 low data coverage, and orders with $>75\%$ of living taxa with cladistic data as having high data coverage.

We investigated whether the available cladistic data for each order was (i) randomly distributed, (ii) overdispersed or (iii) clustered, with respect to phylogeny, using two metrics from community phylogenetics: the Nearest Taxon Index (NTI; [16]) and the Net Relatedness Index (NRI; [16]). NTI is most sensitive to clustering or overdispersion near the tips, whereas NRI is more sensitive to clustering or overdispersion across the whole phylogeny [17]. Both metrics were calculated using the *picante* package in R [18, 19].

NTI [16] is based on mean nearest neighbour distance ($MNND$) and is calculated as follows:

$$NTI = - \left(\frac{\overline{MNND}_{obs} - \overline{MNND}_n}{\sigma(MNND_n)} \right) \quad (1)$$

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 $MNND$ between n randomly drawn taxa, and $\sigma(MNND_n)$ is the standard deviation of these 1000 random $MNND$ values. NRI is calculated in the same way, but $MNND$ is replaced by mean phylogenetic distance (MPD) as follows:

$$NRI = - \left(\frac{\overline{MPD}_{obs} - \overline{MPD}_n}{\sigma(MPD_n)} \right) \quad (2)$$

where \overline{MPD}_{obs} is the observed mean phylogenetic distance of the tree containing only the n taxa with cladistic data. Negative NTI and NRI values show that the focal taxa are more overdispersed across the phylogeny than expected by chance, and positive values reflect clustering.

We calculated NTI and NRI values for each mammalian order separately, at each

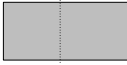




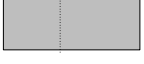











different taxonomic level. For each analysis our focal taxa were those with available cladistic data at that taxonomic level and the phylogeny was that of the order pruned from [11].

