

CarniFOSS: A database of the body mass of fossil carnivores

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Abstract

Motivation: Body mass is one of the most important determinants of animal ecology. Unlike other important traits it is also readily inferable from fossils and it is therefore one of the only traits that can be directly analysed and compared between fossil and contemporary communities. Despite this, no comprehensive database of the body mass of larger clades of extinct species exists. Analysis of fossils has therefore been restricted to small clades or to smaller, potentially biased, subsets of species. We here describe CarniFoss, an open-access database of body masses of all 1,322 extinct species of non-pinniped Carnivoramorpha and two related extinct groups of carnivorous mammals, Hyaenodonta and Oxyaenidae.

Main types of variables contained: We gathered lengths of teeth of fossil and extant species and body mass for extant species and a few of the best-known fossil species. Following this we estimated body mass for all species through phylogenetic imputation.

Spatial location and grain: Global, terrestrial.

Time period and grain: We collected data on all known species within the focal groups. The known species all lived in the Palaeogene, Neogene or Quaternary (i.e., the last 66 Myr).

Major taxa and level of measurement: We searched for data on reported tooth size of all described species of Carnivoramorpha (excluding pinnipeds) and selected extinct related groups (Hyaenodonta and Oxyaenidae). We combined this with measured body mass for all extant species and inferred body mass based on long-bones for selected extinct species, as well as a species-level phylogeny including all extant and extinct species in the group, and inferred the body mass for all species using phylogenetic imputation.

Software format: Data are provided as a series of .csv files, with all metadata in a separate PDF file.

KEYWORDS

body mass, Carnivora, Creodonta, fossil, Hyaenodonta, imputation, Oxyaenidae, tooth length

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1 | INTRODUCTION

While the niche of a species is inherently multidimensional, much can be known about a species by just knowing its mass and its rough taxonomic position. It has repeatedly been highlighted that many factors scale with body mass as a power law (i.e., $x \sim \text{Body mass}^k$), at least within larger groups (Savage et al., 2004). Such relationships include, but are not limited to, metabolic rate (Savage et al., 2004), population density (Pedersen et al., 2017), life span (Healy et al., 2014) and daily movement range (Carbone et al., 2005). In addition to power law relationships, many more complex relationships between ecology and body mass also exist. For energetic reasons all larger carnivorous mammals, for instance, have to rely on prey larger than themselves, whereas smaller species can specialize on either large or small prey (Carbone et al., 1999). The relationship between body mass and range size is also partly energetically driven because larger species require a wider distribution to maintain a sufficiently large population, while small species can range from narrow endemics to widespread species (Gaston & Blackburn, 1996).

Because body mass is both relatively easily measured and highly important, several databases have been amassed to include the body mass of all extant or recently extinct species (e.g., Faurby et al., 2018; Smith et al., 2003). There are no complete or nearly complete databases for extinct species. Even though morphological measurements that can be used to infer body mass are known for the vast majority of extinct species, these are often only reported in the original species descriptions or in papers describing additional species within their respective genera. There are only a few noteworthy exceptions to this, such as the systematic revision of all North American species of Canidae by Xiaoming Wang and colleagues (Tedford et al., 2009; Wang, 1994; Wang et al., 1999). A few efforts to collect data also exist, such as NOW (New and Old Worlds database of fossil mammals) or PBDB (the PaleoBiology DataBase), but both only include mass for a small fraction of species within any larger group. Analyses looking for general patterns in the fossil record (e.g., Smith et al., 2018) therefore have to rely on very incomplete data, which creates a risk of producing biased results, since even small amounts of missing data have the potential to drastically bias conclusions (Sayol et al., 2020).

It is thus clear that there is a need for a more exhaustive database for extinct species, at least for a few selected clades, and we will here provide one such focusing on Carnivora and three related ecologically similar groups: Miacoidea, Hyaenodonta and Oxyaenidae. We do this using a two-step procedure. First, we scan the literature for the size of carnassial teeth (i.e., the modified premolars or molars adapted for shearing meat) for as many species as possible, which we combine with the mass of extant carnivores from PHYLACINE 1.2 (Faurby et al., 2018) and long-bone-derived measurements (estimated based on ulna, humerus tibia and/or femur) for selected extinct species. We primarily relied on carnassial teeth for two main reasons. Firstly, tooth fossils are much more abundant than long-bone fossils, making it possible to retrieve data from a larger fraction of species. Secondly, carnassial size has previously been used as

the main estimator of size within the studied group (e.g., Legendre & Roth, 1988; Morlo, 1999).

