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Cope's rule and the evolution of body size in Pinnipedimorpha (Mammalia: Carnivora)

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Cope's rule describes the evolutionary trend for animal lineages to increase in body size over time. In this study, we tested the validity of Cope's rule for a marine mammal clade, the Pinnipedimorpha, which includes the extinct Desmatophocidae, and extant Phocidae (earless seals), Otariidae (fur seals and sea lions), and Odobenidae (walruses). We tested for the presence of Cope's rule by compiling a large dataset of body size data for extant and fossil pinnipeds and then examined how body size evolved through time. We found that there was a positive relationship between geologic age and body size. However, this trend is the result of differences between early assemblages of small-bodied pinnipeds (Oligocene to early Miocene) and later assemblages (middle Miocene to Pliocene) for which species exhibited greater size diversity. No significant differences were found between the number of increases or decreases in body size within Pinnipedimorpha or within specific pinniped clades. This suggests that the pinniped body size increase was driven by passive diversification into vacant niche space, with the common ancestor of Pinnipedimorpha occurring near the minimum adult body size possible for a marine mammal. Based upon the above results, the evolutionary history of pinnipeds does not follow Cope's rule.

KEY WORDS: **Body size, Cope's rule, diversification, marine mammal evolution, pinniped.**

Body size is a basic trait of organisms, which differs widely between taxa and strongly influences life-history and ecology (Peters 1983; LaBarbera 1986; Bonner 1988). Because of the importance body size plays in organismal biology, study of body size change over time within lineages can provide important insights into the evolution, life history, and physiology of those lineages. One frequently observed trend in body size over time is Cope's rule (Rensch 1948), which describes the tendency for the size of organisms to increase over geological time via natural selection (Cope 1896; Rensch 1948; Benton 2002; but see Polly 1998).

Two distinctive types of processes can lead toward shifts in average body size within a clade. The pattern produced by Cope's rule is a result of an active process, which results from bias in selection toward an increased body size (McShea 2000). For a driven trend, body size across most lineages within a clade of interest will increase concurrently with an increase in minimum body size (Fig. 1A). There will also be a greater number of increases in body size between ancestors and descendents than decreases (McShea 2000). This increase in body size over time is often considered a result of selection for increased ecological specialization associated with benefits of a larger body size (Kingsolver and Pfennig 2004; Van Valkenburgh et al. 2004; Hone and Benton 2005; Raia et al. 2012). These benefits are many, but include increased defense against predation, the ability to exploit a greater variety of food sources, and increased survival during times of environmental stress (Hone and Benton 2005).

Alternatively, a passively driven trend occurs when a shift in body size occurs as a result of diversification of a clade and subsequent filling of available morphospace (McShea 2000; Fig. 1B). This is typically associated with diversification from a single ancestor of minimum possible body size for the lineage (Stanley 1973; Gould 1988; Clauset and Erwin 2008). Over time, minimum body size may or may not shift, and ancestor–descendent comparisons should show no or minimal positive skew (McShea

Body size information archived with paper as Supporting Information.

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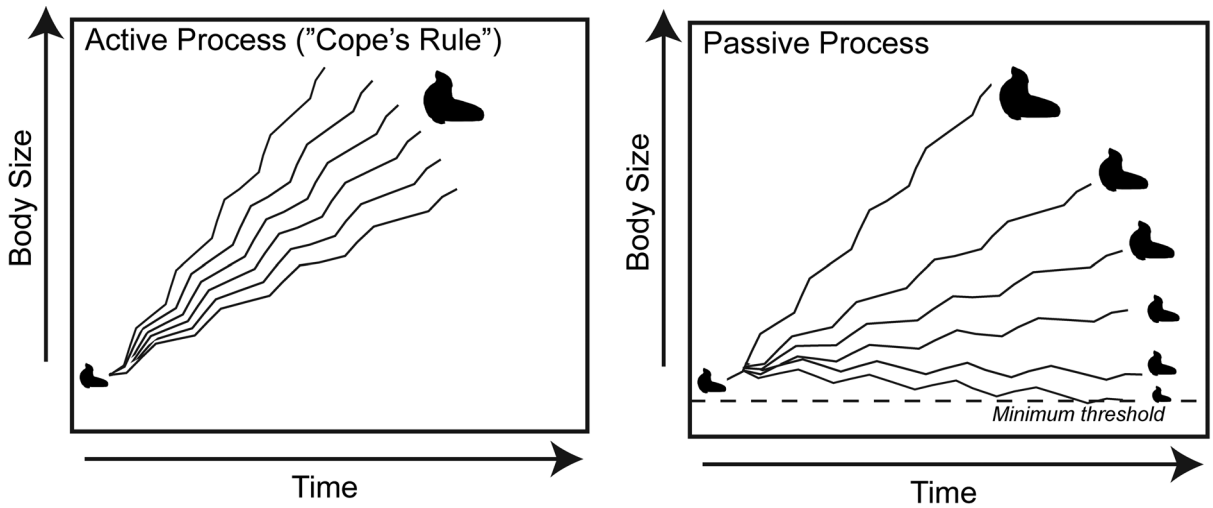

Figure 1. Simplified model demonstrating the differences between changes in the mean character state as a result of active (A) and passive (B) processes.

2000). Even if there is an increase in mean body size, there should not be more positive changes in body size than negative changes.

When tested by applying Bayesian methods to a large phylogeny of extant Mammalia, Cope's rule was not found to be valid, or only weakly so (Monroe and Bokma 2010). Yet, taxonomic level matters when analyzing body size trends, as patterns that are evident at a broad taxonomic level may not be apparent within smaller subclades (Hone and Benton 2007). Furthermore, studies that have incorporated hundreds of fossil taxa have found support for Cope's rule in Mammalia (Alroy 1998; Raia et al. 2012), with the inclusion of fossil taxa improving the ability to estimate ancestral body size (Finarelli and Flynn 2006). Cope's rule has been shown to apply to Canidae (Van Valkenburgh et al. 2004), fissiped Arctoidea (Finarelli and Flynn 2006), and oryzomyine rodents (Avaria-Llautureo et al. 2012), but was found to be invalid for Paleogene mammals (Gingerich 1980) and Equidae (Gould and MacFadden 2004).

Cope's rule has only been tested for terrestrial mammals, and the validity of the rule for marine mammals (cetaceans, sirenians, and pinnipeds) is still unknown. Marine mammals were left out of the macroevolutionary analyses of Alroy (1998) and Raia et al. (2012), and it is unclear if and how many marine mammals were included in the analysis of Monroe and Bokma (2010). Finnareli and Flynn (2006) incorporated extant pinniped body size into their analysis of body size evolution of Caniformia, but a lack of data from fossil taxa meant they could not assess body size evolution in pinnipeds.

