

Comparative description of a female *Enaliarctos emlongi* (Carnivora, Pinnipedimorpha) from the mid-Miocene of Oregon and the evolution of sexual dimorphism within Pinnipedia

by

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A thesis submitted to the Faculty of Graduate and Postdoctoral Affairs in partial fulfillment of the requirements for the degree of

Master of Science

in

Earth Sciences

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ABSTRACT

Sexual selection is an important evolutionary process effecting the behaviour and morphology of many animal groups. Sexual size dimorphism (SSD) often occurs within species as a result of differing mating systems. An important example of this can be observed within pinnipeds. Modern members of this group show two main mating systems: a land based harem system with extreme SSD, and a water based system with minor SSD. How this system evolved is poorly understood, and is analyzed here using a combination of fossil comparisons and geometric morphometrics on modern species. A previously undescribed specimen of *Enaliarctos emlongi*, a fossil relative of pinnipeds, was examined and found to most likely represent an adult female individual, with another known *E. emlongi* specimen representing an adult male. Geometric morphometric and discriminant function analysis showed that species with significant SSD could also be distinguished sexually through cranial shape. Otariids were found to show consistent patterns of cranial diversity across all sampled species, whereas phocids showed a much more variable pattern. *E. emlongi* was found to plot within otariids in cranial morphospace, suggesting a morphological stability between primitive pinnipeds and modern otariids. This, when added to previously noted fossil evidence, suggests that extreme SSD and the related mating systems are plesiomorphic in pinnipeds. This may also have implications for our understanding of the ecology and biogeography of this group, and our broader understanding of sexually selective evolutionary processes.

ACKNOWLEDGMENTS

I would like to thank the staff of the Smithsonian Institution's Natural History museum for access to the modern pinniped collections and fossil material, and for loaning the small skull specimen for use in this study, the staff of the Penn State Quantitative Imaging Lab for use of their microCT scanning equipment, Alex Tirabasso of the Canadian Museum of Nature for his assistance in manipulating the CT scan data and the creation of the 3D model of the middle ear structures, the R Foundation and the various package authors, and for assistance with R and discussions on the statistical methods we would like to thank D. Fraser, J. Claude, T. Hossie, S. Hinic-Frlog, and L. Schmitz. Funding support for this research was provided by NSERC to TMC (Canada Graduate Scholarship) and NR (Discovery Grant).

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INTRODUCTION

Sexual dimorphism refers to differences, generally in appearance (e.g. colouration, size, ornamentation) or behaviour (e.g. mating systems, risk-taking, feeding) between females and males within a given species, which arise as a result of sexual selection (Kissner et al, 2000). Sexual size dimorphism (SSD) is a common result of differing mating systems in animals, and is among the most visible form of sexual dimorphism, with SSD resulting in larger females than males in many groups (Bulté et al, 2008). Among mammals, many groups show some evidence of sexual dimorphism, which typically manifests in males possessing larger bodies or elaborate display structures (Alcock, 2005). Pinnipeds, which includes phocids (seals), otariids (sea lions and fur seals), and odobenids (walrus), are a diverse group of semi-aquatic carnivores with a wide range of reproductive strategies (Nowak et al, 2003). Otariids display some of the most extreme SSD in mammals, and have a gregarious, often harem-based, and highly polygynous mating system (Cassini, 1999; Nowak et al, 2003). By contrast, phocids show only slight polygyny, with males generally mating with one or two females, and have a generally female-choice driven mating system (Nowak et al, 2003). Exceptions to the general phocid mating system can be seen in *Mirounga* and *Halichoerus*, both of which have a land-based, highly polygynous mating system and display extreme SSD (Cassini, 1999). In addition to SSD, a number of other physical traits in pinnipeds appear dimorphic (size and surface area of the sagittal crest, masseteric fossae, neck musculature, and