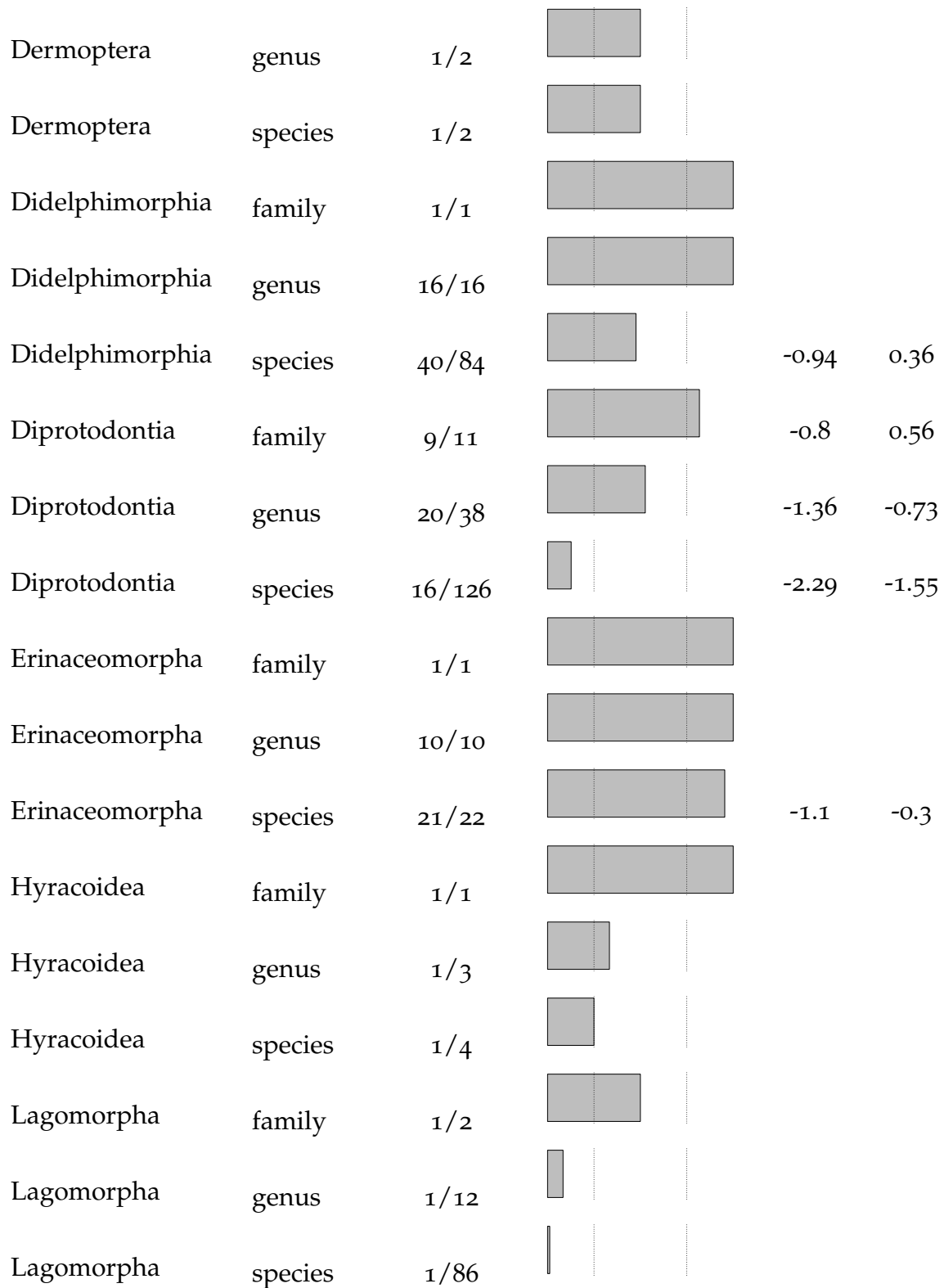
RESULTS

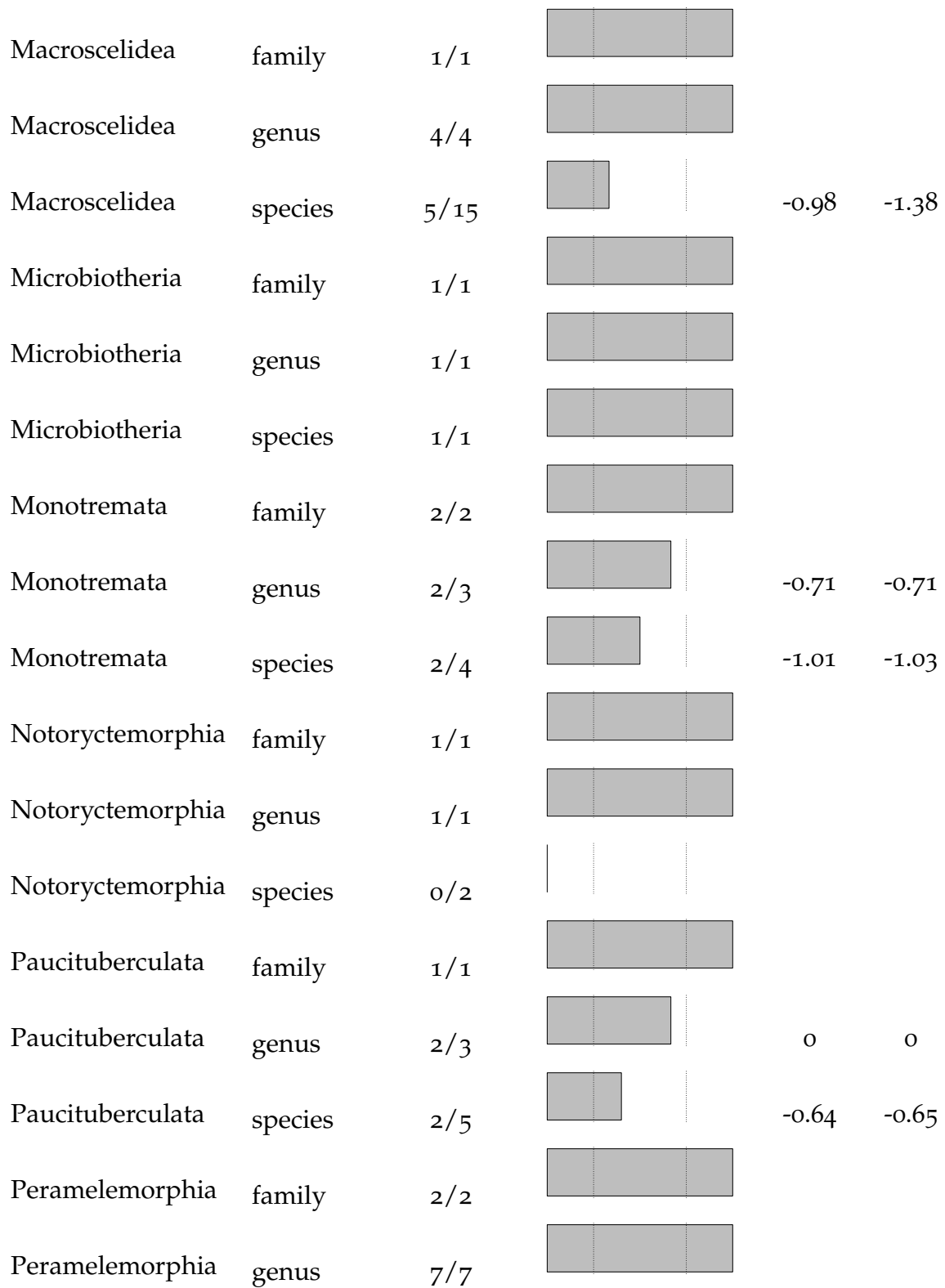
22 of 28 orders have low coverage (<25% species with cladistic data) and six have high coverage (>75% species with cladistic data) at the species-level. At the genus-level, three orders have low coverage and 12 have high coverage, and at the family-level, no orders have low coverage and 23 have high coverage (Table 1).