Constraints and selective pressures on body size in marine mammals are different from those for terrestrial mammals. The increased energetic cost of thermoregulation in water (Downhower and Blumer 1988) will constrain the minimum body size possible for aquatic mammals far above that of the minimum body size of terrestrial mammals. Increased convective heat loss will also increase the maximum body size possible for marine mammals (Clauset 2013). However, other constraints, such as the ability to move on land, are likely to limit maximum body size in pinnipeds below the maximum body size possible for sirenians and cetaceans. Beyond selective pressures shared by terrestrial mammals, selection for increased diving depth and duration will also favor larger body size (Halsey et al. 2006) as larger body size confers increased oxygen storage capability in muscles and blood, and a proportionally reduced metabolic rate (Butler and Jones 1982; Kooyman and Ponganis 1998).

Our study is the first to explicitly test for the presence of Cope's rule in a marine mammal clade, specifically the Pinnipedimorpha (seals, sea lions, and walruses). Kellogg (1922) stated that Cope's rule was assumed to apply to marine mammals, and specifically pinnipeds, but gave no further discussion. Repenning (1976) argued that body size increases were an adaptation for pelagic foraging in pinnipeds, and indicated that the body size of odobenids, otariids, and desmatophocids all increased in size over time, and that these taxa attained larger body size than stem pinniped taxa such as the "enaliarctines." A similar pattern has also been invoked for Phocidae, with the relatively small Phocinae (northern seals) considered to represent the ancestral condition, with larger taxa such as *Mirounga* and Lobodontini (Antarctic seals) representing a more derived condition (Flower 1881; Laws 1959; McLaren 1960; King 1972). Wyss (1994), based on recent cladistic and character analyses (Wyss 1987, 1988), argued that the common ancestor of Phocidae was large in body size, and that subsequent dwarfing had occurred within phocids. All of the above studies were descriptive in nature and did not attempt to rigorously test or define pinniped body size trends through time, and only Wyss (1994) presented his argument within a phylogenetic

context. Prior studies have also lacked body size estimates for fossil taxa. Our study builds on this previous work by rigorously testing for Cope's rule in a phylogenetic context and includes a large database of body size estimates for fossil taxa.

Materials and Methods

SAMPLING

We estimated body size data from fossil and extant pinnipeds from around the world, with an emphasis on fossil taxa from the North Pacific. We focused on this region as there is a well-studied, and nearly temporally continuous fossil record for pinnipeds in this region (Deméré et al. 2003). The North Pacific also was an important center of pinniped evolution, as it preserves the oldest definitive pinnipeds (Mitchell and Tedford 1973), is the most likely center of origin for Otariidae and Odobenidae (Mitchell 1975; Repenning and Tedford 1977; Barnes 1989; Kohno et al. 1995b; Deméré et al. 2003; Churchill et al. 2014a), and the phylogenetic relationships of taxa within this region are well understood (Barnes 1989; Berta 1991; Berta and Wyss 1994; Deméré 1994a; Kohno 1996; Deméré and Berta 2001; Kohno 2006; Boessenecker and Churchill 2013; Churchill et al. 2014a).

Sampling of taxa was limited to taxa with preserved cranial material that has been described or figured in the literature. Measurements used were those described by Churchill et al. (2014b). Fossil taxa examined included nine "enaliarctines," eight desmatophocids, five phocids, sixteen odobenids, and five otariids (Appendix S1). Due to limited sample size, most body size estimates for fossil taxa are based on single specimens. Fossil taxa represented by multiple specimens include *Enaliarctos mealsi* ($N = 2$), *Pteronarctos goedertae* ($N = 6$), *Pacificotaria hadromma* ($N = 2$), *Pinnarctidion rayi* ($N = 2$), *Desmatophoca oregonensis* ($N = 7$), *Allodesmus gracilis* ($N = 6$), *Callophoca obscura* ($N = 5$), *Thalassoleon mexicanus* ($N = 2$), *Proneotherium repenningi* ($N = 3$), *Imagotaria downsi* ($N = 4$), *Pontolis magnus* ($N = 5$), and *Dusignathus seftoni* ($N = 2$).

Sexual size dimorphism is present in extant Otariidae, Odobenidae, and some Phocidae. It is unclear how widespread sexual size dimorphism is in fossil taxa, although it has been identified in "enaliarctines" (Cullen et al. 2014) and Desmatophocidae (Mitchell 1966; Deméré and Berta 2002). Bias from preferential sampling of male or female individuals will skew our estimated body sizes toward higher values or lower values, respectively, than that of the true species average. Sex assignment can be difficult in fossil specimens, especially if they are fragmentary or are from taxa known only from a single individual. Using a combination of the criteria delimited in Cullen et al. (2014), measurement data, and information from the literature (Mitchell 1966; Repenning and Tedford 1977; Barnes and Raschke 1991; Berta 1994; Deméré 1994b; Kohno 1994; Deméré and Berta 2001, 2002, 2005; Kohno 2006; Cullen et al. 2014), we assigned sex whenever possible to specimens used to produce body size estimates. Based on sex assignments, the following taxa are represented by specimens representing both male and female individuals: *Pteronarctos*, *Pacificotaria*, *P. rayi*, *D. oregonensis*, *A. gracilis*, *Callophoca*, *T. mexicanus*, *Imagotaria*, *Pontolis*, and *Valenictus*. Taxa which are likely represented by only female specimens include *Brachyallodesmus*, *A. sadoensis*, *Pithanotaria*, *Callorhinus gilmorei,* and *Pseudotaria*. Taxa represented by only male specimens include *E. mealsi*, *E. tedfordi*, *E. emlongi*, *A. kelloggi*, *A. sinanoensis*, *A. nov*. sp. *T. macnallyae*, *Proterozetes*, *Prototaria primigenia*, *P. planicephala*, *Proneotherium*, *Neotherium*, *Gomphotaria*, and *Ontocetus nov*. sp. All other taxa are represented by individuals that could not be assigned a sex with certainty. Based on these sex assignments, there may be bias toward male individuals in our dataset of "imagotariine" walruses, however these taxa were overall small in body size. This may create a much larger increase in body size from "enaliarctine" taxa to stem odobenids, although is unlikely to influence our ancestral body size reconstructions in later diverging taxa.

Nearly all extant pinniped taxa were included within the ancestral character state reconstruction analysis for body size, with body size averaged across sex and taken from previous compilations of pinniped body size (Lindenfors et al. 2002). Taxa excluded from this analysis include historically extinct taxa (*M. tropicalis*, *Zalophus japonicus*) and taxa for which phylogenetic relationships are still contested (*Neophoca cinerea*; Churchill et al. 2014a).

PRINCIPAL COMPONENTS ANALYSIS

Estimates of body size for fossil taxa were made using the multivariate and single variable regression equations developed by Churchill et al. (2014b), which included separated sets of body size prediction equations for Phocidae and Otariidae, the two clades containing almost all extant pinniped diversity. However, most fossil taxa in this study are either stem taxa outside of extant clades ("enaliarctines") or belong to clades that are extinct (Desmatophocidae), or have limited extant taxonomic diversity (Odobenidae). All these situations prevent the development of robust predictive equations of body size for these groups, which require multiple extant species as a baseline comparison. Furthermore, the phylogenetic relationships of some extinct taxa are still disputed (e.g., *Pinnarctidion*, Desmatophocidae; Barnes 1989; Berta and Wyss 1994), making it unclear which set of regression equations would be most appropriate for different fossil taxa. We addressed this problem by performing a principal component analysis (PCA) on 12 $\log_{10}$ transformed cranial measurements used in the reconstruction of body size in pinnipeds. This allowed us to determine what part of the morphospace the extinct clades fell into, and which set of equations (phocid or otariid) was most appropriate for fossil taxa.

