Quantitative analysis of the influences of phylogeny and ecology on phocid and otariid pinniped (Mammalia; Carnivora) cranial morphology

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Abstract

Pinnipeds (seals, sea lions and walruses) are secondarily marine carnivorans that exhibit a wide range of feeding and reproductive specializations. Extant pinnipeds are split into three families: Phocidae (seals), Otariidae (sea lions) and Odobenidae (walruses). Morphometric analyses were used to examine cranial morphology in otariid and phocid pinnipeds. Phocids are more ecologically and taxonomically diverse than otariids, and this study quantitatively assessed the effects of life history, phylogeny and ecology on cranial morphology in these closely related clades of aquatic carnivorans. Fifty-three to 58 three-dimensional landmarks were gathered from 138 specimens, representing 31 of the 33 extant species of otariids and phocids. Principal components analysis was used to identify major axes of variation, and principal component scores were compared with phylogenetic distances and ecological variables to test for significant correlates of skull morphology. Results showed that phocids exhibit a much greater diversity of adult skull morphology than otariids. Shape differences within adult otariids were dominated by males of only one species, *Otaria flavescens*. In contrast, several species of phocids deviated markedly from the mean phocid morphology. These atypical morphologies were consistently associated with specializations of either feeding or mating strategies. Ontogenetic shape changes are greater, relative to interspecific differences, in otariids than in phocids, and shape dimorphism was observed in only one otariid and two phocid species. Unexpectedly, neither otariids nor phocids showed strong correlations between phylogenetic relationship and cranial morphology. Both clades show strong correlations between cranial shape and some life history and some environmental variables, but phocids show stronger correlations with life-history variables, perhaps reflecting the broad range of reproductive strategies observed in phocids.

Introduction

Pinnipeds are a clade of secondarily aquatic arctoid carnivorans, including 34 extant species dispersed across most of the world's oceans. There are three extant families of pinnipeds: Odobenidae (walruses, 1 sp.); Phocidae (seals, 19 sp.) and Otariidae (sea lions and fur seals, 14 sp.) (Wilson & Reeder, 2005). Although most pinniped species are generalist pierce feeders that grip and swallow their prey whole (Adam & Berta, 2002), the clade displays a wide range of ecological diversity (Reeves et al., 2002). Many species are opportunistic, and their diets may vary annually, between colonies and between individuals within a colony (King, 1983; Sinclair & Zeppelin, 2002; Williams et al., 2007). Some of the notable specialist feeding techniques that have evolved within the group include: (1) suction feeding: Odobenids and *Erignathus barbatus* (Phocidae) use powerful facial musculature to pro-

duce forces large enough to extract molluscs from their shells (King, 1983; Adam & Berta, 2002; Marshall, Kovacs & Lydersen, 2008); (2) filter feeding: *Lobodon carcinophaga* (Phocidae) uses bicuspidate teeth to sieve out krill as water is expelled from the mouth; (3) grip and tear feeding: *Hydrurga leptonyx* (Phocidae) feeds on large warm blooded prey such as penguins and seal pups by shaking the prey to tear off manageable pieces of flesh. Although an otariid, *Arctocephalus gazella*, is also specialized on krill, it does so with pierce feeding and not with the derived filter feeding style of *L. carcinophaga* (Adam & Berta, 2002).

Pinnipeds are similarly diverse in reproductive strategy. Otariids all have large harems, mate and breed exclusively on land, often in rookeries and wean their young over extended periods, up to 2 years (Kovacs & Lavigne, 1992; Schulz & Bowen, 2004). Relatedly, otariids display a high degree of size dimorphism. As with feeding ecology, phocids

display a greater diversity of mating and reproductive strategies than otariids. Young are more precocial (4–50 days to weaning) than otariids and often learn foraging skills after separation from their mothers (Schulz & Bowen, 2004). Phocids breed on land or ice, can mate in water and range from solitary to gregarious social systems (Cassini, 1999). The degree of dimorphism varies across phocids, with some species (e.g. *Histriophoca fasciata*) displaying no size dimorphism, while others (*Mirounga leonina*) exhibit the greatest dimorphism observed among pinnipeds. These differences in reproductive strategy and weaning time between otariids and phocids may have significant repercussions for their evolutionary histories. One hypothesis posits that the greater ecological diversity and geographic range of phocids is attributable to their shorter weaning periods and hence lack of dependence on a stable breeding substrate (land), allowing them to inhabit polar regions that are uninhabitable by otariids (Kovacs & Lavigne, 1992; Schulz & Bowen, 2005).

While there have been several studies of evolutionary morphology and ecological transitions in the other major clades of secondarily aquatic mammals (cetaceans and sirenians), pinnipeds remain relatively understudied in evolutionary history or ecomorphology. Thus far, the majority of research on pinnipeds has focused on taxonomy, phylogenetic relationships, ecology and conservation. The phylogenetic relationships among pinnipeds have been particularly problematic, with recent molecular work (Flynn *et al.*, 2005; Arnason *et al.*, 2006) suggesting a closer relation between otariids and odobenids (forming the Otarioidea clade, while morphological analyses (Adam & Berta, 2002; Deméré, Berta & Adam, 2003) suggest a closer link between phocids and odobenids (Phocomorpha clade). Additionally, there was a longstanding debate on a single (Wyss, 1988) or dual (Muizon, 1982) origin for pinnipeds, but most recent studies support a single origin for pinnipeds, with Musteloidea as its sister clade (Flynn *et al.*, 2005).

The many interesting ecological and life-history differences observed in pinnipeds provide a rich topic for examining the relationships among morphology, ecology and ontogeny. Early studies of pinniped morphology focused on the acquisition of aquatic features in fossil forms and the differences among the three extant families in the degree of specialization (Repenning, 1976), while more recent work has applied quantitative analyses of discrete features to identify four ecomorphological types, based on diet and prey capture strategies (Adam & Berta, 2002): pierce feeders (with characteristic features including homodonty), suction feeders (vaulted palate, mandibular fusion), filter feeders (interdigitating, cuspidate teeth) and grip-and-tear feeders (sharply pointed postcanines, enlarged incisors). A few studies have used two-dimensional (2-D) morphometric analyses of cranial morphology in otariids to test the validity of different otariid species (Brunner, 2003) or to examine shape dimorphism (Sanfelice & de Freitas, 2008). Only one previous study has used 3-D morphometric data to study ecomorphology among pinnipeds, focusing on morphological convergences across the three extant families (Jones & Goswami, 2009).

