



Osteological correlates and phylogenetic analysis of deep diving in living and extinct pinnipeds: What good are big eyes?

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ABSTRACT

Marine tetrapods have evolved different sensory solutions to meet the ecological challenges of foraging at depth. It has been proposed that pinnipeds, like ichthyosaurs, evolved large eyeballs for such demands. Here, we test this hypothesis using morphological and diving data from a comprehensive data set ($n = 54$ species; 435 individual specimens), including living and extinct pinnipeds and other select carnivorans as outgroup taxa. We used bony orbit size as a proxy for eyeball size, and recorded associated skull measurements to control for relative changes in orbit size; for diving depth, we used the deepest dive depth reported in the literature. Our analyses included both standard regressions and those corrected for phylogeny (*i.e.*, independent contrasts). Standard regression statistics showed orbit size was a significantly good predictor of diving depth for phocids and for pinnipeds overall, although there was no correlation for otariids. In contrast, independent contrasts showed little support for a relationship between orbit size and diving depth for any group broader than family level, although this approach did demonstrate deep diving has evolved multiple times in crown Pinnipedia. Lastly, using select fossil taxa, we highlight the need to test adaptive hypotheses using comparative data in an evolutionary context.

Key words: allometry, diving depth, evolution, morphology, phylogenetic independent contrasts, Pinnipedia, skull, vision.

The evolution of marine mammals represents multiple, independent origins of a return to marine habitats from terrestrial ancestry. Marine mammals are thus a polyphyletic group, and they include both living and extinct taxa that exhibit varied ecological and morphological specializations for aquatic life (Williams *et al.* 2000, Berta *et al.* 2003, Uhen 2007). Among marine mammals, pinnipeds (seals, sea lions, and walrus) comprise a clade whose extant members exhibit distinctly amphibious features, which provides an unusual comparative system for studying adaptive traits at the interface of terrestrial and aquatic lifestyles.

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In many respects, comparisons between pinnipeds and cetaceans highlight common evolutionary solutions, independent of phylogeny, for foraging in marine environments (Warheit and Lindberg 1988, Werth 2000, Uhen 2007). Many species of pinnipeds and cetaceans, for example, share common prey items, and their foraging modes overlap in time and space (Clarke 1996, Klages 1996, Pauly *et al.* 1998). Moreover, both groups have evolved suites of morphological, behavioral, ecological, and life history solutions to meet the demands of foraging underwater (Werth 2000), especially with deep diving, in search of prey (Lindberg and Pyenson 2007). Both pinnipeds and cetaceans rank among the deepest tetrapod divers (Schreer and Kovacs 1997), but unlike toothed whales, pinnipeds do not possess echolocation to locate their prey in the low light conditions of the mesopelagic zone (150–1,000 m; Schusterman *et al.* 2000, Berta *et al.* 2003).

Among available sensory systems, pinnipeds possess specialized hearing, vibrissae, and vision for prey detection and capture in their aquatic environment. While the auditory abilities of pinnipeds appear attuned for underwater hearing, this sense seems unable to fulfill the needs for prey detection in all species (Repenning 1972; Kastak and Schusterman 1998, 1999; Schusterman *et al.* 2000). Pinniped vibrissae, or whiskers, are highly specialized (Ling 1977, Gläser *et al.* 2010, Hanke *et al.* 2010), and this tactile sense is an important component of pinniped prey detection (Hyvärinen *et al.* 2009, Hanke *et al.* 2010), especially in benthic-foraging species (Dehnhardt *et al.* 1998, Marshall *et al.* 2006). It has been suggested that pelagic feeding and high-speed swimming may hinder pinnipeds' ability to detect water movement above background noise (Levenson and Schusterman 1999), although experimental and morphological evidence now suggest that the vibrissae of at least harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) can detect hydrodynamic trails left by prey (Dehnhardt *et al.* 2001, Hanke and Bleckmann 2004, Hanke *et al.* 2010). Moreover, the specialized and undulated morphology of harbor seal vibrissae confers a performance advantage over the nonspecialized hair type in sea lions (Gläser *et al.* 2010, Hanke *et al.* 2010). *Zalophus* may overcome such limitations by approaching their prey from below to perceive their silhouettes against light on the water's surface (Hobson 1966). Although 15 of 18 phocid species have undulated vibrissae (Ginter *et al.* 2010, Hanke *et al.* 2010), the behavior of some phocids suggests some integration of vision and foraging as well, for example, approaching prey from below (seen in Weddell seals, *Leptonychotes weddellii*; Davis *et al.* 1999) or making short-scale benthic zigzag prey pursuit movements (seen in crabeater seals, *Lobodon carcinophaga*; Bengston and Stewart 1992).

The visual capabilities of pinnipeds foraging at depth have been assessed using experimental and anatomical studies. Behavioral and experimental studies, for example, have shown that pinniped eyes in general resemble those of nocturnal mammals, with higher light sensitivity and faster darkness adaptation compared to other diurnal, terrestrial mammals (Levenson and Schusterman 1999). Microscopic eye anatomy of the deep-diving *Leptonychotes* shows a well-developed tapetum lucidum and rods and absence of a fovea centralis, indicating a specialization for extreme light sensitivity (Welsch *et al.* 2001). Walruses' (*Odobenus rosmarus*) eyes likewise exhibit morphologies suggesting both color vision (cones) and specializations for short-range underwater use (Kastelein *et al.* 1993). The visual acuity of walruses, however, is lower than that of other pinnipeds, a finding that is consistent with the ecological differences between benthic-feeding walruses and more pelagic phocids and otariids (Kastelein *et al.* 1993). Pinniped visual pigment sensitivity of retinal rods also suggests the importance of underwater vision, with pinnipeds exhibiting blue-shifted pigment

sensitivity values (reflecting specialization for aquatic vision), relative to terrestrial values (Kirk 1994). Additionally, pinniped foraging depth is positively correlated with visual pigment sensitivity, with the deepest-diving pinnipeds showing a more pronounced blue-shift towards light wavelengths common in deeper water (Lythgoe and Dartnall 1970, Lavigne and Ronald 1975, Levenson *et al.* 2006). Lastly, elephant seals (*Mirounga* spp.), which dive well below the photic zone, have pigment sensitivity characteristics corresponding to light wavelengths emitted at depth by bioluminescent organisms (Levenson *et al.* 2006). These findings strongly argue for the importance of vision as a sensory system that is tightly linked with diving in pinnipeds.

The high visual sensitivity of the pinnipeds compared to terrestrial mammals likely evolved during their transition to aquatic life, but without soft tissue preservation in the fossil record, we require osteological correlates of diving to examine the acquisition of visual sensitivity. Given these constraints, we used eye size as a proxy for sensitivity in extant and extinct pinnipeds. In living vertebrates, visual sensitivity is a function of both photoreceptive cell number as well as eye diameter: larger eyes can house more retinal photoreceptive cells, and the absolute size limits incoming light (Walls 1942, Hughes 1977, Martin 1983, Schmitz 2009). Previous studies on nocturnal tetrapods, including both extant archosaurs and placental mammals, have reinforced the importance of absolute eye size (Walls 1942, Hughes 1977); archosaurs, in particular, possess a bony orbit and sclerotic ring that provide a solid proxy for diel patterns in extinct relatives (Schmitz 2009). Among marine taxa, Motani *et al.* (1999) used eye size and aperture (approximated by measuring the bony sclerotic ring of the eye) to assess diving in ichthyosaurs, some of which possessed the absolutely largest eyes of any vertebrate. Based on inferences of ichthyosaur visual sensitivity, Motani *et al.* (1999) argued that ichthyosaurs were capable of seeing in low light conditions and, based on body size, diving to depths of 500 m or more. Humphries and Ruxton (2002) further argued that the large ichthyosaur eyes provided high visual sensitivity *and* acuity, although subsequent tests for acuity (*i.e.*, measuring retinal pooling) are not possible given the constraints of the fossil record. As synapsids, marine mammals lack sclerotic rings and thus the aforementioned proxies for visual acuity are only moderately informative. Fitzgerald (2006) argued that some Oligocene stem mysticetes, like *Janjucetus*, possessed large orbits that reflected putative deep-diving adaptations. Such evolutionary arguments, however, have not been advanced in a comparative context, nor using a single, well-sampled clade with known diving behavior.

Here, we examined the allometry and evolution of deep diving in pinnipeds using skull dimensions (*e.g.*, bony orbit size) as a proxy for visual sensitivity. Crown Pinnipedia¹ provides an ideal clade of marine mammals for testing the correlation between eye size and diving, given their high species richness, abundant representation in curated museum collections, and relatively well-known and reported diving behavior. First, we compared bony orbit size between pinnipeds and their closest extant terrestrial relatives (select arctoid carnivorans). Then, we examined the

¹Here, we follow terminology for crown groups originally articulated by de Queiroz and Gauthier (1992). These concepts essentially argue that higher taxonomic terminology ought to reflect phylogeny (see also Joyce *et al.* 2004). A crown group refers to the common ancestor of all extant members of a taxon plus all of that ancestor's descendants, whether extant or not (De Queiroz and Gauthier 1992); stem-based names are informal, and refer to extinct members outside of the crown group, which are more closely related to the living descendants than to a given outgroup (Budd 2001).

relationship between bony orbit size and other skull metrics *vs.* diving depth, across all pinnipeds, as well as within subclades (*e.g.*, the families Otariidae and Phocidae). We also examined these correlations while accounting for phylogenetic relationships among the sampled taxa (*i.e.*, phylogenetic comparative methods). Lastly, we outlined a framework for understanding the significance of these results in an evolutionary context, by comparing the proposed cranial correlates of deep diving in key fossil pinnipeds.

MATERIALS AND METHODS

Institutional Abbreviations

Extant and fossil specimens studied herein are deposited in collections at the following institutions: Australian Museum, Sydney, Australia (AM); American Museum of Natural History, New York, New York (AMNH); California Academy of Sciences, San Francisco, California (CAS); Canadian Museum of Nature, Ottawa, Canada (CMN); Natural History Museum of Los Angeles County, Los Angeles, California (LACM); University of California Museum of Vertebrate Zoology, Berkeley, California (MVZ); San Diego Natural History Museum, San Diego, California (SDNHM); University of California Museum of Paleontology, Berkeley, California (UCMP); University of Oregon Museum of Natural and Cultural History, Eugene, Oregon (UOMNH); Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A. (USNM); and Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington (UWBM).

Taxonomic Scope

Cranial measurements and associated natural history data were collected for 353 extant pinniped specimens, representing 34 species in 21 genera. This study includes 14 extant species in Otariidae (sea lions and fur seals),² and all 19 extant species in Phocidae (true seals), including the recently extinct *Monachus tropicalis*, as well as the only extant species in Odobenidae (walruses). The advent of molecular systematics has called into question pinniped alpha taxonomy over the past 20 yr, and, consequently, the taxonomic status and monophyly of many otariid genera and species are unclear (Wynen *et al.* 2001, Brunner 2003). While there are more recent phylogenies for pinnipeds (*e.g.*, Fulton and Strobeck 2010, for phocids), for simplicity, in this study we follow the taxonomic opinions of Higdon *et al.* (2007), because their study spans all pinniped taxa in our analysis and is, to date, the most comprehensive reported molecular analysis of pinniped species relationships (based on all available GenBank pinniped sequences; see Table 1 for taxonomic details and Fig. 1A, B for phylogenetic relationships).

²We did not follow Brunner (2003), who reduced *Arctocephalus forsteri* and *A. galapagoensis* to subspecies of *A. australis*, and also relegated *A. townsendi* to a subspecies of *A. philippii*. Instead, we have kept *A. forsteri* and *A. galapagoensis* as nominal species. We also departed from the Taxonomy List of the Society for Marine Mammalogy (SMM) in keeping *A. townsendi* and *A. philippii* within *Arctocephalus*, instead of members of the resurrected genus *Arctophoca*. Our justification follows that of *ad hoc* Committee on Taxonomy member A. Berta, listed in footnote 2 of the SMM Taxonomy List website (Committee on Taxonomy 2009).