All measurements used were those of Churchill et al. (2014b), except for lengths of upper and lower tooth rows, due to severe modification in tooth development in odobenines (displacement of I^3, extensive development of upper canines, molarization of lower canines; Cobb 1933; Deméré 1994a; Horikawa 1995; Boessenecker and Churchill 2013) Extant phocid and otariid measurement data from Churchill et al. (2014b) was supplemented with $\log_{10}$ transformed mean measurement data from sixteen fossil taxa. These include a wide diversity of fossil pinnipeds, with three "enaliarctines" (*E. emlongi*, *Pteronarctos*, *Pacificotaria*), two desmatophocids (*D. oregonensis*, *A. kernensis*), four "imagotariine" walruses (*Proneotherium, Neotherium, Imagotaria, Pontolis*), one dusignathine walrus (*D. seftoni*), one fossil odobenine walrus (*Ontocetus*), and one fossil otariid (*T. mexicanus*). Also included for comparison with fossil odobenids is the extant walrus *Odobenus rosmarus*, with the average values of the two subspecies (Berta and Churchill 2012) and both sexes treated separately. Specimens used for PCA of *O. rosmarus* are listed at the end of Appendix S1. The PCA was performed in R 2.12.1 using the FactomineR package (Lê et al. 2008). We also performed discriminant function analysis (DFA) on this dataset, to determine how well the fossil taxa could be classified as Otariidae or Phocidae by their cranial measurements.

BODY SIZE ESTIMATION

We used total body length as a metric for body size. For marine mammals, total body length produces more accurate estimates of body size than body mass (Churchill et al. 2014b), as it is less prone to variation from seasonal or health-related changes in body mass (Churchill et al. 2014b). Regression equations used to estimate body size are from Churchill et al. (2014b). Whenever possible, we used the all subsets multivariate regression equation in preference to single variable regression equations, as this increased the accuracy of results (Churchill et al. 2014b). For those taxa in this study represented by only fragmentary cranial material, which precluded the use of the multivariate regression equation, single variable regression equations were used. Whenever possible the four most accurate predictors of body size in otariids (basal length of cranium, width of rostrum across canines, bizygomatic width, and length of mandible) and phocids (basal length, width of rostrum across canines, width across the occipital condyles, and height of the occipital) were used. Finally, when the four best predictors were not preserved in a given fossil taxon, regressions based on other present single variables were used. Specific single variable regression equations used in this study are listed in Appendix S1 along with the specimens for which they were used. When single variable regression equations were used, if multiple variables were present, total body length was calculated for different variables and the mean total body length for all measurements were used. If multiple specimens of a given taxon were available, the total body length reported represents the mean total body length for the taxon. A certain degree of uncertainty is present in the total length estimates produced here, either due to variance in the size of specimens examined (when multiple individuals of a single species was present), as well as imprecision in the predictive equations used to compute total length. This uncertainty is presented in Appendix S2.

To assess the accuracy of these predictive equations for estimating the total body length of fossil taxa, we compared total body length estimates derived from the multivariate and single regression equations with known total body length of a fossil taxon. The only fossil taxon available for study that is complete enough to allow total body length to be determined and whose skull is fully prepared and not deformed or otherwise too damaged to be used in the multivariate and single variable regression equations is the holotype of *A. kelloggi* (LACM 4320). This specimen is known from a nearly complete but unarticulated skeleton with a total body length of 258 cm (Mitchell 1966; Barnes 1972). The results of the comparisons between the known total body length of *A. kelloggi* and predictive equations' estimated total body length are discussed in Appendix S3.

ANALYSIS OF BODY SIZE TRENDS

To identify trends in body size through time, we performed two different sets of analyses, focused on among-lineage and within-lineage trends. Prior to performing these analyses, we tested whether there was phylogenetic signal (K) present in body size data; absence of phylogenetic signal in body size would make further testing of Cope's rule pointless (Laurin 2004). To do so, we created a composite phylogeny containing all taxa included within this study, with the topology reflecting that of the most recent comprehensive phylogenetic analyses for the different pinniped clades (Fig. 2). The topology of Odobenidae is that of Boessenecker and Churchill (2013) and the topology of Otariidae follows Churchill et al. (2014a). For Phocidae, the topology of Phocinae is that of Fulton and Strobeck (2010), whereas the topology of Monachinae follows Berta et al. (in press). The topology for Allodesminae follows Kohno (1996), whereas that of *Enaliarctos* follows Berta (1991). Placement of other fossil taxa and clades largely follows that of Berta and Wyss (1994), with the exception of placement of Odobenidae as the sister taxon to Otariidae, consistent with all genotype-based analyses of pinniped phylogeny (Árnason et al. 2006; Higdon et al. 2007; Agnarsson et al. 2010). Taxa not present in our analyses, either because they lack sufficient cranial material to allow the estimation of body size, or were not available for examination, were pruned from the tree. Tests for phylogenetic signal were performed in R using the packages APE (Paradis et al. 2004) and GEIGER (Harmon et al. 2008), with mean K values of greater than 0.5 considered evidence of strong phylogenetic signature. Branch length data were absent for most

