Stanford
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Phylogenetic and fossil evidence for a common body size attractor in marine mammals

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1. Introduction

Evolutionary transitions between terrestrial and aquatic habitats are rare and often have large effects on the evolutionary trajectory of the clade making the transition. Following a single transition from the marine realm to the terrestrial realm, tetrapods have subsequently re-evolved a marine lifestyle at least 30 separate times. At least six of these re-invasions of the water occurred within crown-group mammals and four [sirenians (Sirenia), whales (Cetacea), pinnipeds (Pinnipedia), and otters (Lutrinae)] clades are extant. Although marine mammals are widely known to be larger than their terrestrial sister groups, the extent to which the body size evolution of these clades reflects common constraints of a marine lifestyle remains little studied.

2. Materials and Methods

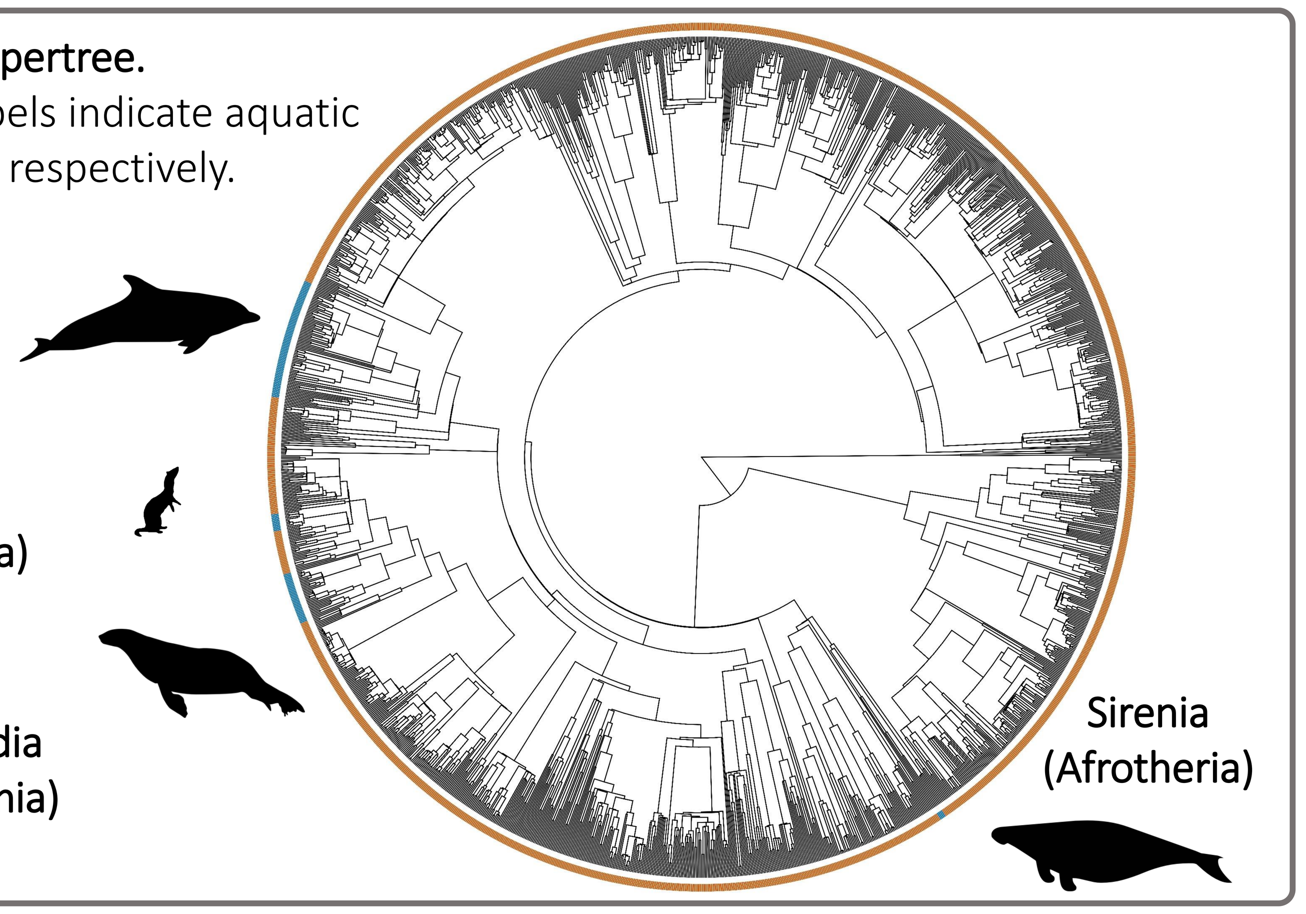
- Body masses of 3832 living and 3005 fossil mammal species (PanTHERIA, NOW, MOM, Heim et al 2015, Tomiya 2013)
- Species/genus level habitat data (GBIF, primary literature)
- Mammal supertree (Bininda-Emonds et al 2007)
- Mammal species fossil ranges (Paleobiology Database)
- Macroevolutionary Ornstein-Uhlenbeck (OU) model fitting
    - Phylogenetic analyses (*OUwie*, Beaulieau et al 2012)
    - Fossil record analyses (*paleoTS*, Hunt 2006)