Table 1. Extant and extinct pinniped species used in this analysis, with specimen means and standard deviations (SD), phylogeny according to Higdon *et al.* (1997).

Higher taxon	Species	Common name	Total		Male		Female		CBL		BZB		OCB		AveOrb	
			<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Otariidae	<i>Arctocephalus australis</i>	South American fur seal	18	9	20.88	3.21	11.98	0.57	4.79	0.23	5.24	0.56	5.24	0.56	5.24	0.56
	<i>Arctocephalus forsteri</i>	New Zealand fur seal	8	4	23.48	1.06	14.20	1.73	5.10	0.31	5.99	0.32	5.99	0.32	5.99	0.32
	<i>Arctocephalus galapagoensis</i>	Galapagos fur seal	7	3	18.51	1.30	11.39	1.24	4.46	0.22	5.01	0.22	5.01	0.22	5.01	0.22
	<i>Arctocephalus gazelle</i>	Antarctic fur seal	10	9	23.40	0.77	14.60	0.99	5.16	0.23	6.15	0.21	6.15	0.21	6.15	0.21
	<i>Arctocephalus pusillus</i>	Cape fur seal	8	4	25.43	3.69	14.74	2.71	5.61	0.69	5.91	0.56	5.91	0.56	5.91	0.56
	<i>Arctocephalus tropicalis</i>	subantarctic fur seal	1	1	20.40		13.41		3.98		5.62		5.62		5.62	
	<i>Arctocephalus philippii</i>	Juan Fernández fur seal	1	1	26.21		16.38		5.54		6.03		6.03		6.03	
	<i>Arctocephalus townsendi</i>	Guadalupe fur seal	3	3	23.90	1.95	13.43	1.70	5.23	0.29	6.07	0.31	6.07	0.31	6.07	0.31
	<i>Gallorhinus iratus</i>	Northern fur seal	15	7	18.81	1.12	10.74	0.59	4.75	0.29	5.35	0.21	5.35	0.21	5.35	0.21
	<i>Eumetopias jubatus</i>	Steller sea lion	17	8	33.22	3.92	19.57	2.99	7.60	0.69	7.26	0.72	7.26	0.72	7.26	0.72
	<i>Neophoca cinerea</i>	Australian sea lion	8	6	27.37	3.08	14.98	2.39	5.65	0.47	5.91	0.60	5.91	0.60	5.91	0.60
	<i>Otaria byronia</i> *	South American sea lion	6	3	29.98	3.87	17.65	2.75	6.17	0.59	6.61	0.73	6.61	0.73	6.61	0.73
	<i>Phocaria bookeri</i>	New Zealand sea lion	11	5	28.68	3.14	15.49	2.53	6.41	0.60	6.74	0.52	6.74	0.52	6.74	0.52
	<i>Zalophus californianus</i>	California sea lion	15	6	25.78	2.60	13.98	2.17	5.88	0.49	5.82	0.40	5.82	0.40	5.82	0.40
	<i>Cystophora cristata</i> *	Hooded seal	13	6	25.73	2.47	19.32	2.41	6.95	0.51	7.24	0.73	7.24	0.73	7.24	0.73
	<i>Erignathus barbatus</i>	Bearded seal	20	11	22.11	0.70	12.70	0.69	6.85	0.37	4.95	0.25	4.95	0.25	4.95	0.25
	<i>Halichoerus grypus</i>	Gray seal	13	6	24.39	4.15	14.66	3.25	6.65	0.49	4.96	0.44	4.96	0.44	4.96	0.44
<i>Histriophoca fasciata</i> *	Ribbon seal	8	3	19.26	1.00	12.12	0.69	5.84	0.43	4.98	0.44	4.98	0.44	4.98	0.44	
<i>Hydrurga leptonyx</i>	Leopard seal	14	3	38.74	2.81	20.87	2.99	8.38	0.62	8.77	0.64	8.77	0.64	8.77	0.64	
<i>Leptonychotes weddellii</i>	Weddell seal	8	1	26.86	2.18	16.22	1.75	7.56	0.75	6.91	0.79	6.91	0.79	6.91	0.79	
<i>Lobodon carcinophaga</i>	Crabeater seal	8	5	27.20	3.11	14.55	1.52	7.81	0.36	5.99	0.59	5.99	0.59	5.99	0.59	
<i>Mirounga angustirostris</i>	Northern elephant seal	8	4	38.38	11.20	24.67	6.34	9.92	1.18	10.45	2.30	10.45	2.30	10.45	2.30	
<i>Mirounga leonina</i>	Southern elephant seal	7	3	42.18	10.14	29.49	6.85	10.89	1.26	12.46	2.39	12.46	2.39	12.46	2.39	
<i>Monachus monachus</i> *	Mediterranean monk seal	3	1	28.17	1.66	18.80	2.04	6.47	0.45	7.14	0.5	7.14	0.5	7.14	0.5	
<i>Monachus schauinslandi</i> *	Hawaiian monk seal	15	4	24.82	0.98	14.83	0.86	5.84	0.27	6.02	0.27	6.02	0.27	6.02	0.27	
<i>Monachus tropicalis</i> *	Caribbean monk seal	11	6	26.61	1.36	16.12	1.02	6.26	0.37	7.10	0.55	7.10	0.55	7.10	0.55	
<i>Ommatophoca russii</i>	Ross seal	7	2	23.17	1.36	16.80	1.36	7.88	0.28	7.17	0.56	7.17	0.56	7.17	0.56	
<i>Pagophilus groenlandicus</i>	Harp seal	22	4	20.30	1.15	11.47	0.74	6.04	0.28	5.16	0.28	5.16	0.28	5.16	0.28	
<i>Phoca largha</i>	Largha seal	4	2	20.15	0.45	12.17	1.06	5.98	0.05	4.98	0.19	4.98	0.19	4.98	0.19	
<i>Phoca vitulina</i> *	Harbor seal	22	11	21.01	1.19	12.80	0.96	5.80	0.28	5.07	0.28	5.07	0.28	5.07	0.28	
<i>Pusa caspica</i> *	Caspian seal	3		18.43	0.45	10.07	0.06	5.10	0.26	4.87	0.15	4.87	0.15	4.87	0.15	

Continued

Table 1. (Continued)

Higher taxon	Species	Common name	Total		Male		Female		CBL		BZB		OCB		AveOrb	
			n	n	n	n	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Stem phocids	<i>Pusa hispida</i> *	Ringed seal	21	6	9	16.60	0.81	9.89	0.48	5.34	0.26	4.64	0.26			
	<i>Pusa sibirica</i> *	Baikal seal	7		4	14.95	0.76	9.02	0.68	5.04	0.15	4.20	0.42			
Desmatophocidae	† <i>Aerophoca longirostris</i>		1			31.4		13.8		6.8		6.5				
	† <i>Leptophoca lentis</i>		2			21.1		11.4		5.2		6.25				
	† <i>Pisophoca pacifica</i>		1			27.8		15.3		6.3		6.7				
	† <i>Allodermus gracilis</i>		1			40.45		18.7		10.3		9.64				
	† <i>Allodermus kelloggi</i>		1			37.15		20.7		9.4		8.91				
Odobenidae	† <i>Desmatophoca oregonensis</i>		1			32.4		17.7		6.89		6.49				
	<i>Odobenus rosmarus</i>	Walrus	11	1	1	36.54	2.52	23.47	2.54	11.51	2.79	5.61	0.39			
Stem pinnipeds	† <i>Aviukus cedroensis</i>		1			NA		17.2		NA		5.96				
	† <i>Imagotaria doensis</i>		1			28.85		16.0		8.2		5.46				
	† <i>Neotherium mirum</i>		1			27.1		14.19		6.26		4.75				
	† <i>Valenictus chulanistaensis</i>		5	4	1	36.13	4.24	21.33	3.52	10.23	1.25	5.02	0.68			
	† <i>Puffila darwini</i>		1			12.96		8.74		2.47		2.50				
	† <i>Enaliarctos meadii</i>		1			NA		13.18		4.57		4.91				
	† <i>Pacificotaria badromma</i>		1			21.3		12.62		5.1		4.17				
Mustelidae	† <i>Pinnarctidium bishopi</i>		1			NA		10.5		4.9		4.02				
	† <i>Pteronarctos goodertae</i>		1			20.7		11.74		5.2		4.26				
	† <i>Pteronarctos pteronot</i>		2			21.25	0.07	12.35	0.25	5.16	0.06	4.27	0.06			
	<i>Enhydra lutris</i>	Sea otter	27	12	15	12.71	0.43	10.00	0.34	4.28	0.18	2.30	0.11			
	<i>Gulo gulo</i> *	Wolverine	5	1	4	14.04	0.67	9.72	0.73	3.58	0.17	1.99	0.07			
Ursidae	<i>Lontra canadensis</i> *	North American river otter	11	7	4	11.31	0.44	7.40	0.40	3.30	0.19	1.61	0.09			
	<i>Ursus arctos</i> *	Brown bear	17	8	9	33.98	2.81	22.13	3.22	6.87	0.67	3.89	0.36			

Note: Column headings: condylobasal skull length (CBL); bizygomatic breadth (BZB); occipital condylar breadth (OCB); sample size (n); mean (\bar{x}); standard deviation (SD). Dagger symbol denotes fossil species; asterisk indicates species was not used in diving analysis; cross indicates the recently extinct species *Monachus tropicalis*. Skulls of unknown sex used in this analysis make up any difference between the male and female specimens and the total number of specimens. NA indicates damage to the skull and therefore a lack of a measurement. Blank SD fields indicate measurements based on one specimen (e.g., *Arctocephalus philippii*, *A. tropicalis*, and many fossil species).

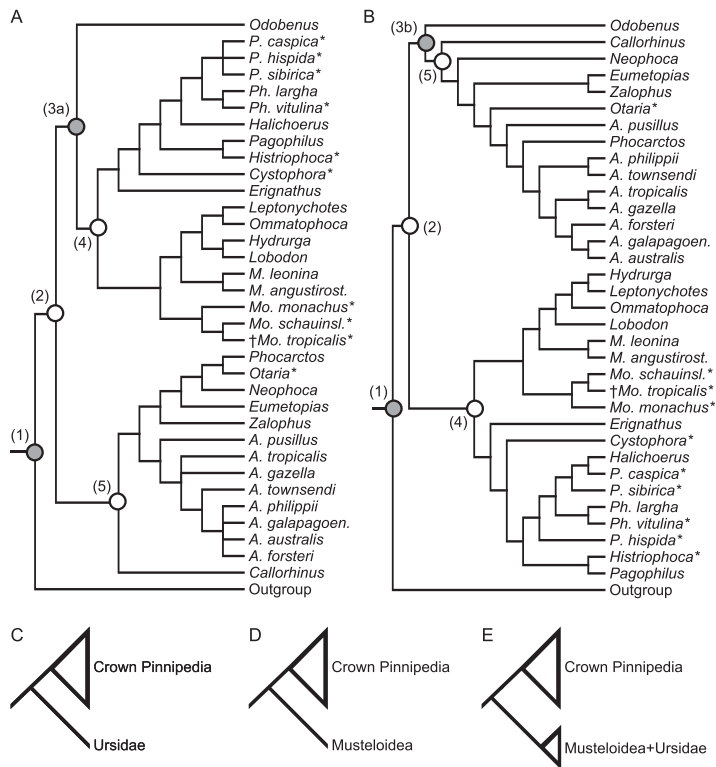


Figure 1. Phylogenetic trees and relationships among pinniped taxa in this study. (A) Morphological phylogeny, pruned from Deméré *et al.* 2003; (B) Molecular phylogeny, pruned from Higdon *et al.* 2007. Numbered nodes refer to clades defined as follows: (1) crown Pinnipedia + arctoid carnivoran outgroup, (2) crown Pinnipedia, (3a) *Odobenus* + Phocidae, (3b) *Odobenus* + Otariidae, (4) crown Phocidae, and (5) crown Otariidae. Asterisks indicate taxa not used in diving analyses; cross indicates the recently extinct species *Monachus tropicalis*. White circles represent nodes for crown clades, and gray circles represent unnamed or unstable clades. Taxon abbreviations: A. = *Arctocephalus*; *angustirost.* = *angustirostris*; *galapagoen.* = *galapagoensis*; M. = *Mirounga*; Mo. = *Monachus*; P. = *Pusa*; Ph. = *Phoca*; *schauinsl.* = *schauinslandi*. Hypothesized pinniped outgroups: (C) Ursidae, (D) Musteloidea, (E) a clade composed of both Musteloidea and Ursidae.