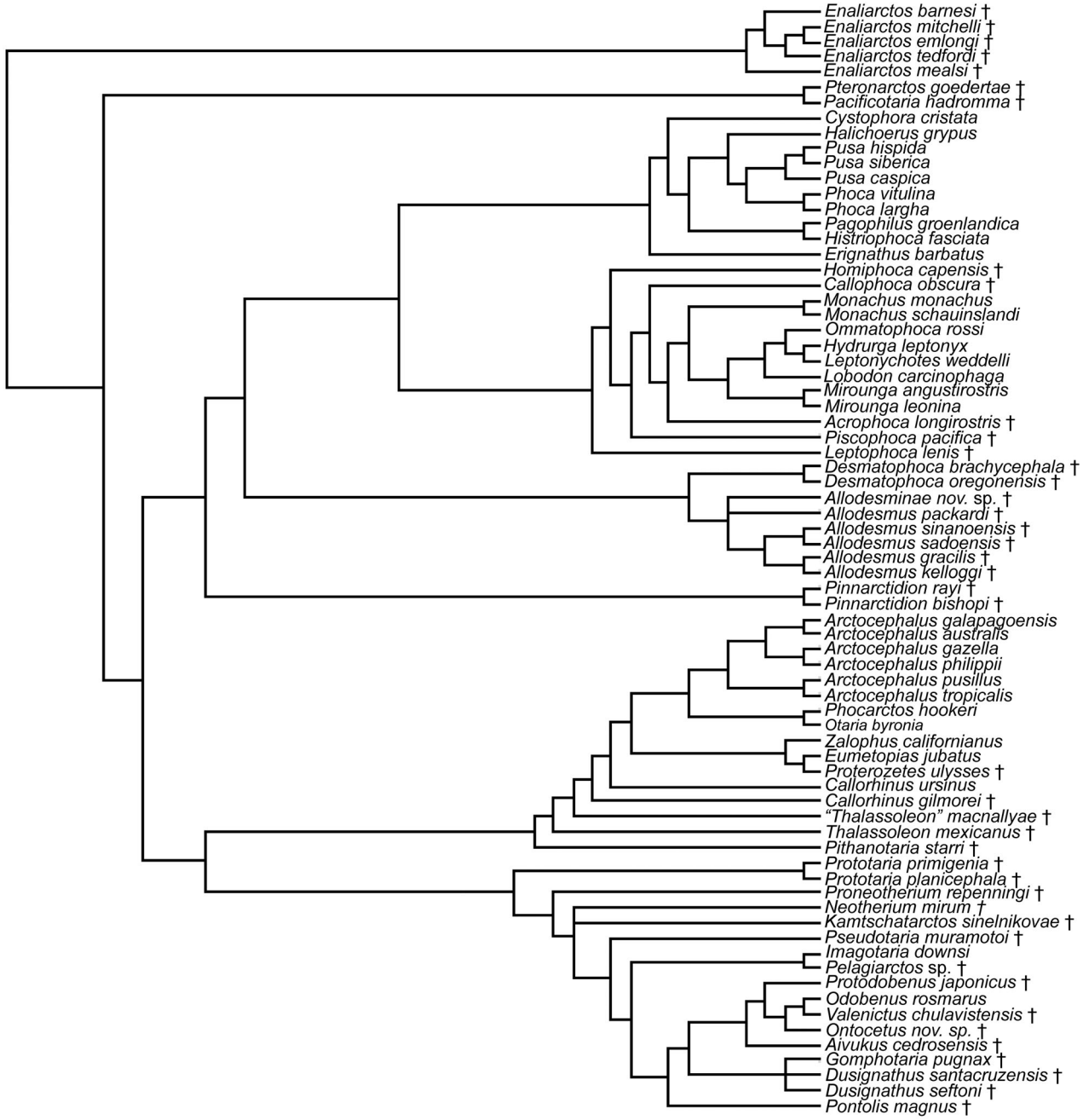

Figure 2. **Composite phylogeny of Pinnipedimorpha used in this study. Topology of tree follows Boessenecker and Churchill (2013) for Odobenidae, Churchill et al. (2014a) for Otariidae, Fulton and Strobeck (2010) for Phocinae, Berta et al. (in press) for Monachinae, Kohno (1996) for Allodesminae, Berta (1991) for *Enaliarctos*, and Berta and Wyss (1994) for overall placement of extinct clades. Extinct taxa indicated by "†."**

of the phylogenies used for our composite tree, so we performed our phylogenetic tests with 10,000 randomly generated branch lengths.

If there was a phylogenetic signal in the body size data, we then proceeded with the next two sets of analyses. First, we determined whether there was a significant trend in increasing body size over time. To do this, we first determined if the body size data were normally distributed, using normal Q–Q plots; if the data were normally distributed, it was not log-transformed. If the data were found to be non-normal, the body size estimates were converted to the $\log_{10}$ scale. Extant taxa were excluded from this analysis; first appearance data remains poorly known for most extant taxa, and the extant clades Phocidae and Otariidae have relatively poorly known fossil records (Deméré et al. 2003).

After assessing the normality of the data, we then tested whether there were consistent trends between geologic age of fossil taxa and body size among pinniped lineages. We compiled data from the literature on the youngest and oldest occurrences of taxa included in this study, and then determined the median geologic age of each taxon. Geologic age data for all fossil taxa are presented in Appendix S4. We tested the correlation between the youngest, median, and oldest possible age of fossil taxa and estimated body size data using Spearman rank correlation tests ($\alpha = 0.05$).

We also tested for directional change in body size within pinniped lineages using the methods of Laurin (2004), Carrano (2005), and Butler and Goswami (2008). To do so, we determined the ancestral body size at every node in a composite phylogeny of Pinnipedimorpha containing all taxa within this study (Fig. 2). We fitted the composite phylogeny described above to the fossil record in Mesquite 2.75 (Maddison and Maddison 2011). To generate branch length data, we used geologic age data from the fossil record for extinct taxa and extant taxa with fossil records older than the Holocene to determine the average amount of time an individual pinniped species persisted ($N = 43$, mean $= 2.64$ Myr). We then set all branch lengths in the phylogeny as equal to this value. We performed ancestral character state reconstruction for the $\log_{10}$ body size for every node in the tree. These data were then used to determine the change in body size between ancestors and descendants for terminal tips of the tree as well as internal nodes. We then determined the mean change, median change, and sum change in body size for Pinnipedimorpha, Desmatophocidae, Phocidae, Odobenidae, and Otariidae. We also determined the number of positive and negative changes in body size within each of the above clades. The number of positive and negative changes in body size were then assessed using nonparametric Chi-squared goodness of fit tests to determine if there were a greater than expected number of decreases or increases in body size compared to a null expectation of an equal number of increases and decreases in body size within a lineage through time.

Results

PRINCIPAL COMPONENTS ANALYSIS

The PCA of 12 $\log_{10}$ transformed cranial measurements indicated that ~89% of the variation within the measurements was best explained by the first two components (Fig. 3). Component one explained 78.32% of the variation and reflected the difference in size between taxa. Component two explained 10.34% of the variation and reflected the shape of the bullae, orbital region, and length of the postcanine tooth row. The PCA clearly segregated Otariidae from Phocidae. All fossil taxa either overlapped with the otariid morphospace (Desmatophocidae, *Thalassoleon*) or clustered separately below but adjacent to the otariid morphospace ("enaliarctines," Odobenidae), and away from the phocid morphospace.

The DFA performed on the 12 $\log_{10}$ transformed cranial measurements was able to classify fossil phocid and otariid taxa with 100% accuracy. When the morphospaces of extant Otariidae and Phocidae were used to classify fossil taxa, 93.75% of the "enaliarctines," desmatophocids, and odobenids were classified as similar to Otariidae with a 99.99% posterior probability. Only the odobenid *D. seftoni* was classified as similar to phocids, again with 99.99% posterior probability. The latter result however contradicted the PCA plot, which still showed fossil walruses clustering separately from phocids. Based on these results, we used only body size predictive equations developed for Otariidae to estimate body size in "enaliarctines," desmatophocids, and odobenids.