Following this we estimate the body mass of all extinct species based on phylogenetic imputation (Goolsby et al., 2016), based on a species-level phylogeny of our focal group (Faurby et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Data collection

For this study, we used the taxonomy of Faurby et al. (2019). The sole exception to this was five species accepted by Faurby et al. (2019), which we discovered to be objective synonyms as part of the present work. These five species (*Miacis uintensis*, *Uintacyon major*, *Mustela larteti*, *Schlossericyon viverroides* and *Stenogale aurelianensis*) were therefore excluded. We searched the literature and collected information on the lengths of carnassial teeth. Despite this we were not able to get information on all species. A small fraction of species either lack any known carnassial teeth or alternatively, particularly for species only discussed in older papers, the descriptions were sparse and lacked any measurements of the fossils they described. In total, we gathered tooth data on 193 out of 203 species of Hyaenodonta and Oxyaenidae, 1,027 out of 1,119 species of extinct terrestrial Carnivoramorph (non-pinniped Carnivora and Miacoidea) and 110 out of 259 extant or historically extinct non-pinniped Carnivora. Different taxonomic groups varied in the availability of tooth data for extant species. We had data on at least one species for all families with extinct species only known from fossils but not the three families lacking any fossil species (Nandiniidae, Prionodontidae and Eupleridae). Among remaining families, coverage ranged from 12% in Viverridae to 92% in Felidae (and to 100% in the monospecific Ailuridae). Our coverage includes the vast majority of extant subfamilies, but we lack representatives of Viverridae: Paradoxurinae, Viverridae: Hemigalinae, Ursidae: Ailuropodinae and Mustelidae: Taxidiinae. The information was retrieved from 337 references and supplemented with data from the PBDB and personal observations by the last two authors. For one species (*Zodiocyon zetesios*) we were not able to track down the species description or other descriptions of its morphology.

2.2 | Analyses

We inferred all missing values by phylogenetic imputation using Rphylopars (Goolsby et al., 2020). This method effectively works similarly to the better known process of ancestral state reconstruction, with two main differences: (a) it incorporates the estimated correlation structure between the variables, that is, if two or more traits are found to evolve in a correlated fashion this correlation is incorporated into the imputation of missing values rather than treating each trait as evolving independently; (b) in addition to estimating the values of all internal nodes as normal ancestral state reconstruction,

phylogenetic imputation also infers the values for all tips with one or more missing values (Johnson et al., 2021). We assumed evolution under the Pagel's lambda model, which means that the data can evolve through Brownian motion if the data suggest it but does not explicitly require any degree of phylogenetic signal in the data if none is present. All imputations were performed for each of the 1,000 trees provided by Faurby et al. (2019).

Since the analyses are conditional on the phylogeny used, we tested the effects of drastic transformations of the trees to estimate the stability of the results to phylogenetic errors. For 20 of the trees, we estimated body masses based on the actual trees as well as for Pagel's lambda of .5 and .05 and calculated the correlations between the actual results and the results for the transformed trees. The empirical lambdas were high (it was e.g., .93 across trees for the imputations for carnivores we discuss in 2.2.2). Since the results as we will discuss later were very similar when inferred with these very low lambdas it suggests that while our results may be informed by the underlying phylogeny, the influence of phylogenetic errors should be relatively small.

All analyses were performed in R 4.0.2 (R Core Team, 2020) and relied on functions from the packages *ape*, *geiger* and *Rphylopars* for analyses (Goolsby et al., 2020; Pennell et al., 2014; Paradis & Schliep, 2019) and *maptools* and *vioplot* (Adler & Kelly, 2020; Bivand & Lewin-Koh, 2020) for plotting.