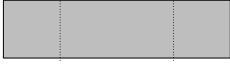






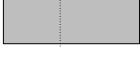


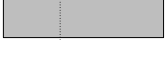


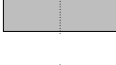


Table 1: Number of taxa with available cladistic data for mammalian orders at three taxonomic levels. The left vertical bar represents low coverage (<25%); the right vertical bar represents high coverage (>75%). Negative Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) values indicate phylogenetic overdispersion; positive values indicate phylogenetic clustering. Significant NRI or NTI values are in bold. *p < 0.05; **p < 0.01; ***p < 0.001.




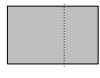



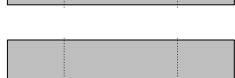
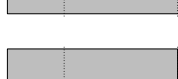





Order	Taxonomic level	Proportion of taxa	Coverage	NRI	NTI
Afrosoricida	family	2/2			
Afrosoricida	genus	17/17			

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			





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			

Only six orders had significantly clustered data (Afrosoricida and Pholidota at the species-level, and Carnivora, Cetartiodactyla, Chiroptera and Soricomorpha at both species- and genus-level) and none had significantly overdispersed data (Table 1).

Figure 1 shows randomly distributed OTUs with cladistic data in Primates (Figure 1A) and phylogenetically clustered OTUs with cladistic data in Carnivora (mainly Canidae; Figure 1B).