BODY SIZE ESTIMATES

Total body length estimates for fossil taxa, including regression equations used, are presented in Appendix S1. For Otariidae, Odobenidae, Desmatophocidae, and "enaliarctines," we used the multivariate predictive regression equation for Otariidae, shown here:

$$1.9 \times \mathrm{Log}\,(\textit{basal length of skull}) - 0.66 \times \mathrm{Log}\,(\textit{palate length}) + 0.4,$$

which had a R^2 of 0.83, percent prediction error of 2.66%, and a standard error of estimation of 10.62%. For Phocidae, we used the following multivariate predictive equation:

$$0.37 \times \mathrm{Log}\,(\textit{width of skull across canines}) + 0.80 \times \mathrm{Log}\,(\textit{width across occipital condyles}) + 1.39,$$

which had a R^2 of 0.94, percent prediction error of 2.83%, and a standard error of estimation of 13.34%.

ANALYSIS OF BODY SIZE TRENDS

Fossil pinniped body size was found to have a strong phylogenetic signal ($K = 0.8 \pm 0.08$), indicating that further tests of body size trends in Pinnipedimorpha were warranted. A Q–Q plot (Appendix S5) indicated that the body size data were not normally distributed. Taxa that violated the assumption of normality included the largest (*P. magnus*) and the smallest (*P. bishopi*) species in this study. Because fossil pinniped total length data were not normally distributed, all total length data were $\log_{10}$ transformed. When median geologic age and $\log_{10}$ total length was plotted, a negative relationship was found between geologic age of fossil taxa and body size (Fig. 4), evident even when the imprecision of total length estimates and geologic age are taken into account. Spearman rank correlation tests indicate that the negative relationship is significant, regardless if the

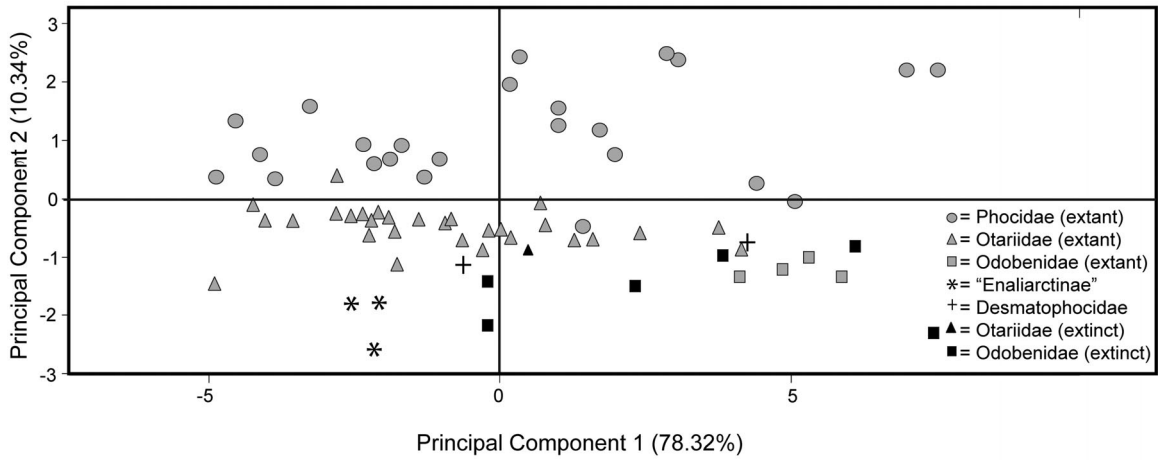

Figure 3. Bivariate plot of principal component one versus principal component two, based on 12 cranial measurements used to predict body size in pinnipeds (Churchill et al. 2014). Only taxa in which all 12 cranial measurements are preserved are included within the PCA.

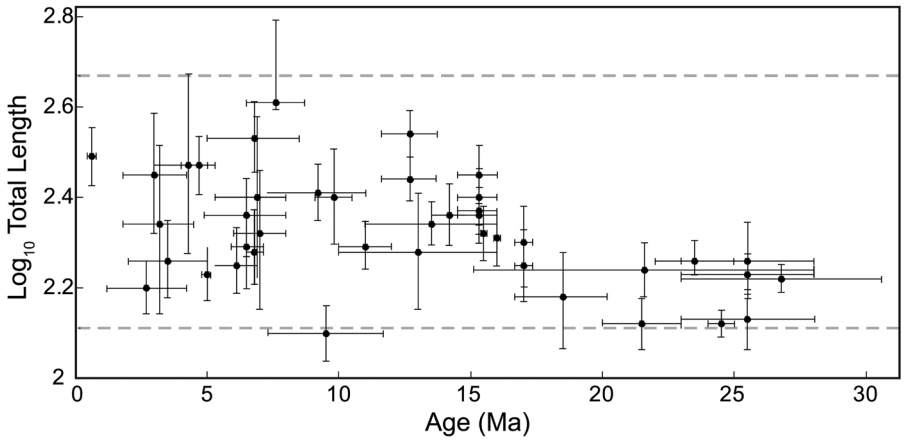

Figure 4. Relationship between median age of fossil taxon and total length, showing a pattern of increasing body size toward the present. Vertical error bars represent error associated with total length estimate, from error in estimation (percent prediction error) and variation in body size estimates from multiple equations or individuals. Horizontal error bars represent the minimum and maximum age of a fossil specimen. Total length of fossil taxa is listed in Appendix S1. Age of taxa is listed in Appendix S3.

youngest ($P = 0.002$), median ($P = 0.003$), or oldest ($P = 0.003$) possible geologic age of taxa is used. This indicated that overall, the mean body size of pinnipeds has increased through time, with later evolving taxa reaching larger body sizes than earlier occurring forms. Although there was variation in the maximum size of pinniped taxa through time, there were only minor variations in minimum pinniped body size, with the earliest pinnipedimorph taxa being only slightly smaller or within the same size range as extant taxa. Fossil pinniped taxa largely occur within the envelope of body size displayed by extant marine pinnipeds, and achieved maximum disparity in body size by the late Miocene.

To test for body size trends within pinniped lineages, we determined the ancestral body size for every node in our composite phylogeny (Appendix S6). These data were then used to summarize ancestor–descendent body size trends for Pinnipedimorpha, Desmatophocidae, Phocidae, Odobenidae, and Otariidae (Table 1). Generally, the mean, median, and sum body size change recorded for the different clades was zero or close to zero. Very little skew in body size change was evident for most clades, although Desmatophocidae showed slight skew toward increasing body size. There were no significant differences in the number of negative and positive changes in body size within a lineage, and only Desmatophocidae showed a slight but not significant increase in body size over time (Fig. 5).

Discussion

CHANGE IN PINNIPED BODY SIZE IN THE NORTH PACIFIC

Previous studies (Repenning 1976) have suggested that otariids and odobenids evolved from relatively smaller ancestors, and that over time both clades independently achieved larger body size as

Table 1. Results of ancestor–descendent comparisons of reconstructed $\log_{10}$ body size in Pinnipedimorpha and component clades.

