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The evolution of aquatic mammals toward a nearly universal large size? Evidence from phylogenetics and fossils

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1. Introduction

Most mammal species live on land, but the largest mammals live in the oceans. Aquatic and terrestrial habitats clearly impose differing selective pressures on body size. However, the quantitative study of body size evolution in mammals and other major animal clades typically focuses on either terrestrial or marine clades independently, thus failing to capture the dynamics of size evolution associated with the transition between land and water. Consequently, the extent to which the rate, magnitude, and outcome of size change associated with habitat transitions are shared among clades remains unknown, leaving open the question of whether the apparently common phenomenon of size increase associated with the acquisition of an aquatic lifestyle reflects idiosyncratic responses of individual clades versus a common response to universal constraints.

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**

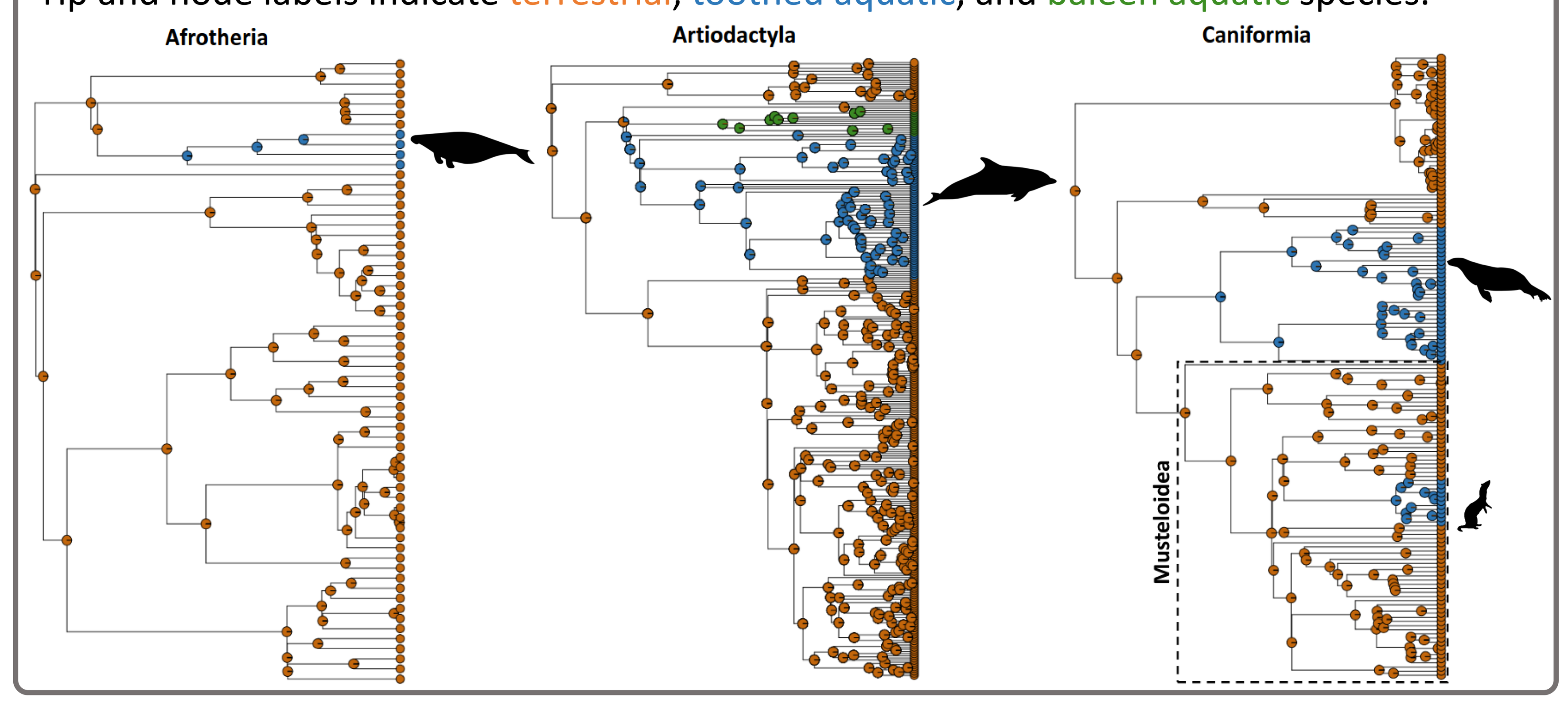


Figure 2.1: **Habitat reconstruction for the four clades of interest.** Tip and node labels indicate terrestrial, toothed aquatic, and baleen aquatic species.