Specimens were selected for this study on the basis of (1) preservation of skull morphology, (2) age of the individual, and (3) contribution to the overall breadth of phylogenetic sampling. Adults were preferentially sampled to avoid confounding ontogenetic effects; we determined relative age based on suture fusion of the palate and braincase. Because of the absence of full suture fusion in adult *Mirounga* spp. (Fig. 2C, D; King 1972), in this genus we based our evaluation of maturity on skull size. Lastly, the rarity of some pinniped species hindered attempts to broaden phylogenetic sampling and, consequently, our data set primarily included abundantly curated taxa.

Phylogenetic relationships between crown Pinnipedia and its nearest outgroup have long been contentious (Berta 2009), and there remains no strong consensus on

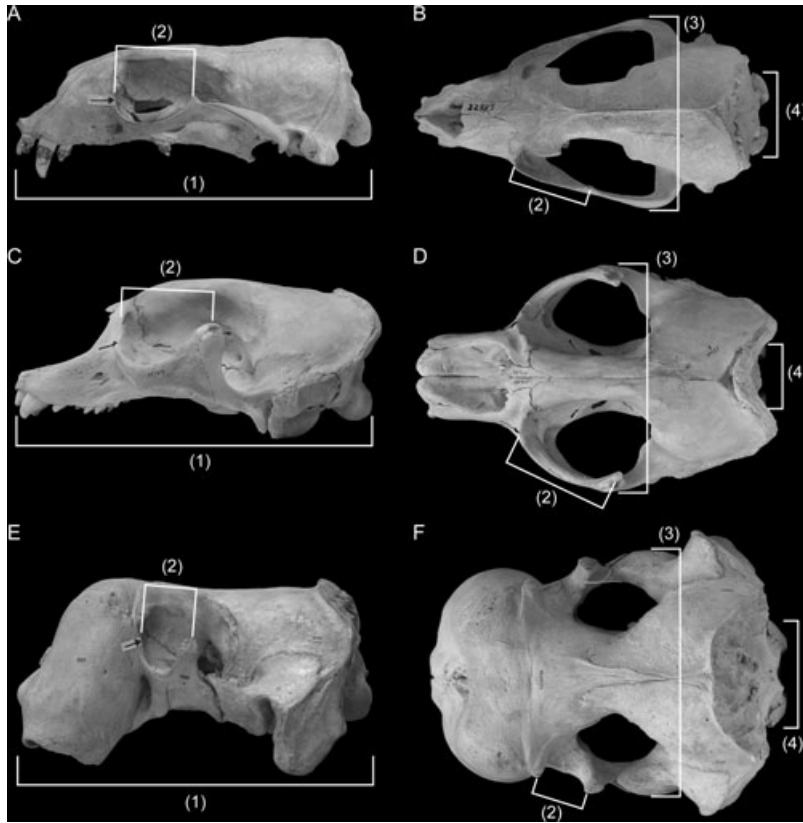


Figure 2. Exemplar pinniped skulls, identifying morphometric measurements used in this study. (A, B) Lateral and dorsal views of female *Eumetopias jubatus* (UCMP 22889); (C, D) Lateral and dorsal views of female *Mirounga angustirostris* (CAS 23764); (E, F) Lateral and dorsal views of male *Odobenus rosmarus* (CAS 20776). Arrows on masking tape represent anterior-most apex of the orbital margin. Numbers denote measurements: (1) CBL, (2) ORB, (3) BZB, and (4) OCB. See text and Table 2 for further details about measurements.

the pinnipeds' sister taxon among carnivorans (Bininda-Emonds 2000, Delisle and Strobeck 2005, Árnason *et al.* 2006, Bininda-Emonds *et al.* 2007, Dasmahapatra *et al.* 2009). The traditional morphological and paleontological hypotheses for pinniped evolution posited a diphyletic origin, with "otarioid" pinnipeds (a grouping of otariids, *Odobenus*, and their fossil relatives) evolving from an arctoid (ursid) relative, and phocid pinnipeds (true seals) evolving from a different arctoid (mustelid) ancestry (McLaren 1960, Tedford 1976, Repenning *et al.* 1979, Muizon 1982). Though the hypothesis of pinniped diphyly is still advocated by some workers (*e.g.*, Koretsky and Barnes 2006), extensive morphological (Wyss 1989, Wyss and Flynn 1993, Berta and Wyss 1994) and molecular (Sarich 1969, Árnason and Widegren 1986, Árnason *et al.* 1995, Lento *et al.* 1995, Flynn and Nedbal 1998, Bininda-Emonds *et al.* 1999, Flynn *et al.* 2000, Davis *et al.* 2004, Flynn *et al.* 2005, Árnason *et al.* 2006, Fulton and Strobeck 2006, Higdon *et al.* 2007, Dasmahapatra *et al.* 2009) analyses nearly unanimously support pinniped monophyly. Morphological analyses have suggested

Ursidae as sister to pinnipeds (Wyss and Flynn 1993; Fig. 1C), whereas different molecular analyses have identified either Ursidae (Vrana *et al.* 1994) or Musteloidea (Árnason and Widegren 1986, Flynn and Nedbal 1998, Bininda-Emonds *et al.* 1999, Yu *et al.* 2004, Flynn *et al.* 2005, Fulton and Strobeck 2006, Yu and Zhang 2006; Fig. 1D) as sister taxa. Yet another hypothesis posits that Ursidae and Musteloidea form a clade that is sister to Pinnipedia, based on molecular evidence (Bininda-Emonds *et al.* 2007; Fig. 1E). To account for these different sister relationships, our morphometric analysis included a sample of brown bears (*Ursus arctos*) to represent ursids, and three different mustelid species to represent musteloids: sea otters (*Enhydra lutris*), North American river otters (*Lontra canadensis*), and wolverines (*Gulo gulo*). For analyses comparing diving with skull measurements, we used a published diving depth and duration for *E. lutris*, and set diving depth and duration at 0 m and 0 min, respectively for remaining outgroups.

In this comparative study, we also examined the relationships of our skull measurements in select fossil pinniped taxa. Fossil pinnipeds are predominantly described on the basis of diagnostic cranial material (*e.g.*, Deméré 1994a), and all of the cranial measurements we examined for extant pinnipeds were applied to fossil taxa as well. Although a comprehensive evaluation of fossil pinnipeds was outside of the scope of this study, we selected candidate taxa that were represented by nearly complete cranial material and are significant in pinniped phylogeny; this list of taxa included 16 fossil species in 14 genera (see Table 1 for taxonomic details and Fig. 3 for phylogenetic relationships).

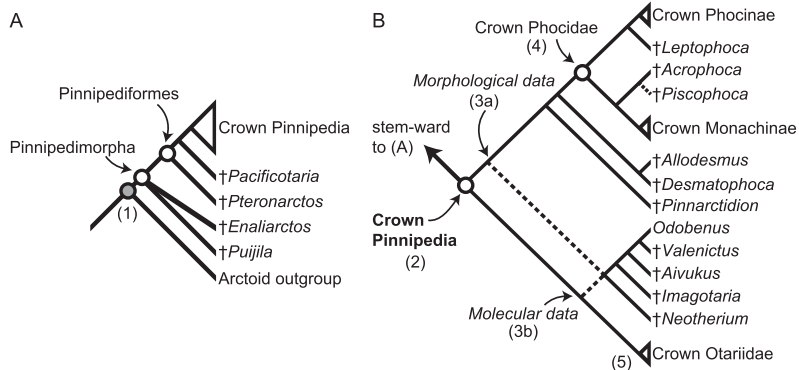


Figure 3. Pinniped phylogeny, including basal branching lineages and extinct taxa. (A) crown and stem pinnipeds, including Pinnipedimorpha and Pinnipediformes (white circles), which are defined by extinct taxa. The position of *Puijila* is based solely on its sister relationship with *Enaliarctos* in the analysis by Rybcynski *et al.* (2009); (B) Interrelationships among crown pinniped family level clades differ at key basal branches; dashed line denotes alternative branching topologies, based on morphological or molecular data sets. Composite phylogeny modified from Deméré *et al.* 2003 and Kohno 2006, for the position of basal pinnipediformes and *Pinnarctidion*; dashed line for *Piscophoca* refers to its tentative placement as the sister taxon to *Acrophoca*, following Deméré *et al.* 2003. Numbered nodes refer to clades defined as follows: (1) crown Pinnipedia + arctoid carnivoran outgroup, (2) crown Pinnipedia, (3a) *Odobenus* + Phocidae, (3b) *Odobenus* + Otariidae. See text for more details about nodal reconstruction and comparisons with extinct terminal taxa.

Cranial Measurements

On each skull, we recorded five measurements: condylobasal skull length (CBL), bizygomatic breadth (BZB), occipital condyle breadth (OCB), and the average of the right and left orbital breadths (AveOrb) (Fig. 2, Table 2; see species values in Table 1). These measurements are essentially homologous across all carnivorans, although two of them were topographic maxima (BZB and OCB). Orbit size was defined by a line from the dorsal most point on the postorbital process of the zygomatic arch to the anterior most point on the medial margin of the bony orbit (Fig. 2), which follows the same measurement of Brunner (2003; fig. 1, Table 1). Orbital measurements are not necessarily homologous because the targeted landmark is a topographic point, rather than a suture or contact, given that the ultimate aim of this study is a functional proxy for orbit size. All morphological measurements were averaged for all individuals within each species, and all individual right and left orbital measurements were averaged together (arithmetic mean), for a resulting species average orbital measurement (AveOrb).

Diving Data

Published diving studies report a wide range of diving variables, such as maximum and average dive depth, duration, and rate. Many of these variables are often correlated with one another: for example, increased dive duration is positively correlated with dive depth because it takes more time to reach greater depths (Feldkamp *et al.* 1989, Harcourt *et al.* 1995, Costa and Gales 2003, Pitcher *et al.* 2005). Additionally, body mass and diving are positively correlated for many diving vertebrates because diving performance is constrained by metabolic rate and the ability to store oxygen in blood and muscle, and increases in body mass provide a metabolic advantage (Schreer and Kovacs 1997, Kooyman and Ponganis 1998, Mottishaw *et al.* 1999, Wright and Davis 2006). To investigate the relationship between orbit size and diving, we compiled published natural history data for mean body mass and maximum dive depth and duration. These data were predominantly culled from the valuable compilation of Schreer and Kovacs (1997: Table 1), and we supplemented their taxonomic coverage with additional data (see Table 3). While there are concerns

Table 2. Cranial measurements used in this study. All measurements reflect symplesiomorphies that are available on both stem and crown pinnipeds.