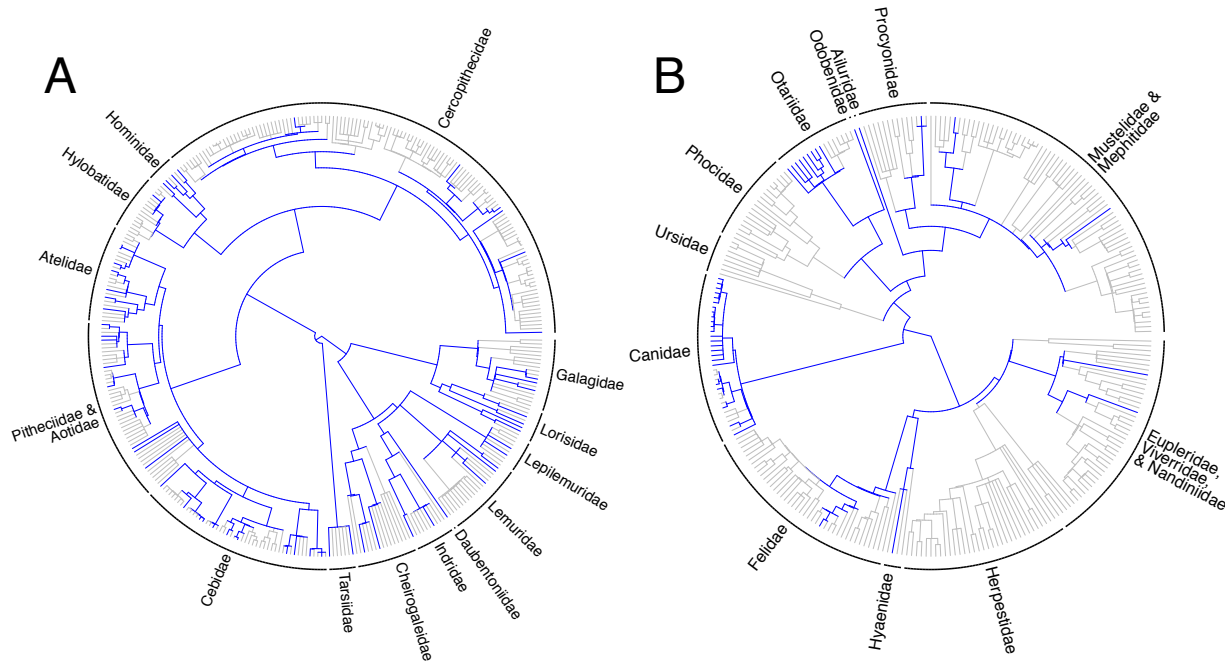


Figure 1: Phylogenetic distribution of species with available cladistic data across two orders (A: Primates; B: Carnivora). Blue branches indicate available cladistic data for the species.

DISCUSSION

Our results show that although phylogenetic relationships among living mammals are well-resolved (e.g. [11, 20]) , most of the data used to build these phylogenies is molecular, and very little cladistic data is available for living mammals compared to fossil mammals (e.g. [21, 22]). This has implications for building Total Evidence

120 phylogenies containing both living and fossil mammals, as without sufficient cladistic
121 data for living species, fossil placements in these trees are very uncertain [9].

122 The number of living mammalian taxa with no available cladistic data was
123 surprisingly high at the species-level: only six out of 28 orders have a high coverage of
124 taxa with available cladistic data. This high coverage threshold of 75% of taxa with
125 available cladistic data represents the minimum amount of data required before
126 missing data has a significant effect on the topology of Total Evidence trees [9]. Beyond
127 this threshold, there is considerable displacement of wildcard taxa (*sensu* [23]) and
128 decreased clade conservation [9]. Therefore we expect difficulties in placement of fossil
129 taxa at the species-level in most mammalian orders, but fewer issues at higher
130 taxonomic levels. This point is important from a practical point of view because of the
131 slight discrepancy between neontological and palaeontological species concepts. While
132 neontological species are described using morphology, genes, distribution etc.;
133 palaeontological species can be based only on morphological, spatial and temporal data
134 (e.g. [22]). Therefore, most palaeontological studies use genus as their smallest OTU
135 (e.g. [22, 21]), so data availability at the genus-level in living mammals should be our
136 primary concern when building phylogenies of living and fossil taxa.

137 When few species have available cladistic data, the ideal scenario is for them to
138 be phylogenetically overdispersed to maximize the possibilities of a fossil branching in
139 the right clade. The second best scenario is that species with cladistic data are randomly
140 distributed across the phylogenies. Here we expect no special bias in the placement of

fossils [9], it is therefore encouraging that for most orders, species with cladistic data were randomly distributed across the phylogeny. The worst case scenario for fossil placement is that species with cladistic data are phylogenetically clustered. Then we expect two major biases to occur: first, fossils will not be able to branch within a clade containing no data, and second, fossils will have higher probability of branching within the most sampled clade by chance. Our results suggest that this may be problematic at the genus-level in Carnivora, Cetartiodactyla, Chiroptera and Soricomorpha. For example, a Carnivora fossil will be unable to branch in the Herpestidae, and will have more chance to randomly branch within Canidae (Figure 1B).

Despite the absence of good cladistic data coverage for living mammals, the Total Evidence method still seems to be the most promising way of combining living and fossil data for macroevolutionary analyses. Following the recommendations in [9], 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. Such an effort would be valuable not only to phylogeneticists, but also to any researcher focusing understanding macroevolutionary patterns and processes.

ETHICS STATEMENT

N/A

DATA ACCESSIBILITY STATEMENT

All data and analysis code is available on GitHub
(https://github.com/TGuillerme/Missing_living_mammals).

