

Reconstructing Body Size in Extinct Crown Cetacea (Neoceti) Using Allometry, Phylogenetic Methods and Tests from the Fossil Record

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Abstract Living cetaceans exhibit interspecific size ranging across several orders of magnitude, and rank among the largest vertebrates ever. Details of how cetaceans evolved different body sizes, however, remain obscure, because they lack basic morphological proxies that have been traditionally used in other fossil vertebrates. Here, we reconstruct the body size of extinct crown group cetaceans (Neoceti) using different regression methods on extant skull and length data, in a phylogenetic context. Because most fossil cetaceans are fragmentary, we developed regression equations to predict total length based on cranial metrics that are preserved on most fossil crania. The resultant regression equations are based on a database of skull and length data from most extant lineages of cetaceans ($n=45$ species; 272 specimens), sampling all living mysticete genera and all major clades of odontocetes. In generating predictive equations, we compared both conventional species data regression and independent contrast regression methods, as

well as single trait predictors and a new approach that combines the advantages of a partial least squares (PLS) multivariate regression with independent contrasts. This last approach leverages the predictive power of using multiple correlated proxies. Lastly, we used the rare occurrences of fossil cetaceans with preserved total lengths to test the performance of our predictive equations for reconstructing body size from skull measurements alone. Our results demonstrate that incorporating information about phylogenetic relationships and multiple cranial measures in PLS scaling studies increases the accuracy of reconstructed body size, most notably by reducing prediction intervals by more than 70%. With this empirical foundation, we highlight the outline of major features in the evolution of body size for Neoceti and future opportunities to use these metrics for paleobiological questions.

Keywords Cetacea · Fossil record · Body size · Allometry · Independent contrasts · Partial least squares

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Introduction

Perhaps no variable has a greater singular impact on an organism's biology than its size. In the past 30 years, the study of body size and scaling in comparative biology has emerged as a coherent line of investigation that impacts community ecology, biomechanics, physiology, functional morphology, and paleobiology (LaBarbera 1989; Damuth and MacFadden 1990; Brown 1995; Thomason 1997; Currey 2004; Bonner 2006). For many biological questions, comparisons in organismal size often span several orders of magnitude. Classic scaling studies have used extant cetaceans (or crown Cetacea) as superlative extremes of large body size in comparison with other mammals,

vertebrates, and even metazoans (Calder 1984; Schmidt-Nielsen 1984). No living or extinct vertebrate rivals the mass of the largest cetaceans, such as blue whales (*Balaenoptera musculus*). Even the smallest living cetaceans are relatively large compared to the majority of terrestrial mammals, including their closest living artiodactylan sister taxa (see body masses listed in Nowak 1999). However, extant cetaceans are obligately aquatic, unlike their nearest relatives. Previous authors have highlighted this underlying functional difference (i.e., the buoyancy of water and release from gravity's terrestrial constraint) as an important factor that has permitted the evolution of large body size for crown cetaceans (e.g., Slijper 1962). This explanation implies that the wide range in extant cetacean body size (total lengths ranging from 1 to 30 m) is related to a dramatic ecological transition in their evolutionary history. However, the evolutionary processes underlying this correlation remain largely unexplored.

Since the Triassic, many tetrapod clades have undergone similar transitions from terrestrial to aquatic lifestyles (Carroll 1997). In the Cenozoic, many other marine mammal lineages independently evolved aquatic lifestyles from terrestrial ancestry, but it is the relatively rich and well-studied fossil record of early cetaceans that has become a textbook case for illustrating macroevolutionary transitions. Fossils of stem Cetacea (more widely known as the paraphyletic group Archaeoceti) from the middle and late Eocene provide the basis for understanding the range of musculoskeletal, sensory, ontogenetic, and ecological shifts that allowed early cetaceans to transition from a semi-aquatic to an obligately aquatic lifestyle (Thewissen and Bajpai 2001; Thewissen and Williams 2002; Gingerich 2005a; Gingerich et al. 2009). Although most early cetaceans are represented by incomplete skeletal material, body size estimates have been generated for some stem cetaceans, based on thoracic vertebral centra size and using regression data from extant marine mammals (Gingerich 1998; Gingerich et al. 2001). Such estimates, coupled with isolated comparisons of individual elements, place the largest of the semi-aquatic early cetaceans (remingtonocetids and protocetids) between 390–750 kg (Gingerich 1998; Gingerich et al. 2009). The first obligately aquatic stem cetaceans, like basilosaurids, are better represented from near-complete skeletons, and have been estimated to approach sizes between 1140–5840 kg (see median values reported by Gingerich 1998; also see Marino et al. 2000, 2004; Uhen, 2004). The discrepancy in body size classes between semi-aquatic and obligately aquatic Eocene cetaceans is largely connected to their initial transition from land to sea (Gingerich 2005a), but these stem taxa are not directly related to living cetaceans, and thus they provide limited data for understanding the evolutionary origins for the extremely broad size range witnessed in crown cetaceans.

Resolving this evolutionary history requires a better understanding of body size in extinct crown cetaceans (or Neoceti sensu Fordyce and Muizon 2001), which is a task hindered by several challenges. First, complete skeletons of fossil Neoceti are rare, and the great majority of fossil taxa consist of isolated crania (Uhen and Pyenson 2007; Fordyce 2009). Second, standard body size proxies in mammalian paleobiology (e.g., molar dimensions, limb bone cross-sectional area) are uninformative in Neoceti, because they possess highly derived dentition and lack weight-bearing limbs. To overcome these challenges, some authors have advocated using body size proxies solely derived from single cranial measurements that are patent in fossil taxa. For example, Marino et al. (2003, 2004) reconstructed the history of brain size evolution in toothed whales using endocranial volumes calculated from occipital condyle breadth (OCB), a proxy also advocated by Uhen (2004). Bianucci et al. (2008) used the breadth across the postorbital processes of the frontals to estimate size in fragmentary remains of fossil beaked whales (Ziphiidae) from South Africa. Clementz et al. (2009) and Sarko et al. (2010) also used occipital condyle breadth for estimating body size in fossil sirenians, a group that shares similar constraints because of a parallel evolutionary history (Domning 2001).

In this paper, we provide a method for reconstructing body size in fossil Neoceti using allometric equations that relate multiple cranial measurements to total length in extant cetaceans. We improve on earlier reconstruction methods in two ways: 1) we incorporate a multivariate partial least squares (PLS) regression approach to leverage the predictive value from multiple correlated measurements of the skull with total length; and 2) we account for phylogenetic relationships using independent contrasts. For the first consideration, we aimed to generate more informative predictions of body size by using a combination of multiple measurements (i.e., body size proxies), rather than using a single predictive metric. Such a multivariate approach also minimizes the effects of non-uniform allometry across the clade, which are readily apparent between living toothed and baleen whales (crown groups Odontoceti and Mysticeti, respectively). For the second consideration, we incorporate independent contrasts to account for the non-independence of comparative data. Felsenstein (1985) first articulated a quantitative framework for assessing the impact of evolutionary relationships in comparative studies with the concept of independent contrasts. Since this time, phylogenetic comparative methods have emerged as a robust set of methodological tools for understanding the phylogenetic underpinnings of comparative datasets from extant taxa (Garland et al. 1992, 2005; Garland and Ives 2000). Paleobiologists have already adopted phylogenetic comparative methods for estimating

body size in extinct mammals (Reynolds 2002; Muhlbachler and Solounias 2006; Sears et al. 2008) and, in some cases, demonstrated the utility of these methods in conjunction with fossil data for evaluating ancestral states (Polly 2001; Finarelli and Flynn 2006).

The size reconstruction method presented herein relies on an extensive dataset of cranial measurements from extant Neoceti, including all living genera of Mysticeti and nearly every family of Odontoceti. This dataset includes vouchered museum specimens that also have total length measurements, which is a standard measurement for cetologists (Mackintosh and Wheeler 1929; Norris 1961). We conduct single and multivariate standard regressions to determine how well these cranial measurements predicted body size in extant Neoceti. We then use phylogenetic methods to reanalyze these relationships with independent contrasts. For verification and comparison, we test our predictions of body size for fossil Neoceti using rare fossil specimens where total body length is preserved, in addition to cranial material. Finally, we apply these phylogenetic multivariate relationships to interpolate the body length for key fossil Neoceti where body lengths are unavailable. Our results indicate that incorporating both multiple predictor variables and phylogenetic relatedness limit confounding assumptions, provide more consistent predictions in our test cases, and most significantly, improve the confidence (i.e., reduce the prediction interval) of our reconstructed body size estimates. At a broader scope, these robust and quantified estimates of body size in fossil crown cetaceans reveal a pattern of recently derived large body size that may underlie a changing ecological role for Neoceti in the Neogene. Moreover, such size estimates enhance the picture of size evolution in cetacean history from the earliest semi-aquatic cetaceans through to the vast size range of modern taxa.

Institutional Abbreviations (in Main Text and Captions)

LACM, Division of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, U. S. A.; OU, Geology Museum, University of Otago, Dunedin, New Zealand; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, University of California Museum of Paleontology, Berkeley, California, U. S. A. See Appendices for other institutional abbreviations.

Materials and Methods

Taxon Sampling

Our extant taxon dataset consisted of 272 adult individual specimens from 45 species of Neoceti, collected from

curated natural history collections in both Northern and Southern hemispheres. (See Appendix 1 in the Supplementary Information for full list of institutions, taxa, and specimens). Among mysticetes, we collected body size measurement data from every living genus, and nearly every species. Species not included were either unavailable or taxonomically unstable (e.g., *Balaenoptera edeni-B. brydei* complex; see Sasaki et al. 2006). Among odontocetes, we collected body size measurement data on all major lineages (Nikaido et al. 2001), thereby sampling all recent physeterids, kogiids, platanistids, inioids, and most delphinoids. Because of its rarity, it was not possible to include *Lipotes vexillifer*, even though it singularly represented a lineage of odontocetes (Pyenson 2009). The adult body size of *Lipotes* does fall within the range for its near relatives, and therefore its absence from the dataset likely poses no serious sampling issues. The otherwise broad and thorough taxonomic sampling of this study provides a solid foundation for developing regression equations, particularly in a phylogenetic context. Our dataset included only physically mature specimens. We judged skeletal maturity on the basis of suture fusion in the cranium and the degree of porosity on the occipital condyles (see more references and details in Supplemental Information). Recent work (Walsh and Berta 2011) has borne the validity of such qualitative metrics for Balaenopteroidea, and we presume that they broadly apply to all Neoceti, in the absence of any quantitative evidence otherwise. Lastly, we averaged all specimen values within a species, irrespective of sex. With the exception of *Physeter*, living Neoceti are not especially sexually dimorphic in terms of adult body size (see, e.g., Mackintosh and Wheeler 1929) and thus we were not concerned about artificially depressing male size and enhancing female values (Gingerich et al. 1982; Gordon 2003).