Code	Measurement	Parameter
1 CBL	Condylobasal skull length	From anterior tip of premaxillae to posterior margin of occipital condyles.
2 AveOrb	Average orbital size	Average of right and left bony orbital measurements (ORB), defined as the line from the dorsal most point on the postorbital process of the zygomatic arch to the anterior most point on the medial margin of the bony orbit.
3 BZB	Bizygomatic breadth	Maximum skull breadth at the zygomatic arches.
4 OCB	Occipital condylar breadth	Maximum breadth on lateral margins of the occipital condyles.

Table 3. Extant pinniped diving data used in this study. Column headings are: maximum depth reported in the literature (Max. depth); maximum dive duration reported (Max. duration); mean body mass (Mean mass). Where no sex is listed for the species, it was not reported. M + F denotes an average of the published male and female values. Asterisks indicate species not used in diving analysis, see text. Abbreviations in superscript are as follows: A = depth limited by water depth; B = depth limited by range of pressure sensor; C = mean of male, 300 kg, and female, 160 kg, body weights; D = mass not reported, total body length reported as 2 m, average published weight for 2.4 m female (300 kg) used in analysis; E = approximated from figure in Parrish *et al.* (2002); F = mean body weight of 10.9–18.1 kg range; G = mean body weight of 5–14 kg range; H = mean of male, 320 kg, and female, 200 kg, body weights.

Family	Species	Sex	Max. depth (m)	Max. duration (min)	Mean mass (kg)	Source
Otariidae	<i>Arctocephalus australis</i>	F	170	7	45	Schreer and Kovacs (1997)
	<i>Arctocephalus forsteri</i>	M + F	346	12.1	74.4	Page <i>et al.</i> (2005)
	<i>Arctocephalus galapagoensis</i>	F	115	8	30	Schreer and Kovacs (1997)
	<i>Arctocephalus gazella</i>	F	240	10	106	Schreer and Kovacs (1997), Lea <i>et al.</i> (2002)
	<i>Arctocephalus pusillus</i>	F	204	8	80	Schreer and Kovacs (1997)
	<i>Arctocephalus tropicalis</i>	F	208	6.5	50	Georges <i>et al.</i> (2000)
	<i>Arctocephalus philippii</i>	F	90	3.71	48.1	Francis and Boness (1998)
	<i>Arctocephalus townsendi</i>	F	82	18	50	Schreer and Kovacs (1997)
	<i>Callorhinus ursinus</i>	F	207	8	50	Schreer and Kovacs (1997)
	<i>Eumetopias jubatus</i>	M + F	438	16	270	Schreer and Kovacs (1997), Pitcher <i>et al.</i> (2005)
	<i>Neophoca cinerea</i>	F	105	8.3	105	Schreer and Kovacs (1997), Costa and Gales (2003)
	<i>Otaria byronia</i> *	F	112 ^A	6	140	Schreer and Kovacs (1997)
	<i>Phocartos bookeri</i>	F	550	12	160	Schreer and Kovacs (1997), Costa and Gales (2000)
	<i>Zalophus californianus</i>	F	482	15	110	Schreer and Kovacs (1997)
	Phocidae	<i>Cystophora cristata</i> *	M + F	1016 ^B	52	230 ^C
<i>Erignathus barbatus</i>		M + F	250	22.5	310	Schreer and Kovacs (1997)
<i>Halichoerus grypus</i>		M + F	383	22.5	182.5	Schreer and Kovacs (1997), Beck <i>et al.</i> (2003)
<i>Hydrurga leptonyx</i>		M	424.5	9.35	197.5	Kuhn <i>et al.</i> (2005)
<i>Leptonychotes weddellii</i>		M + F	655.5	73	392.5	Kooyman <i>et al.</i> (1980), Schreer and Kovacs (1997), Harcourt (2001), Evans <i>et al.</i> (2004)

Continued

Table 3. (Continued)

Family	Species	Sex	Max. depth (m)	Max. duration (min)	Mean mass (kg)	Source
	<i>Lobodon carcinopaga</i>	M + F	528	15	250	Schreer and Kovacs (1997), Harcourt (2001)
	<i>Mirounga angustirostris</i>	M + F	1389.5	69.5	1,300	Schreer and Kovacs (1997)
	<i>Mirounga leonina</i>	M + F	1193	104.5	2,300	Schreer and Kovacs (1997)
	<i>Monachus monachus</i> *	F	78 ^A	15	300 ^D	Gazo and Aguilar (2005)
	<i>Monachus schauinslandi</i> *	M + F	500 ^B	20 ^E	222.5	Parrish <i>et al.</i> (2002), Nowak (1999)
	<i>Onmatophoca rossii</i>	M + F	792	30	154	Blix and Nordøy (2007)
	<i>Pagophilus groenlandicus</i>	F	370	16	120	Schreer and Kovacs (1997)
	<i>Phoca largha</i>		100	10	100	Schreer and Kovacs (1997)
	<i>Phoca vitulina</i> *		508 ^B	28	100	Schreer and Kovacs (1997)
	<i>Pusa hispida</i> *		222 ^A	26	80	Schreer and Kovacs (1997)
	<i>Pusa sibirica</i> *	M + F	300 ^B	68	33.75	Stewart <i>et al.</i> (1996), Schreer and Kovacs (1997)
Odobenidae	<i>Odobenus rosmarus</i>	M	100 ^A	13	1900	Schreer and Kovacs (1997)
Mustelidae	<i>Enhydra lutris</i>		97	4	40	Schreer and Kovacs (1997)
	<i>Gulo gulo</i>	M + F	0	0	14.5 ^F	Paitschniak-Arts and Larivière (1995); diving set at 0 m and 0 min
	<i>Lontra canadensis</i>	M + F	0	0	9.5 ^G	Larivière and Walton (1998); diving set at 0 m and 0 min
Ursidae	<i>Ursus arctos</i>	M + F	0	0	450 ^H	Paitschniak-Arts (1993); diving set at 0 m and 0 min

with the accuracy and validity of using maximum diving depth, we argue that these concerns would be amplified with using mean depth. We suggest that maximum dive depths are more indicative of the physiological limits of the species, whereas mean depths are more likely to reflect a composite of behavioral or environmental factors (*e.g.*, diel-migrating prey, or habitat variation between populations).

Diving data were not available for all taxa: *Monachus tropicalis*, *Histiophoca fasciata*, and *Pusa caspica* were included in the morphometric data set for allometric analysis, but the lack of diving data precluded their use in the diving analyses. Furthermore, as some taxa have recorded diving depths that were limited by either the range of the pressure sensor or water depth, we chose to focus on data that accurately depicted the depth capability of the species. Therefore, the following taxa were excluded from diving analyses: *Cystophora cristata*, *Monachus monachus*, *M. schauinslandi*, *Otaria byronia*, *Phoca vitulina*, *Pusa hispida*, and *P. sibirica*. Although depth records for male otariids are severely underrepresented in the published literature, our morphological data showed no significant differences when comparing males individually, females individually, or all specimens averaged together (see Statistical Analyses). Therefore, we used a compilation of both sexes for all our analyses to maximize the taxonomic coverage of our data sample (see Table 3). Lastly, maximum dive depth and mass were log-transformed to meet normality where indicated.

Statistical Analyses

To investigate the effects of sexual dimorphism in our data set, we compared the slopes of the lines using GraphPad Prism version 5.00 for Mac OS X (GraphPad Software, San Diego, CA) for bivariate plots of orbit size *vs.* our morphological measurements and orbit size *vs.* depth and body mass, among males and females separately, and males and females combined together. Essentially, this comparison is equivalent to an *F*-test to determine whether males or females, alone, differed significantly from a data set comprising all measured specimens averaged together within species. As the three data sets did not differ significantly ($P < 0.05$), we used all specimens averaged within a species for the remainder of the analyses.

To test the correlation of orbit size with diving depth, we first examined whether pinnipeds differ from their proposed outgroups in orbit size. Testing each species separately against one outgroup species avoids the problems of comparing specimens at different taxonomic levels, as averaging all pinniped species (comprising three ecologically and taxonomically distinct families) into a composite, higher taxonomic grouping and then comparing that grouping to one species of Ursidae would not be statistically valid. Additionally, using species averages for *t*-tests is problematic because there is only one ursid species represented in our data set (*U. arctos*). Therefore, to determine the difference between each pinniped species and each of the four measured outgroup species, we conducted separate Welch's two-sample *t*-tests comparing specimens within each pinniped species to specimens within each outgroup species for both absolute orbit size (AveOrb) and relative orbit size (AveOrb standardized to CBL). Welch's two-sample *t*-tests are appropriate when the variances are not assumed to be equal. We judged differences in orbit sizes between in- and outgroup taxa as significant when $P < 0.05$. These analyses were conducted in R (ver. 2.6.1, R Development Core Team 2008).

We explored the relationships among orbit size, skull morphology, diving depth and duration, and body mass using general linear modeling (GLM) to determine whether orbit size is correlated with diving depth. We also investigated the relationship between dive duration and body mass, both which have been suggested to be correlated with diving depth (Schreer and Kovacs 1997, Kooyman and Ponganis 1998, Mottishaw *et al.* 1999), even when controlling for phylogeny (Halsey *et al.* 2006b). We examined the relationships between orbit size (response variable) and the three skull measurements (CBL, BZB, and OCB, as explanatory variables), both within and among pinniped families. We also analyzed all morphological measurements in relation to diving depth and duration and body mass, among all pinnipeds, as well as partitioned by family. In all cases, we started the GLM with all parameters and then used model selection procedures based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) and R^2 Adjusted to determine the best model that balanced the explanatory variables and variance explained. Lower AIC_c values indicate a more parsimonious model that better explains patterns in the data, while penalizing for the addition of trivial parameters. Just as with AIC_c , we used R^2 Adjusted because it accounts for parameter number. Significant parameters in the linear models were also tested as the sole predictors in the model. GLM analyses were conducted in R.

Phylogenetic Independent Contrasts

Over the last two decades, comparative biologists have increasingly recognized that values for taxonomic data are not independent; instead, they are related to one another by genealogical history, as indicated by phylogenetic relationships (Garland *et al.* 1992, Garland and Ives 2000). This understanding has led to the establishment of comparative methods to study how phylogeny impacts comparative data among taxa that are related to one another using different phylogenetic hypotheses (*i.e.*, phylogenetic trees). Among various approaches, we examined correlated trait evolution in our data sets using Felsenstein's (1985) phylogenetically independent contrasts (PICs). Contrasts essentially represent the calculated trait at the most recent common ancestor between two lineage pairs; interested readers can consult Garland and Ives (2000) for a description of the procedure. We calculated contrasts using log-transformed data entered into Mesquite 2.6 (Maddison and Maddison 2009) with the Phenotypic Diversity Analysis Program module of PDTREE (Midford *et al.* 2006).

In examining our data, we used two different phylogenetic hypotheses: a morphological phylogeny from Deméré *et al.* (2003), and a molecular phylogeny of pinniped relationships from Higdon *et al.* (2007) (Fig. 1A and B, respectively). These two hypotheses differ in several ways. First, molecular analyses place the position of *Odobenus* as sister to Otariidae, whereas morphological analyses place it as sister to Phocidae. Second, subclades within both Otariidae and Phocidae also differ in the placement of select species and genera (Fig. 1). Among otariids, molecular analyses fail to recover the monophyletic *Arctocephalus* clade proposed by morphologists, and they recover a sister relationship between *Eumetopias* and *Zalophus*. Molecular and morphological analyses correspond well in recovering the long-standing phocid subfamilies Monachinae and Phocinae, although some discrepancies exist for the placement of *Phoca* spp. and *Pusa* spp. For both trees, we pruned the tree under consideration to only the taxa covered in this study. For examining independent

contrasts, we set all branch lengths to 1.0, which minimizes type I error (also known as a false positive) rates and is a reasonable assumption in trees where branch length information is absent or uninformative with composite phylogenies (Ackerly 2000). Also, in the molecular tree, we subtracted one degree of freedom for each branch in the single polytomy of the *Arctocephalus* clade (Purvis and Garland 1993, Garland and Díaz-Uriarte 1999). To test for correlated trait evolution, we performed independent contrast correlations between skull traits and diving traits using both molecular and morphological tree topologies, and quantified the strength and significance of these relationships using PIC Pearson product-moment correlation coefficients (r) and two-tailed P -values and sign tests (following Hofman *et al.* 2008).