	Mean change	Sum change	Skew	Median change	n	Positive changes	Negative changes	χ^2	P
Pinnipedimorpha	−0.001	−0.043	−0.117	−0.002	142	65	74	0.583	0.445
Desmatophocidae	0.008	0.105	−1.188	0.022	14	8	5	0.692	0.405
Phocidae	−0.002	−0.084	0.095	−0.008	45	19	25	0.818	0.366
Otariidae	−0.001	−0.010	0.065	−0.005	31	12	18	1.200	0.273
Odobenidae	0.002	0.070	−0.143	0.009	33	18	14	0.5	0.480

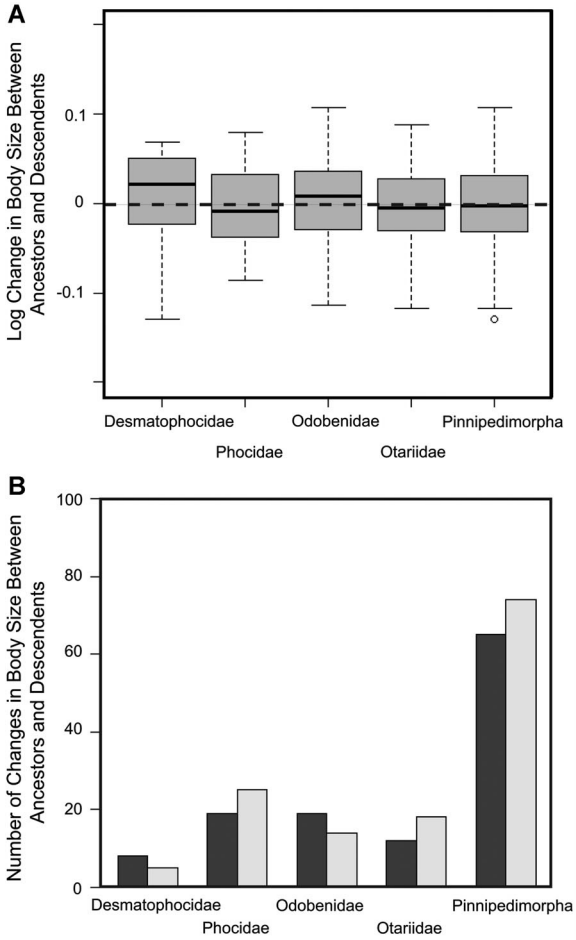

Figure 5. Comparisons of within-lineage change in $\log_{10}$ total length among Desmatophocidae, Phocidae, Odobenidae, Otariidae, and Pinnipedimorpha. Boxplot A summarizes total change in $\log_{10}$ total length within pinniped lineages, with 0 change indicated by the dashed line. Barplot B illustrates total number of positive (black) and negative (gray) total length changes for each clade.

a result of increased adaptation to a pelagic lifestyle. Our study indicated that the common ancestor of Otariidae and Odobenidae was smaller than later diverging members of their respective lineages.

The earliest known described otariid, *Pithanotaria starri* from the Tortonian of California (Deméré et al. 2003), represents one of the smallest known otariids (est. total length = 126 cm; Appendix S2). This is comparable to the smallest extant adult otariid, female *Arctocephalus galapagoensis* (120 cm) in size. Older, undescribed otariid taxa are known, however these appear to represent similarly sized animals (Kohno et al. 2007). Most other Miocene and Pliocene otariid taxa were larger than *Pithanotaria* but within the same range of body size as that exhibited by extant Otariidae. Indeed, stem otariids such as *T. macnallyae* and possibly *C. gilmorei* are reconstructed as having comparable body sizes to the earliest diverging crown otariid, *C. ursinus*. These taxa would have been the smallest members of the local pinniped faunas, and are far smaller than contemporary odobenid taxa.

Our ancestral character state reconstruction indicated initial size increases within Otariidae beginning in the common ancestor of northern sea lions and southern otariids. This tendency for increased body size was later reversed in southern fur seals (*Arctocephalus*), which showed progressive miniaturization within their lineage. Both shifts in body size are recent, as the radiation of crown Otariidae was confined to the Pliocene and Pleistocene (Yonezawa et al. 2009). The development of small body size in southern fur seals may explain the convergence in pelage between this clade and *Callorhinus*, as reduced body size may have necessitated the development of thick underfur to aid in thermoregulation, because blubber is insufficient by itself at a small body size for insulation (Iverson 2008; Liwanag et al. 2012).

It is unclear why miniaturization occurred in southern fur seals. One driver may have been reproductive isolation: most otariid taxa can readily hybridize across species and genera (Berta and Churchill 2012), but extreme differences in body size such as that between sea lions and fur seals reduces the chance of successful mating (Miller et al. 1996). Separation of niche space from the larger southern sea lions (*Phocarctos*, *Neophoca*, and *Otaria*) may have also been an important factor.

Within Odobenidae, the ancestrally reconstructed total length was 195 cm, smaller than almost all other fossil walruses. Early and middle Miocene" imagotariines" (stem odobenids) showed a range in total length of ~200–225 cm, comparable to that exhibited by extant *Zalophus* and slightly larger than their "enaliarctine" ancestors, although some of this difference may be due

to bias from overrepresentation of male stem odobenids in our dataset. Odobenids showed drastic size increases during the late Miocene, cumulating in the largest odobenid ever, *P. magnus,* at over 4 m in total length. Large body size (~250–335 cm total length) is also present in the Dusignathinae (double-tusked walruses). Odobenines showed a greater variation in body size, with earlier taxa more similar in size to sea lions (i.e., *Aivukus*: 207 cm total length), with later diverging taxa reaching enormous sizes, such as the 3-m-long *Ontocetus nov*. sp. from Japan, as well as the extant *Odobenus*.

Desmatophocidae appeared to show the greatest tendency to evolve larger body sizes in our study. The earliest known desmatophocids, the desmatophocines, have estimated body sizes ranging from the "enaliarctine" sized (~130 cm total length; *D. brachycephala*) to sea lion sized (~200 cm total length; *D. oregonensis*). They were replaced by the Allodesminae in the middle Miocene, which attained even larger size, with taxa examined in our study reaching up to 3 m in length, although cranial material from Japan suggests even larger individuals (Kohno 1996; Kohno et al. 2007). These taxa were considered to be large pelagic predators, ecologically similar to *Mirounga* (Mitchell 1966), although rigorous studies of their ecology have not been performed. Allodesmine taxonomy is contentious (Barnes 1972; Barnes and Hirota 1995; Kohno 1996; Mitchell 1966; Deméré and Berta 2002), and it is unclear how many species were present. Our analysis used Barnes and Hirota (1995) as a baseline for eastern North Pacific taxonomy, but the genera and species within Allodesminae may be oversplit (Deméré and Berta 2002). Future taxonomic work may change the results presented here, and show that Desmatophocidae followed Cope's rule.