Measurements

Among all vertebrates, the large size of many cetaceans pose logistical challenges towards collecting morphometric data that are rivaled only by sauropod dinosaurs. For cranial measurements, we measured specimens using either a 2 m anthropometer or forestry calipers (up to 1.8 m); both tools work equally effectively. For specimens whose crania exceeded the upper limit of anthropometers and large calipers, we used a 30 m transect tape measure, measuring distances between linear points on parallel surfaces (e.g., floors or walls, depending on the orientation of the crania) that were orthogonal to desired measurement plane (Fig. 1). For body size measurements, we selected total length (TL), a value that has been historically used by cetologists and marine mammalogists since the early twentieth century (Mackintosh and Wheeler 1929; Norris 1961). As opposed to body mass, which is an extremely difficult value to

measure reliably for cetaceans heavier than ~100 kg (Gambell 1970; Lockyer 1976), total length is mostly invariant to fluid loss and distortion once the specimen is on land. Moreover, since its inception for the pelagic whaling industry, TL has become a standardized measurement that is usually recorded along with attendant natural history data for cetaceans. We actively selected vouchered museum specimens that possessed this attendant data for inclusion in our dataset.

We selected symplesiomorphic cranial measurements (Fig. 1) that would thus be present in both crown lineages of Neoceti as well as extinct stem taxa belonging to those lineages. These measurements are either traditional from the mammalogical literature, or standard landmarks (see, e.g., Perrin 1975; Mead and Fordyce 2009). We also selected cranial measurements as proxies based on their preservational quality (i.e., their likelihood of preservation in fragmentary fossil taxa). Unusually well-preserved specimens may have complete rostra (often missing teeth), but diagenetic processes related to fossilization can still distort the shape and thus proportions of the skull (as with ichthyosaurs, which are also preserved in marine sediments; Motani 1997). Fortunately, most fossil cetacean taxa are not distorted in the cranial regions (i.e., the region posterior of

the rostrum), and the selected cranial proxies are also located near relatively dense bone, which increases the likelihood of preservation and non-distortion. Thus, the measurements selected for this study were: a) relatively accessible, even on large skulls; b) they consisted of six variables, including total length, which made data collection reasonable and not overly time-consuming; c) the skull measurements were all symplesiomorphies, and therefore detectable on both stem and crown lineages within Neoceti; and d) the skull measurements were easily identified on fossil skulls, and the least likely to deform or become lost through diagenesis and taphonomic alteration. Appendix 1 in the Supplementary Information describes these specific anatomical points in detail.

Phylogenetic Hypotheses

Topologies—To reconstruct body size in extinct cetaceans within a comparative context, we focused our selection of phylogenetic hypotheses on molecular trees for two reasons. First, molecular studies of Neoceti phylogeny have generally used a much broader taxonomic sampling of living cetacean species than morphological ones. Second, molecular phylogenetic trees ought to have greater inde-

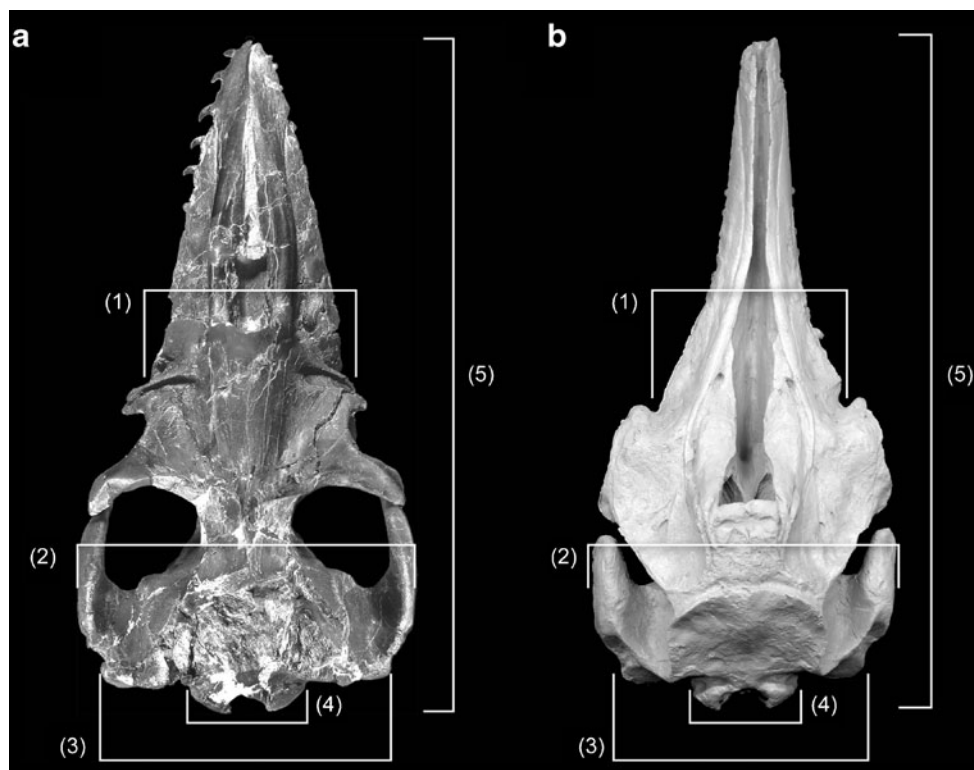


Fig. 1 Morphological landmarks of the cetacean skull used in this study. **a** *Aetiocetus weltoni* (UCMP 122900); and **b** *Waipatia maerewhenua* (cast of OU 22095), both scaled to approximately the same condylobasal length, with anterior towards page top. Landmarks denoted as follows: 1) width of antorbital notches or antorbital process

of maxillae (AON); 2) bizygomatic width (BIZYG); 3) exoccipital width (EXOCC); 4) occipital condyle breadth (OCB); and 5) condylobasal length (CBL). Note that symplesiomorphic landmarks illustrated here are readily available in all crown cetaceans. *Aetiocetus weltoni* image courtesy of T. A. Deméré

pendence from size-related or size-influenced characters used to build morphological data sets. In the past 15 years, extant cetacean systematics have undergone a renaissance, with molecular data providing a wealth of phylogenetic data for generating robust hypotheses of relationships among major extant lineages (e.g., Nikaido et al. 2001; Sasaki et al. 2006), although species-level resolution is preferred for comparative datasets using extant species data at branch termini (i.e., tips). At the onset of this study, May-Collado and Agnarsson (2006) provided the most comprehensive cetacean phylogeny at the species level, especially for odontocetes. May-Collado and Agnarsson (2006), however, had poor sampling of extant mysticetes, and thus we built a composite phylogeny with Sasaki et al. (2006) providing a species level resolution for relationships among living Mysticeti (Fig. 3). More recently, Agnarsson and May-Collado (2008), McGowen et al. (2009), and Steeman et al. (2009) have produced species level phylogenies of extant cetaceans, but they do not differ fundamentally for most intrafamilial relationships among Neoceti.

Because we could not collect body size data for all species listed in these latter studies, we pruned our selected trees to generate topologies representing our dataset (Fig. 2) (See Appendix 2 in the Supplementary Information for specific pruning and compilation of Operational Taxonomic Units). These permutations consist of the following trees (see Fig. 2 and Table 1): Set 1) for odontocetes, we pruned May-Collado and Agnarsson (2006) (Fig. 2b); Set 2) for mysticetes, we used two different topologies reported in Sasaki et al. (2006), including a fully resolved topology and one with an unresolved relationship between *Eschrichtius* and balaenopterids (Fig. 2c, d); and Set 3) for all cetaceans, we considered the phylogeny of May-Collado and Agnarsson (2006) alone as well as two composite trees generated by combining May-Collado and Agnarsson (2006) for odontocetes with each of the Sasaki et al. (2006) trees (Fig. 2a). In combining the two phylogenies, we assumed a sister relationship between odontocetes and mysticetes, a relationship that is well supported in existing phylogenies of cetaceans and other artiodactylans