General Equation of an OU Model:

$$dX(t) = \alpha[\theta - L(t)]dt + \sigma dB(t)$$

$L(t)$: initial body size	**α: strength of selection**
$dX(t)$: change in body size	**σ: intensity of random drift**
$dB(t)$: random variation	**θ: body size optimum**

Figure 2.1: Mammal supertree. Blue and orange tip labels indicate aquatic and terrestrial species, respectively.



3. Results

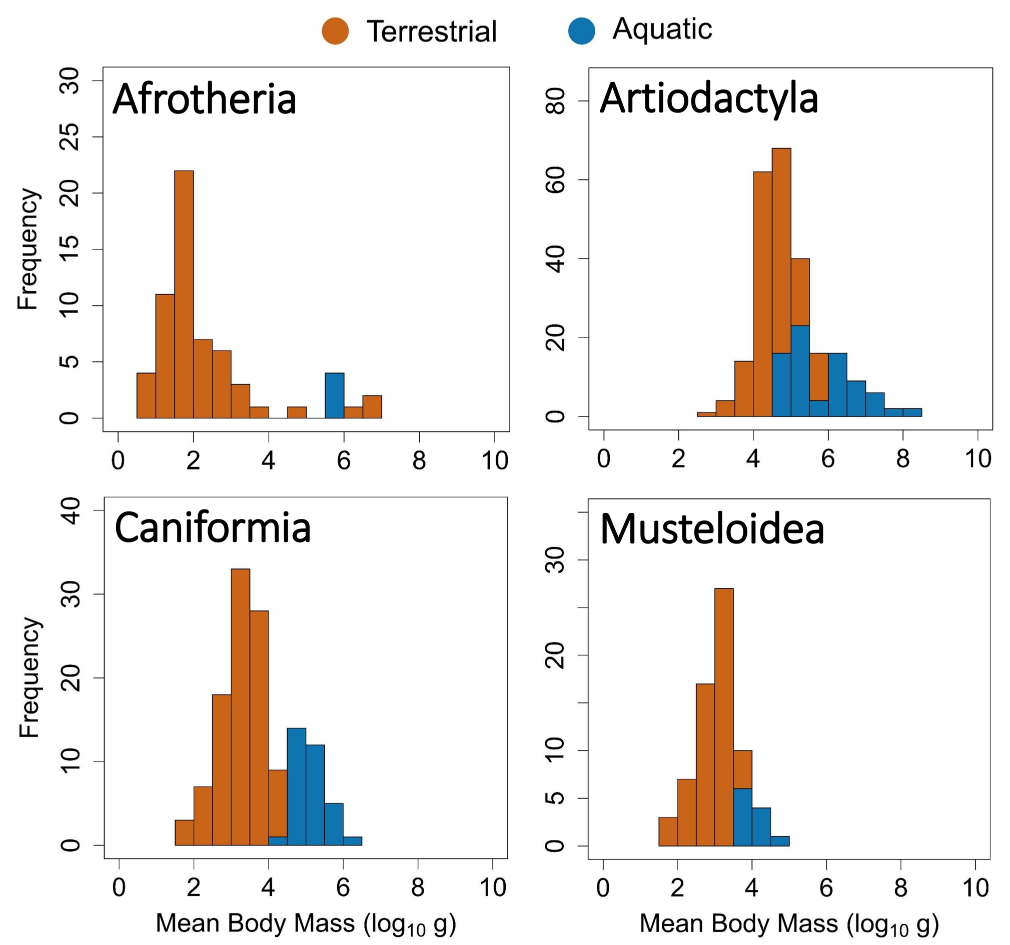


Figure 3.1: Extant mammal species body sizes. Histograms of mammal species body sizes, separated by clade.