other muscle attachment areas; rostral width; mandibular tooth row length; canine cross-sectional area), and thought to be related to display and intra-specific combat (Howell, 1929; Cassini, 1999; Nowak et al, 2003; Brunner et al, 2004). The mating systems of modern pinnipeds are summarized in Table 1, and the degree of SSD present in a pinniped species appears to be closely linked to their mating systems, with greater SSD associated with larger harems (Cassini, 1999). This close linkage could allow predictions of behaviour to be made by examination of the degree of SSD in a species, when natural history or ecological observations are missing. This could be of use for paleontological studies, as while it is relatively easy to determine in living populations, reproductive behaviour can be difficult to infer when only dealing with skeletal material, particularly fossilized skeletal material. Fossil vertebrate remains are relatively rare in the geological record, due to the low likelihood of fossilization, and complete fossil skeletons even more so. In order to identify and study sexual dimorphism and infer breeding strategies in extinct vertebrates, morphological patterns and features must be found that are related to those behaviours. The origin and evolution of these behaviours and mating systems is not yet well resolved, partially due to the incomplete nature of the fossil record, although their close association in modern forms could allow the use of morphology in fossil forms to make inferences of behaviour (Berta et al, 1989; Cassini, 1999; Lindenfors et al, 2002; Rybczynski et al, 2009; Jones and Goswami, 2010). Unfortunately, for most fossil vertebrates, including pinnipeds, are often known from a single, or a few, specimens. Consequently, alternative explanations for

differing morphologies (ontogeny, phylogeny, etc...) must be rejected before sexual dimorphism can be reasonably considered.

The relationships of early pinnipeds, represented by Oligocene to Miocene aged fossils, are poorly (Berta et al, 1989; Berta, 1991; Rybczynski et al, 2009). Most of the fossil taxa are basal to crown-group pinnipeds, belonging to the more broadly defined Pinnipedimorpha (basal taxa + crown group)(Berta, 1991; Rybczynski et al, 2009). *Puijila darwini* appears to be among the most basal of the known fossil material. It was found in a lacustrine deposit of the Haughton Formation, Devon Island, (Nunavut, Canada) and represents a transitional morphological stage between a terrestrial and more fully aquatic taxa (Rybczynski et al, 2009). Amongst other fossil pinnipedimorph taxa, *Enaliarctos* is the most studied with the largest sample size, and includes five species (*E. mealsi*, *E. emlongi*, *E. barnesi*, *E. mitchelli*, and *E. tedfordi*), although the validity of the genus has been questioned (Berta et al, 1989; Berta, 1991). *Enaliarctos* has been described as a 'meta-taxon', as no unequivocal synapomorphies are shared between all *Enaliarctos* species (Berta, 1991). Collected from near-shore marine deposits (Berta, 1989; Berta, 1991; Bebej, 2008) of north-western Oregon, the various *Enaliarctos* species have a stratigraphic range from the upper Oligocene Yaquina Formation to the lower to middle Miocene Nye Mudstone and Astoria Formation (Berta, 1991). The latter two units also host other early pinniped taxa, such as *Pinnarctidion*, *Pteronarctos*, and *Pacificotaria* (Barnes, 1992; Berta, 1994A; Berta, 1994B). *Enaliarctos* has a fully flippers manus and pes, making it morphologically more similar to a modern pinniped

(Berta, 1989; Berta, 1991; Rybczynski et al, 2009) than to *Puijila*. Considerable work remains in order to further illuminate the early evolution of this group.

Multivariate statistical methods, such as geometric morphometrics, have been used to examine aspects of ontogeny, sexual dimorphism, ecology, and phylogenetics within many animal groups, including pinnipeds (Kissner et al, 2000; Brunner et al, 2004; Bulté et al, 2008; Sanfelice and de Freitas, 2008; Jones and Goswami, 2010). Work by Jones and Goswami (2010) examined phocids and otariids with the purpose of quantitatively assessing the influence of ecology and phylogeny on cranial morphology. This was accomplished through 3D geometric morphometrics of skulls and correlation statistics with phylogeny and ecological variables. They concluded that phocids showed much greater morphological diversity than otariids, that several phocid species deviated greatly from the “mean phocid morphology”, and that neither otariids nor phocids showed strong associations between morphological diversity and phylogeny. However, their methods are somewhat problematic and potentially weaken their conclusions. The methods of Jones and Goswami (2010) are used here, albeit with considerable modification to account for potential problems with their analysis, such as: 1) low sample sizes (often under five individuals per species), 2) uninformative specimens (many individuals of uncertain sex or ontogenetic stage), and 3) comparisons using “mean phocid morphology” despite considerable morphological and ecological diversity within said family, previously mentioned low sample sizes, and inclusion of juveniles (pers. obs.).

