Morphological Grouping and Body Mass Prediction Models

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Every facet of an organism's function is affected by its body size, for example, heart rate, metabolism, organ size and function, feeding ecology, and locomotion. Using body size to assess the function and size of organs in extant mammals is relatively straightforward. However, estimating the body size and organ function of transitional fossil species, such as the Eocene whales, is difficult. The Eocene whales are diverse in body size and structure resulting from changes in habitat, locomotion, and feeding mechanism. Therefore, an all-encompassing allometric model will not provide the most accurate body size estimation for each fossil whale family and consequently, a less accurate organ function assessment. The goal of my research is to predict the body size of the Eocene whales using morphological models of extant mammals as guides. The first stage is the morphological grouping and body mass prediction models using modern mammal skeletons.

Two principles guide the building of allometric models for body mass estimation. First, allometric equations are formulated using data sets compiled from animals of similar function and structure. Second, allometric equations cannot be extrapolated beyond the range of data from which they are constructed. Given the diversity of morphology found within the Eocene whales, I chose 80 species from 24 families of modern aquatic, semi-aquatic, and terrestrial mammals to satisfy these two requirements. The families chosen are shown in Table 1.1.

Table 1.1 Families used in the Linear Regression and PCA analyses

Balaenopteridae	Phocidae
Delphinidae	Odobenidae
Iniidae	Mustelidae
Monodontidae	Ursidae
Phocoenidae	Canidae
Physeteridae	Cervidae
Pontoporiidae	Moshidae
Eschrichtiidae	Tragulidae
Ziphiidae	Suidae
Trichechidae	Tayassuidae
Otariidae	Tapiridae
Phocidae	Hippopotamidae

Figure 1.1 Modern Morphological Groups Used

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I measured the skull, vertebrae, and appendicular bones of the 80 chosen species I calculated an average body mass representative of each species using recorded body weights. The variables measured are shown in Table 2.1 and examples are shown in Figure 2.1.

Figure 2.1 Variables Measured

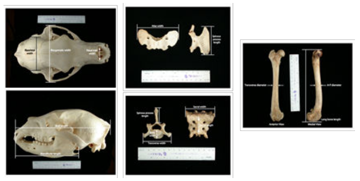


Table 2.1 Measurements for Linear Regression and PCA

Appendicular	Skull	Vertebral
Humerus length	Skull length	C1 transverse width
Humerus a-p diameter midshaft	Bimastoidal width	C1 transverse width
Humerus m-l diameter midshaft	Biparieal width	C1 vertebral foramen width
Radius length	Bizygomatic width	C1 vertebral foramen height
Radius a-p diameter midshaft	Postorobital width	C2 spinous process length
Radius m-l diameter midshaft	Nasal inlet width	C2 body height (w/ dens)
Ulna length	Pharyngeal width	C2 body width
Ulna a-p diameter midshaft	Bicondylar width	C2 vertebral foramen width
Ulna m-l diameter midshaft	Foramen magnum width	C2 vertebral foramen height
Femur length	Foramen magnum length	C7 body height
Femur a-p diameter midshaft	Skull height (basion-bregma)	C7 body width
Femur m-l diameter midshaft	Mandibular ramus length	C7 vertebral foramen width
Femur length	Mandibular corpus length	C7 vertebral foramen height
Femur a-p diameter midshaft	Coronoid process height	C7 inferior width
Femur m-l diameter midshaft		C7 transverse width
Tibia length		C7 spinous process length
Tibia a-p diameter midshaft		Sacral superior width
Tibia m-l diameter midshaft		S1 body width
		S1 vertebral foramen width
		S1 vertebral foramen height

For each PCA analysis completed, I created a linear regression equation to predict body size from the skeletal variables used in each analysis and the calculated average body sizes. I tested these prediction models using the measurements from 12 representative skeletons that were not included in the data set used to create the model, specifically *Odocoileus virginianus, Tragulus napu, Hippopotamus amphibus, Tapirus indicus, Sus scrofa, Canis lupus lycaon, Nyctereutes procyonid, Ehydra lutris, Gulo gulo, Neophoca cinerea, Lobodon carinophagus,* and *Ursus maritimus.*

For the prediction model using all skeletal variables, the standard error of the estimate (SEE) for all 12 test individuals ranged from 0.3359 – 0.7496. For the skull variables, the SEE ranged from 0.1260 – 0.3197. For the limb variables, the SEE ranged from 0.1716 – 0.3964. For the vertebral variables, the SEE ranged from 0.1511 – 0.2851. The predictions from each model are similar to each other and to the ranges used to build the average body weight for the models. These small SEE values substantiate the accuracy of these predictive models and the reliability of their respective confidence intervals (CI) and prediction intervals (PI) for the models. The 95% CI and PI are not presented here due to size limitations (available on request). These results support the use of these linear regression models to predict the body mass of the Eocene whales in the second stage of this project.