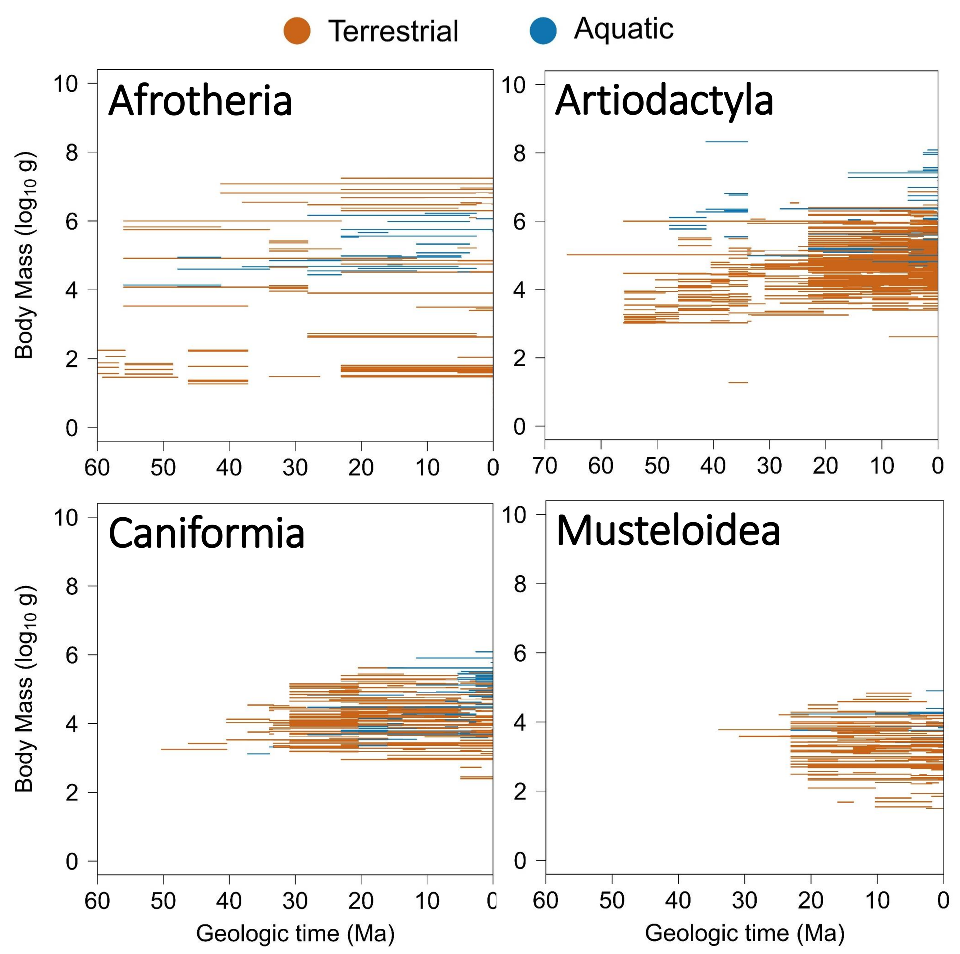
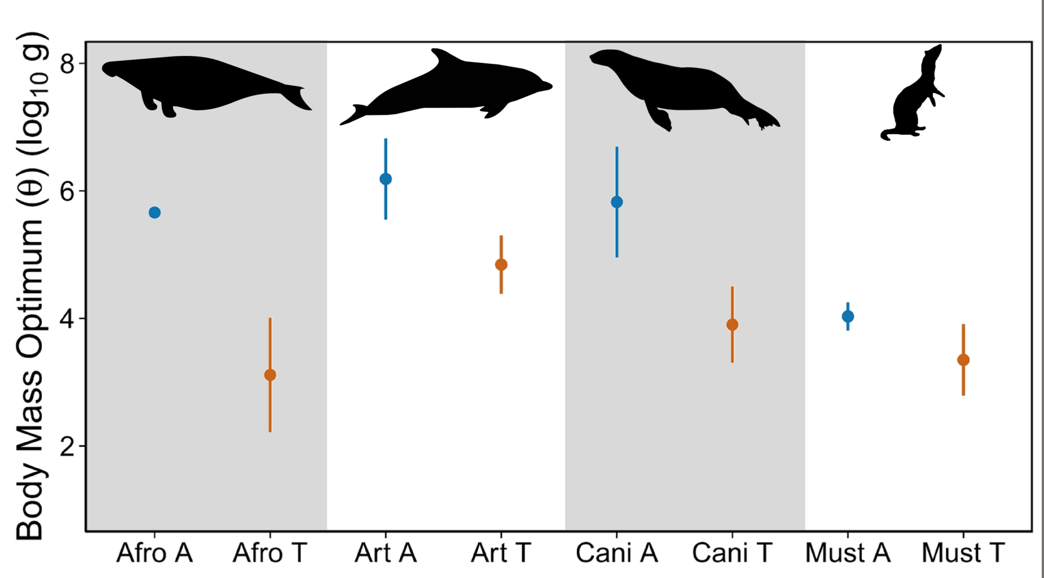