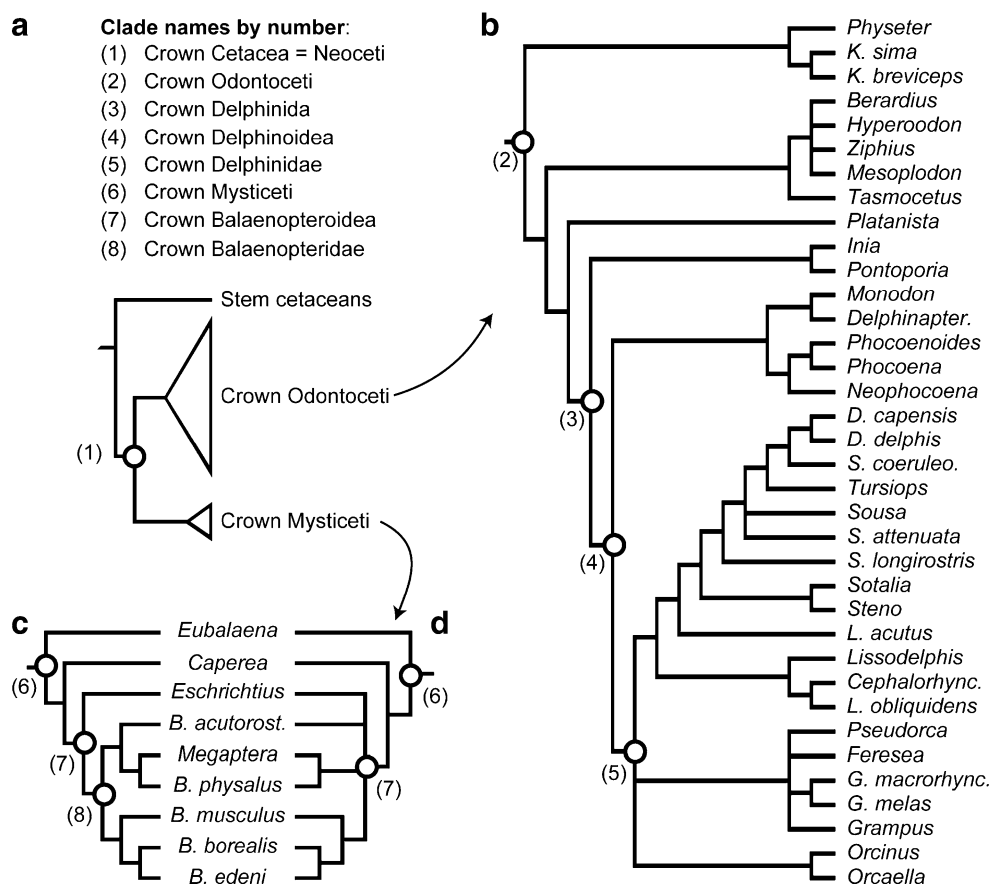


Fig. 2 **a** Molecular phylogenetic trees of extant Neoceti used in this study; **b** May-Collado and Agnarsson (2006) for odontocetes; **c** Sasaki et al. (2006) for mysticetes with resolution for Balaenopteroidea; and **d** Sasaki et al. (2006) for mysticetes with an unresolved polytomy for Balaenopteroidea. For crown Neoceti, encompassing all the extant cetaceans sampled in our morphometric dataset, we used either May-

Collado and Agnarsson (2006)'s full tree, pruned to the taxa in our dataset, or a composite of trees from **b**) + **c**) or **b**) + **d**). Abbreviations: *acutorost.* = *acutorostrata*; *Cephalorhync.* = *Cephalorhynchus*; *coeruleo.* = *coeruleoalba*; *Delphinapter.* = *Delphinapterus*; *macrorhync.* = *macrorhynchus*

Table 1 Reconstruction results for single variable regressions to predict total length in *Atocetus* and *Balaenoptera siberi*, with varying phylogenetic tree reconstructions and branch length transformations. Values are all reported in centimeters. Deviations from actual TL for each fossil taxon are reported as “% dev.” Phylogenetic trees are as follows: Tree 1: May-Collado and Agnarsson (2006) for all cetacean species; Tree 2: May-Collado and Agnarsson (2006) for odontocetes plus Sasaki et al. (2006):fig. 3 for mysticetes; Tree 3: May-Collado

and Agnarsson (2006) for odontocetes plus Sasaki et al. (2006):fig. 5 for mysticetes; Tree 4: May-Collado and Agnarsson (2006) for odontocetes only; Tree 5: Sasaki et al. (2006):fig. 3 for mysticetes; Tree 6: Sasaki et al. (2006):fig. 5 for mysticetes. All1: all branch lengths equal to 1; Grafen's: Grafen (1989)'s branch length transformation; Ultramet.: ultrametricizing. Assuming a star phylogeny is equivalent to conventional regression techniques

Phylogenetic Hypothesis		Single Variable Regression (bizegomat width)						
Tree	BL Model	<i>n</i>	Exponent (\pm 95% CI)	R^2	<i>Atocetus</i> prediction range	% dev.	<i>Balaenoptera siberi</i> prediction range	% dev.
Star	N/A	45	0.95 \pm 0.11	0.96	[64 – 142 – 313]	–18%	[506 – 1119 – 2475]	47%
Tree 1	All 1	42	0.95 \pm 0.10	0.89	[94 – 128 – 173]	–26%	[805 – 1072 – 1427]	41%
	Grafen's	42	0.92 \pm 0.10	0.89	[82 – 129 – 204]	–25%	[818 – 1052 – 1354]	39%
	Ultramet.	42	0.94 \pm 0.10	0.89	[90 – 129 – 187]	–25%	[794 – 1060 – 1416]	40%
Tree 2	All 1	45	0.93 \pm 0.10	0.89	[93 – 129 – 180]	–25%	[776 – 1066 – 1465]	40%
	Grafen's	45	0.92 \pm 0.10	0.89	[79 – 130 – 213]	–25%	[754 – 1041 – 1438]	37%
	Ultramet.	45	0.94 \pm 0.10	0.89	[87 – 129 – 191]	–26%	[768 – 1056 – 1452]	39%
Tree 3	All 1	45	0.92 \pm 0.10	0.89	[92 – 129 – 181]	–26%	[777 – 1039 – 1389]	37%
	Grafen's	45	0.93 \pm 0.10	0.89	[80 – 129 – 208]	–25%	[742 – 1036 – 1448]	36%
	Ultramet.	45	0.94 \pm 0.10	0.89	[88 – 129 – 188]	–26%	[779 – 1047 – 1407]	38%
Tree 4	All 1	36	0.98 \pm 0.11	0.90	[93 – 126 – 171]	–27%	N/A	N/A
	Grafen's	36	0.94 \pm 0.10	0.90	[82 – 131 – 208]	–25%	N/A	N/A
	Ultramet.	36	0.96 \pm 0.11	0.89	[89 – 130 – 189]	–25%	N/A	N/A
Tree 5	All 1	9	0.84 \pm 0.29	0.86	N/A	N/A	[635 – 1046 – 1724]	38%
	Grafen's	9	0.87 \pm 0.33	0.81	N/A	N/A	[577 – 1037 – 1865]	36%
	Ultramet.	9	0.87 \pm 0.33	0.82	N/A	N/A	[624 – 1042 – 1741]	37%
Tree 6	All 1	9	0.84 \pm 0.24	0.86	N/A	N/A	[687 – 1025 – 1528]	35%
	Grafen's	9	0.89 \pm 0.33	0.78	N/A	N/A	[657 – 1030 – 1613]	36%
	Ultramet.	9	0.88 \pm 0.30	0.81	N/A	N/A	[692 – 1038 – 1558]	37%

(Agnarsson and May-Collado 2008; McGowen et al. 2009; Steeman et al. 2009). In total, we used six different tree topologies as a basis for generating clade-specific reconstructions of body size within Neoceti.

Branch lengths—Many comparative methods, like the independent contrasts approach used below, require normalization of trait values (i.e., contrasts) by accounting for branch lengths between taxa and ancestral nodes (Schluter et al. 1997; Cunningham 1999; Garland et al. 2005). Branch lengths and molecular evolution rates were not equally reported among the published phylogenetic hypotheses in our study; moreover, it is likely that such values would have differed among our phylogenetic hypotheses. Thus, we tested our body size reconstructions over a range of three possible branch length models, implemented with the PDAP module (Midford et al. 2006) of Mesquite 2.0 (Maddison and Maddison 2009). We first assumed all branch length segments were equal, effectively assuming that the absolute contrasts between each node were directly comparable. Additionally, we considered branch length models using ultrametricized trees and Grafen's branching model (Grafen 1989), each of which sets independent

branch segment length in a topology-dependent manner. We selected these permutations agnostically, with no presumption about which model would best describe cetacean size evolution. We used these three alternative branch length models to bound a wide range of possible models of evolutionary rates. This approach enabled us to detect whether our conclusions depended on specific phylogenetic hypotheses or were robust across the range of possible resolutions and branching models. In all, we considered six different topologies each with three different branch length models for a total of eighteen phylogenetic hypotheses. Lastly, we conducted a conventional regression that technically assumed a star phylogeny (i.e., all taxa equally related to all others). We decided to keep this regression separate from the other phylogenetic hypotheses for convention and ease of comparison.

Regression Models

The major goal of this study was to provide body size reconstructions for fossil cetaceans and compare the results of different regression approaches. Both single and multi-

variate approaches are prevalent in the literature on body size reconstruction in paleobiology (see, e.g., Mendoza et al. 2006; Sears et al. 2008). In some cases, fossil taxa may not preserve all the desired variables, and thus multivariate predictor variables are not feasible. On the other hand, for instances where fossil taxa do have multivariate predictors (e.g., for complete specimens, or for composite values from multiple specimens), the statistical value of added predictors can warrant using multivariate approaches. In total, our study assessed the following types of regression models (a shorthand for each model listed, hereafter, listed in parentheses): a single predictor, non-phylogenetic regression (single non-IC); a single predictor regression with independent contrasts (single IC); a multivariate non-phylogenetic regression (PLS non-IC); and a multivariate regression with independent contrasts (PLS IC). Below, we expand on the regression methods used to develop both IC and PLS models.

Independent contrasts (IC)—Because all organisms share a common evolutionary history, taxa are not independent samples in comparative datasets. Thus, any investigation of interspecific scaling relationships must account for the phylogenetic relationships of the taxa under consideration. Felsenstein (1985)'s independent contrasts method provides a statistical technique for assessing this aspect of comparative datasets, which we adopt here. Using Mesquite 2.0 (Maddison and Maddison 2009), we recorded the contrasts between log-transformed values of body size (total length) and each individual cranial predictor, for each of the six phylogenetic hypotheses. We normalized these contrasts to each of the three branch length permutations, and exported these values into JMP Version 7 (SAS Institute Incorporated 2007) for statistical regressions. We reflected the independent contrasts around the origin to force regressions through the origin, which satisfied the requirement that no change in predictors resulted in no change with dependent variables. Degrees of freedom for confidence and prediction intervals were adjusted to use the original number of taxa minus the number of polytomies in each phylogenetic hypothesis.

Prediction intervals—As Garland and Ives (2000) emphasized, incorporating phylogeny into regression models can sometimes improve predicted values for unsampled taxa. In other words, independent contrasts can reduce prediction intervals (PIs) for reconstructed trait values of unknown species (via interpolation or extrapolation). This beneficial property arises because the methodological approach requires reconstructing only the contrasted trait value between the target lineage and its nearest node in the phylogenetic tree (Garland et al. 1999; Garland and Ives 2000:figs. 1 and 2). To accomplish phylogenetic independent contrast reconstructions within the phylogeny of Neoceti, we first placed the target extinct taxon sister to the appropriate sub-clade. If phylogenetic resolution of the target taxon was lacking or uncertain, we resolved its position as a branch

splitting off from the last common ancestral branch that was shared among all alternative phylogenetic hypotheses for that taxon's placement. The phylogenetic position of fossil taxa in our reconstruction (Fig. 3) therefore does not necessarily represent a statement of their best-supported sister relationships, but rather the node from which contrasts were reconstructed. The resulting reconstruction was therefore valid for any resolution with respect to more derived clades (Garland and Ives 2000). To provide the most conservative reconstructions, we always selected the most stemward possible node as a starting point when uncertainty existed for the placement of a fossil taxon (see Fig. 3).