In this study, we focus on intrafamilial patterns of cranial morphology within the two major families of pinnipeds, otariids and phocids. We conduct separate 3-D morphometric analyses of otariids and phocids to assess how different factors have affected their evolutionary histories. Specifically, we test the following hypotheses:
(1) Phocids and otariids share common axes of shape variation due to their shared aquatic habitat.
(2) Phylogeny is the dominant influence on cranial morphology within otariids and phocids.
(3) Cranial morphology reflects ecological and life-history differences within otariids and phocids.

Methods

Landmarks

3-D landmark data were collected from cranial specimens using an Immersion Microscribe G2X digitizer (Immersion Corp., San Jose, CA, USA) with 0.2 mm accuracy. Landmarks were selected based on unambiguous identification and homology across all specimens and were widely distributed across the cranium. Landmark measurements were repeated three times, and landmarks with standard deviations >1 mm, on specimens ranging from 20 to 50 cm in skull length, were excluded from further analysis. A total of 37 dorsal landmarks and 49 ventral landmarks were digitized and later merged with a least-squares algorithm in MATHEMATICA 6.0.1 (Wolfram Research Inc., Champaign, IL, USA), using 10 landmarks common to both views (Table 1, Fig. 1). Next, 12 midline points were used as a mirroring plane to fill in gaps in symmetrical landmarks. Both stages offered an opportunity to measure error, and specimens with high error were removed from the analysis. Out of the original 76 landmarks, 23 were removed from the analyses of otariids and 18 were removed from the analyses of phocids, leaving 53 and 58 landmarks, respectively, in the final analysis.

Specimens

Specimens were measured from the collections at the University of Cambridge Museum of Zoology and the Natural History Museum in London. Thirteen of the 14 extant otariid species and all of the 19 extant phocid species were sampled. A total of 127 phocid and 70 otariid specimens were digitized (Appendix S1). For the otariid study, 24 specimens were removed before analysis due to high error or missing landmarks, leaving a total of 46 specimens. In addition an analysis was conducted without any young specimens, which included a total of 32 specimens. For the phocid study, 92 specimens were analysed, after 35 specimens had been removed due to high error or missing landmarks.

Every attempt was made to equally sample both genders, with the final distribution of specimens composed of 43% male (59 specimens), 30% female (42 specimens) and 27% unsexed (37 specimens). Thirty-three per cent of the specimens sampled were infant or juvenile (46 specimens; Appendix S1). The young specimens used in this study were

Table 1 Cranial landmarks used in analyses

Number	Landmarks
1	Anterior interpremaxilliary suture[a]
2	Nasal width midline
3	Nasal width[b]
4	Premaxilla–nasal–maxilla suture[b]
5	Nasal–frontal midline suture
6	Maxilla–frontal–nasal suture[b]
7	Jugal–maxilla anterodorsal suture (p)[b]
8	Postorbital process/interobital width[a,b]
9	Antorbital process[b]
10	Jugal–squamosal anterior suture[b]
11	Jugal posterodorsal process[b]
12	Parietal–occipital midline suture
13	Foramen magnum dorsal extreme (p)[a]
14	Premaxilla–maxilla venterolateral suture (p)[b]
15	Canine anterior[b]
16	Canine posterior[b]
17	Canine labial[b]
18	Cheek teeth anterior[b]
19	Cheek teeth posterior[b]
20	Maxilla–premaxilla midline suture
21	Maxilla–palatine midline suture
22	Palatine–maxilla lateral suture[b]
23	Midline between ultimate molars[b]
24	Posterior interpalatine suture
25	Jugal–maxilla posteroventral suture (p)[a,b]
26	Jugal–squamosal posteroventral suture[a,b]
27	External auditory meatus lateral extreme[b]
28	Auditory bulla anteromedial extreme[b]
29	Auditory bulla posterior extreme[b]
30	Mastoid process lateral extreme[b]
31	Mastoid process posterior extreme[b]
32	Basion
33	Occipital condyle venteromedial[a,b]
34	Occipital condyle dorsomedial[b]

Landmark numbers refer to Fig. 1. (p) represents landmarks used only in the phocid analyses.
[a]Overlapping landmarks that were used to unify the dorsal and ventral views.
[b]Symmetrical landmarks, gathered from right and left side.
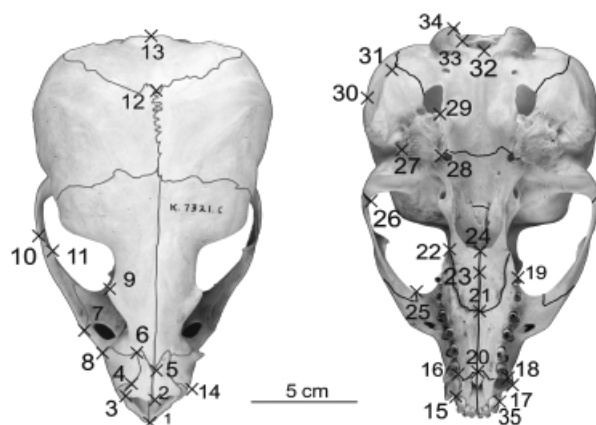

Figure 1 Landmarks collected and included in final analysis, shown on *Arctocephalus gazella*. Numbers correspond with landmarks listed in Table 1. Symmetrical landmarks are shown on one side only.

Procrustes analysis and principal components analysis (Zelditch *et al.*, 2004) were conducted separately for otariids and for phocids. First, analyses were conducted with all male, female and young specimens, to assess ontogenetic patterns across each clade. A second analysis was conducted with only adults, both male and female, to identify dimorphism in each clade. Because of some uncertainties in ages and gender of specimens, to maximize the number of specimens in the analyses, actual specimen values, rather than species averages were used in the principal components analysis to assess differences both within and across species in cranial shape. It should be noted that sexes (males and females, unknowns removed) and/or ages (juveniles/subadults and adults) were separated and gender-specific species averages used in the further analyses, described below.

Phylogenetic signal

The amount of phylogenetic signal in otariid and phocid cranial shape was tested using non-parametric correlation analysis. A patristic distance matrix was constructed using a composite phylogeny from Arnason *et al.* (2006) and Wynen *et al.* (2001) (Fig. 2). Euclidean distances between each pair of species were calculated from principal component (PC) scores for each of the first four principal components to generate four shape distance matrices. As mentioned above, separate analyses were conducted for male and female specimens, and only adult specimens were included in generating the distance matrices. Each shape distance matrix was then compared with the patristic distance matrix using Spearman's rank correlation analysis. Analyses were conducted in PAST (Hammer, Harper & Ryan, 2001).