Figure 3.2: Mammal fossil ranges. Fossil ranges and average body sizes of mammal species.

Figure 3.3: Body size optima. Median optima (θ) as estimated by OUwie analyses separated by clade and habitat. Error bars represent 2 standard errors. Silhouettes for reference. Of note is the similarity between the aquatic optima of Afrotheria, Artiodactyla, and Caniformia, despite their very different terrestrial optima, and the overlap of the terrestrial and aquatic Musteloid optima.



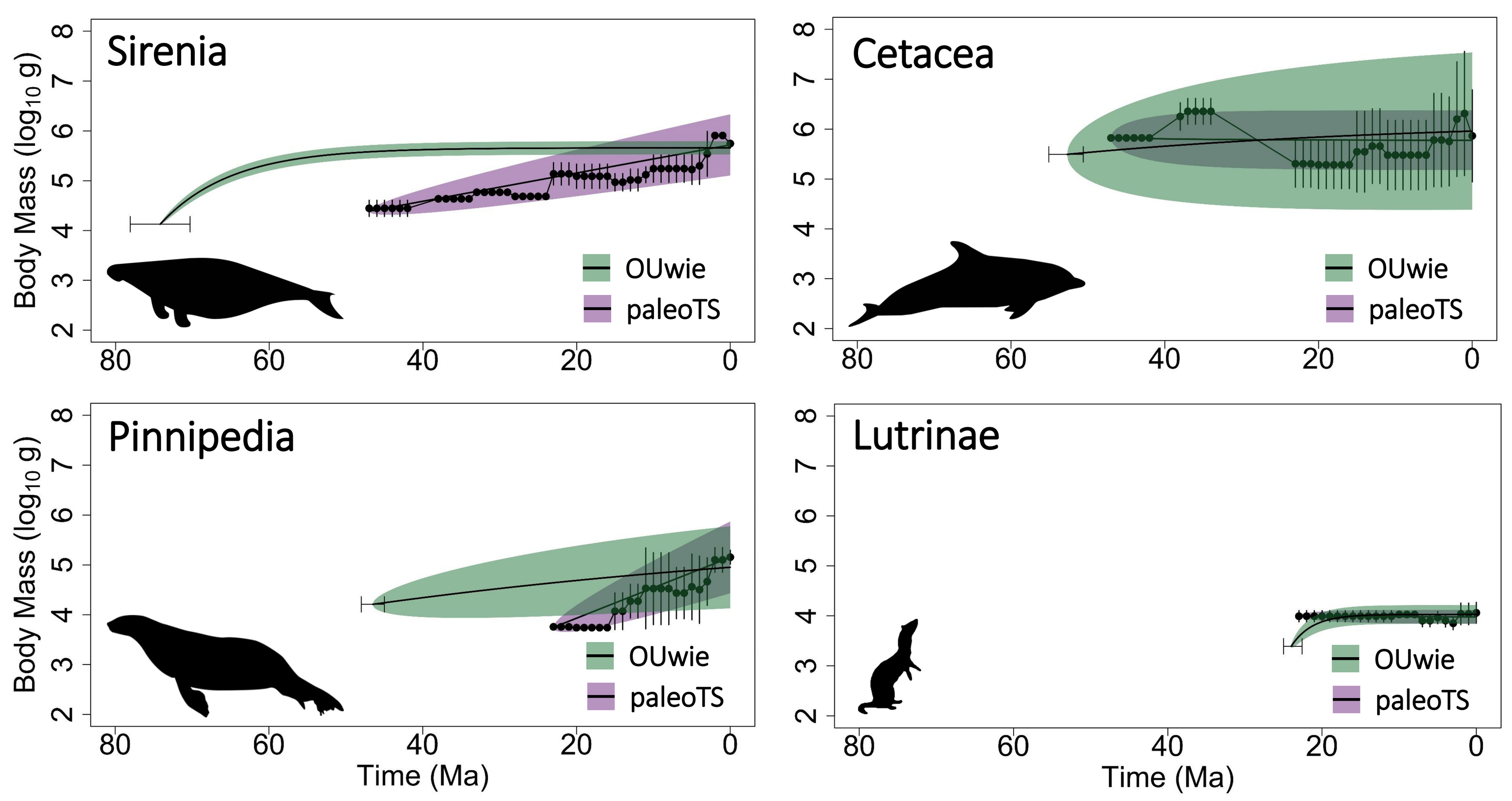


Figure 3.4: Comparison of results of phylogenetic and fossil analyses. Overlay of Ornstein-Uhlenbeck processes using average parameters as estimated by OUwie phylogenetic and paleoTS fossil analyses for individual clades. Points and error bars within paleoTS results represent average raw data and variance, respectively, per Myr time bin. Significant differences between the results of the phylogenetic and fossil analyses of Sirenia, Pinnipedia, and Lutrinae. Phylogenetic analyses tend to infer larger α parameters than the fossil analyses, while fossil analyses tend to infer continued increase, even in the modern.

	BM1	BMS	OU1	OUM	OUMV	OUMA	OUMVA
Afrotheria	0.00	0.02	0.00	0.00	0.11	0.00	**0.85**
Artiodactyla	0.00	0.00	0.00	0.14	0.21	0.08	**0.39**
Caniformia [- Mustelidae]	0.00	0.06	0.00	0.02	**0.62**	0.05	0.24
Musteloidea	0.17	**0.25**	0.06	0.12	0.08	0.11	0.17