2.2.1 | Hyaenodonta and Oxyaenidae

We relied on the two to three sets of carnassial teeth present in this group, that is, P4/m1, M1/m2 and M2/m3 for most Hyaenodontidae and P4/m1 and M1/m2 for Oxyaenidae and hyaenodontid Limnocyoninae that lack m3 (unlike the rest of Limnocyoninae, *Prolimnocyon* has a small m3, but because it is greatly reduced, we will analytically treat it as lacking, just as in the other Limnocyoninae). The primary estimator of body mass was the average length of lower carnassial teeth, that is, the average of the length of m1 and m2 for Oxyaenidae and Limnocyoninae and the average of m1, m2 and m3 for the remaining Hyaenodontidae. This has previously been found to be a robust estimator of body mass for the group, while at the same time being available for a substantially larger subset of species than bone or skull measurements (Morlo, 1999). We also gathered data on m1–m3 (or m1–m2 for species lacking m3) when these were reported instead of the length of the individual teeth. Out of 203 hyaenodontid and oxyaenid species in our phylogeny (Faurby et al., 2019), we found measurements of the lower molar row or all lower molars individually for 146 species. For 47 species we found data on some upper or lower carnassial teeth but not all lower molars, while for the last 10 species we did not find any reported molar size measurements. For the 47 species lacking information on some, but not all, teeth, we estimated the size of the missing teeth by an initial round of phylogenetic imputation (Goolsby et al., 2016). Since the relationship between m1 and m2 may be influenced by the presence or absence of m3, we inferred the sizes of missing teeth in three

separate imputations, one for species with m3 (most Hyaenodontida) and one for each of the two clades lacking m3 (1: Oxyaenidae and 2: Limnocyoninae). We created tables with logarithms of the lengths of all upper and lower carnassial teeth for each of the groups and imputed all missing values.

Imputations require body masses for some of the species but these cannot be inferred directly based on tooth measurement from these two groups since they lack extant closely related analogues and have a morphologically distinct dentition compared to carnivores. We therefore first estimated body mass based on seven metrics relying on preserved long-bones for 20 species. Three metrics [based on equations for the relationship between body mass and femur cortical cross-sectional area, femur distal articular (condylar) area or humerus cortical cross-sectional area] were obtained from Anyonge (1993). Two metrics (based on the relationship between body mass and tibia and ulna length) were obtained from Figueirido et al. (2011). The last two metrics, based on the relationship between body mass and humerus or femur length, were the means of independently derived equations from Anyonge (1993) and from Figueirido et al. (2011). Only 3 out of 20 species had information on all these metrics but for each species we used the median of all metrics that could be calculated as the measure of mass.

We first calculated the mean lower carnassial tooth size for each species. This was the mean of (non log-transformed) length of m1 and m2 for Oxyaenidae and Limnocyoninae and the mean of m1, m2 and m3 for the remaining Hyaenodontida. We then created a table with the logarithm to this mean length and the logarithm to body mass and imputed all missing values. The 10 species lacking morphological data had mass and tooth sizes inferred solely by the phylogeny.

2.2.2 | Carnivoramorpha (non-pinniped Carnivora or Miacoidea)

For this group we primarily searched for sizes of the single set of carnassial teeth P4/m1, especially for species that went extinct before 1500 AD since no direct measurements are available for these. We also gathered tooth sizes for 109 out of 241 extant species (representing 58 out of 105 genera). The data on extant species were solely used for inferring the evolutionary patterns and not to infer the mass of the species themselves and a near complete coverage of extant species is therefore less important than for extinct species. In total, we gathered data on P4 for 593 species and m1 for 1,019 species resulting in at least one tooth measurement for 1,137 species. We gathered body mass data on all 259 species that are either extant or at least survived until 1500 AD from Faurby et al. (2018). This was supplemented with previously inferred body mass based on long-bones of 24 selected extinct species from extinct families or subfamilies (Anyonge, 1993; Figueirido et al., 2011; Heinrich & Houde, 2006).

We created a table with logarithms of body mass and the lengths of P4 and m1 and imputed all the missing values. The 118 species

lacking morphological data had their body mass inferred solely by the phylogeny.

3 | PATTERNS IN DATA

3.1 | Reliability and precision

All the raw measurements were found to be highly correlated, which indicates that the imputations we use them for are also likely to be reliable. The correlations were highest for the measurements of mass based on long-bone metrics for Hyaenodonta and Oxyaenidae. The smallest pairwise correlation between any of the seven metrics based on standard non-phylogenetic correlations was .97 (which was for mass inferred from femur versus humerus length). The evolution of the average carnassial tooth length body mass was inferred to be highly correlated in Hyaenodonta and Oxyaenidae and had a median correlation across the trees of .91 (range .89–.95). The correlation between the length of the carnassial teeth and body mass for Carnivoramorpha was slightly lower (P4 versus mass, median .80 range .77–.81; m1 versus mass, median .80 range .78–.82), while the evolution of the sizes of the two carnassial teeth was found to be more correlated (median correlation .93 range .92–.94).