AUTHORS' CONTRIBUTIONS

T.G. and N.C conceived and designed the experiments. T.G. performed the experiments and analysed the data. T.G. and N.C. contributed to the writing of the manuscript. All authors approved the final version of the manuscript.

COMPETING INTERESTS

We have no competing interests.

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References

- [1] Slater GJ, Harmon LJ. Unifying fossils and phylogenies for comparative analyses of diversification and trait evolution. *Methods Ecol Evol.* 2013;4(8):699–702.
- [2] Fritz SA, Schnitzler J, Eronen JT, Hof C, Böhning-Gaese K, Graham CH. Diversity in time and space: wanted dead and alive. *Trends Ecol Evol.* 2013;28(9):509 – 516.
- [3] Eernisse D, Kluge A. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. *Mol Biol Evol.* 1993;10(6):1170–1195.
- [4] Ronquist F, Klopstein S, Vilhelmsen L, Schulmeister S, Murray D, Rasnitsyn A. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Syst Biol.* 2012;61(6):973–999.
- [5] Pyron R. Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Syst Biol.* 2011;60(4):466–481.
- [6] Schrago C, Mello B, Soares A. Combining fossil and molecular data to date the diversification of New World Primates. *J Evolution Biol.* 2013;26(11):2438–2446.
- [7] Beck RM, Lee MS. Ancient dates or accelerated rates? Morphological clocks and the antiquity of placental mammals. *P Roy Soc B-Biol Sci.* 2014;281(20141278):1–10.

- [8] Slater GJ. Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary. *Methods Ecol Evol.* 2013;4(8):734–744.
- [9] Guillerme T, Cooper N. Effects of missing data on topological inference using a Total Evidence approach. *Mol Phylogenet Evol.* 2016;94, Part A:146 – 158.
Available from:
<http://www.sciencedirect.com/science/article/pii/S1055790315002547>.
- [10] O’Leary MA, Kaufman S. MorphoBank: phylophenomics in the cloud. *Cladistics.* 2011;27(5):529–537.
- [11] Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, et al. The delayed rise of present-day mammals. *Nature.* 2007 03;446(7135):507–512.
- [12] Wilson DE, Reeder DM. *Mammal species of the world: a taxonomic and geographic reference.* vol. 1. JHU Press; 2005.
- [13] Wagner PJ. Exhaustion of morphologic character states among fossil taxa. *Evolution.* 2000;54(2):365–386.
- [14] Brazeau MD. Problematic character coding methods in morphology and their effects. *Biol J Linn Soc.* 2011;104(3):489–498.
- [15] Harrison LB, Larsson HCE. Among-Character Rate Variation Distributions in Phylogenetic Analysis of Discrete Morphological Characters. *Syst Biol.* 2015;64(2):307–324.

- 213 [16] Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. Phylogenies and community
214 ecology. *Ann Rev Ecol Syst.* 2002;p. 475–505.
- 215 [17] Cooper N, Rodríguez J, Purvis A. A common tendency for phylogenetic
216 overdispersion in mammalian assemblages. *P Roy Soc B-Biol Sci.*
217 2008;275(1646):2031–2037.
- 218 [18] Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, et al.
219 Picante: R tools for integrating phylogenies and ecology. *Bioinformatics.*
220 2010;26:1463–1464.
- 221 [19] R Core Team. R: a language and environment for statistical computing. Vienna,
222 Austria; 2015. Available from: <http://www.R-project.org>.
- 223 [20] Meredith R, Janečka J, Gatesy J, Ryder O, Fisher C, Teeling E, et al. Impacts of the
224 Cretaceous terrestrial revolution and KPg extinction on mammal diversification.
225 *Science.* 2011;334(6055):521–524.
- 226 [21] O’Leary MA, Bloch JL, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, et al.
227 The placental mammal ancestor and the postK-Pg radiation of placentals. *Science.*
228 2013;339(6120):662–667.
- 229 [22] Ni X, Gebo DL, Dagosto M, Meng J, Tafforeau P, Flynn JJ, et al. The oldest known
230 primate skeleton and early haplorhine evolution. *Nature.* 2013;498(7452):60–64.
- 231 [23] Kearney M. Fragmentary taxa, missing data, and ambiguity: mistaken
232 assumptions and conclusions. *Syst Biol.* 2002;51(2):369–381.