Ecological signal

To analyze correlations of skull shape with ecological attributes, data on 11 ecological variables were collected from the literature (Reeves *et al.*, 2002; Schulz & Bowen,
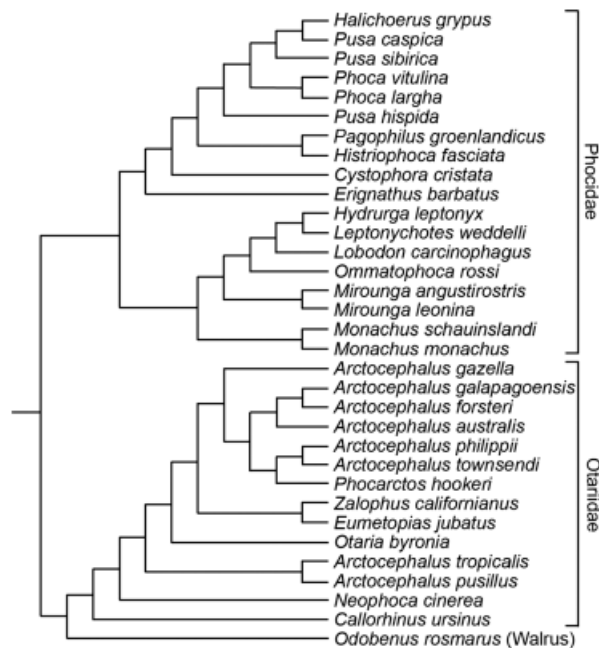
primarily identified based on original age data acquired during specimen collection. Additional young specimens without original data available were identified based on the presence of significantly open sutures. Note that, for many species, particularly phocids, sutures closure occurs well after weaning, but before sexual maturity, which may result in an overestimate of specimen age (Schulz & Bowen, 2004). For this reason, specimens with closed sutures that were not labelled as adult were treated as of unknown age.

Data analysis

Cranial shape

The unified, mirrored dataset was then entered into MORPHO-LOGIKA 2.5 (O'Higgins & Jones, 2006), and generalized

Figure 2 Composite phylogeny for extant pinnipeds (Wynen *et al.*, 2001; Arnason *et al.*, 2006).

2004; Ferguson & Higdon, 2006). These variables are separated into life-history variables and environmental variables. Life-history variables include sexual size dimorphism (male/female mass in kg), gestation time (days), neonate mass (kg), weaning time (months), growth rate (kg day^{-1}), time to female reproductive maturity (days) and longevity (months). Data on growth rates were not available for most phocids, and this variable was excluded from analyses involving that clade. Environmental variables include latitude, temperature (°C), productivity and seasonality. Marine primary productivity was measured using ^{14}C uptake and simulated fluorescence techniques (C(g) m^{-2} year^{-1}) (Ferguson & Higdon, 2006). Seasonality was measured as the annual variation coefficient of the monthly primary productivity, averaged over 20 years, taken from measures of soil evapotranspiration in coastal weather stations (S. H. Ferguson, pers. comm.).

Ecological variables were compared with PC scores, using Pearson's product–moment correlation analysis. PC scores were averaged across adult specimens of each species, separately for males and females, and young (infant and juvenile) specimens were excluded from ecology analyses. Because closely related species have the potential to be more similar in morphology or ecology, phylogenetically independent contrasts (Felsenstein, 1985) were obtained with COMPARE 4.6b (Martins, 2004), using the phylogeny shown in Fig. 2 (Wynen *et al.*, 2001; Arnason *et al.*, 2006). A significance value of $P < 0.05$ was used in all analyses. Because multiple analyses were conducted, a Bonferroni correction was also applied. However, because both independent contrasts and Bonferroni corrections greatly reduce the ability to recover statistically significant results, particu-

larly with relatively small datasets, we also report the results of analyses without a Bonferroni correction.

Results

Cranial shape analyses

Otariidae

Ontogenetic changes in cranial shape represented a large amount of the observed variation among otariids. PC1 represented 28.1% of the total variation and clearly separated young and adult specimens (Fig. 3). The shape transition from juveniles to adults involved an elongation of the nasal and palate regions and growth of the canines and mastoid process. Cranial growth in otariids appeared to involve similar shape changes in all species, as PC1 separated all juveniles from all adults (Fig. 3). Male *Otaria flavescens* specimens were the only group to cluster separately, at the negative end of PC1.

Because ontogenetic changes dominated the otariid morphospace, a second analysis was run without young specimens (Fig. 4). When only adults were analyzed, PC1 and 2 represented 33.5 and 12.2% of total shape variation, respectively. Shape variation represented on PC1 was concentrated around the nasal and palate regions. Male *O. flavescens* specimens, with a wide nasal opening, enlarged palate and broad, recessed nasal bones, defined the negative end of PC1 (Fig. 4).

Species did not cluster strongly on PC3 and 4 (Fig. 5), which represented 9.5 and 7.4% of the total variation, respectively. PC3 was dominated by basicranial and dental landmarks, while PC4 was dominated by palatal landmarks.

Phocidae

In phocids, PC1 and 2 were primarily defined by species with ecological specializations (Fig. 6). The specialist feeders *L. carcinophaga* and *H. leptonyx* fell on the positive end of PC1. Conversely, *Cystophora cristata* (specialized nasal display), *M. leonina* (large harems, male fighting, male proboscis) and *E. barbatus* (suction feeder) were found at the negative PC1. Species with the largest shape differences between young and adult specimens (*Halichoerus grypus*, *C. cristata*, *M. leonina*) were all found at the negative end of PC1. These taxa overlapped with those that show a large difference in male and female morphology (*C. cristata*, *M. leonina*). Unfortunately, *Mirounga angustirostris* was represented by only a single juvenile specimen, but it is likely that an adult male specimen would also have fallen toward the negative end of PC1.