Following taxon placement at a node, we rerooted the entire tree to that point, in Mesquite 2.0 (Maddison and Maddison 2009). We reconstructed the root node trait values and calculated the contrasts between cranial predictor values from the root node to the target taxon. In our single predictor variable regression, we calculated the prediction interval for the reconstructed total length of the target taxon using the formula from Garland and Ives (2000). As a result of this method, the prediction interval increased with the magnitude of the contrast. Prediction intervals were symmetric around the log of the data and became non-symmetric when we converted back to a linear scale for reporting.

Multivariate Partial Least Squares (PLS)—Scaling studies have traditionally used bivariate regressions with comparative data, using both living and extinct datasets (e.g., Gingerich et al. 1982; Damuth and MacFadden 1990; Gordon 2003). Unlike single trait predictors, multivariate approaches can increase the accuracy of predictions by incorporating variation from more than one predictor variable (e.g., Mendoza et al. 2006). However, simply adding additional morphological variables into a multivariate regression to predict body size does not necessarily improve the statistical model's performance, because each of the predictor measurements can be highly correlated with one another. As a result, each additional measurement beyond the first variable is likely to only add a small increment of independent predictive information to the model. Moreover, adding more variables to a model reduces its statistical power, effectively fitting "noise," or uninformative variability in the data in addition to the predictive trend in body size. As a result, simply incorporating additional highly correlated predictors into a multiple regression rarely improves model performance (Selvin 1995).

However, the use of multiple morphological measurements could improve our predictions of body size if the informative components of each morphological measurement could be incorporated without markedly increasing the number of independent variables in the model. A general approach to this type of problem is to construct a set of new variables formed from linear combinations of the

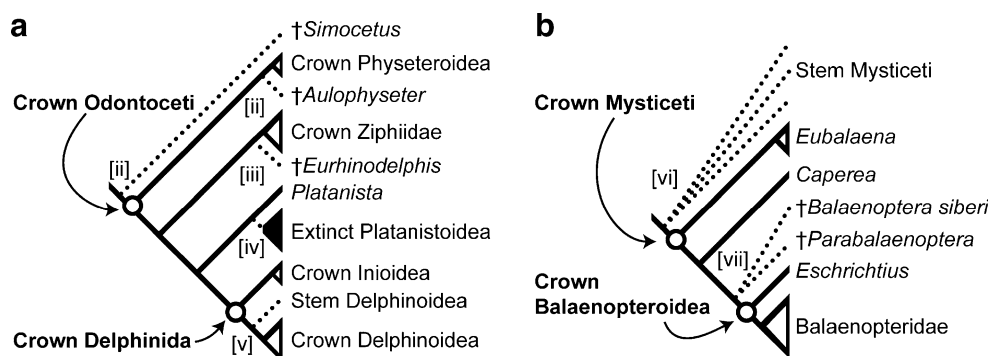


Fig. 3 Phylogenetic placement of select fossil cetacean taxa on a molecular phylogenetic tree. Note that these positions reflect the most conservative placements for reconstructions based on the re-rooting methods used in this study, rather than their likely systematic

positions. Trees follow **a** Sasaki et al. (2006) for mysticetes, resolved; and **b** May-Collado and Agnarsson (2006) for odontocetes. For references about systematic position in fossil cetaceans, see references in Table S1

predictor variables. These linear combinations, or canonical variables, can be constructed to maximize a desired statistical measure in the data. For example, the ubiquitous Principal Components Analysis (PCA) constructs canonical variables that capture the greatest amount of variation in the component variables (Selvin 1995).

Rather than describing the variation of a set of predictor variables (as PCA does), we specifically wanted to evaluate how well multiple variables can capture the variation in a dependent variable (i.e., in this study, body size). To accomplish this regression, we followed a partial least squares (PLS) approach, which constructs canonical variables from multiple morphological measurements such that each canonical variable was independent and maximized the covariance between the predictor and dependent variables (Tobias 1997; McGuire 2010). PLS constructs linear combinations of both predictor and dependent variables that best capture the covariance between the two sets, and hence it is applicable to multiple predictor and multiple dependent variables. However, because our current interest is only in predicting body size, we restricted our analysis to a single dependent variable and constructed canonical variables only from the predictor variables. PLS also permitted us to restrict our regressions to only the most significant canonical variable(s). In effect, this approach allowed us capture the covariance between body size and a relatively large set of morphological measurements with a very reduced set of predictor variables.

Many different regression approaches have been used to understand the allometry of body size in fossil vertebrates. For example, Gingerich and Smith (1984) and Gordon (2003) argued that least square approaches are ideal for generating predictive equations, whereas other authors (Jadwiszczak 2001; Reynolds 2002) have used variations of the major or reduced major axis (MA or RMA) approach. We followed Gingerich and Smith (1984) and Gordon (2003), using the rationale stated by LaBarbera (1989) for using least squares (ordinary and partial) to reconstruct body size in extinct Neoceti. In this study, we extended an independent contrasts

approach to a PLS context by using the contrasts of our five cranial proxies as the component variables in a PLS regression with the contrasts in total length. Extracting coefficients for the canonical predictor variable allowed us to reconstruct extinct Neoceti total length by predicting the contrast in the total length value between the tip value for the extinct taxon and its nearest node, paralleling the single variable independent contrast approach. Prediction intervals were obtained by substituting the first PLS linear combination of skull morphometrics contrasts into the independent contrasts prediction interval equation from Garland and Ives (2000) using a custom MATLAB (MathWorks, Natick, Massachusetts) script.

Testing Predictions Using the Fossil Record

We tested our body size reconstructions for crown cetaceans in unique instances where both a complete skull and total length were preserved in a fossil taxon. For these tests, we used two particular fossil exemplars, one representing fossil odontocetes and another fossil mysticetes. Such preservation is exceedingly rare, and the available sample size for fossil specimens with complete specimens is very limited. Some authors (e.g., Brand et al. 2004) have reported complete specimens in the field, but very few complete skeletons are known in museum collections globally.

For odontocetes, we selected an undescribed kentriodontid from the late Miocene Sycamore Canyon Member of the Puente Formation, in San Bernardino County, California (LACM locality 7503). Here, we provisionally refer this specimen (LACM 150117) to the kentriodontid genus *Atocetus* (Muizon 1988; L. G. Barnes, pers. comm., 2008). LACM 150117 preserves a skull in articulation with the complete skeleton, with total length (TL) of 173 cm (see Fig. S1). Because this specimen was molded and casted prior to preparation, the original articulation of the skeletal elements was preserved intact. Kentriodontidae represents a basal group of delphinidans or delphinoids (Fordyce and Muizon 2001; Fordyce 2009), but the phylogenetic rela-

tionships of kentriodontids have remained volatile, and many workers suggest that the group may be para- or polyphyletic (Geisler and Sanders 2003). Recent work by Geisler et al. (2011:figs. 5 and 6) has placed *Atocetus nasalis* (the type species of the genus) as the sister taxon to crown Delphinoidea. For mysticetes, we used the paratype specimen of *Balaenoptera siberi* (SMNS 47307), from the late Miocene of the Pisco Formation in Peru. Notably, SMNS 47307 preserves an entire articulated skeleton, including a complete skull and an intact vertebral column with a total length (TL) of 760 cm (Pilleri and Pilleri 1989). Deméré et al. (2005) incorporated information about the paratype in an analysis of balaenopteroidean relationships. Results from this analysis placed *B. siberi* well within the crown clade of Balaenopteridae (Deméré et al. 2005). Although *B. siberi* exhibits many key characters that are diagnostic of Balaenopteridae, it is possible that *B. siberi* is also a stem member to crown Balaenopteridae, i.e., closer to crown Balaenopteridae than to Eschrichtiidae. However, because Eschrichtiidae has been frequently recovered within Balaenopteridae (see Deméré et al. 2005; Sasaki et al. 2006; see Marx 2010:fig. 1, for a review), we reconstructed *B. siberi* stem to crown Balaenopteroidea (Fig. 3b).

Within the context of independent contrasts used in this study, the lineages of the aforementioned extinct taxa were placed in a phylogenetic position on a molecular backbone (Fig. 3) according to their most conservative relationship with their most likely parental clade (Tables 4, S1). We emphasize that this placement is not necessarily the most likely phylogenetic placement of these taxa. This distinction was important for re-rooting procedures described herein, because it implied that the lineage terminating in the extinct taxon can be placed anywhere within its parental clade without affecting reconstructed lengths. This situation arises because the reconstructed contrast in length diverges from the first shared node between the taxon of interest and the more derived sister clade. Thus, we placed *B. siberi* most conservatively outside of crown Balaenopteroidea and *Atocetus* in a conservative position as outside of Delphinoidea (Fig. 3).

Results

Scaling Relationships in Extant Neoceti

All four classes of regression models, i.e., single variable both non-IC and ICs (Fig. 4a, c and Table 1) and PLS non-IC and IC (Fig. 4b, d and Table 2), revealed comparable relationships both in terms of the scaling exponent and the percentage of variation in total length explained by the skull metrics (R^2). Slopes did not differ significantly from one, indicating that cranial metrics scale isometrically with body

length when considering either conventional (i.e., non-IC) or IC regressions (regression f -test, $p > 0.1$). The high correlation between crown cetacean cranial and length measurements was not surprising given previous work (e.g., Kemper and Leddard 1999; Uhen 2004), but our results indicated that this strong scaling relationship across extant Neoceti holds even when phylogeny is appropriately incorporated into the regression model.