A sequential pattern of large body size evolution is apparent in the North Pacific (Fig. 6), with different clades generally occupying the large body size niche at different times. The first large pinnipeds to evolve were the Allodesminae, who were contemporaneous with small- and medium-sized "imagotariines." The Allodesminae became rare shortly after the middle Miocene, with the latest known record from the Tortonian of Washington state (Bigelow 1994) and California (Repenning and Tedford 1977). At this time the first large odobenids appeared. Odobenids continued to be the dominant large-sized pinniped throughout the remainder of the Miocene and the Pliocene in the North Pacific. By the end of the Pleistocene, Odobenidae were almost completely extinct. Only the extant *Odobenus* survived, restricted to the Arctic Ocean. At some time in the late Pliocene to Pleistocene, the current large North Pacific pinnipeds, *Mirounga* and otariid sea lions, evolved or entered the North Pacific. (Deméré et al. 2003; Boessenecker 2011, 2012).

Although large body size can provide benefits, it also confers disadvantages, including the need for increased amounts of food (Hone and Benton 2005) and greater susceptibility to extinction (Cardillo et al. 2005). These factors may have influenced the extinction dynamics within pinnipeds. Odobenids throughout the late Miocene and early Pliocene included a variety of taxa of varying body size. In contrast, the allodesmines were almost entirely large. This suggests that Allodesminae were more specialized and vulnerable to extinction when compared with odobenids. The greater size diversity of Odobenidae in the Neogene may explain the longer dominance of this clade in the North Pacific. Although speculative, competition may have also played a role in allodesmine extinction, as there is possible overlap in time and space between the first giant walruses (*Pontolis*) and the last allodesmines; greater dental and palate diversity in odobenids (Deméré 1994a) may have also played a role. Further work on Neogene pinniped faunas may help resolve patterns underlying the extinction and replacement of large pinniped taxa in the North Pacific.

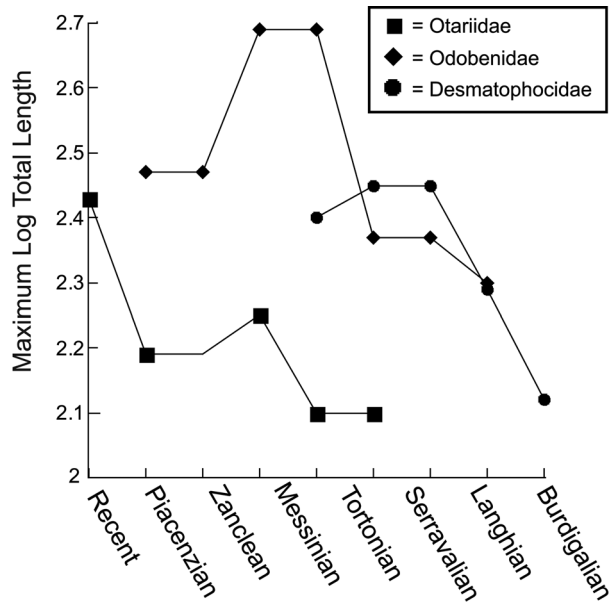

Figure 6. Maximum total length of North Pacific pinniped clades by stage. Body size estimates are presented in Appendix S1, whereas taxa are binned by stage according to Table 2.

EVOLUTION OF PHOCID BODY SIZE

Interpretation of body size trends within Phocoidea has been controversial, with miniaturization and Cope's rule both cited as occurring within the clade (Laws 1959; McLaren 1960; King 1972; Wyss 1994). Our analysis found little evidence that Phocidae evolved from large ancestors. Reconstruction of total length in the common ancestor of Phocoidea, *Pinnarctidion*, and the clade comprising Phocidae and Desmatophocidae all indicated a total length (~140–170 cm) comparable to their small (~150–170 cm total length) "enaliarctine" ancestors. The common ancestor of Phocidae had a reconstructed total length of 204 cm, smaller than most extant monachines.

Monachines and phocines showed very different patterns of body size change. Monachinae showed a trend toward increased body size. Stem monachines were smaller than extant taxa at ~180–190 cm in total length, the one exception being *Callophoca*, at nearly 3 m in total length. The evolution of taxa from stem monachines through *Monachus* and *Mirounga* showed a pattern of increasing body size. This is partly reversed within Lobodontini, with both size increases and decreases occurring.

Phocinae showed the opposite pattern, with the earliest diverging lineages being larger than the later diverging taxa. Although Wyss (1994) identified only one trend toward decreasing body size in Phocinae, we identify two possibly separate reductions in size, with separate trends toward reduced body size within the *Histriophoca–Pagophilus* clade and the *Phoca–Pusa* clade. However, this would in part support Wyss (1994), as members of these clades show the most pronounced ontogenetic juvenilization, and reduction in body size may be a result of heterochronic processes.

However, interpretation of the evolution of body size in Phocidae remains tentative. Unlike other pinniped clades, the fossil record for Phocidae is poorly known, especially for Phocinae. Rigorous cladistic analyses of Phocinae are lacking, and only a small number of fossil monachines have appeared in studies (Berta et al. in press; Berta and Wyss 1994; Cozzuol 2001; Koretsky and Holec 2002). In addition, many fossil phocids are known only from fragmentary and isolated postcranial material, making estimation of body size using the regression equations of Churchill et al. (2014b) impossible. Because of the above problems, only five fossil taxa could be incorporated into this study. With additional fossil material, a pattern of miniaturization may be recovered in Phocinae. Alternatively, reductions in body size may be relatively recent phenomena, and further analysis will reveal that reduction in body size happened independently for several phocine genera.

COPE'S RULE IN PINNIPEDS

By testing both among and within lineage evolution of body size, we determined the pattern of body size evolution in Pinnipedimorpha, and whether there was consistent selection toward larger body size. Our analysis showed that later diverging pinniped taxa reached larger body sizes than earlier diverging forms, indicating that mean body size had increased through the Cenozoic. This would seem to support the assertions of previous studies that have argued that most pinniped groups had smaller ancestors (Laws 1959; McLaren 1960; King 1972; Repenning 1976).

When the data were summarized as stage-level time slices (Table 2; Fig. 7A), most of the pattern of change in pinniped body size through time can be interpreted to be a result of the difference between the relatively small basal pinniped taxa of the Oligocene and early Miocene (Chattian, Aquitanian, and Burdigalian stages),

Table 2. Fossil pinniped taxa included in this study, sorted by epoch and stage.