Evaluating Ancestral Nodes with Fossil Data

To compare select fossil taxa with data from extant pinnipeds, we compared terminal tip data (*i.e.*, species values) to reconstructed ancestral node values at key positions in pinniped phylogeny. Foundational studies in phylogenetic comparative methods have led to the realization that both parsimony and likelihood approaches are equally useful and, sometimes, complementary, for reconstructing ancestral states on a phylogeny (Schluter *et al.* 1997, Cunningham 1999). We used squared change parsimony (Maddison 1991) in Mesquite 2.0 (Maddison and Maddison 2009) to reconstruct continuous traits at specific nodes because likelihood methods are better suited for reconstructing discrete traits (which were not in this study) and because squared change parsimony performs as well as maximum likelihood (ML) when ML assumes Brownian motion models of evolution (Polly 2001, Finarelli and Flynn 2006). We reconstructed two specific traits, (1) AveOrb and (2) the ratio of AveOrb to BZB, for key nodes in pinniped phylogeny, using both morphological and molecular topologies for interrelationships among crown Phocidae, crown Otariidae, and *Odobenus*. CBL was not used in these comparisons because it was not universally preserved among all the fossils included in this sample. For extinct taxa, we specifically compared nodal values with branch termini, as a rough heuristic for the amount of evolutionary change. More sophisticated methods for comparing extinct taxa with ancestral nodes do exist (Polly 2001, Finarelli and Flynn 2006), but such approaches are beyond the scope of this study. By incorporating fossil data in this study, our aim was to outline potential hypotheses about the evolution of deep-diving traits in pinniped phylogeny. The incomplete nature of many fossil pinniped skulls precluded using all of our morphological measurements, and so we relied on complete specimens and ignored taxa missing the relevant morphological data; the inclusion of fossil data here ought to provide a basis for attempting more comprehensive studies using fossil data in the future.

RESULTS

In addressing the relationship between pinniped orbit size and diving depth using a comparative data set, we had three main objectives: (1) determine whether pinnipeds possessed larger eyes than their nondiving outgroup taxa, (2) assess orbit size (absolute and relative) across pinniped taxa in relation to other cranial variables, and (3) determine the correlation between orbit size and diving measures. This study also made an explicit approach to understand the stated relationships using both nonphylogenetic (*i.e.*, traditional regression statistics) and PICs. We subsequently

review the relevance and significance of the findings arising from this overall approach in the Discussion section.

Cranial Allometry Relative to Outgroups

Generally, eye size is a proxy for visual sensitivity in mammals (Kiltie 2000), and we would expect, *a priori*, that pinnipeds orienting and hunting at deep depths should differ in eye size from nondiving taxa (*i.e.*, the outgroup species in this analysis). The results of the Welch's two sample *t*-tests indicated that most pinniped species did indeed have significantly larger absolute orbit sizes ($P < 0.05$) than any of the proposed outgroup taxa (see Table S1). All pinniped species had significantly larger orbits than all three mustelid species, and nearly all pinniped species had significantly larger orbits than *Ursus arctos*. The only exception was the phocid *Pusa sibirica*, which had an orbit size larger than *Ursus*, but not with statistical significance ($P = 0.32$). Notably, this species has the smallest average skull size and body mass of all pinnipeds studied. This exception highlights the importance of considering orbit size relative to skull size and body mass (see later).

When examining relative orbit sizes (AveOrb standardized to CBL), using Welch's *t*-tests between each pinniped species and each outgroup species, all pinniped species had significantly larger relative orbit sizes than outgroup taxa ($P < 0.05$), with the exception of *Odobenus rosmarus* (see Table S2). *Odobenus* had larger relative orbit size ($P < 0.05$) compared to all outgroup taxa, except when compared to *Enhydra*, which actually had significantly larger relative orbit size than *Odobenus* ($P < 0.001$). The small relative orbit size of walruses was not surprising because *Odobenus* is a shallow-diving pinniped that forages for mollusks buried in the seafloor substrate and given this benthic feeding ecology, it is likely that walruses, like sea otters, rely more heavily on well-developed vibrissae than vision. In sum, the results indicate that most pinniped species had significantly larger orbits, even when standardized to skull size, as compared with their nondiving outgroup taxa.

The results of linear regression analyses show increasing orbit size among all species in the analysis with increasing skull size (Fig. 4), though with negative allometric relationships (*i.e.*, linear regression with a slope < 1.0), such that larger skulls, on average, have proportionately smaller eyes. The one exception is the positive allometry of AveOrb relative to condylar breadth (OCB) shown by phocids (Fig. 4C). Fig. 4 also illustrates that extant pinnipeds exhibit larger eyes than the ursids and mustelids, both absolutely and for their skull size, with phocids and otariids having relatively larger eyes than the walrus.

We used GLM analysis to examine the correlation between orbit size (AveOrb) and our skull measurements (CBL, BZB, and OCB) for all pinnipeds, and at a finer taxonomic level (families). Overall, morphological results from GLM show the significance of the correlation between orbit size and BZB, regardless of taxonomic level or the inclusion of fossil taxa. According to the ranking by AIC_c, the best single predictor of orbit size for Pinnipedia was BZB ($P < 0.001$, R^2 Adj. = 0.78; Table 4), and this pattern held regardless of inclusion of extinct taxa. The inclusion of extinct pinnipeds decreased the R^2 Adj. value slightly (R^2 Adj. = 0.68 for all Pinnipedia; R^2 Adj. = 0.61 for extinct Pinnipedia only) but did not affect the significance. This result was not entirely unexpected because skull width largely accommodates the anatomical space required for the eyes and their associated tissues; this result also suggests that BZB could potentially be used as a rough proxy for

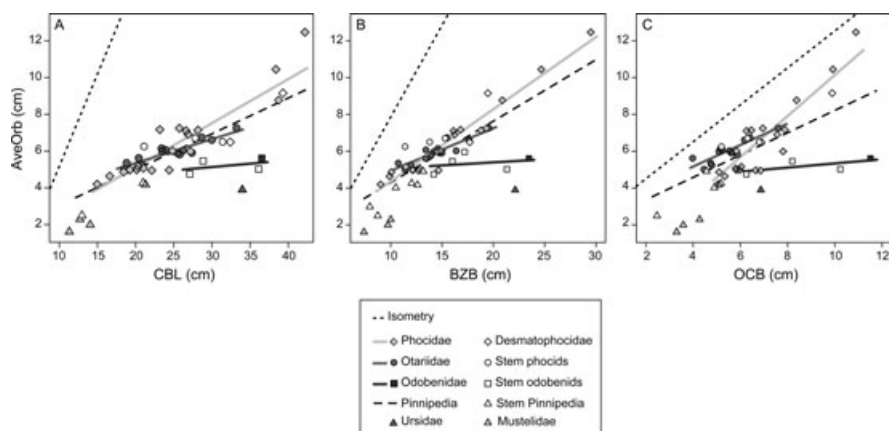


Figure 4. Allometric results using linear least squares regression of orbit size (AveOrb) and additional skull measures: (A) CBL; (B) bizygomatic breadth (BZB); (C) occipital condylar breadth (OCB). Infilled points indicate extant taxa; empty outlines indicate fossil taxa: open circles = fossil phocids (stem Phocidae); open diamonds = Desmatophocidae (Phocoidea); open squares = fossil odobenids; open triangles = stem pinnipeds. The isometric line, with slope equal to 1, is arbitrarily set at $y = 4$ in all panels.

bony orbit size because it directly reflects the accommodation of the eyeballs in the cranium. In models containing BZB as one of multiple predictors, BZB was usually the only significant predictor. When analyzed by family, the GLM results show a pattern similar to the overall Pinnipedia results, and exhibit the importance of BZB. However, the best single predictor of orbit size in otariids is CBL ($P < 0.001$, R^2 Adj. = 0.83).

Correlation of Morphology and Diving Ability

We compared models for diving depth by taxon based on sets of our skull measurements only, or a combination of our skull measurements, mass, and diving duration (Table 5). Because these models require both morphological data and known diving data, extinct taxa were not included. The general linear model for pinniped diving depth as predicted by all skull parameters (AveOrb, CBL, BZB, and OCB), was significant ($P < 0.05$), and based on AIC_c weights, this combination of skull parameters ranked fourth best among all models; AveOrb was the only significant parameter, ($P < 0.05$). This result indicates that orbit size was the best morphological predictor in our data set for diving depth among all pinnipeds, and indeed the model with AveOrb as the sole predictor for pinnipeds ranks third among all models. Surprisingly, the top model lacked both mass and duration, and instead contained only skull parameters (AveOrb, BZB and OCB; overall model: $P < 0.001$, R^2 Adj. = 0.56), with all parameters significant. The model containing duration as the only parameter ranked fifth ($P < 0.001$, R^2 Adj. = 0.43), and the model with both duration and orbit size ranked second ($P < 0.001$, R^2 Adj. = 0.48). These results do not contradict previous suggestions about the correlation between diving depth and mass and/or duration, but linear regression shows orbit size to be a better predictor of depth, especially because orbit size was a significant predictor in 9 of the top 10 models.

Table 4. Ranking of top five candidate models for orbit size at different taxonomic levels by Akaike's Information Criterion corrected (AIC_c).

Taxon	Model, predicting AveOrb	n	P	R^2 Adj.	AIC_c	ΔAIC_c
Pinnipedia (extant)	BZB ^c	34	<0.001	0.78	-107.04	0
	BZB ^c + OCB	34	<0.001	0.78	-105.69	1.34
	CBL + BZB ^b	34	<0.001	0.78	-104.73	2.31
	CBL + BZB ^b + OCB	34	<0.001	0.79	-103.34	3.69
	CBL ^c	34	<0.001	0.72	-98.93	8.11
Pinnipedia (extant and extinct)	BZB ^c	49	<0.001	0.68	-120.42	0
	BZB ^c + OCB	47	<0.001	0.65	-113.18	7.24
	CBL + BZB	45	<0.001	0.65	-108.48	11.94
	CBL ^c	45	<0.001	0.63	-107.27	13.15
	CBL + BZB + OCB	45	<0.001	0.65	-106.08	14.34
Fossil Pinnipedia (extinct only)	BZB ^c	15	<0.001	0.61	-23.72	0
	OCB ^b	13	0.002	0.61	-20.39	3.32
	CBL ^b	11	0.002	0.69	-17.40	6.32
	CBL + BZB	11	0.002	0.78	-17.26	6.46
	BZB + OCB	11	0.010	0.61	-16.93	6.79
Phocidae (extant)	BZB ^c	19	<0.001	0.93	-68.34	0
	BZB ^c + OCB	19	<0.001	0.93	-66.40	1.94
	CBL + BZB ^b	19	<0.001	0.93	-65.88	2.46
	CBL + BZB ^b + OCB	19	<0.001	0.93	-63.27	5.07
	CBL ^c	19	<0.001	0.87	-57.17	11.18
Phocidae (extant and extinct)	CBL + BZB ^b	22	<0.001	0.90	-73.34	0
	BZB ^c	22	<0.001	0.88	-73.30	0.04
	BZB ^c + OCB	22	<0.001	0.88	-70.66	2.67
	CBL + BZB ^b + OCB	22	<0.001	0.90	-70.33	3.01
	CBL ^c	22	<0.001	0.83	-64.84	8.50
Phocoidea (extant and extinct)	CBL + BZB ^c	24	<0.001	0.89	-78.99	0
	BZB ^c	24	<0.001	0.87	-78.55	0.44
	BZB ^c + OCB	24	<0.001	0.88	-77.19	1.79
	CBL + BZB ^b + OCB	24	<0.001	0.89	-76.47	2.51
	CBL ^b + OCB	24	<0.001	0.84	-70.57	8.42
Otariidae (extant)	CBL ^c	14	<0.001	0.83	-67.45	0
	BZB ^b + OCB	14	<0.001	0.86	-66.81	0.64
	BZB ^c	14	<0.001	0.82	-66.58	0.87
	CBL + BZB	14	<0.001	0.85	-65.98	1.47
	CBL + OCB	14	<0.001	0.83	-64.14	3.3

Note: The dependent variable in all cases is average orbit size, AveOrb, and independent variables are other skull parameters (CBL, BZB, and OCB). See Table 2 for measurement details. All variables have been log transformed to meet normality. Column headings are: number of species (n); whole model P -values (P); R^2 adjusted for number of parameters (R^2 Adj.); small sample AIC (AIC_c); and distance from best model (ΔAIC_c). P -values for individual predictors are given by: $P^a < 0.05$; $P^b < 0.01$; $P^c < 0.001$. Phocoidea includes Phocidae (extant and extinct) as well as the desmatophocids.