PCs 1 through 4 contributed 20.4, 17.9, 13.1 and 8.9%, respectively, to the total shape variation. PC1 was dominated by landmarks focused around the nasal region, where many dimorphic display features are concentrated (proboscis in *M. leonina*, nasal bladder in *C. cristata*). Species near the negative end of PC1, *C. cristata*, *M. leonina* and *E.*
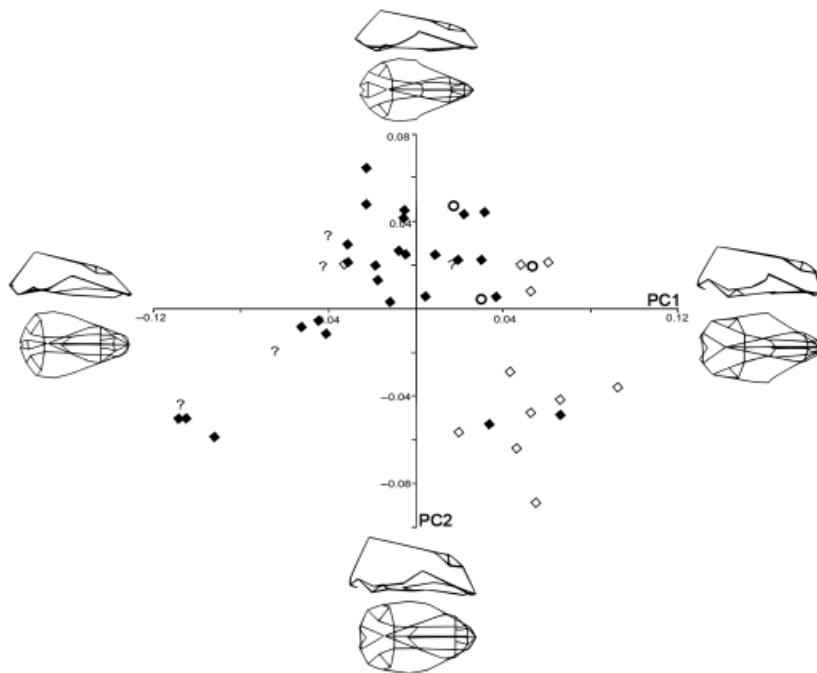
Figure 3 Principal components analysis of Otariidae showing the first two principal components. Wireframes represent the position of landmarks in lateral (top) and dorsal (bottom) views in specimens at the extremes of each axis. ◇, infant and juvenile; ○, subadult; ◆, adult; ?, unknown age.
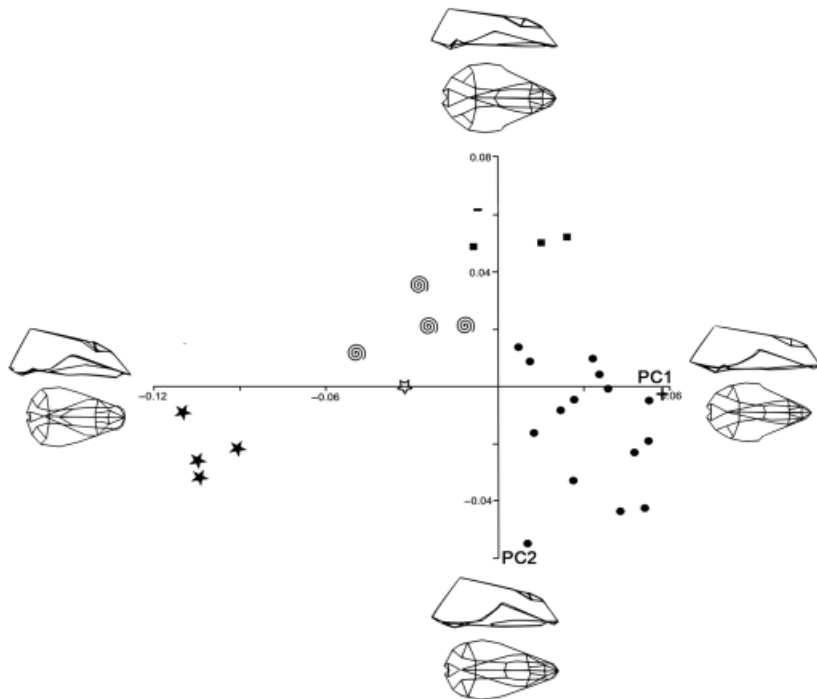

Figure 4 Principal components analysis of Otariidae, excluding infant and juvenile (young) specimens, showing principal components one and two. ●, *Arctocephalus* (sp.); +, *Callorhinus ursinus*; ◎, *Eumetopias jubatus*; –, *Neophoca cinerea*; ★, *Otaria flavescens* male; ☆, *O. flavescens* female; square, *Zalophus californianus*.

barbatus, exhibit larger nasal openings, with reduced and recessed nasal bones, and shorter, rounder skulls, while specimens at the positive end of PC1 displayed elongate, pointed skulls. PC2 represented shifts from narrow interorbital regions and enlarged auditory bullae at the negative end, involving mainly female and juvenile specimens of *M.*

leonina and *C. cristata*, species, to broad interorbital regions and enlarged nasal openings at the positive end.