Epoch	Stage	Age	Taxa	Mean total length (cm)
Pliocene	Piacenzian	3.6–2.588	*Homiphoca capensis, Dusignathus seftoni, Valenictus chulavistensis, Callorhinus gilmorei*	209
	Zanclean	5.332–3.6	*Homiphoca capensis, Callophoca obscura, Dusignathus seftoni, Protodobenus japonicus, Ontocetus nov.* sp., *Valenictus chulavistensis, Thalassoleon mexicanus, Callorhinus gilmorei*	228
Miocene	Messinian	7.246–5.332	*Piscophoca pacifica, Callophoca obscura, Acrophoca longirostris, Pontolis magnus, Gomphotaria pugnax, Aivukus cedrosensis, Protodobenus japonicus, Ontocetus nov.* sp., *Thalassoleon mexicanus, T. macnallyae*	250
	Tortonian	11.608–7.246	*Allodesminae nov.* sp., *Leptophoca lenis, Piscophoca pacifica, Acrophoca longirostris, Pseudotaria muramotoi, Imagotaria downsi, Pontolis magnus, Gomphotaria pugnax, Dusignathus santacruzensis, Aivukus cedrosensis, Pithanotaria starri, Thalassoleon mexicanus*	236
	Serravallian	13.65–11.608	*Allodesmus sadoensis, A. sinanoensis, A. kelloggi, A. gracilis Leptophoca lenis, Neotherium mirum, Kamtschatarctos sinelnikovae, Pseudotaria muramotoi, Pelagiarctos thomasi, Pithanotaria starri*	236
	Langhian	15.97–13.65	*Brachyallodesmus packardi, Allodesmus kelloggi, A. gracilis, Leptophoca lenis, Proneotherium repenningi, Neotherium mirum, Kamtschatarctos sinelnikovae, Pelagiarctos thomasi*	230
	Burdigalian	20.43–15.97	*Desmatophoca oregonensis, Prototaria primigenia, P. planicephala, Proneotherium repenningi*	203
	Aquitanian	23.03–20.43	*E. mealsi, E. emlongi, Pteronarctos goedertae, Pacifcotaria hadromma, Desmatophoca brachycephala*	164
Oligocene	Chattian	28.1–23.03	*Enaliarctos mealsi, E. barnesi, E. tedfordi, E. mitchelli, E. emlongi, Pinnarctidion bishop, P. rayi*	163

Age of individual taxa is listed in Appendix S3.

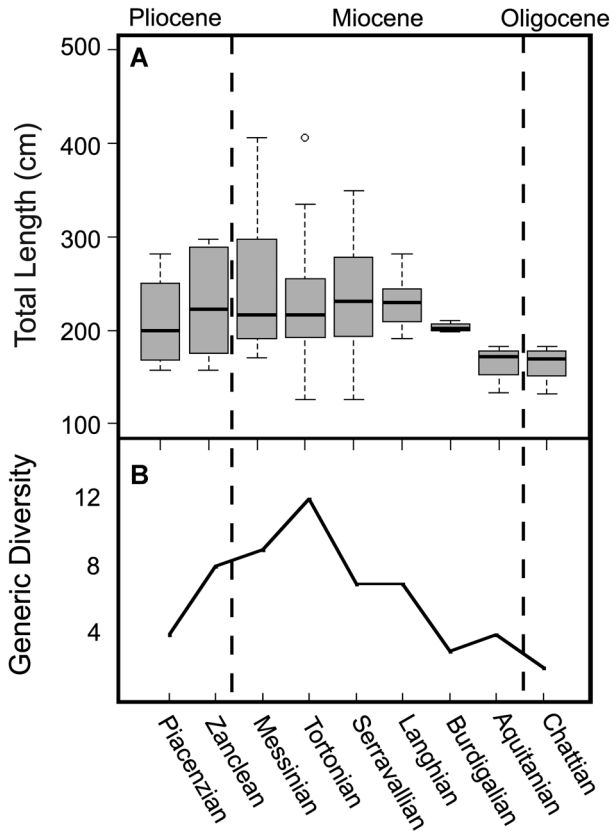

Figure 7. Boxplots of total length data for fossil pinniped taxa binned by geologic stage (A), compared with generic diversity (B). Dashed lines separate the Pliocene and Miocene epochs and the Miocene and Oligocene epochs. Mean total length and taxonomic composition of each stage are presented in Table 2.

and younger taxa that were generally larger but more variable in size. Thus most of the pattern appears to have been driven by an initial increase in body size during the middle Miocene (Langhian-Serravalian).

The increase in pinniped body size was associated with an increase in pinniped generic diversity (Fig. 7B). These changes in diversity and body size occurred around the same time or somewhat earlier than the rapid increase in cetacean diversity (Marx and Uhen 2010), which has been shown to be related to changes in global primary productivity (Suto et al. 2012). Pinnipeds, much like whales, may have seen an increase in diversity coincident with an increase in global primary productivity. As early pinnipeds were close to the minimum body size possible for an endothermic marine mammal (Downhower and Blumer 1988), diversification led to increased mean body size as species departed from the lower body size constraint (Stanley 1973; Fig. 1B). Pinnipedimorph body size was not undergoing selection for larger body size, as posited by Repenning (1976), but rather change in body size occurred through passive forces. Ancestor–descendent comparisons failed to show a significant difference between positive and negative changes in body size for any pinniped clade, which strongly supports the idea that change in body size over time has largely been the result of passive drivers, not active selection favoring increased body size (McShea 1994, 2000). Further evidence was also provided by minimum body size, which is highly variable over the time period examined in this study, but does not show a steady increase as expected in active selection toward larger body size. Instead, small taxa, some similar or smaller in size than early pinnipedimorphs, occurred throughout the Neogene (and today).

Our analysis is biased toward the North Pacific. The oldest definitive records of Phocidae date from the Burdigalian to Langhian of the North Atlantic and North Africa (Koretsky 2001; Deméré et al. 2003; Koretsky and Domning 2014), however phocid evolution and diversity in this region is poorly known. For our study we were only able to examine one early phocid, *Leptophoca lenis*, which had an estimated total body length of ~190 cm, larger than earlier diverging pinnipedimorphs, but comparable in size to geologically older desmatophocids. Because of this sampling bias, it is impossible to tell whether the pattern observed in this study holds true for pinnipeds globally, or if the increase in body size in phocids in the North Atlantic occurred earlier or later than the increase in the North Pacific.

Recent studies have confirmed the validity of Cope's rule in mammals, but this rule does not apply to pinnipeds. This indicates the importance of testing evolutionary trends at varying taxonomic levels (Hone and Benton 2007). The findings of this study contrast with previous research on Caniformes and Canidae (Van Valkenburgh et al. 2004; Finarelli and Flynn 2006), which supported increasing body size through time. This implies that evolutionary pressures affecting body size in terrestrial mammals may not be the same as those affecting their marine relatives. This finding somewhat agrees with previous work from Bininda-Emonds and Gittleman (2000), who found slight, although insignificant, differences in the evolution of body size between fissiped and pinniped carnivorans.

Alternatively, while past studies on Carnivora have reconstructed body size in fossil taxa and operated under a phylogenetic paradigm, they did not use rigorous ancestor–descendent comparisons to test for Cope's rule. Thus, while the prior studies have indicated a positive increase in body size within some lineages, these trends may only apply to specific lineages and are not universal at higher taxonomic levels. Further tests of Cope's rule are thus needed to determine the applicability of this trend across Carnivora.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. List of taxa and specimens examined for this study, with estimated age, size, and regression equation used.
Appendix S2. Uncertainty in fossil total length estimates.
Appendix S3. Comparisons of estimated and known body size in *Allodesmus kellogii* (LACM 4320).
Appendix S4. Age and locality data for pinniped taxa included in this study.
Appendix S5. Normal Q–Q plot of untransformed (A) and $\log_{10}$ transformed (B) fossil pinniped total length.
Appendix S6. Reconstructed ancestral body size.