Table 5. Ranking of candidate models for diving depth at different taxonomic levels by AIC_c , with only the top five models shown.

Taxon	Model, predicting diving depth	<i>N</i>	<i>P</i>	R^2 Adj.	AIC_c	ΔAIC_c
Pinnipedia	AveOrb ^c + BZB ^a + OCB ^a	24	<0.001	0.56	6.48	0
	Duration + AveOrb	24	<0.001	0.48	8.71	2.23
	AveOrb ^c	24	<0.001	0.44	9.10	2.63
	AveOrb ^c + CBL + BZB + OCB	24	<0.001	0.55	9.26	2.79
	Duration ^c	24	<0.001	0.43	9.42	2.94
Phocidae	OCB ^b	10	<0.05	0.64	1.70	0
	AveOrb ^b	10	<0.05	0.58	3.32	1.62
	CBL + OCB ^a	10	<0.05	0.68	3.65	1.95
	BZB ^b	10	<0.05	0.56	3.74	2.04
	AveOrb + LogOCB	10	<0.05	0.63	4.95	3.25
Otariidae	Mass ^b	13	<0.05	0.44	1.20	0
	Mass ^a + AveOrb	13	<0.05	0.46	2.79	1.59
	Mass ^a + Duration	13	<0.05	0.38	4.63	3.43
	OCB	13	0.097	0.16	6.36	5.16
	AveOrb	13	0.099	0.16	6.41	5.20

Note: Only extant pinnipeds are included in this analysis. The dependent variable in all cases is diving depth, and independent variables are our skull parameters (CBL, BZB, OCB, and AveOrb, see Table 2), as well as mass and dive duration (see Table 3). All skull measurements, mass, and dive depth have been log transformed to meet normality. Column headings are: number of species (*n*); whole model *P*-values (*P*); R^2 adjusted for number of parameters (R^2 Adj.); small sample AIC (AIC_c); and distance from best model (ΔAIC_c). *P*-values for individual predictors are given by: $P^a < 0.05$, $P^b < 0.01$, $P^c < 0.001$.

The models for diving depth examined at the level of family show that Phocidae and Otariidae exhibit two very different patterns than the model for all pinnipeds (Table 5). The top five phocid models contain only skull parameters; both mass and duration are surprisingly absent. The top model for phocid diving depth contains OCB as a single predictor ($P < 0.05$, R^2 Adj. = 0.64), followed closely by orbit size as a single predictor in the second best model ($P < 0.05$, R^2 Adj. = 0.58). Otariids, in contrast, exhibit a pattern of dive duration, mass, and AveOrb, in various combinations, in four of the top five models predicting dive depth. The top three models all contain mass as a significant predictor (either as the only parameter in the best model, or in combination with orbit size or duration). The difference between phocids and otariids illustrates the importance of examining data at lower taxonomic levels, as the divergent patterns are obscured in an analysis at the level of Pinnipedia.

Result of Independent Contrast Analyses

We used PICs to understand how consideration of phylogeny affected putative cranial correlates of diving and mass across extant pinnipeds. Notably, these analyses all used *Enhydra* as the sole outgroup because all other potential outgroup carnivorans were assigned an effective diving depth of zero, which unnecessarily complicates independent contrast analyses. We analyzed our comparisons using two different kinds of phylogenetic trees (morphological and molecular), as well as evaluating subclades

within crown pinnipeds (*i.e.*, crown groups Otariidae and Phocidae). Generally, there were no serious numeric differences between results from morphological and molecular trees. With only a few exceptions, correlations between cranial metrics and diving depth yielded no statistically significant correlations using PICs (Table 6). Specifically, bivariate plots of positivized contrasts between OCB, AveOrb, BZB, and mass *vs.* depth produced weak correlations, with R^2 values <0.38 for Pinnipedia, Otariidae, and Phocidae, for both molecular and morphological trees. The comparison of AveOrb *vs.* depth was significant for Pinnipedia ($P = 0.03$ and 0.04 , for morphological and molecular trees, respectively), although the R^2 values were below 0.19 . Similarly, the comparison of OCB *vs.* depth verged on significance for Phocidae ($P = 0.11$ and 0.06 , for molecular and morphological trees, respectively), but R^2 values were less than 0.38 . Despite a large literature across tetrapods about the scaling of mass and diving depth, the best correlation we could find within Pinnipedia was in otariids, with R^2 values between 0.32 and 0.37 that were significant ($P = 0.04$ and 0.03 , for molecular and morphological trees, respectively).

Results of PICs for cranial metrics comparing AveOrb, OCB, and BZB *vs.* mass (Table 6) showed very strong and highly significant correlations, regardless of tree topology. Of the cranial metrics, Pinnipedia and Phocidae showed low but significant correlation values for comparisons of AveOrb *vs.* mass (R^2 values 0.26 – 0.35). Otariids, in contrast, showed a strong and significant correlation between orbit size and body mass. Correlations between skull width (BZB) and mass were similarly strong and significant for Pinnipedia and Otariidae, but the correlation for phocids was weaker. Lastly, OCB and BZB were very tightly correlated with mass, across all subclades and regardless of tree topology.

To visualize comparisons of traits like AveOrb and diving depth in a phylogenetic context, we mapped squared change parsimony reconstructions of these traits on a morphological phylogeny (Fig. 5; see Fig. S1 for a traits mapped on a molecular phylogeny). Trait values for extant pinnipeds largely reflect the aforementioned results from morphometric analyses: all pinnipeds have larger bony orbits than *Enhydra* (both absolutely and proportionately; see results from Welch's *t*-tests, Table S1, S2). Fine binning of the color values showed a clear distinction between the evolution of bony orbit size and diving: whereas bony orbits show no major evolutionary patterns (with the exception of monachine phocids), deep diving evolved multiple times among unrelated lineages of pinnipeds. This striking visual juxtaposition provides an alternative summary of the PIC data, indicating that there is no correlation between orbit size and diving depth across all pinnipeds, when phylogeny is considered. *Mirounga* spp. provide a compelling exception to this statement because their orbit size values depart sharply from the reconstructed ancestral states (Fig. 5). Although their ability to dive deeply may be related to their body size (see Fig. 6 and Fig. S2), they nonetheless possess large orbits for their skull size (Table S2), ranking along with other extinct and extant phocids as having the absolutely and relatively largest orbit sizes of all pinnipeds.

Comparisons with Select Fossil Data

To better understand the evolutionary transformations of the continuous traits studied herein, we included select fossil taxa in our ancestral node reconstructions. The sample data set included fossil pinnipeds from both the stem and crown groups. Although often incomplete, the fossil taxa that we selected shared most of the key measurements used for the extant taxa. We did not intend for these exemplars to

Table 6. Results of Felsenstein's (1985) contrasts correlation (*i.e.*, PICs) using morphometric and diving trait values and mass.

Correlation	Tree type	Clade	r^2	r	P	Sign test	n
AveOrb <i>vs.</i> DEPTH	Molecular	Pinnipedia	0.19	0.43	0.031	0.541	24
		Otariidae	0.19	0.43	0.142	0.774	12
		Phocidae	0.21	0.45	0.193	1	9
	Morphological	Pinnipedia	0.14	0.37	0.068	0.307	24
		Otariidae	0.11	0.34	0.262	0.388	12
		Phocidae	0.19	0.43	0.215	1	9
BZB <i>vs.</i> DEPTH	Molecular	Pinnipedia	0.03	0.17	0.427	0.839	24
		Otariidae	0.03	0.18	0.556	0.388	12
		Phocidae	0.21	0.46	0.189	1	9
	Morphological	Pinnipedia	0.02	0.12	0.555	0.541	24
		Otariidae	0.02	0.16	0.613	0.388	12
		Phocidae	0.23	0.48	0.162	1	9
MASS <i>vs.</i> DEPTH	Molecular	Pinnipedia	0.07	0.27	0.194	0.839	24
		Otariidae	0.32	0.57	0.044	0.388	12
		Phocidae	0.28	0.53	0.119	1	9
	Morphological	Pinnipedia	0.05	0.22	0.28	0.307	24
		Otariidae	0.37	0.61	0.03	0.146	12
		Phocidae	0.24	0.49	0.156	1	9
OCB <i>vs.</i> DEPTH	Molecular	Pinnipedia	0.03	0.18	0.382	0.541	24
		Otariidae	0.14	0.37	0.216	0.146	12
		Phocidae	0.29	0.54	0.113	1	9
	Morphological	Pinnipedia	0.01	0.1	0.638	1	24
		Otariidae	0.05	0.23	0.459	0.774	12
		Phocidae	0.38	0.61	0.064	1	9
AveOrb <i>vs.</i> MASS	Molecular	Pinnipedia	0.35	0.59	< 0.01	0.008	30
		Otariidae	0.85	0.92	< 0.01	0.003	13
		Phocidae	0.34	0.58	0.024	0.267	14
	Morphological	Pinnipedia	0.28	0.53	< 0.01	0.008	30
		Otariidae	0.71	0.84	< 0.01	0.003	13
		Phocidae	0.26	0.51	0.052	0.581	14
BZB <i>vs.</i> MASS	Molecular	Pinnipedia	0.62	0.79	< 0.01	0.001	30
		Otariidae	0.6	0.77	< 0.01	0.022	13
		Phocidae	0.36	0.6	0.019	0.092	14
	Morphological	Pinnipedia	0.54	0.74	< 0.01	0.002	30
		Otariidae	0.51	0.72	< 0.01	0.022	13
		Phocidae	0.3	0.55	0.036	0.267	14
OCB <i>vs.</i> MASS	Molecular	Pinnipedia	0.84	0.92	< 0.01	0.001	30
		Otariidae	0.78	0.88	< 0.01	0.092	13
		Phocidae	0.55	0.74	< 0.01	0.022	14
	Morphological	Pinnipedia	0.77	0.88	< 0.01	0.001	30
		Otariidae	0.61	0.78	< 0.01	0.022	13
		Phocidae	0.53	0.73	< 0.01	0.092	14

Note: Abbreviations for morphometric traits follow the rest of the test; for molecular and morphological trees, see Figure 1. Statistical abbreviations, from left to right, are as follows: r = Pearson product-moment correlation coefficient; P = two-tailed P -value; sign test = two-tailed sign test; n = number of contrasts.