3. Results

	BM_1	BM_S	OU_1	OU_M	OU_{MV}	OU_{MA}	OU_{MVA}
Afrotheria	0.00	0.03	0.00	0.00	0.29	0.00	**0.44**
Artiodactyla	0.00	0.00	0.00	0.09	**0.31**	0.23	0.13
Caniformia [- Lutrinae]	0.02	0.15	0.01	0.04	0.34	0.02	**0.41**
Musteloidea	0.15	**0.27**	0.06	0.04	0.06	0.12	0.21

least support 0.0 0.2 0.4 0.6 0.8 1.0 *most support*

	BM_1	BM_S	OU_1	OU_M	OU_{Ma}
Afrotheria	0.47	0.00	**0.53**	0.00	0.00
Artiodactyla	0.00	0.06	0.00	0.00	**0.93**
Caniformia [- Lutrinae]	**0.90**	0.08	0.02	0.00	0.00
Musteloidea	0.00	0.01	0.00	**0.63**	0.36

Table 3.1: **OUwie and paleoTS model support.**
Top: Median AIC_c weight values for OUwie analyses over 100 Bayesian iterations; bottom: AIC_c weight values for paleoTS analyses. Bolded values represent best-fit models. Models are as follows: BM_1 fits a single σ^2 rate across entire group; BM_S fits a model with different σ^2 rates for each habitat; OU_1 fits a single θ across entire group; OU_M fits different θ for each habitat, holding σ^2 and α constant; OU_{MA} fits different θ and α, holding σ^2 constant; *OUMV* fits different θ and σ^2, holding α constant; and OU_{MVA} fits different θ, α, and σ^2 parameters. For paleoTS analyses, OU_M fits different θ for each habitat, holding σ^2, α, and the ancestral state constant; OU_{Ma} fits different θ and ancestral states, holding σ^2 and alpha constant.

Note that, across OUwie analyses, separate OU models best fit Afrotheria, Artiodactyla, and Caniformia, while there is little consensus for Musteloidea. However, note high support from paleoTS analyses for the BM_1 model for Caniformia and split OU models for Musteloidea.

Figure 3.1: **Body size optima.** Model-averaged median optima (θ) as estimated by OUwie analyses (circles) and mean modern body sizes (triangles) separated by clade and habitat. Error bars represent model-averaged median 2σ.

Of note is the similarity between the aquatic optima of Afrotheria, Artiodactyla, and Caniformia, despite their very different terrestrial optima. Also of note is the similar terrestrial and aquatic optima in Musteloidea, which are both different from those of the other aquatic clades.