The PLS, multivariate approach produced higher R^2 values in both the conventional and IC contexts. This result was not entirely attributable to simply increasing the number of variables in the model. Rather, cross-validation within each PLS regression (non-IC or IC) showed that only the first canonical variable significantly contributed to the model. Thus, although we used five measurements to predict body size, there was only a single free predictor variable in each PLS regression model. The increased explanatory power of PLS regression resulted from leveraging the explanatory power of multiple skull metrics rather than from over-fitting noise in the model.

Independent contrasts typically produced regressions with lower R^2 values than conventional, non-IC regressions (compare Tables 1 and 2). Contrasts (differences) in length measurements are usually smaller than the absolute magnitude of the trait and hence contrasts can be more sensitive to random variation, which effectively creates a lower signal to noise ratio. However, the higher R^2 values for non-IC regressions likely arose from the non-independence of each species value artificially inflating the strength of the regression relationship. Cranial metric IC regressions were consistent across all tree topologies and branch length transformations when the entire clade of Neoceti was considered, although it is noteworthy that Trees 5 and 6 produced weaker relationships (lower R^2 values) than the other topologies (Table 1). This result manifested from the smaller taxonomic sampling of these latter trees (only mysticetes), which reduced statistical power and broadened confidence intervals. Despite the weaker explanatory power, the scaling exponent was not significantly different between odontocetes and mysticetes or between each subgroup and Neoceti as a whole (f -tests for equal slopes, $p > 0.1$).

Reconstructing Fossil Neoceti of Known Size

Overall, there were only small differences in the scaling relationships between the different classes of regression models. However, when we reconstructed unknown total lengths from fossil skull measurements of taxa not included in the original dataset, we determined that the multivariate, phylogenetic approach provided greater resolution and accuracy in addition to being less susceptible to taxon specific variation in single skull metrics and providing

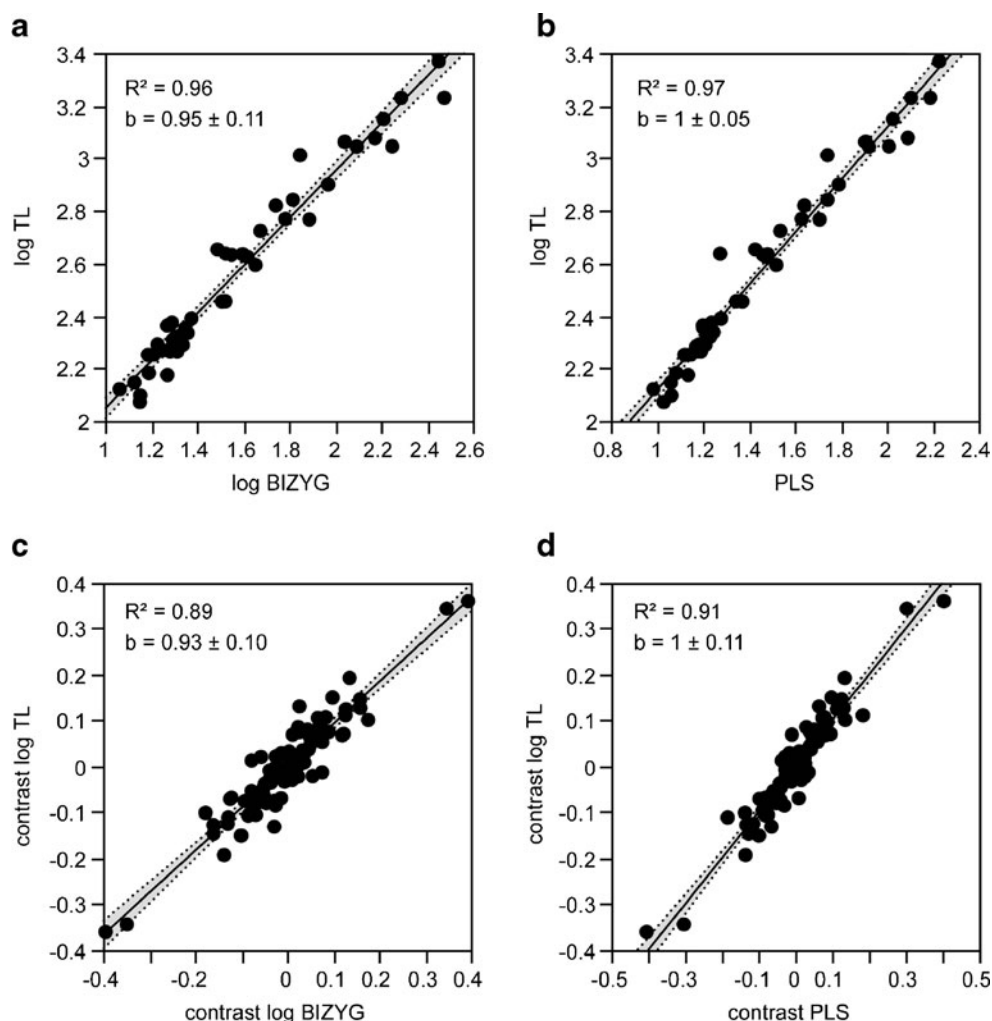


Fig. 4 Regressions for comparative datasets of extant Neoceti total length versus cranial measurements. **a** Conventional regression of the data for total length (TL) for a given single variable (bizygomatic width) without phylogenetic context; **b** Conventional regression using

the first predictor variable from the partial least squares (PLS) approach; **c** Independent contrasts regression using a single predictor skull metric; and **d** Independent contrasts regression using the PLS approach

statistical independence of samples. We tested the efficacy of our regression models on two examples of fossil Neoceti that preserved TL. While many of the regression models predicted similar mean reconstruction values, the primary difference in performance between the models was narrowing the prediction intervals. Fundamentally, this reduction may be a more important indicator of performance than the actual reconstructed value because the prediction interval represents the range of total lengths for which we have 95% statistical confidence that the true value occupied. For reconstructing body size in the target fossil odontocete, a specimen of the kentriodontid genus *Atocetus*, most single trait regression equations consistently underestimated its actual TL between -52% to -3% , although condylobasal length (CBL) overestimated TL by 13% (Table 3). The average of the single trait values underestimated TL by -19% (Table 3), which was similar to the PLS reconstruction that

underestimated the length of the *Atocetus* specimen by -21% (Table 3). Compared with single traits, PLS equations did produce narrower prediction intervals except when compared to occipital condyle breadth (OCB), but the latter underestimated length by over 50% (Table 3). Incorporating a phylogenetic context (IC reconstructions) still underestimated TL in *Atocetus*, although IC reconstructions for *Atocetus* narrowed the minimum and maximum boundaries across all single reconstructions by an average of 50% compared to conventional (non-IC) regressions (Fig. 5, Table 3). In the IC regression, a PLS approach provided an additional narrowing of the prediction intervals by 16% .

We also reconstructed TL in a target fossil mysticete, *Balaenoptera siberi*. In this case, all reconstructions (i.e., single and PLS traits and non-IC and IC) overestimated TL for this fossil taxon. Non-IC single trait and PLS reconstructions overestimated TL between $2\text{--}49\%$, with

Table 2 Reconstruction results for multivariate PLS regressions to predict total length in *Atocetus* and *Balaenoptera siberi*, with varying phylogenetic tree reconstructions and branch length transformations. Values are all reported in centimeters. Deviations from actual TL for

each fossil taxon are reported as “% dev.” Because the PLS predictor is already a linear combination of multiple measurements, the slope is always scaled to a value of one. Phylogenetic trees and branch length transformations are labeled as in Table 1

Phylogenetic Hypothesis		Multivariable PLS Regression							
Tree	BL Model	<i>n</i>	Exponent (\pm 95% CI)	R ²	<i>Atocetus</i> prediction range	% dev.	<i>Balaenoptera siberi</i> prediction range	% dev.	
Star	N/A	45	1 \pm 0.05	0.97	[63 – 137 – 299]	–21%	[458 – 1000 – 2183]	32%	
Tree 1	All 1	42	1 \pm 0.10	0.90	[105 – 140 – 188]	–19%	[739 – 974 – 1285]	28%	
	Grafen's	42	1 \pm 0.10	0.91	[94 – 141 – 212]	–18%	[786 – 984 – 1232]	29%	
	Ultramet.	42	1 \pm 0.10	0.89	[102 – 147 – 212]	–15%	[734 – 979 – 1306]	29%	
Tree 2	All 1	45	1 \pm 0.09	0.90	[105 – 141 – 188]	–19%	[731 – 967 – 1280]	27%	
	Grafen's	45	1 \pm 0.11	0.91	[94 – 143 – 217]	–17%	[743 – 977 – 1286]	29%	
	Ultramet.	45	1 \pm 0.10	0.89	[101 – 146 – 211]	–16%	[724 – 978 – 1320]	29%	
Tree 3	All 1	45	1 \pm 0.10	0.90	[102 – 141 – 193]	–19%	[731 – 958 – 1256]	26%	
	Grafen's	45	1 \pm 0.11	0.91	[94 – 143 – 218]	–17%	[726 – 975 – 1309]	28%	
	Ultramet.	45	1 \pm 0.11	0.89	[101 – 146 – 211]	–16%	[732 – 979 – 1308]	29%	
Tree 4	All 1	36	1 \pm 0.12	0.89	[104 – 142 – 194]	–18%	N/A	N/A	
	Grafen's	36	1 \pm 0.10	0.91	[93 – 145 – 224]	–16%	N/A	N/A	
	Ultramet.	36	1 \pm 0.12	0.88	[107 – 149 – 209]	–14%	N/A	N/A	
Tree 5	All 1	9	1 \pm 0.14	0.96	N/A	N/A	[781 – 969 – 1202]	27%	
	Grafen's	9	1 \pm 0.17	0.95	N/A	N/A	[725 – 960 – 1270]	26%	
	Ultramet.	9	1 \pm 0.16	0.95	N/A	N/A	[761 – 961 – 1214]	27%	
Tree 6	All 1	9	1 \pm 0.15	0.95	N/A	N/A	[800 – 882 – 973]	16%	
	Grafen's	9	1 \pm 0.18	0.95	N/A	N/A	[827 – 960 – 1114]	26%	
	Ultramet.	9	1 \pm 0.18	0.94	N/A	N/A	[813 – 948 – 1104]	25%	

the predicted TL from OCB providing the least deviation from actual TL; however, minimum and maximum boundaries for all single traits were broad, ranging on average from 393–2415 cm (Table 3). As with *Atocetus*, PLS reconstruction in *B. siberi* improved predicted TL accuracy by ~15% from averages of single trait reconstructions. By comparison, the predicted IC values, for both single traits and PLS, were closer to the actual TL of *B. siberi*, ranging in overestimation between 13-37%. Notably, IC reconstructions in *B. siberi* again markedly narrowed the prediction intervals by 68%, to an average TL range of only 704–1351 cm (Table 3). A PLS IC approach reduced this range subsequently by 16% to 743–1286 cm.