PC3 of this analysis appeared to show a strong phylogenetic signal with monachine phocids displaying positive values, and phocine phocids showing negative values. Monachines, at the positive end of PC3, have wide interorbital
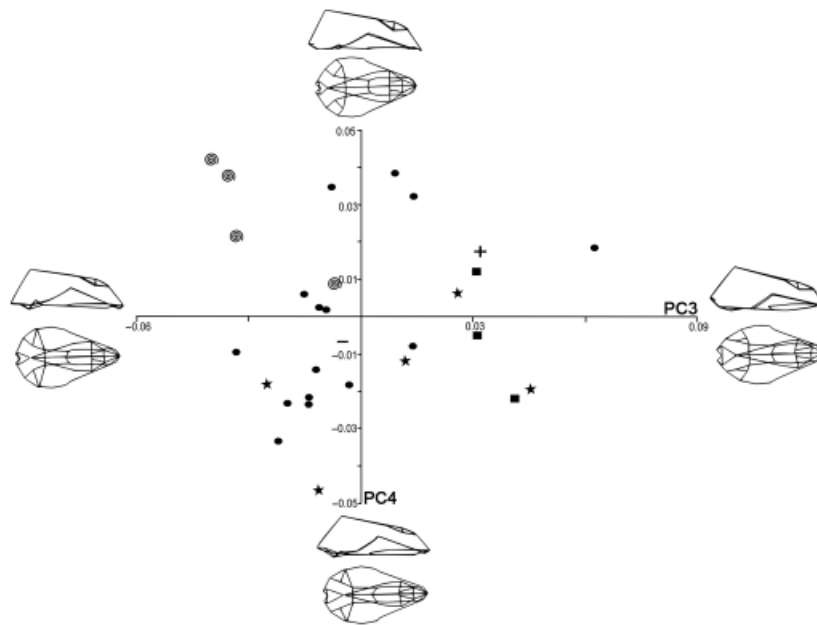
Figure 5 Principal components analysis of Otariidae, excluding infant and juvenile (young) specimens, showing principal components three and four. Symbols as in Fig. 4.
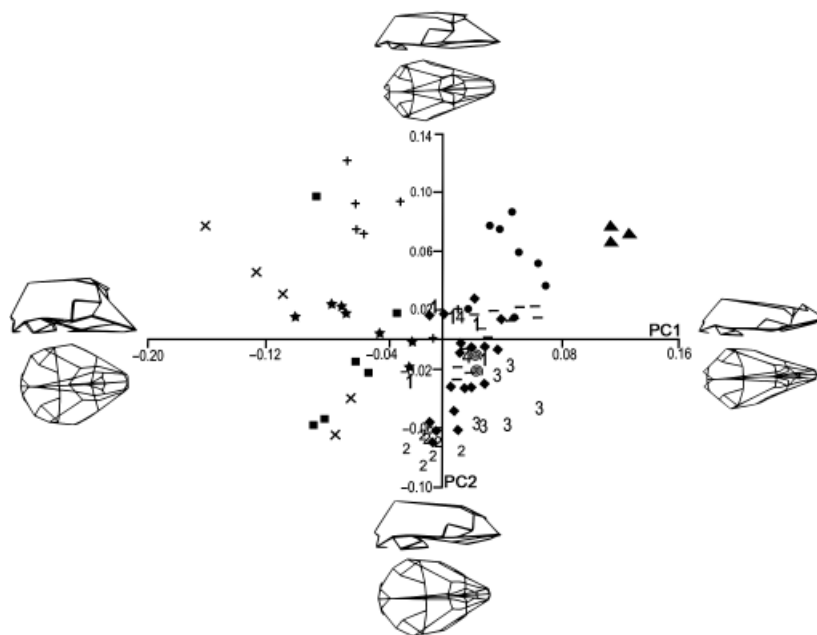

Figure 6 Principal components analysis of Phocidae, showing principal components one and two. +, *Halichoerus grypus*; ■, *Mirounga leonina*; ×, *Cystophora cristata*; ▲, *Hydrurga leptonyx*; •, *Lobodon carcinophaga*; ★, *Erignathus barbatus*; –, *Pusa* (sp.); ◆, *Phoca* (sp.); ◉, *Ommatophoca rossii*; 1, *Monachus* (sp.); 2, *Histriophoca fasciata*; 3, *Lepidium weddellii*; 4, *Pagophilus groenlandicus*.

regions, larger auditory bullae and an anterior expansion of the maxilla beyond the nasals, whereas phocines, at the negative end, display narrower nasals (Fig. 7). PC4 was dominated by dorsoventral rotation of the cranium, ranging from a straight skull at the positive end to a dorsally oriented, or upturned, snout at the negative end.

Again the edges of the occupied morphospace were dominated by specialist phocid species. *E. barbatus* (suction feeder) specimens clustered in the second quadrant, negative PC3 and positive PC4, while *L. carcinophaga* (filter feeder) defined the positive end of PC4. *Ommatophoca rossii* occu-

pied the positive end of PC3 and *C. cristata* (large nasal display) and the landlocked seals *Pusa caspica* and *Pusa sibirica* showed large negative scores on PC4.

Analyses excluding young specimens showed very similar results to those with all specimens included, as can be seen in Fig. 8 (PC1 and 2, representing 25.8 and 17.4%, respectively) and Fig. 9 (PC3 and 4, 13.9 and 7.2%, respectively). This indicates that ontogenetic shape changes are not as important as interspecific shape differences in phocids, in contrast to the pattern observed in otariids.
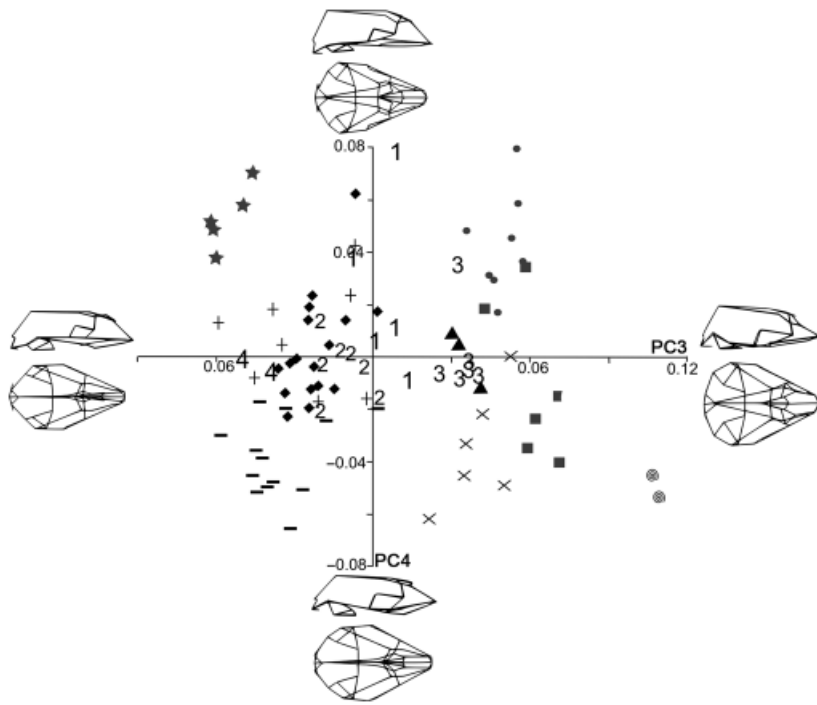
Figure 7 Principal components analysis of Phocidae, showing principal components three and four. Symbols as in Fig. 6.
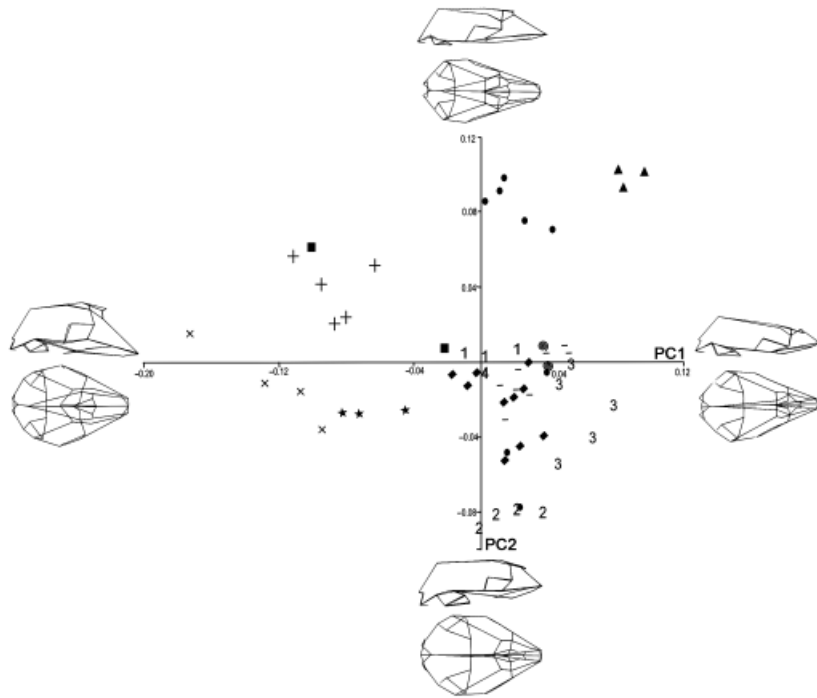