Our conclusions were highly robust to phylogenetic uncertainties. For Hyaenodonta and Oxyaenidae all correlations between inferred body mass based on the actual trees, and body mass inferred based on trees transformed with Pagel's lambda of .5 or even .05, were above .99. For Carnivoramorpha the correlations were around .98 between estimates for the actual trees and transformations with Pagel's lambda of .5, and between .95 and .96 for transformations with Pagel's lambda of .05. Even researchers disagreeing with parts of the phylogeny used to infer body masses can therefore safely use the inferred body masses in downstream analyses.

As another test of the reliability of the results, we looked at the overall distribution of inferred body mass (Figure 1). The estimated body mass of all Carnivoramorpha was between the body masses of the smallest extant Carnivora, that is, around 100 g, to 1,000 kg, which has been suggested to be the theoretical maximum body mass of carnivorans (Carbone et al., 2007). The estimated body masses of hyaenodonts on the other hand were occasionally larger than this suggested maximum. Six species have inferred body masses above 1,000 kg; five Miocene hyaenodonts, all belonging to the same subfamily (the three species of *Hyainailouros* and the two monospecific genera *Megistotherium* and *Sivapterodon*), and one member of Oxyaenidae (*Sarkastodon mongoliensis*). Six hyaenodonts also have inferred body masses smaller than any known carnivore (estimated masses between 2 and 80 g) but they belong to six separate genera

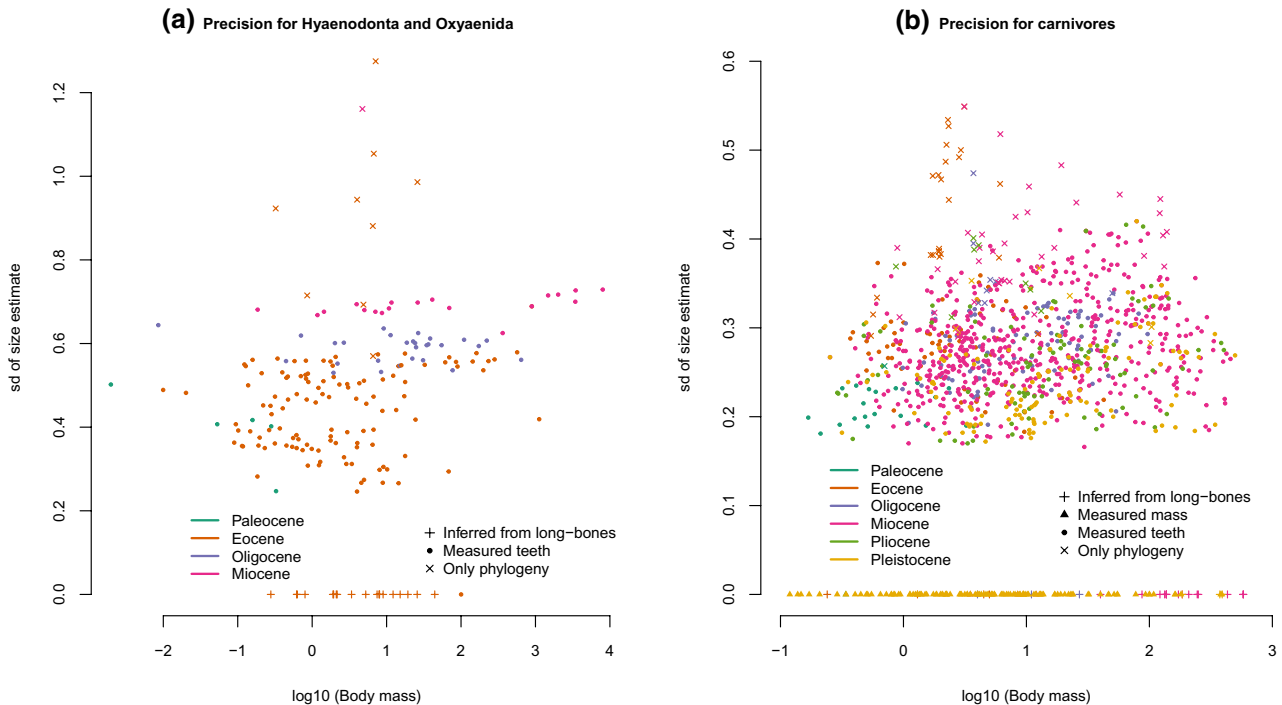


FIGURE 1 Estimated standard deviations in the inferred mass of all extinct species based on Rphylopar (Goolsby et al., 2020). Only species known from fossils are included and the different colours represent the age of the most recent record of each taxon [based on the set of records analysed by Faurby et al. (2019), and only including records where both the minimum and maximum age of the fossil fall within the same epoch]. Species are further grouped by data availability (symbols). Species with data on tooth size but not measured body masses or long-bone data are coded as 'Measured teeth', while species inferred solely from phylogeny are coded as 'Only phylogeny'. We stress that the standard deviations shown on the y axes solely refer to the uncertainties associated with the imputations. This means that while these imputation-associated uncertainties by definition are equal to 0 for the species with 'Measured mass', and 'Inferred from long-bones' the actual body masses of such species are not known without error