Table 3.1: OUwie model support. Median AIC_c weight values over 100 Bayesian iterations. Bolded values represent best-fit models. Models are as follows: *BM1* fits a single σ^2 rate across entire group; *BMS* fits a model with different σ^2 rates for each habitat; *OU1* fits a single θ across entire group; *OUM* fits different θ for each habitat, holding σ^2 and α constant; *OUMA* fits different θ and α, holding σ^2 constant; *OUMV* fits different θ and σ^2, holding α constant; and *OUMVA* fits different θ, α, and σ^2 parameters. Separate OU models best fit Afrotheria, Artiodactyla, and Caniformia, while Brownian motion models best fit Musteloidea.

4. Conclusions

- Mammals living in aquatic environments have higher optimal body sizes than their terrestrial counterparts.
- Results suggest the existence of a body size attractor that has been discovered independently by three mammalian clades.
- The fossil record suggests it often takes a long time for body size to increase, implying there is low pressure to get bigger.
- Some groups may still be getting larger, although preliminary analyses suggest there may be an upper limit without key innovations (e.g. baleen whales).
- The sustained small size of aquatic mustelids could indicate the presence of a second attractor at small size or competitive exclusion from the ~1 ton attractor.
- Differences between phylogenetic and fossil analysis results may be indicative of poor method assumptions or low power.

References

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Silhouettes from phylopic.org