Figure 8 Principal components analysis of Phocidae, excluding infant and juvenile (young) specimens, showing principal components one and two. Symbols are as in Fig. 6.

Phylogenetic signal

Otariids

In otariids, cranial shape differences did not correlate significantly with patristic distance, a measure of phylogenetic relationship, for any of the first four principal components in either adult males or adult females (Table 2).

Phocids

In phocids, cranial shape differences among males were significantly correlated with patristic distance on PC2 (Table 2; $r = 0.37$, $P \ll 0.001$) and on PC3 ($r = 0.23$, $P < 0.001$). Among females, cranial shape differences and patristic distance were significantly correlated only on PC3 ($r = 0.53$, $P \ll 0.001$).
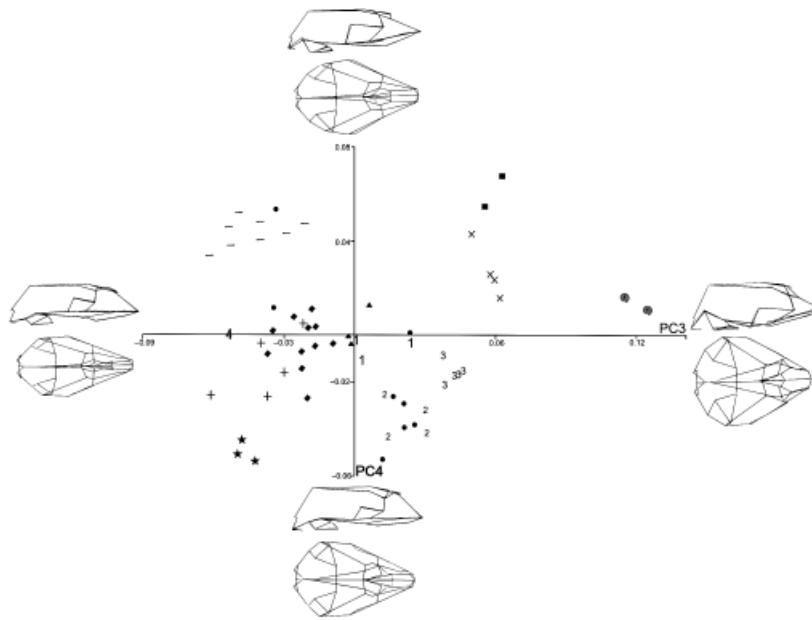
Figure 9 Principal components analysis of Phocidae, excluding infant and juvenile (young) specimens, showing principal components three and four. Symbols as in Fig. 6.

Table 2 Results of Spearman's rank correlation analysis of Euclidean distances between species and phylogenetic relatedness

PC	Otariidae				Phocidae			
	Male r	P	Female r	P	Male r	P	Female r	P
1	0.026	0.83	−0.120	0.38	0.087	0.21	0.007	0.93
2	0.225	0.06	−0.031	0.82	**0.374**	**<0.001**	0.000	0.99
3	−0.070	0.53	−0.156	0.25	**0.231**	**<0.001**	**0.531**	**<0.001**
4	0.060	0.62	0.146	0.29	0.036	0.61	−0.051	0.53

Euclidean distances were calculated separately for each of the first four principal components. Significant results in bold.

Ecological signal

Otariids

Female otariids showed significant correlations between skull shape and growth rate (PC1), weaning time (PC4), gestation time (PC4) and temperature (PC4; Table 3). Correlations that were significant only without a Bonferroni correction include weaning time (PC2), productivity (PC2), dimorphism (PC3) and latitude (PC3). Male otariids only showed significant correlations without a Bonferroni correction, for growth rate (PC1 and 3), temperature (PC1 and 2), dimorphism (PC3), growth rate, productivity (PC4) and seasonality (PC4).

Phocids

Female phocids showed a significant relationship between time to female maturity and PC4 (Table 3). Without a Bonferroni correction, there were also significant correlations between skull shape and gestation time (PC1), productivity (PC1), weaning time (PC2), dimorphism (PC3 and 4) and gestation time (PC3). Skull shape in male phocids was not significantly correlated with any ecological variables when a Bonferroni correction was applied. Without the correction, male skull shape was correlated with dimorphism (PC1 and 4), gestation time (PC1), weaning time (PC1 and 2), productivity (PC1), temperature (PC2), time to female maturity (PC3), longevity (PC3) and seasonality (PC3).

Discussion

Comparison of cranial shape in otariids and phocids: adult morphology

Life in the aquatic realm might be expected to impose similar pressures or constraints on cranial shape evolution in both otariids and phocids, which should be reflected in similar loadings of variables on the major axes of variation. In both otariids and phocids, landmarks in the nasal region contributed greatly to PC1, demonstrating that the rostral region of pinnipeds is a focal region of morphological adaptations (Figs 4 and 8). However, palatal landmarks also contributed to PC1, as well as PC 2 and 4, in otariids, while phocids showed a more general shift from a rounded to a narrow skull on PC1.