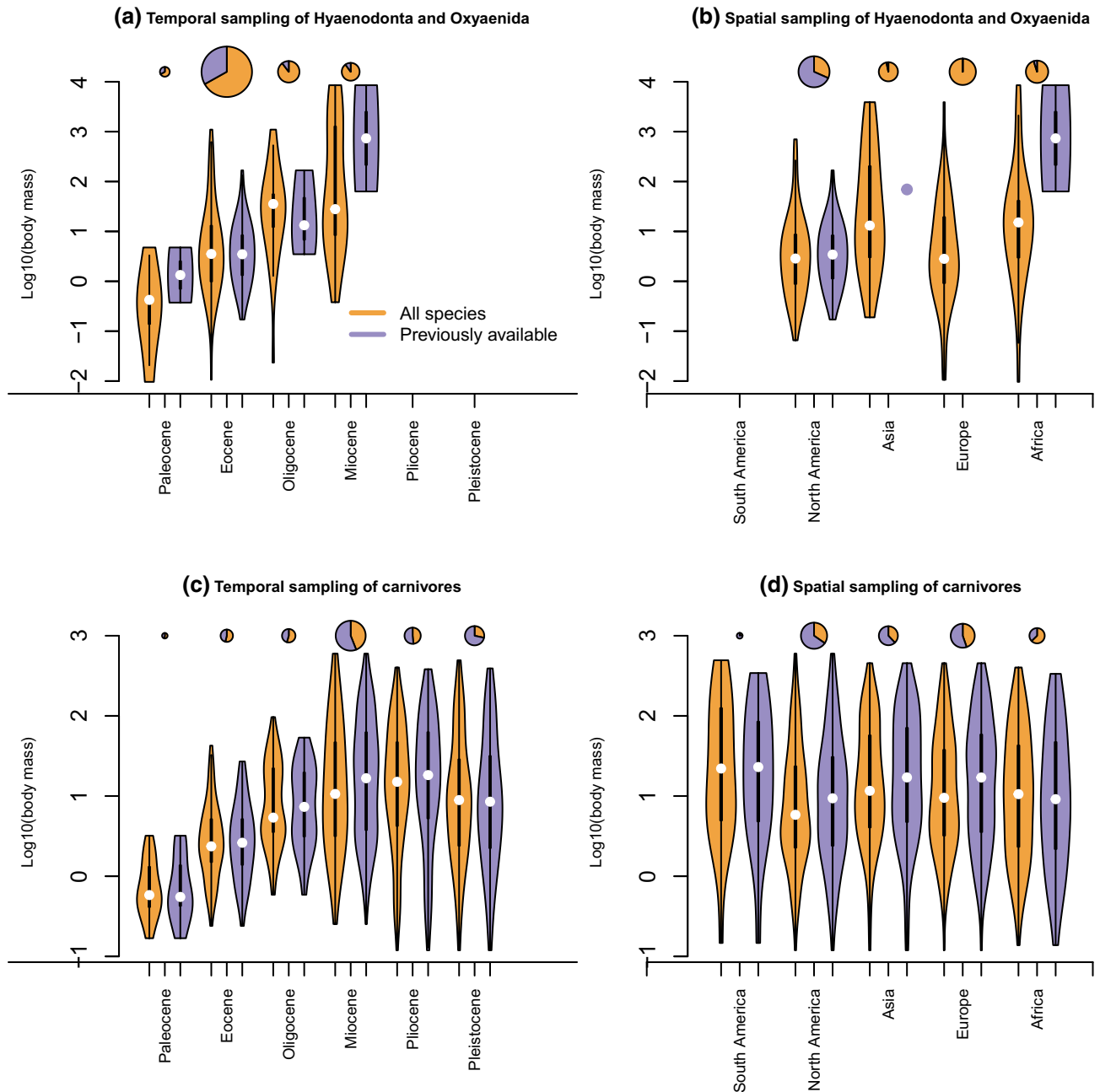


FIGURE 2 Body mass distributions of all carnivoramorphans, hyaenodontids or oxyaenids known from an epoch or a continent. Only species known from fossils are included [based on the set of records analysed by Faurby et al. (2019)], and assignment is only based on records where both the minimum and maximum age of the fossil fall within the same epoch. The pie charts show the fraction of species in each group that has previously available estimated body mass. The areas of the pies are proportional to the number of species known from each continent or epoch within each subplot but are not standardized between subplots

(*Boualitomus*, *Eoproviverra*, *Parvagula*, *Prolimnocyon*, *Thereutherium*, *Tinerhodon*) from multiple subfamilies and are from different epochs.