As with the comparisons between scaling exponents and regression strengths, we discovered that branch length transformations had little impact on independent contrast reconstruction values, when all other factors were held constant (Table 2; see also Pyenson 2008). Similarly, our analyses also compared phylogenetic reconstructions with different tree topologies, but the different resolutions (e.g., Sasaki et al. 2005:fig. 3 versus fig. 5) did not improve the reconstruction values of total length provided the more complete cetacean phylogenies (Trees 1–3) were used for predictions.

Reconstructing Fossil Cetaceans with Skulls Only

Based on the successful reconstruction of TL in *Atocetus* and *B. siberi*, we proceeded to reconstruct TL in other fossil cetaceans that are not represented by complete skeletons. For reconstructing TL in fossil Neoceti, we used the most resolved, composite phylogenetic tree (Tree 3 from Tables 1 and 2), which preserved statistical power and consistency between reconstructions. We could not justify separate allometric equations for odontocetes and mysticetes given the similar scaling relationships in our data (i.e., compare slopes for different trees in Tables 1 and 2). We selected Grafen’s (1989) branch length transformation because it generally generated the longest branch length estimates for reconstructed taxa, and we therefore considered it to be most conservative transformation for generating prediction intervals.

Table 4 summarizes the results of these reconstructions, displaying the range of predicted total lengths based on PLS and other single trait proxies. These fossil Neoceti are only represented by complete or incomplete crania that do not preserve TL, and they were therefore suitable for our regression models. Because the extant size range of our Neoceti dataset included a wide range of both absolute total

Table 3 Reconstruction results for single variable regressions to predict total length in *Atocetus* and *Balaenoptera siberi*, with Tree 3 [May-Collado and Agnarsson (2006) for odontocetes plus Sasaki et al. (2006):fig.5 for mysticetes] and Grafen (1989)'s branch length transformation. Values are all reported in centimeters. Deviations from

actual TL for each fossil taxon are reported as “% dev.” Abbreviations: AON, antorbital notch width; BIZYG, bizygomatic width; CBL, condylobasal length; EXOCC, width across exoccipitals; OCB, occipital condyle breadth

Tree 3 & Grafen's branch length transformation			<i>Atocetus</i> reconstruction (TL=173 cm)				<i>Balaenoptera siberi</i> reconstruction (TL=760 cm)			
			TL predicted	% dev.	TL min	TL max	TL predicted	% dev.	TL min	TL max
non-IC	single traits	OCB	83	-52	27	255	776	2	252	2391
		BIZYG	142	-18	64	313	1119	47	506	2475
		EXOCC	145	-16	59	357	1135	49	461	2797
		AON	168	-3	75	376	975	28	435	2183
		CBL	195	13	78	484	913	20	367	2271
		Avg. single	141	-19	57	349	974	28	393	2415
		PLS	PLS	137	-21	63	299	1000	32	458
IC	single traits	OCB	100	-42	59	168	894	18	639	1252
		BIZYG	130	-25	79	213	1042	37	754	1438
		EXOCC	138	-20	81	234	1093	44	773	1547
		AON	165	-5	95	285	1011	33	705	1449
		CBL	186	8	125	277	857	13	660	1114
		Avg. single	141	-19	85	231	975	28	704	1351
		PLS	PLS	143	-17	94	217	978	29	743

lengths and length contrasts, the reconstructions required only interpolation within the regression plots (Fig. 4). Without preserved TL we could not assess the accuracy of the single variable versus PLS approaches directly in these fossils, but no one single proxy consistently reconstructed TL closer to the PLS estimate than to any other. Bizygomatic width (BIZYG) was the most consistent, deviating less than 10% from PLS for 9/14 fossil Neoceti, as compared with other single traits reconstructions that were precise less frequently and deviated from the PLS predicted lengths more reliably (Table 4). Of the other individual proxies: antorbital notch width (AON) approximated PLS reconstructions within a range of 6-19%, and mostly overestimated the PLS predicted length; OCB rarely approached PLS predicted length values, mostly underestimating these values, between -6% and -31%; the width across the exoccipitals (EXOCC) performed closer to PLS predicted length values, producing near identical reconstructed total lengths in *Prosqualodon*, and deviated less than 10% from PLS for 7/14 fossil cetaceans; and CBL seemed to perform the least consistently compared with PLS predicted length values, ranging from 1% deviation in *Simocetus* to a full 50% deviation in *Eurhinodelphis*.

Across all of the reconstructed fossil taxa (Table 4), incorporating PLS methods improved the average confidence of our predictions by decreasing the prediction interval 12% from conventional methods. The large differences in the magnitude of the prediction intervals around

reconstructions of similarly sized variables arise from the differences in the amount of contrast that fossil taxa have with the nearest node in the phylogenetic reconstructions (Fig. 3). For example, the prediction interval in *Parabalaenoptera* is less than half of that of the comparably sized *Pelocetus* because the independent contrasts in its length measurements were smaller. More precisely, the reconstructed TL nodal value at node [vii] in Fig. 3b (from which the change in the TL was reconstructed for *Parabalaenoptera*) was longer than the nodal values for *Pelocetus* (node [vi] in Fig. 3b).

Discussion

Because marine mammals have undergone dramatic evolutionary and morphological transformations from their independent terrestrial ancestries, many of the traditional body size proxies used in mammalian paleobiology are either absent or uninformative. Moreover, the procedure of reconstructing body size within a taxonomic group from a single trait is susceptible to allometric relationships that differ across lineages within that group. We have developed an approach that combines 1) a comprehensive dataset of extant Neoceti, 2) the strength of a phylogenetic context (IC) for improving fossil reconstructions (following Garland and Ives 2000), and 3) a multivariate regression technique that allows a suite of cranial measurements (PLS) to act as a single proxy for reconstructing body length in extinct

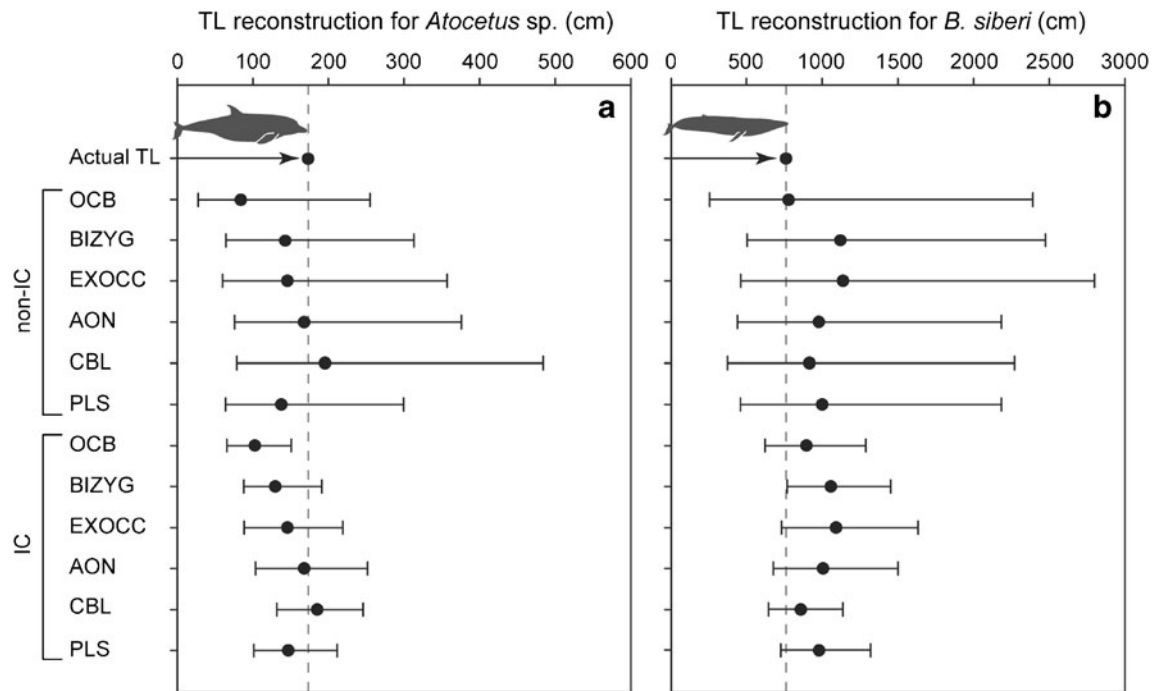


Fig. 5 Reconstruction comparisons for exemplar fossil Neoceti. Different reconstruction models for **a** *Ato cetus* sp. and **b** *Balaenoptera siberi* follow those described in the text. Abbreviations: BIZYG:

bizygomatic width; IC: independent contrast-based results, using branch length and reconstruction methods in the text; non-IC; star phylogeny; PLS: partial least squares of all measurements from Fig. 1

Neoceti. Our approach improved prediction intervals by over 70% over conventional, single variable regression approaches. We demonstrated that the explicitly phylogenetic and multivariate approach provided a more consistent reconstruction of the rare fossil taxa that preserve TL. Finally, we applied this approach to reconstructing select fossil Neoceti that are represented by isolated crania. Because the majority of the cetacean fossil record consists of such representation, we suggest that our approach can improve the historical perspective on body size changes in this clade.