Table 3 Correlation analyses of ecological variables against the first four principal components of cranial shape in phocids and otariids (no young), using independent contrasts

	Otariidae								Phocidae							
	Female				Males				Females				Males			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Life-history variables																
Sexual size dimorphism	0.29	0.32	0.64*	−0.48	0.46	0.04	0.69*	−0.31	−0.21	−0.17	0.50*	0.60*	−0.48*	0.25	0.09	0.60*
Gestation time	−0.44	0.31	−0.36	−0.76**	−0.6	0.32	0.22	−0.09	0.55*	0.10	−0.50*	0.08	0.56*	−0.17	−0.31	0.04
Weaning time	−0.22	−0.66*	0.07	0.73**	0.04	0.31	−0.09	−0.32	0.41	−0.53*	−0.08	0.00	0.48*	−0.66*	0.07	−0.03
Growth rate	−0.81**	−0.45	0.35	−0.36	−0.54*	−0.06	0.21	−0.69*								
Female maturity	0.00	0.09	−0.12	0.39	0.09	−0.07	−0.11	0.27	0.25	0.05	−0.74**	−0.26	0.44	−0.04	−0.52*	0.14
Longevity	0.15	0.37	0.38	−0.34	−0.04	−0.19	0.08	0.13	0.02	0.21	−0.25	0.05	0.04	0.25	−0.52*	0.14
Environmental variables																
Latitude	−0.11	0.07	0.55*	0.16	0.10	0.44	0.18	0.01	−0.21	−0.28	−0.38	−0.32	−0.14	−0.30	−0.09	−0.36
Temperature	0.20	−0.27	0.47	0.76**	0.72*	0.52*	−0.13	0.07	−0.34	0.16	0.23	0.30	−0.38	0.48*	−0.43	0.02
Productivity	0.27	0.63*	−0.41	−0.46	−0.46	0.30	0.03	0.52*	−0.58*	−0.10	0.43	−0.11	−0.55*	0.15	0.23	−0.24
Seasonality	−0.31	−0.35	0.33	−0.50	−0.37	−0.31	−0.12	−0.69*	−0.08	−0.21	0.19	0.10	−0.12	−0.18	0.54*	0.29

There was not enough data to include age to female maturity in analyses of otariids. Seasonality and neonate mass were not significantly correlated with any principal components.

*$P<0.05$.

**$P<0.05$ with Bonferroni correction.

Orbital landmarks contributed much of the variation of PC 2 and 3 for phocids (Figs 8 and 9), but did not play a significant role in otariid skull shape. This greater importance of orbit morphology in phocids than in otariids could reflect the superior diving capacities of phocids (Ferguson & Higdon, 2006). Bony orbit size, a proxy for eye size, has been linked to diving capacity in pinnipeds (Berg & Pyenson, 2008). Unfortunately, in this case the ecological data were not comprehensive enough to permit a correlation analysis of maximum recorded diving depth with cranial shape. It is worth noting, however, that shallow divers, such as *H. grypus*, group at the positive end of PC2, corresponding with small orbit size, while deep divers, such as *M. leonina*, group at the negative end of PC2 (Fig. 6), which is consistent with the hypothesis that diving capacity is an influence on cranial shape in phocids. Phocids also showed a concentration on bullar morphology (PC 2 and 3) and dorsoventral rotation of the skull (PC4), neither which appear to be a major source of variation in otariid skull morphology. Thus, while both clades showed high loadings of nasal characters on PC1, nearly all otariid variation was concentrated in the rostral region. Phocids instead displayed significant variation across the skull, from the rostrum to the orbits and bullae, as well as more global shifts in skull shape.

There are also differences in the distribution of otariid and phocid species within their respective morphospaces. When only adults were analysed, only *O. flavescens* clearly separated from other otariids (Fig. 4), reflecting several aspects of *O. flavescens* cranial morphology that are distinct from other otariids. Males have been described as having an upturned snout, related to mating display (King, 1983), and it has been suggested that males and females display adapta-

tions for suction feeding (Adam & Berta, 2002). The only other dietary specialist among otariids, *A. gazella*, a krill feeder, does not display unusual cranial morphology in comparison with other otariids. Most other otariid species are generalist feeders with large size dimorphism (Ferguson & Higdon, 2006), but little shape dimorphism. In contrast, phocids showed strong species separation in the principal components analysis, with specialist species defining the edges of the occupied morphospace (Fig. 8).

Comparison of cranial shape in otariids and phocids: ontogeny and dimorphism

In addition to differences in adult cranial shape variation, there were also striking differences in ontogenetic shape variation between otariids and phocids. Ontogenetic shape changes were large relative to interspecific differences in all otariid species (Fig. 3), but only in a few phocids (Fig. 6). Within phocids, species exhibiting significant changes in skull shape during ontogeny were concentrated toward the negative end of PC1 (Fig. 6), illustrating that these species share an aspect of common morphology. Previous work examining interfamilial differences across all pinnipeds (Jones & Goswami, 2009) found that these species had adult cranial shapes that converged on odobenid (walrus) morphology. Some of these more derived morphologies relate to feeding adaptations, such as in *E. barbatus*, while others reflect reproductive adaptations, as in *C. cristata*.

The result that otariids show larger ontogenetic shape changes relative to interspecific differences than observed in phocids may partially reflect the later weaning times of otariids (Ferguson & Higdon, 2006), such that a larger

percentage of young otariid specimens would be expected to still be suckling at death. In contrast, phocids wean faster, and thus more of the young phocid specimens may be expected to have a more similar diet, and more similar cranial morphology, to adults of their species. The separation on PC1 of young and adult specimens of otariids (Fig. 3) may thus represent a separation of suckling and solid-feeding individuals, while only a few phocid specimens are likely to have still been suckling when they died. However, *C. cristata*, a phocid with a weaning time of just 4 days (Ferguson & Higdon, 2006), exhibits a large ontogenetic change in cranial morphology (Fig. 6), suggesting that weaning time alone does not explain the differences observed in phocid and otariid ontogenetic shape trajectories. A detailed study with known age data for phocids and otariids is needed to rigorously assess the relationship between weaning time and ontogenetic shape changes in these clades.