Table 3. 1 Predicted Values for Test Mammals

Test Mammals	All Variables		Limb Variables		Skull Variables		Vertebral Variables	
	Fit (kg)	SE Fit	Fit (kg)	SE Fit	Fit (kg)	SE Fit	Fit (kg)	SE Fit
Odocoileus virginianus	89.5	0.4877	51.0	0.2623	55.2	0.184	85.5	0.2388
Tragulus napu	3.0	0.7006	4.1	0.2292	5.1	0.1681	4.5	0.2746
Hippopotamus amphibus	1478.4	0.5413	1008.2	0.3006	2491.4	0.3197	1720.4	0.2742
Tapirus indicus	284.9	0.4093	272.3	0.3261	300.7	0.1819	333.5	0.2195
Sus scrofa	175.5	0.7469	89.5	0.229	77.2	0.2937	64.8	0.2659
Canis lupus lycaon	34.5	0.3809	49.5	0.2694	49.4	0.126	53.8	0.196
Nyctereutes procyonid	2.4	0.6814	3.7	0.1716	5.0	0.2173	3.4	0.2284
Enhydra lutris	53.5	0.6875	26.6	0.3964	49.2	0.2199	25.4	0.2851
Gulo gulo	42.0	0.5874	14.2	0.1807	30.0	0.2872	18.6	0.2176
Neophoca cinerea	153.2	0.5249	264.6	0.2686	165.4	0.1671	206.9	0.2431
Lobodon carcinophagus	219.5	0.3359	153.1	0.2319	413.4	0.1927	270.1	0.1959
Ursus maritimus	176.3	0.5073	157.1	0.2913	153.5	0.1899	267.4	0.1511

Four PCA analyses were performed using all measured variables, only the skull variables, only the limb variables, and only the vertebral variables. Figure 2.1 shows PCA Factor 1 vs Factor 2 for all variables measured. This graph shows a clear delineation between the aquatic and terrestrial families. Figure 2.2 is PCA Factor 2 vs 3 for all variables measured and identifies five morphological groups: Aquatic, Semi-aquatic, Semi-terrestrial, Large Terrestrial and Small Terrestrial.

Four PCA analyses were performed using all measured variables, only the skull variables, only the limb variables, and only the vertebral variables. Figure 2.1, 2.2, 2.3 and 2.4 show PCA Factor 1 vs Factor 2 vs 3 for each PCA analysis. Three of these graphs show a clear delineation between the aquatic and terrestrial families. Figure 2.1 is PCA Factor 1 vs 2 vs 3 for all variables measured, and it identifies four morphological groups: Aquatic, Semi-aquatic, Semi-terrestrial, and Terrestrial. Viewing Fac 2 vs Fac 3 for this analysis shows a division into 5 groups by separating the Terrestrial group into a Small Terrestrial group and a Large Terrestrial group. Only Fig 2.3 does not separate the aquatic mammals, whales and manatees, into separate groups. These results suggest that the differences between the appendicular and vertebral skeletons of these mammals are distinct. Therefore, these elements can be used to separate aquatic and terrestrial mammals morphologically. In contrast, the skulls of these mammals share many similar characteristics and do not allow for such distinct grouping as a single characteristic. Nevertheless, when the skull is considered with the other skeletal elements, the combination of morphological characteristics separate these mammals into distinct morphological groups reflective of their size, habitat, and method of locomotion.

Figure 2.1 Fac 1 vs Fac 2 vs Fac 3 All Variables

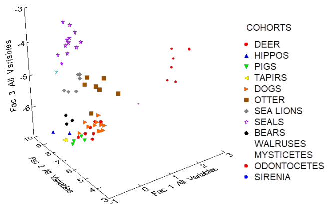


Figure 2.2 Fac 1 vs Fac 2 vs Fac 3 Limb Variables

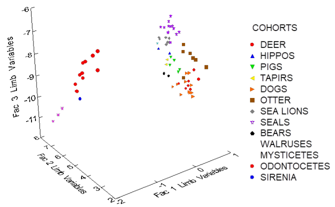


Figure 2.3 Fac 1 vs Fac 2 vs Fac 3 Skull Variables

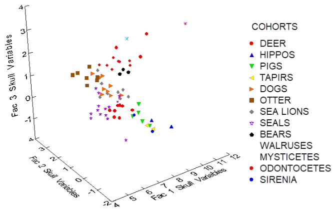
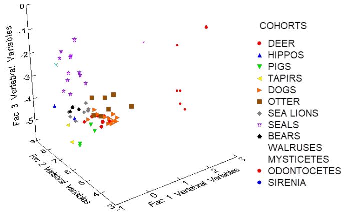


Figure 2.4 Fac 1 vs Fac 2 vs Fac 3 Vertebral Variables



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