Reconstructing Body Size Using Total Length

Vertebrate paleobiologists have long sought to reconstruct body size in extinct taxa, but the fragmentary preservation of most fossil taxa and the absence of modern relatives have been the two most significant hurdles for generating quantified estimates of body size in extinct vertebrates. Fossil mammals have been a notable exception, given the higher abundance of extinct taxa with relatively complete skeletons and the happenstance of living descendents, or extant analogues with similar body plans (Damuth and MacFadden 1990). Nonetheless, estimating body size in the fossil record is a perilous undertaking, given the variance in body size of a single individual, whose body mass can fluctuate daily, seasonally, geographically, through ontogeny and reproduction (Van Valkenburgh 1990). Because of the difficulties in estimating single values for a metric such

as body mass, we focused our efforts for reconstructing body size in extinct cetaceans (Neoceti) using their total length (TL). This linear metric is comparable across all extant taxa and it is less or negligibly variant to the factors that affect body mass (especially after reaching skeletal maturity), because body mass is susceptible to errors from measurement in piecemeal, fluid and tissue loss during carcass dismemberment (Gambell 1970), and strongly linked to seasonal, sexual, and regional variations (Lockyer 1976). While the strong correlation between TL and adult body mass has been well documented for both mysticetes and odontocetes (Mackintosh and Wheeler 1929; Nishiwaki 1950; Gambell 1970; Perrin 1975; Lockyer 1976; Uhen 2004), TL is more widely reported in the literature for other marine vertebrates (e.g., teleosts, elasmobranchs, and Mesozoic marine reptiles). Because of the abundant specimen data available from the whaling industry and long-term stranding programs, some cetological studies have sought to predict the body size of living cetaceans using proxy metrics (e.g., Stuart and Morejohn 1980; Kemper and Leddard 1999), but few have explored the implications of such proxies for illuminating evolutionary patterns in the fossil record (Lindberg and Pyenson 2006). In this study, we favored the approach of using total length as a valid size metric. If body mass estimates are necessary, reconstructed changes in length can be converted to changes in body mass via a third power relationship under assumptions of isometry and defensible mass estimates for

Table 4 Reconstruction results for select fossil cetaceans using the PLS or single variable independent contrast regressions based on the May-Collado and Agnarsson (2006) and Sasaki et al. (2006) resolved tree with Grafen's branch length transformation (Tree 3). Data are

reported as [minimum bound – predicted length (in bold)– maximum bound] for 95% prediction intervals. Intervals are asymmetric because they were converted from the log values

Fossil taxon	PLS	OCB	BIZYG	EXOCC	AON	CBL	Phylogenetic position on Fig. 3
<i>Kentriodon pernix</i>	[95 145 220]	[81 136 227]	[91 150 245]	[99 167 284]	[72 125 217]	[114 169 251]	[v]
<i>Simocetus rayi</i>	[131 241 445]	[91 193 409]	[111 299 472]	[137 296 641]	[131 292 652]	[136 243 435]	[i]
<i>Waipatia maerewhenua</i>	[162 257 409]	[130 230 405]	[138 239 413]	[147 264 476]	[157 288 530]	[179 279 433]	[iv]
<i>Zarhinocetus errabundus</i>	[168 266 424]	[180 318 561]	[121 210 363]	[118 213 384]	[131 241 444]	[258 402 625]	[iv]
<i>Squalodon bellunensis</i>	[170 270 429]	[125 221 390]	[143 246 426]	[138 248 447]	[156 286 527]	[243 378 587]	[iv]
<i>Janjucetus hunderi</i>	[167 294 520]	[142 286 573]	[165 323 630]	[157 323 663]	[154 325 685]	[146 250 430]	[vi]
<i>Aetiocetus cotylalveus</i>	[173 306 540]	[137 276 554]	[141 275 539]	[170 350 717]	[161 339 715]	[188 323 554]	[vi]
<i>Prosqualodon davidis</i>	[192 306 486]	[163 288 509]	[187 323 558]	[169 305 548]	[193 356 654]	[171 265 413]	[iv]
<i>Eurhinodelphis cochteuxi</i>	[230 384 640]	[169 317 594]	[169 310 568]	[166 317 607]	[183 358 701]	[472 770 1255]	[iii]
<i>Diorocetus hiatus</i>	[286 539 1016]	[216 457 966]	[255 548 1176]	[214 476 1060]	[270 601 1340]	[332 622 1165]	[vi]
<i>Aulophyseter moreni</i>	[413 687 1143]	[347 647 1208]	[335 610 1111]	[377 719 1371]	[417 816 1597]	[376 610 989]	[ii]
<i>Aglaoctetus moreni</i>	[411 725 1279]	[248 497 994]	[360 704 1374]	[351 721 1479]	[423 894 1889]	[480 825 1418]	[vi]
<i>Pelocetus calvertensis</i>	[443 782 1380]	[292 584 1170]	[419 818 1599]	[350 720 1477]	[455 963 2039]	[471 809 1390]	[vi]
<i>Parabalaenoptera bauliensis</i>	[684 885 1146]	[589 810 1114]	[596 811 1102]	[634 881 1225]	[724 1017 1429]	[750 961 1233]	[vii]

a closely related taxon. We emphasize that body mass estimates in larger cetaceans is an exercise fraught with uncertainty and that many of the reported literature values are from tertiary sources, although a simple isometric conversion may suffice for an initial comparison in the absence of reliable body mass estimates.

Estimating Body Size in Extinct and Fossil Marine Mammals

Despite the challenges for reconstruction body size in extinct organisms, several studies have attempted to estimate body size in fossil marine mammals, although with a limited comparative scope or sample size of specimens. These case studies are instructive, with respect to fossil Neoceti, because they illuminate the kinds of methodological considerations that are shared by other obligate and semi-aquatic mammals with different terrestrial ancestries. To reconstruct the body size of the extinct Steller's sea cow (*Hydrodamalis gigas*), Scheffer (1972) adopted a method pioneered by Colbert (1962) for dinosaurs, and built a scale clay model using skeletal information obtained from three relatively complete specimens. Scheffer (1972) determined that the calculated weight (based on assumptions of specific gravity) closely matched previous estimates based on G. Steller's original observations (Domning 1978:95–100). To reconstruct body size in desmostylians, Inuzuka (1996) also used the

clay model method, although such approaches are difficult to ground truth because of the notable lack of modern analogues for this clade of extinct mammals, which possessed enigmatic ecological and locomotory preferences. Gingerich (2005b) outlined a promising multivariate approach, suggesting that Desmostylia shared limb proportions most closely with polar bears (*Ursus maritimus*). Clementz et al. (2009) used OCB as a body size proxy for Tethys-Mediterranean occurrences of the dugongid genus *Metaxytherium*, but this study lacked an explicit allometric basis for its use in extant specimens (see their citation of Bianucci et al. 2008 as rationale). Sarko et al. (2010) recently provided the necessary empirical underpinnings for such an allometric relationship in extant sirenians, by evaluating the performance of different cranial and length measurements for predicting both weight and TL in Florida manatees (*Trichechus manatus latirostris*) and dugongs (*Dugong dugon*), with a comprehensive, specimen-based dataset. In agreement with our results (Table 3), Sarko et al. (2010) found that different cranial measurements predicted body size better than others for different taxa, although Sarko et al. (2010) did not combine single predictors into a multivariate approach.

Estimating Body Size in Fossil Cetaceans (Neoceti)

Researchers have devised similar approaches to estimating body size in fossil cetaceans, although these studies have

generally relied on single traits, singleton samples, and conventional regression methods. Gingerich (1998) and Marino et al. (2000) provided the first set of body size estimates for fossil cetaceans, but these estimations focused on body mass calculations for stem cetaceans, such as protocetids and basilosaurids (Gingerich et al. 2001; Uhen 2004). Because of the fundamental differences between Neoceti and stem cetacean bauplans, such body mass estimates are not meaningfully comparable for the allometric analyses desired in this study. Marino et al. (2003, 2004) first proposed using OCB as a proxy for body size in fossil Neoceti. Marino et al. (2003, 2004) cited the strong correlation of OCB with body mass (Pearson $r=0.89$; $R^2=0.79$, in each study, respectively), although these statistics pertain to a dataset compiled from an unreported combination of published skeletal lengths and personal observations. Relying on preliminary results from the analyses presented herein (i.e., Pyenson and Lindberg 2003; Pyenson and Sponberg 2007), Pyenson and Haasl (2007) reconstructed the body size of a Miocene cetotheriid hosting a molluscan whale-fall assemblage from central California, using EXOCC as a proxy for body size. Separately, Bianucci et al. (2008) presented body size estimates for an enigmatic assemblage of fossil ziphiids from South Africa using postorbital skull width. In that study, Bianucci et al. (2008) supported the use of this proxy by showing allometric relationships in a supplemental regression analysis, but the extant dataset used only a single trait and was taxonomically restricted to Ziphiidae. Bianucci et al. (2010) cited Pyenson and Lindberg (2003) as the basis for using OCB in estimating the body size of the ziphiid *Messapicetus gregarius*, from the Pisco Formation of Peru. More recently, Lambert et al. (2010) presented body size estimates for the stem physeteroid *Livyatan* and a selection of fossil mysticetes from late Paleogene through the Recent. Their estimates, which included select odontocetes and mysticetes, were based on BIZYG and conventional allometric regressions using specimen-based datasets with known TL (Lambert et al. 2010). Notably, Lambert et al. (2010)'s reconstructions of TL in *Livyatan* were interpolated from extant *Physeter* data, which can attain total lengths of 20 m in mature males (Nishiwaki 1950). In the present study, all of our reconstructions were encompassed by the extant size range of Neoceti, a fact that strengthens the statistical basis of our extinct reconstructions (interpolations vs. extrapolations) and carries important considerations about the evolution of body size as well.