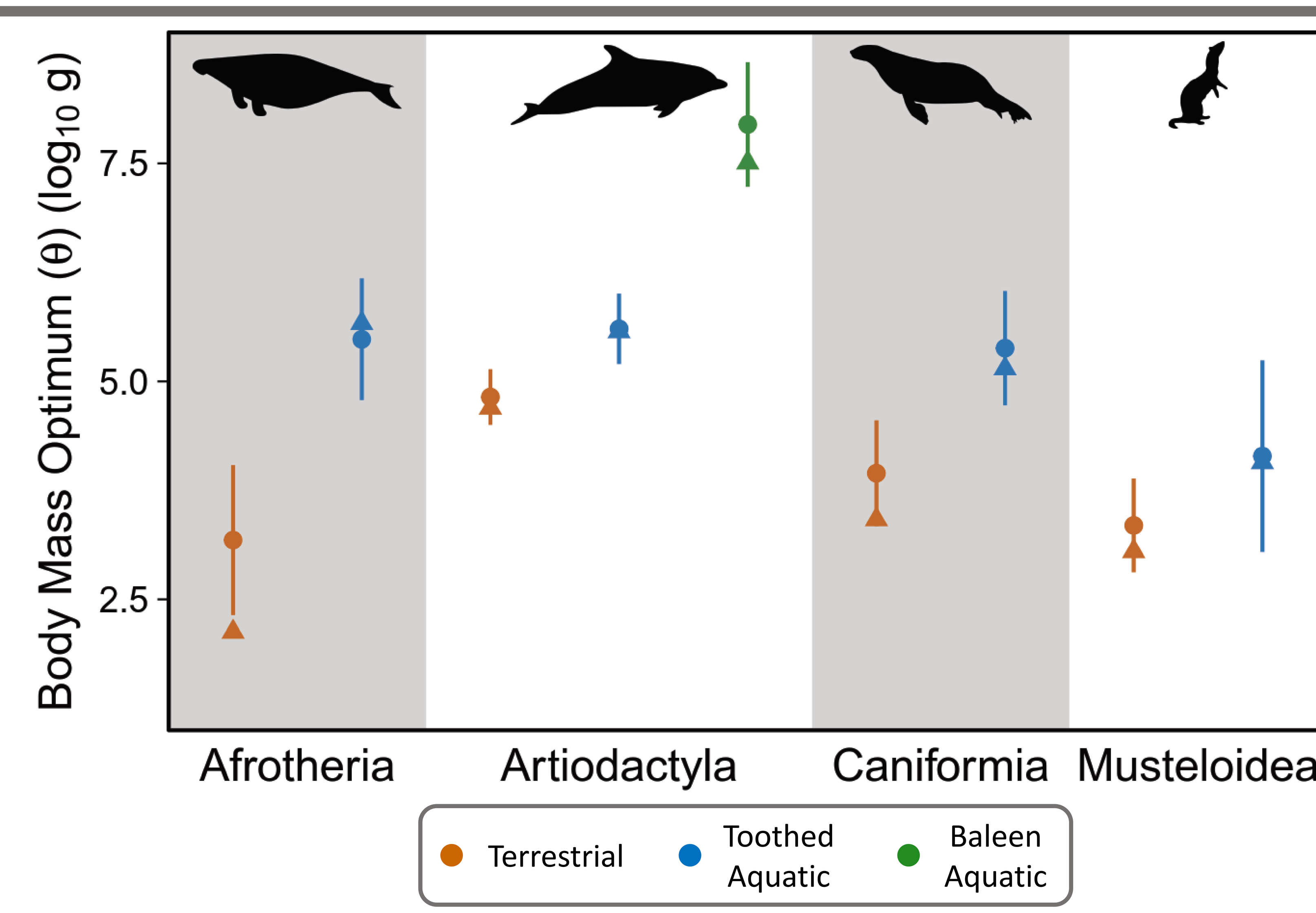
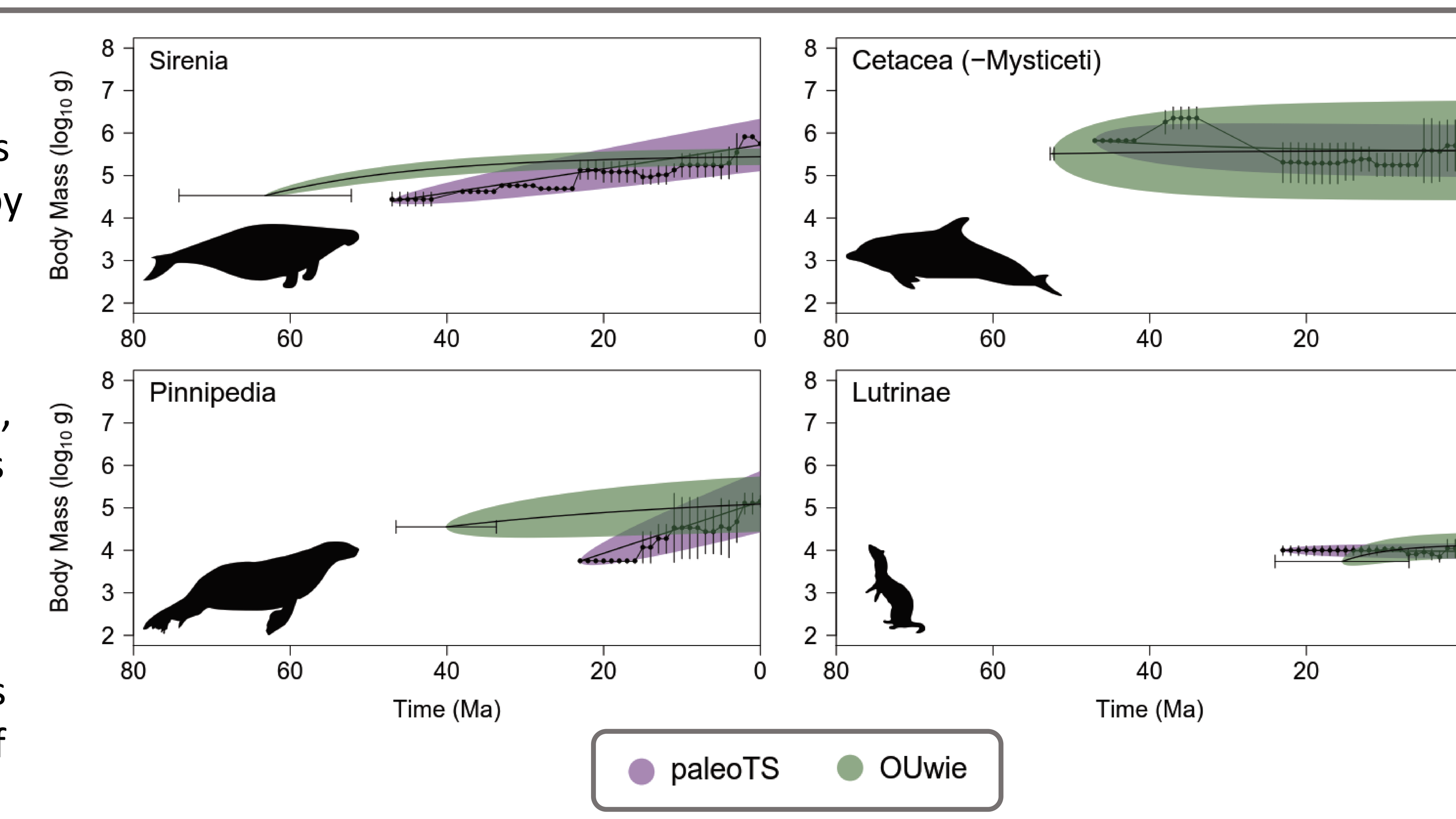


Figure 3.2: **Comparison of results of phylogenetic and fossil analyses.** Overlay of Ornstein-Uhlenbeck processes using average parameters as estimated by OUwie phylogenetic and paleoTS fossil analyses for individual clades. Points and error bars within paleoTS results represent average raw data and variance, respectively, per Myr time bin. Error bars associated with the OUwie curve origins indicate the extents of branches associated with aquatic transitions.

Note the differences between the results of the phylogenetic and fossil analyses of Sirenia and Pinnipedia.



4. Conclusions

- 3 out of 4 mammal groups living in aquatic environments have *larger optimal body sizes* than their terrestrial counterparts.
- Results suggest the existence of a *body size attractor* (~500 kg) that has been discovered independently by these three aquatic clades, coupled with shared relatively rapid selection toward, and limited deviation from, this attractor (not shown here).
- Some groups may still be getting larger, although analyses suggest there may be an *upper limit* without help from key innovations (e.g. baleen).
- The sustained small size of aquatic mustelids could indicate the presence of a *second attractor* at a smaller size *or competitive exclusion* from the 500 kg attractor.
- Analyses of the fossil record find *indistinguishable optima* (with large error), but produce different model support.

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