Estimations of the body mass of extinct animals necessarily have a large element of uncertainty (Figure 1), and while our results should be reliable overall there may be significant over- or underestimates for some species. These errors will almost certainly have a strong phylogenetic signal. In this regard, we note that the five hyaenodonts estimated to be larger than 1,000 kg were all closely

related, and if the body mass is drastically overestimated in one of them, it may likely be so in all five. It is further important to note that, because we rely on phylogenetic imputation to understand the relationship between tooth size and body mass, species for which the body mass of closely related species is available can have their body mass inferred more precisely. Due to the temporal patterns in the species with body mass that was not phylogenetically imputed (i.e., extant species with measured masses or extinct species with masses

inferred based on long-bones), Miocene species generally have the lowest precision for both hyaenodonts and carnivorans (Figure 1). As intuitively expected, we found that mass inferred solely based on phylogeny had a substantially higher uncertainty than mass inferred based on tooth size (Figure 1), and since these species represent only a small fraction of all species, we suggest that users of our data consider omitting them from any analyses relying on this database.

3.2 | Biases in previously available data

Previously available data on body mass might represent a biased subset of species. In order to assess this, we compared the previously available body masses [based on Smith et al. (2018); NOW, New and Old Worlds fossil mammals; and Faurby et al. (2018)] broken down by geography or epoch (Figure 2). We found substantial biases in the previously available data. In particular, we found that larger species and North American species are disproportionately likely to have previously available data. For Carnivoramorphia we further found that more recent species are more likely to have existing data, whereas the pattern is the opposite in hyaenodonts and oxyaenids, where older species are more likely to have previous estimates of body mass.

We tested these visual patterns by logistic regressions using a full model with size, presence in any given continent and presence in any given time period as predictors. For Hyaenodonta and Oxyaenidae we could not include presence in Europe as a potential predictor since there is not a single European species in the databases we compared our data to. This means that the effect of presence in Europe is associated with lower probability of having previous data but that the size of this effect is statistically unidentifiable. Among the testable predictors, the only significant one was a positive effect of presence in North America on the probability of having data already available ($p < .001$). For Carnivoramorphia many predictors were significant (all with $p < .001$). Both Pleistocene and Miocene taxa were significantly more likely to have data previously available (with stronger effect sizes for Pleistocene taxa). Since species may be present in several continents and widespread species may be more likely to have previously available data, presence in any of the five continents had significant positive effects but the effects sizes varied drastically, with stronger effects for presence in North America (3.37, SE 0.36), weaker effects for Africa (1.13, SE 0.38) and Asia (1.74, SE 0.29), and intermediate for South America (2.41, SE 0.65) and Europe (2.46, SE 0.33).

4 | CONCLUDING REMARKS

We hope that the database we provide here may stimulate body mass related research. The group we focus on here likely constitutes a monophyletic clade (aside from the marine pinnipeds) making them suitable for evolutionary analyses of trait evolution. They also nearly constitute an ecological guild although a few herbivorous species occur in the group (Faurby et al., 2018) and there

were at times a few other co-occurring mammalian clades specialized on vertebrate prey such as Mesonychia, Arctocyonidae or Cimolestidae (Halliday et al., 2015). Our database may therefore also provide input data for analyses focusing on guild structure through time and space. One guild can, however, not be completely understood in isolation and we hope that this database motivates other researchers to develop similar resources for some of the main herbivore groups, which would further open up research into multiple additional fields, such as community structure or co-evolution of predators and prey.

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DATA AVAILABILITY STATEMENT

All data are given in the Supporting Information and are also available on Dryad (<https://doi.org/10.5061/dryad.fttdz08t5>). In addition, CarniFOSS is freely available, and will continue to be updated, on Github (<https://github.com/sorenfaurby/CarniFOSS>) We encourage users to highlight additional data sources and any errors in the database to the corresponding author.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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