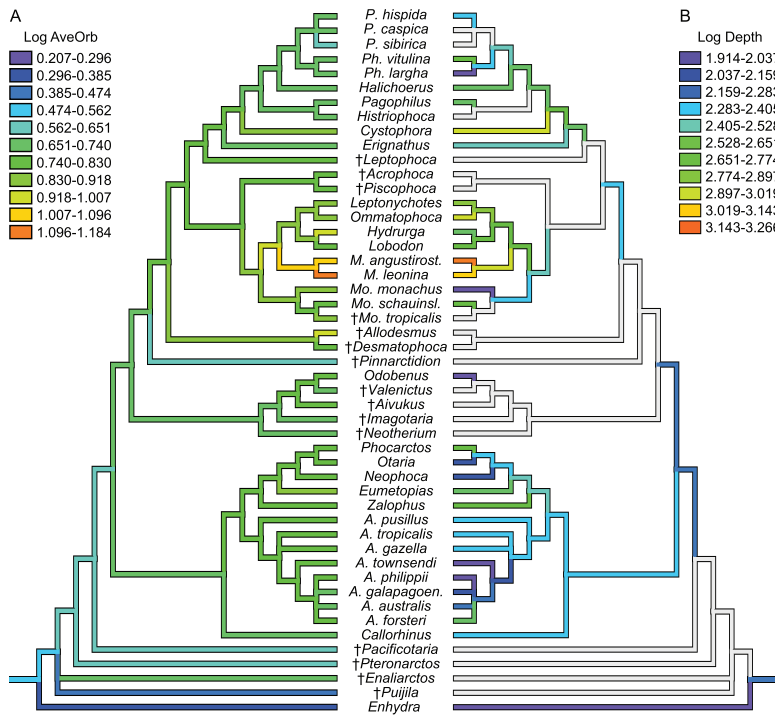


Figure 5. Results from PICs with mirrored phylogenetic trees tracing the evolution of orbit size and diving depth in crown pinnipeds. Phylogenetic tree follows the molecular hypothesis of Figure 1B. (A) Log AveOrb (cm) compared with (B) Log Depth (m). Traits are mapped using squared change parsimony; trait values are binned by color at regular intervals. Taxa abbreviations follow the caption to Figure 1. See text for more details.

provide a full taxonomic coverage of fossil pinnipeds, rather to partially illuminate evolutionary transitions as a way to stimulate future work. Ancestral node reconstructions showed relative orbit size at different nodes in pinniped phylogeny (Fig. 3). Nodal reconstructions were made using square changed parsimony, computed by Mesquite (Maddison and Maddison 2009; see Table 7, S3). Along the stem, basal pinnipeds show values of relative orbit size that are comparable with those of living taxa, although *Puijila*'s value is smaller, and much closer to the nodal value of Pinnipedia and its sister taxon (Fig. 5). Given *Puijila*'s tentative placement in pinniped phylogeny as sister to *Enaliarctos* (Rybcynski *et al.* 2009), it is unclear if its comparatively smaller orbit size reflects the ancestral state in pinniped phylogeny. Among crown pinnipeds, we investigated evolutionary changes in stem phocids, extinct crown phocids, and stem odobenids. For stem phocids, such as *Pinnarctidion* and *Desmatophoca*, their relative orbit size values matched the ancestral node for crown Phocidae closely, although *Allodesmus* was a notable departure, with some of the proportionally largest bony orbits in the data set. As the sister taxon of *Desmatophoca*, we presume that this value represents independent evolution along the lineage leading to *Allodesmus*. Extinct crown phocids, like *Acrophoca*, *Piscophoca* and *Leptophoca*, exhibited the proportionally largest orbit sizes (along with *Allodesmus*); *Leptophoca* had

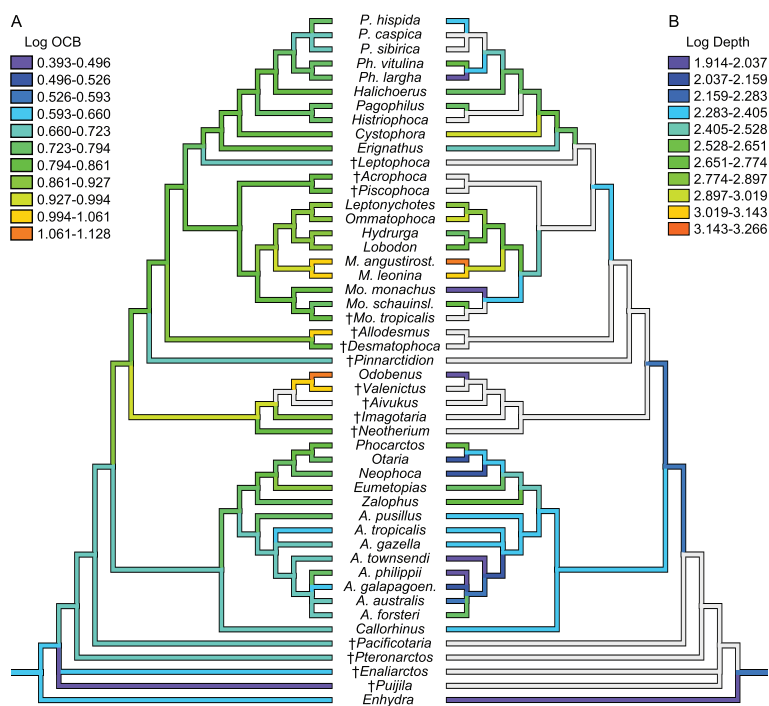


Figure 6. Results from PICs with mirrored phylogenetic trees tracing the evolution of body mass and diving depth in crown pinnipeds. Phylogenetic tree follows the composite morphological hypothesis of Figure 3A, B. (A) Log OCB (occipital condyle breadth, a proxy for body mass) (cm) compared with (B) Log Depth (m). Traits are mapped using squared change parsimony; trait values are binned by color at regular intervals. Taxa abbreviations follow the caption to Figure 1. See text for more details.

the proportionally largest orbits of any pinniped, living or extinct (Table S3). Interestingly, according to nodal reconstructions (Table 7, S3), stem odobenids had relatively much larger bony orbits than *Odobenus*. Some of the relatively smallest bony orbits were exhibited by *Valenictus* and *Odobenus*; as sister taxa, these values indicate shared evolutionary changes in skull dimensions that belong to their derived clade (see Table S3).

DISCUSSION

First, our results indicate pinnipeds have proportionately larger bony orbits than their nearest relatives, including putative living sister taxa. Our analyses indicate that this statement is true of nearly all living pinnipeds, whether compared with *Enhydra*, *Ursus*, or various living mustelids. Extinct crown group pinnipeds adhere to this pattern, although stem pinnipeds differ slightly, especially *Puijila*, the putative basal most pinniped. We suspect that this difference along the stem to crown Pinnipedia reflects meaningful evolutionary transformations that occurred during their ecological transition from terrestrial ancestry late in the Paleogene and in the early

Table 7. Reconstructed nodal values for key clades in pinniped phylogeny.

Tree	Node	Clade	LogAveOrb	LogBZB	LogDepth	AveOrb:BZB
Molecular	1	Pinnipedia + outgroup	0.5	1.08	2.1	0.26
Molecular	2	Crown Pinnipedia	0.64	1.16	2.22	0.3
Molecular	3b	<i>Odobenus</i> + Otariidae	0.71	1.22	2.15	0.31
Molecular	4	Otariidae	0.73	1.14	2.23	0.39
Molecular	5	Phocidae	0.71	1.17	2.41	0.35
Morphological	1	Pinnipedia + outgroup	0.5	1.07	2.09	0.27
Morphological	2	Crown Pinnipedia	0.64	1.14	2.2	0.32
Morphological	0.125	<i>Odobenus</i> + Phocidae	0.71	1.24	2.2	0.3
Morphological	4	Otariidae	0.71	1.1	2.3	0.4
Morphological	5	Phocidae	0.5	1.07	2.09	0.27

Note: Reconstructed nodes follow those listed in Figure 3, especially with different topologies for the relationship of *Odobenus* and its sister taxon, depending on molecular or morphological phylogeny.

Neogene, but we concede that this supposition lacks support from independent data sets (*e.g.*, isotopic evidence).

The second aspect of our study investigated ecomorphologic correlations within crown pinnipeds. When we compared cranial measurements with diving depth across our sample of living pinniped species using the common practice of linear regression, we found that general linear models could adequately predict maximum depth, given sufficient cranial variables, and in some cases cranial measures were better predictors of maximum dive depth than either dive duration or body mass. We compared these models for diving depth based on only one predictor, either mass, dive duration, or orbit size, for all pinnipeds in the analysis, and for phocids and otariids separately. For otariids, mass was the best predictor of dive depth, followed by the combination of mass and orbit size. In contrast, when examining the data at the level of either all pinnipeds or the family Phocidae, orbit size was a much better predictor of dive depth than mass. Interestingly, for both pinnipeds and phocids, the best models for diving depth (lowest *P*-value and highest R^2) were based on one or more cranial measures rather than dive duration or mass. These results illustrate the importance of examining the effects of linear modeling at the smallest taxonomic level possible, in this case by family, as the differences between otariids and phocids are obscured at a higher taxonomic level.

We also investigated these correlations using regression statistics based on phylogenetic relationships. We adopted a dual comparative approach in this study (*i.e.*, nonphylogenetic and phylogenetic) because we wanted to demonstrate how rigorous analyses that seek ecomorphologic relationships require a phylogenetic context. In fact, both approaches rely on phylogenetic hypotheses about organismal relationships: traditional, nonphylogenetic statistics simply assume an unresolved, star phylogeny (with all lineages equally related to one another) whereas PICs use one or more hypotheses with resolved relationships to understand the correlations between traits (Garland *et al.* 1992, Garland and Ives 2000). Here, when we accounted for different phylogenetic relationships, correlations between orbit size and diving depth lost both strength and significance, with only monachine phocids providing an intriguing exception. In Monachinae, ancestral states of bony orbit size and diving depth are comparable with other phocids, but leading to the genus *Mirounga*, the pattern of increasing bony orbit size corresponded to a stepwise increase in diving depth (Fig. 5). We tentatively suggest that absolutely and relatively large eyeball size

in *Mirounga* confers selective advantages for extreme deep diving, although other features are likely involved with deep-diving evolution in this clade, such as large body size (Fig. 6). This finding is largely consistent with experimental studies of foraging depth and pigment sensitivity in *Mirounga* spp. (Hochachka and Mottishaw 1998, Levenson and Schusterman 1999), and highlights the importance of considering physiological and anatomical data when testing adaptational hypotheses (Hochachka 2000).

Although orbit size was highly correlated with mass, in both linear modeling and independent contrasts results, the failure to recover a strong correlation between mass and diving across pinnipeds (Table 6) is surprising, given the work by Halsey *et al.* (2006*a, b*), which focused on a broad taxonomic data set of diving marine tetrapods (*e.g.*, seabirds, cetaceans, and pinnipeds), and explicitly tested long-standing correlations between body size and diving depth and duration. Halsey *et al.* (2006*b*) showed that diving depth and body size scaled positively, across all diving marine tetrapods, with a coefficient roughly equaling 0.33. Their findings, which controlled for phylogenetic relationships between clades of diving tetrapods, were consistent with the oxygen storage/usage hypotheses (Butler and Jones 1982) that have dominated much of the diving literature for several decades. In turn, their findings suggested that the allometry of deep diving in marine tetrapods is controlled by a size-dependent physiological capacity to use and store oxygen. These scaling relationships have long been noted in the diving literature for pinnipeds, which contrasted the ecological discrepancy between large-bodied, deep-diving pelagic pinnipeds (*e.g.*, *Mirounga*) and comparatively smaller and shallower-diving nearshore species (*e.g.*, *Zalophus*; Kooyman 1989; Costa 1991, 1993; Costa *et al.* 2004). Similarly, typical, shallow-diving otariids (*e.g.*, *Zalophus*) and phocids (*Phoca vitulina*) have demonstrably less light-sensitive eyes that are slower to adapt to low-light conditions than those of deeper-diving phocids, such as *Mirounga angustirostris* (Levenson and Schusterman 1999, Southall *et al.* 2002).