Predicting Body Size in Extinct Neoceti

In this study, we outlined a multivariate and phylogenetically controlled method for reconstructing body size in fossil cetaceans. Because of taphonomic constraints and

their high diagnostic value, cranial measurements provided the ideal source of data for body size proxies to generate predictive equations. For the first set of reconstructions in our analysis, we tested our regression equations using some of the few fossil cetaceans that preserved total length. Such specimens are unusually rare in the cetacean fossil record; there are likely few other vouchered specimens extant in museum collections with adequate stratigraphic provenance (contra unrecovered, but reportedly complete skeletons from the Pisco Formation of Peru [Brand et al. 2004]). In general, our predictions overestimated TL for *B. siberi* and underestimated TL for *Atocetus* (Table 3). This difference may ultimately reflect an underlying biological reality about body size values at the nodes of these branches. Alternatively, the discrepancies between actual TL and our reconstructed values, which were built from size information from closely related living relatives, might reflect evolutionary allometric changes that occurred along the lineage to *Atocetus* and *B. siberi* from their ancestral states. Whenever possible, we urge using multivariate approaches with the maximum amount of information for reconstructing body size. However, conventional multivariate regression will likely not improve reconstructions because multiple measurements are already highly correlated by organismal allometry. PLS enables incorporating multiple measures without adding free parameters to the regression model (Tobias 1997). While specific skull proxies may appear appealing for reconstructing fossil taxa when we consider only *Atocetus* or *B. siberi*, single traits did not perform best for both cases. For example, OCB performed well for reconstructing *B. siberi*, but not *Atocetus*; while AON was sufficient for *Atocetus*, it was relatively poor for *B. siberi* (Table 3). Given the variability of single trait performance, and the strength of the multivariate regressions, we favor a PLS reconstruction approach. Ultimately, the consistency and >70% improvement in prediction intervals compared to conventional single proxy regressions indicate that the multivariate and phylogenetically grounded approach provides the highest confidence for predicting fossil body sizes.

Best Single Proxy Alternative

While a multivariate approach may be ideal, there are many cases where fossil taxa are incompletely preserved, providing only a subset of the available proxies for estimating body size. Fossil marine mammalogists would find greater use from a single proxy that performs best when all five cranial metrics are not equally available (and thus the PLS linear combination cannot be calculated). Based on *Atocetus* and *B. siberi* reconstructions (Table 3), it initially seems that CBL provided the best universal predictor of body size in fossil Neoceti. This result is somewhat surprising, given that skull length varies widely in cetaceans, and especially in lineages

with longirostral skulls, such as eurhinodelphinids (e.g., *Eurhinodelphis*) and many platanistoids (e.g., *Zarhinocetus*). Of all single traits, CBL performed well in both the odontocete and the mysticete reconstructions (deviating 8% and 13%, respectively, from actual TL). However, we propose two compelling reasons not to adopt CBL as a single predictor for body size in fossil cetaceans. First, among living cetaceans, longirostral skulls seem to be correlated with specific ecomorphologic modes, such as freshwater or fluvial habitats. For hyperrostral fossil taxa like *Eurhinodelphis* and *Zarhachis*, where the rostrum accounts for >75% of skull length, CBL as a single predictor produces TL values that were 50–100% greater than other cranial proxies (Table 3). Second, and more importantly, we suggest it is unwise to use CBL as a universal proxy because of the vagaries of taphonomy, which rarely permit the preservation of cetacean skulls with an intact CBL, especially when rostra are elongate and delicate (Schaefer 1972). Lastly, given the constraints of our phylogenetic controls, we recommend a single proxy that maximizes the number of sampled taxa because single trait values that were uniquely effective for only odontocetes or only mysticetes relied on much smaller sample sizes than a single proxy using data across all Neoceti.

Based on this line of thinking, we propose adopting BIZYG as a best alternative single proxy for body size in fossil Neoceti, as Lambert et al. (2010) suggested. BIZYG reconstruction values closely tracked PLS values (Fig. 5) and also performed on par with the average single trait predictors for reconstruction *Atocetus* and *B. siberi* (Table 3). BIZYG did deviate more from actual TL of the latter two test specimens than other single trait proxies such as AON and CBL, but from a taphonomic view, BIZYG is abundantly preserved on most specimens of fossil odontocetes and mysticetes that justify taxonomic description. Therefore, given these aforementioned considerations, we think BIZYG makes the best choice as a universal neocete size predictor when the measurements needed for the PLS approach are not available. We provide reconstruction equations for the PLS regression, which require all five measurements, and BIZYG as the best alternative single proxy, in the Supplemental Information (Supplemental Equations). These equations are different for the reconstruction nodes on the phylogeny (roman numerals in Fig. 3) because they depend on contrast data from cranial data derived from specific nodes elaborated in the Supplemental Information. To reconstruct future fossil taxa, we recommend first placing target taxa in the most conservative ancestral position on the phylogenetic trees in Fig. 3 and then computing values from the equations for that node.

Evolution of Body Size in Cetacea

The resultant reconstructions of select fossil cetaceans in this study were plotted through time, based on stratigraphic

age, to depict a broad outline of body size evolution in Neoceti (or crown Cetacea) since the late Oligocene (Fig. 6; see similar outlines in Lambert et al. 2010; Fitzgerald 2010). In the late Oligocene, both odontocetes and mysticetes had very similar body sizes, about 250 cm, which is approximately the adult size of the living bottlenose dolphin (*Tursiops truncatus*). Notably, this size range is mainly represented by stem members of Mysticeti (*Aetiocetus*) and Odontoceti (*Simocetus*), which may have had slightly different body plan proportions than members of crown Mysticeti and Odontoceti, based on cervical vertebrae and forelimb elements associated with crania from some stem members of these lineages (e.g., Barnes et al. 1994 for aetiocetids). If we assume that this approximate size range in the Oligocene represents a value similar to that for the ancestral node of crown Cetacea, it is notably smaller than TL for basilosaurid sister taxa, such as *Dorudon* (485 cm, as estimated for adult specimens by Uhen 2004) and *Basilosaurus* (~1600 cm; Gingerich et al. 1990). How body size evolved along the stem leading to crown Cetacea remains unclear, but the proxies used herein provide an opportunity to resolve this pattern more clearly, pending the discovery of more complete material from stem taxa.

By the early Miocene, body size categories for mysticetes (represented in this outline by *Aglaoctetus*), exhibited the largest size categories of the time, at about 750 cm. The upper size boundary for cetaceans seems to plateau throughout the Miocene, a pattern largely supported by Lambert et al. (2010:fig. 7). We suggest that the absence of Miocene mysticetes larger than 1000 cm may be real, given the thorough sampling from this time period (Uhen and

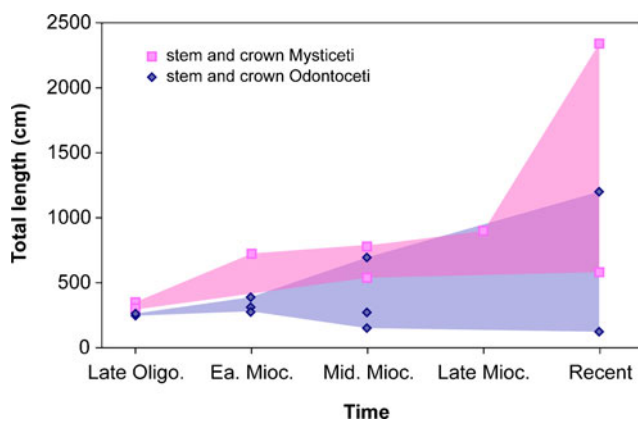


Fig. 6 A broad outline of body size evolution in Cetacea, using the reconstructed total length values (in cm) generated by this study (PLS values only) and actual measurements from Recent taxa. Red denotes mysticetes and blue denotes odontocetes. Note that no Pliocene age fossils were included and that extant taxa were the upper and lower adult species sizes within mysticetes (*Balaenoptera musculus* and *Caperea marginata*) and odontocetes (*Physeter macrocephalus* and *Neophocoena phocoenoides*). Ea. = early; Mid. = middle; Mioc. = Miocene; Oligo. = Oligocene

Pyenson 2007) and because the presence of skeletal elements from fin or blue whale-sized mysticetes (2200–3000 cm in length) would be readily recognized in the field or in museum collections. While odontocetes seem to have reached the lower limit of their size category that persists to today, mysticetes evolved notable difference in size between the late Miocene and the Recent. For Recent taxa, only the largest and smallest species of living mysticetes and odontocetes were plotted. This discrepancy in maximal body size suggests that the evolution of extremely large mysticetes (> 1500 cm) is a relatively recent phenomenon in the history of cetaceans. The delayed achievement of maximal body size in cetaceans contrasts sharply with the relatively early onset of maximal large body size in the evolutionary history of placental terrestrial mammals, which occurred ~10 Ma after their origin (Smith et al. 2010). We suggest that the latter pattern in mysticetes invites closer testing for possible intrinsic and extrinsic factors during the late Neogene that may promoted the extreme gigantism in extant crown mysticetes (Goldbogen et al. 2010). Incorporating data from Oligocene through Pliocene fossil cetacean assemblages will better illuminate this pattern, and refining this broad outline is the direct focus of future work.

Overall, this pattern of body size evolution is broadly congruent with an outline illustrated previously by Trammer (2005), who featured unreferenced data with similar time resolution; the evolutionary pattern for mysticetes reported here is also consistent with the richer dataset presented by Lambert et al. (2010:fig. 7). Although such evolutionary patterns may reflect the expected outcome of continuous values evolving in a diffusion model (Stanley 1973), other models of body size evolution have been recently advanced to explain such patterns in mammals (Clauset and Erwin 2008). Eventually, we expect that more substantive datasets of cetacean body size across the Cenozoic can also help answer whether this pattern differs from their terrestrial artiodactylan sister clades, perhaps reflecting a divergent signal for obligate aquatic lifestyles. Fossil data on body size in extinct Neoceti can also better test the niche-filling hypothesis of early neocete evolution advanced by Slater et al. (2010), who examined the evolution of disparity in Neoceti using extant data alone.

Conclusions

We reconstructed the body size of fossil cetaceans using multivariate and phylogenetically controlled regression equations based on a comprehensive sample of measurements from living cetacean species. Specifically, we used a set of cranial proxies to estimate body size in fossil cetaceans, because the fossil record of described cetacean

taxa is mainly represented by skulls. Our reconstructions also were controlled for phylogenetic effects (by using IC regressions) by including the best phylogenetic estimate for the systematic position of fossil taxa. Lastly, we used the rare occurrences of fossil taxa with preserved total lengths to test our predicted lengths using only skull measurements. Our results demonstrate that incorporating phylogenetic relationships in scaling studies can increase the confidence of reconstructed body size and provide a way of examining body size distributions of cetaceans through time. We conclude that PLS multivariate regression equations that incorporate independent contrasts provide the best body length proxy, but when the five necessary measurements (BIZYG, AON, CBL, EXOCC, and OCB) are not available for calculation of the PLS linear combination, then BIZYG is the best alternative single proxy. We provide reconstruction equations for both of the latter in the [Supplemental Information files](#).

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