Table 1: Comparison of modern pinniped breeding strategies. Modified from Cassini et al, 1999.

Characteristic	Pinniped group	
	Otariidae	Phocidae
Female density	Highly gregarious	Solitary to moderately gregarious, some highly gregarious
Mating system	Polygyny	Slight polygyny, some more highly polygynous
Birthing location	Land	Ice and/or Land
Mating location	Land	Water, some on land

The purpose of this study is to integrate paleontological comparisons of fossil material and neontological multivariate statistical analyses of modern taxa in order to determine the evolution of mating systems and SSD in pinnipeds, and isolate a method that can be used to assess similar situations in other vertebrate groups. Here we provide a more detailed examination of a small fossil skull, originally referred to a juvenile of *E. emlongi* by Berta (1991), and provide evidence that this specimen more likely represents a mature female of *E. emlongi*. The dental, cranial, and middle ear morphology are discussed, as are the sex and maturity of the individual, in order to assess the validity of the original referral. This species, and another fossil taxon (*Desmatophoca*) previously considered as dimorphic, will be discussed in the context of pinniped phylogeny and the evolution of SSD in pinnipeds. We also performed a large-scale quantitative study of modern male and female pinniped cranial morphometrics, with the purpose of identifying trends in sexual size and shape dimorphism across all major phocid and otariids lineages, and using them, with the phylogeny and fossil forms, to determine the evolutionary history of pinniped SSD and mating strategies. Specifically, this study tests the hypotheses that: 1) Intra-specific cranial diversity in modern pinnipeds is closely related to sexual dimorphism, and can be used to predict the reproductive strategy of a given species, and 2) There is a deep evolutionary origin for predictable skull shape differences in sexually dimorphic pinnipeds.

METHODS

Fossil Material for Comparative Description.—The described fossil specimen is USNM 314290 (cf. *Enaliarctos emlongi*), with primary comparisons made to USNM 250345 (*Enaliarctos emlongi* holotype), and additional comparisons made to USNM 314540 (*E. emlongi* referred snout), USNM 314295 (*E. barnesi* holotype), USNM 335375 (*E. barnesi* referred skull), USNM 206273 (*E. tedfordi* holotype), USNM 314325 (*Pinnarctidion rayi* holotype), and USNM 167648 (*Pacificotaria hadromma* holotype).

Institutional Abbreviations.—USNM/NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anatomical Abbreviations.—c, canine; f, frontal; if, incisive foramen; jf, jugular foramen; ju, jugal; m1, first molar; mf, mandibular fossa; mx, maxilla; n, nasal; o, occipital; oc, occipital condyle; p, promontory; p3, third premolar; p4, fourth premolar; pl, palatine; pmx, premaxilla; pop, postorbital process; rw, round window; sc, sagittal crest; sq, squamosal; tb, tympanic bulla; tc, tympanic crest.

Extant Material for Morphometric Analysis.—Skulls of adult male and female individuals, representing most major extant phocid and otariids lineages (Figure 1), were selected from the collections of the Canadian Museum of Nature (CMN), in Ottawa, Canada, and the Smithsonian Institution's National Museum of Natural History (NMNH), in Washington, D.C. A combination of suture fusion and



Figure 1: Pinniped phylogeny, modified from Nyakatura and Bininda-Emonds (2012). Arrows indicate modern taxa sampled for this study. Fossil taxon (*Enaliarctos emlongi*) shown at base of tree.