Our results depart from these simple comparisons by providing a broad taxonomic sampling to control for the impact of phylogeny on these ecologically related traits. In contrast to Halsey *et al.* (2006*a, b*), we find that PICs do negate scaling relationships between body size and dive depth within pinnipeds (Table 6). Large body size and deep diving did not co-evolve in pinnipeds, although evolving large body size may be an important step toward accessing prey resources in the pelagic and bathypelagic zones (see Lindberg and Pyenson 2007 for cetaceans), and it is likely related to other life history traits under sexual selection (*e.g.*, polygyny, Bartholomew 1970).

Despite the lack of correlation with body size evolution, our results do show that deep diving originated independently several times (Fig. 5, 6). Thus, our results suggest that different pinniped lineages independently evolved physiological adaptations for deep diving (*e.g.*, bradycardia, larger body size for increased oxygen storage, ability to function anaerobically and respond to increasing pressure; Kooyman and Ponganis 1997, Hochachka and Mottishaw 1998) without necessarily evolving commensurate changes that might be predicted for their visual sensory system (*e.g.*, large eyes). In other words, crown pinniped visual sensory evolution, as indicated by orbit size, seems decoupled from evolutionary changes of physiological systems that are more fundamentally related to the exigencies of deep diving (with the exception of Monachinae). In a comprehensive assessment of cranial modularity in pinnipeds, Jones and Goswami (2010) proposed that major differences in the amount of interspecific variation between phocids and otariids were similarly explained by underlying ecological differences between major pinniped lineages. We suspect that

similar subclade analyses within monophyletic diving marine tetrapod groups may display similarly contrasting patterns between morphology and ecology, and we urge further such analyses within diving groups with abundant diving data (*e.g.*, cetaceans and seabirds).

A major caveat in these results concerns the use of bony orbits of the skull as an osteological proxy for eyeball size, which we presumed was broadly related to visual sensitivity. Because pinnipeds do not possess sclerotic rings like non-synapsid tetrapods, we relied on cranial dimensions to provide an upper limit of eyeball diameter in pinnipeds. This proxy, however, conceals more complex patterns and anatomical features related to vision. For example, Pütter (1903), in his seminal work on eye anatomy in aquatic mammals, indicated that living pinnipeds generally possess the same number of optical nerve tract fibers as terrestrial carnivores (~100,000–200,000); *Mirounga*, however, has significantly more (~750,000), placing it within the range of humans. These neuroanatomical features, twinned with physical dimensions of the cornea, rods and cones of the retina, retinal resolution, and dark-adjusting capacity point to a plurality of features beyond mere eyeball size that influence vision in the photic zone (Welsch *et al.* 2001, Kröger and Katzir 2008); this suite of highly specialized traits may indicate pinnipeds have taken a different path of visual adaptation than other diving taxa. Nevertheless, our objective was to find an osteological proxy for diving that could be applied to extinct taxa, for which the soft tissue characteristics of the eye do not preserve (*cf.* Schmitz 2009). While GLM suggests orbit size is a good predictor of diving depth for extant taxa, this relationship was not supported using PICs, and there may be other osteological features in pinnipeds that correlate with diving depth better than orbit size.

It is possible that pinniped vision in aquatic environments is controlled by both intrinsic and extrinsic factors, each of which may correlate with phylogeny, habitat, or ecology. Intrinsic factors relating to pinniped vision may include densely packed rods and cones, specialized retinæ, and blue-shifted wavelength sensitivities, whereas extrinsic factors could explain differences among environmental types. For example, the differing predominant habitats of otariids (temperate) and phocids (polar) vary in daily photoperiod, and therefore a strong differential exists in the amount of light available in the water column to be used to hunt prey. Ferguson and Higdon (2006) analyzed pinniped environmental and life history variables, and found that biogeographic groups (subpolar/polar, temperate, tropical) clustered better than taxonomic groups, corroborating the importance of selection pressures related to such basic environmental parameters in pinniped ecology. Habitat will also affect visual capabilities in water, as taxa inhabiting lakes, nearshore sandy environments, and ice floes are likely to experience very different sediment loads in the water column while hunting for prey. In short, there are many factors that could be confounding our analysis of pinniped diving and visual capabilities.

One unexpected finding of this study was the highly significant correlation between body mass and OCB, which held for both major families within pinnipeds as well as the group in its entirety. We stress that this correlation does not likely reflect a functional relationship, but rather indicates that body mass scales with a linear measurement. Also, the strength of this scaling is independent of phylogeny. Therefore, we propose that OCB can be used as a metric to approximate body mass among crown pinnipeds, both living and extinct. Notably, such a measurement has also been used as a body size proxy in other marine mammals (Uhen 2004, Pyenson and Sponberg 2011, Clementz *et al.* 2009, Sarko *et al.* 2010). This feature is relatively robust and, though not universally preserved on fossil pinniped skulls, it

provides a means to estimate a life history trait (*i.e.*, body size) that would otherwise be unavailable in an extinct taxon.

Unlike the early evolution of cetaceans and sirenians (Domning 2001, Thewissen and Williams 2002), the early stages of pinniped evolution are less clearly understood. The oldest stem pinnipeds (basal pinnipedimorphs) exhibit clear ecomorphological features shared with living pinnipeds (Berta *et al.* 2003), suggesting that pelagic specializations in locomotion and feeding systems were already present by the early Miocene (~23–17 MYA). In this study, we attempted to illuminate subtle transitions between stem and crown pinniped lineages using select fossil examples throughout pinniped phylogeny. If the recently discovered *Puijila* is truly a relictual basal pinnipedimorph, then it indicates that the ancestral states of many basal pinniped postcranial morphologies were convergent with extant sea otters and other mustelids (Rybcynski *et al.* 2009). Interestingly, *Puijila*, among all other supposed stem pinnipeds, possessed the relative bony orbit values that most closely matched the ancestral node with pinniped outgroups. Among extinct crown pinnipeds, *Allodesmus* ranked among those with the relatively largest bony orbit values, approximating that of *Mirounga*, and exceeded only by extinct crown phocids. Given that *Mirounga*'s values likely demonstrate a compelling example of an adaptive feature (see earlier), we propose that *Allodesmus* was similarly a deep-diving taxon. This proposal is largely congruent with environmental reconstructions of its depositional environment (Pyenson *et al.* 2009), which indicate that *Allodesmus* inhabited a middle Miocene ocean that shared many features with the upwelling zones that living *Mirounga* inhabits. Auxiliary evidence from stable isotope analyses may strengthen this claim, although a recent analysis of the postcranial skeleton of *Allodesmus* suggested that it employed an unusual swimming mode, which was potentially nonanalogous with extant pinnipeds (Pierce *et al.* 2011). Lastly, our study demonstrated that the extinct odobenid *Valenictus* possessed relative orbit sizes nearly matching that of *Odobenus*, its sister taxon, a finding that is largely congruent with previous interpretations of its likely paleoecological role (Deméré 1994b).

Conclusions

Living pinnipeds are among the premier deep-diving marine mammals. To meet the extraordinary challenges of diving to depth, pinnipeds have evolved physiological solutions (*e.g.*, bradycardia, large body size, response to increasing pressure) that parallel those for cetaceans, although they have evolved different sensory and behavioral solutions (*e.g.*, vibrissae, more light-sensitive eyes, blue-shifted visual pigment sensitivity, altered swimming patterns to maximize prey detection) for foraging in the photic zone. Previous authors have suggested that deep-diving marine tetrapods possessed large eye sizes as an adaptation for foraging at depth. We tested this hypothesis among pinnipeds using a comprehensive morphological data set, complementary diving data, and select outgroups and fossil taxa. Through linear modeling, we determined that bony orbit size adequately predicted maximum dive depth for both extant Pinnipedia and Phocidae, and that when analyzed using PICs, deep diving evolved multiple times independently, though not necessarily accompanied by increasing orbit size. We did, however, demonstrate that large orbit size was potentially an adaptation for deep diving in the clade of monachine phocids, especially in elephant seals (*Mirounga* spp.). We also reconstructed orbit size at key ancestral nodes in pinniped phylogeny, and compared these values to select fossil pinnipeds

that preserved these features. This exercise demonstrated clear patterns along the basal stem lineages of Pinnipedia, and for stem lineages of subclades within Pinnipedia as well (*e.g.*, Phocidae, Odobenidae). Interestingly, our results stand in contrast to other allometric studies among diving marine tetrapods (Halsey *et al.* 2006*a, b*), which have demonstrated strong scaling relationships between body size and diving depth, even accounting for phylogeny. We suspect that better taxonomic sampling of the underlying morphological traits related to visual sensory systems in pinnipeds will illuminate evolutionary signals that are masked by simple proxy measurements such as orbit size. Also, we hope that other investigations on the ecomorphology of diving tetrapods will use similar data sets to investigate the universality of scaling relationships, along with their potential phylogenetic and ecological underpinnings.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1. Results from PICs with mirrored phylogenetic trees tracing the evolution of orbit size and diving depth in crown pinnipeds. This figure is a pruned version of Figure 1B, showing only taxa with both comparable metrics: (A) Log AveOrb (cm) compared with (B) Log Depth (m). Traits are mapped using squared change parsimony; trait values are binned by color at regular intervals. These results formed the basis for PIC regression and ancestral node comparisons (Table 6, 7). See text for more details.

Figure S2. Results from PICs with mirrored phylogenetic trees tracing the evolution of body mass and diving depth in crown pinnipeds. This figure is a pruned version of Figure 1B, showing only taxa with both comparable metrics: (A) Log Mass (kg) compared with (B) Log Depth (m). Traits are mapped using squared change parsimony; trait values are binned by color at regular intervals. These results formed the basis for PIC regression and ancestral node comparisons (Table 6, 7). See text for more details.

Table S1. Results of Welch's two-sample *t*-tests comparing absolute orbit size (AveOrb) in individual pinniped species to outgroup species, see text for more details. Column headings are: mean (\bar{x}), standard deviation (SD), sample size (*n*), *t*-statistics (*t*), and *P*-value (*P*). Where *t*-statistic > 0, orbit size in the pinniped species

is larger than in the outgroup species. *Arctocephalus philippii* and *A. tropicalis* could not be included in this analysis as the sample sizes were too small ($n = 1$).

Table S2. Results of Welch's two-sample t -tests comparing relative orbit size (Ave-Orb/CBL) in individual pinniped species to outgroup species, see text for more details. Column headings are: mean (\bar{x}), standard deviation (SD), sample size (n), t -statistics (t), and P -value (P). Where t -statistic > 0 , relative orbit size in the pinniped species is larger than in the outgroup species. *Arctocephalus philippii* and *A. tropicalis* could not be included in this analysis as the sample sizes were too small ($n = 1$). Note: *Odobenus rosmarus* is the only pinniped species with statistically smaller eyes than an outgroup taxon, *Enhydra lutris*.

Table S3. Fossil values for relative orbit size in select fossil pinnipeds. The ratio between BZB and average orbit size (AveOrb) were rounded to two decimal places. Species values are monospecific except for *Allodesmus* and *Pteronarctos*, which represent *A. kelloggi* (LACM 4320) and *A. gracilis* (UCMP 81708), and *P. goedertae* (LACM 123883) and *P. piersoni* (LACM 127972, 128002), respectively.