Cranial shape differences due to dimorphism were not as significant as ontogenetic differences in otariids. Significant shape differences were observed in only one species of otariid (*O. flavescens*) and two species of phocid (*M. leonina* and *C. cristata*). As noted above, male *O. flavescens* have been described in the literature (King, 1983) as having an 'upturned snout', and *M. leonina* and *C. cristata* have facial displays for mating in the form of a proboscis and a nasal bladder, respectively. In fact, a similar anatomical solution to the problem of producing a male facial display (wider nasal opening with recessed nasals) has been reached three times convergently; in the phocines (*C. cristata*), monachines (*M. leonina*) and otariids (*O. flavescens*). This may reflect a limited range of functionally possible adaptations for organisms that are highly adapted for swimming and cannot involve their postcrania in mating displays.

Phylogenetic signal in cranial shape

Surprisingly, neither clade showed a strong phylogenetic signal in cranial morphology. Phylogenetic relationship is the strongest correlate of cranial shape in comparisons across the three extant pinniped families (Jones & Goswami, 2009), but this higher-level pattern does not simply translate to the intrafamilial level, despite relatively basal splits in both otariids and phocids. Phocids are divided into phocines and monachines, which likely diverged in the early Miocene, at least 16 million years ago (Deméré *et al.*, 2003). Otariids are primarily divided into otariines and potentially para-phyletic arctocephalines (Wynen *et al.*, 2001), which likely diverged in the middle to late Miocene. However, none of these subfamilies showed greater similarity in cranial shape, suggesting a large degree of convergence within each family.

The only significant correlations between cranial shape and phylogenetic relatedness were in phocids (Table 2), with PC2 (males and females) and 3 (males only). Because phocids are ecologically and reproductively diverse, it is perhaps more understandable that they would display a

large amount of variation and convergence in cranial shape. The ecologically and reproductively uniform otariids, however, show no phylogenetic signal in cranial shape at all, perhaps due to the relatively limited range of skull morphology in this clade.

Ecological correlates of cranial shape

As phylogeny does not appear to constrain phocid or otariid skull morphology, it is reasonable to expect that ecological variables have had a relatively greater influence on cranial morphology. Indeed, in phocids, both phocines and mon-achines displayed derived morphologies that define the extremes of PC1. For example, the phocine *M. leonina* and the monachine *C. cristata* both occupied the negative end of PC1 (Fig. 6). Both are gregarious, breeding in large colonies, are highly dimorphic, and display extreme male cranial modifications for mating displays. These convergences in facial morphology appear to overprint the phylogenetic signal in phocids, and indeed phocids showed strong correlations between cranial shape and both life-history and environmental variables, although life-history variables dominate (Table 3). Significant correlations between both gestation and weaning time and each of the first two principal components reflect the diversity of reproductive strategies observed in phocids. After a Bonferroni correction is applied, phocids display only a single significant correlation, between age at female maturity and female cranial shape, again suggesting that aspects of life history are more influential than environmental variables in phocid cranial evolution.

Otariids also showed a mix of life-history and environ-mental variables with significant correlations with cranial shape, but environmental variables appeared more impor-tant than in phocids. Gestation time, weaning time, growth rate and temperature were all significant correlates of cranial shape in females after Bonferroni correction, but latitude, productivity, seasonality, dimorphism also corre-lated with male or female cranial shape without the correc-tion (Table 3). Although young specimens were not included in the ecological analyses, the significance of multiple life-history variables is consistent with the importance of onto-genetic shape changes described above. The significance of the environmental variables is perhaps less straightforward, as most otariids are generalists and ecologically quite uni-form. However, these results may primarily reflect the unusual otariid *O. flavescens*, which deviates from other otariids in cranial morphology and inhabits some of the coldest regions among otariids (Ferguson & Higdon, 2006), possibly driving the strong association with environmental variables.

Further considerations and conclusions

Phocids are more ecologically diverse than otariids, which is reflected in clearer interspecific differences in cranial shape

reported here (Figs. 4 and 8) and in a previous study directly comparing cranial shape across the three clades of pinnipeds (Jones & Goswami, 2009). Several species of phocids display feeding (*E. barbatus*, *H. leptonyx*, *L. carcinophaga*) and reproductive (*M. leonina*, *C. cristata*) specializations, and these species were unsurprisingly those observed in this study to have the most divergent cranial morphologies among phocids. Phocids are more specialized for aquatic life (e.g. deeper diving capacity, polar occupation, improved hearing capabilities) than are otariids, which maintain greater locomotory ability on land. Because phocids are not bound to land for breeding, like otariids are, they have access to a greater range of environments that otariids (Cassini, 1999), perhaps driving their great ecological and morphological diversity. Otariids instead are stuck, in a sense, between specializations for feeding in the aquatic realm and ancestral dependence on land for breeding.

An alternative hypothesis relates to age of each clade; the otariid crown group is geologically younger, sharing a more recent common ancestor, than the phocid crown group. There are no extinct genera in crown Otariidae, and members of the extant clade diverged only recently, with no unambiguous pre-Pleistocene representatives of crown Otariidae. Deméré *et al.* (2003) tentatively suggested a pre-11 mya divergence date for living otariids. In contrast, representatives of crown Phocidae are known from the middle Miocene, requiring a divergence of the phocine and monachine subfamilies before 16 mya. Furthermore, while nearly all extinct otariids are stem taxa, nearly all known extinct phocids fall within the crown group. Although the dataset in this study is insufficient to test this hypothesis, the effect of this differential pruning of the otariid and phocid trees could be tested by including fossil specimens into the study to examine whether stem otariids had more diverse skull morphologies than observed in the crown group.

In conclusion, otariids and phocids display disparate patterns of cranial evolution: (1) phocids displayed a much greater range of skull morphology than otariids, in which interspecific differences were dominated by only *O. flavescens*; (2) surprisingly, neither clade showed strong associations between phylogenetic relatedness and cranial shape, likely reflecting a high degree of convergence among monachine and phocine phocids, but only a lack of cranial diversity in otariids; (3) both clades show significant correlations between aspects of cranial shape and ecological variables, although life-history variables dominate in phocids, potentially reflecting their greater diversity of reproductive strategies; (4) ontogenetic variation in skull morphology was much greater relative to interspecific differences in otariids than phocids, perhaps due to their extended weaning times. Shape dimorphism was observed in only one otariid species (despite universal body mass dimorphism) and two phocids. Future analyses should include fossil taxa to establish the relationship among the ecological, reproductive and morphological traits discussed here and to elucidate the factors driving the disparate evolutionary patterns of phocids and otariids.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of specimens measured.

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