specimen collection age data were used to establish the adult status of specimens, particularly for taxa (such as among the phocids) where complete suture fusion has been noted before sexual maturity (Jones and Goswami, 2010). Where possible, 20 specimens were used per species, equally divided between males and females, although low availability or poor condition did prevent this in some cases. Phocid species included *Pusa hispida* (n=20, 50% male), *Halichoerus grypus* (n=15, 47% male), *Cystophora cristata* (n=20, 50% male), *Erignathus barbatus* (n=14, 50% male), *Monachus tropicalus* (n=20, 50% male), *Leptonychotes weddellii* (n=8, 50% male), and *Hydrurga leptonyx* (n=10, 30% male). Otariids included *Callorhinus ursinus* (n=20, 50% male), *Arctocephalus australis* (n=9, 33% male), and *Eumetopias jubatus* (n=20, 50% male). Additionally, the fossil taxon *Enaliarctos emlongi* (n=2, 50% male) was added into the analysis, to help assess which modern pinniped groups more closely reflect the cranial dimorphism of the earliest pinnipeds. Information relating to each individual specimen, and associated measurements, can be found in Appendix 1.

Data Collection.—Skulls specimens, without mandibles, were placed in a photostand and photographed using a Canon Rebel XSI digital camera, at an approximate distance of 180 cm in order to reduce parallax (*sensu* Rybczynski et al, 2010). Measurements of skull length were also made at this time, utilizing digital calipers with 0.1 mm accuracy, and repeated three times to ensure precision. (measurements can be found in Appendix 1). Landmark coordinates

were obtained directly from specimen photographs using the Pointpicker plugin for ImageJ (Thévenaz, 2012). Thirty-one landmarks, adapted from several other mammalian (primarily pinniped) dimorphism studies, were selected from dorsal (1-12) and ventral views (13-31) with the purpose of capturing skull shape and the positions of features of morphological, ontogenetic, or functional importance (Table 2, Figure 2)(Brunner et al, 2004; Sanfelice and de Freitas, 2008; Jones and Goswami, 2010; Rybczynski et al, 2010). A number of skulls were damaged on one side of the skull, as a result of prior collection practices (*pers. obs.*) so only one side of the skull was given landmarks in dorsal and ventral views, This approach also removes variation due to individual asymmetry. Landmark coordinate-sets were compiled on a species level, and on an individual level, and are included in Appendix 2.

Analysis.—The average total skull length for each species (found in Appendix 1). Additionally, the relative difference in skull length between males and females of each species was computed, with a two-tailed t-test assuming unequal variance.

Morphometric analysis protocols followed in this study were modified from those of Rybczynski et al (2010) and Jones and Goswami (2010). The analysis was conducted using the R program suite, with coding from the ‘Shapes’ (Dryden and Mardia, 1998; Dryden, 2012), ‘Abind’ (Plate and Heiberger, 2011), ‘Calibrate’ (Graffelman, 2012), ‘MASS’ (Ripley, 2012), and ‘Car’ (Fox and Weisberg, 2012) packages, as well as packages contained within the book ‘Morphometrics with R’

Table 2: Morphological landmarks used in this study. Adapted from: (Sanfelice and de Freitas, 2004; Jones and Goswami, 2010).

Number	Landmark
1	intermaxillary suture anterior extreme
2	nasal width lateral
3	nasal width medial
4	nasal-frontal midline suture
5	maxilla-frontal-nasal suture
6	interorbital width / jugal-maxilla anterodorsal suture
7	antorbital process
8	jugal posterodorsal process
9	jugal-squamosal anterior suture
10	parietal-occipital suture dorsolateral margin
11	parietal-occipital suture midline
12	foramen magnum dorsal extreme
13	basion
14	occipital condyle posteromedial
15	occipital condyle anterolateral
16	mastoid process lateral extreme
17	auditory bulla posterior extreme
18	external auditory meatus lateral extreme
19	auditory bulla anteromedial extreme
20	basispheno-basioccipital suture lateral
21	posterior interpalatine suture
22	maxilla-palatine midline suture
23	maxilla-premaxilla midline suture
24	incisive foramen posterior extreme
25	incisive foramen anterior extreme
26	canine anterior
27	canine posterior
28	canine medial
29	canine lateral
30	cheek teeth anterior
31	cheek teeth posterior

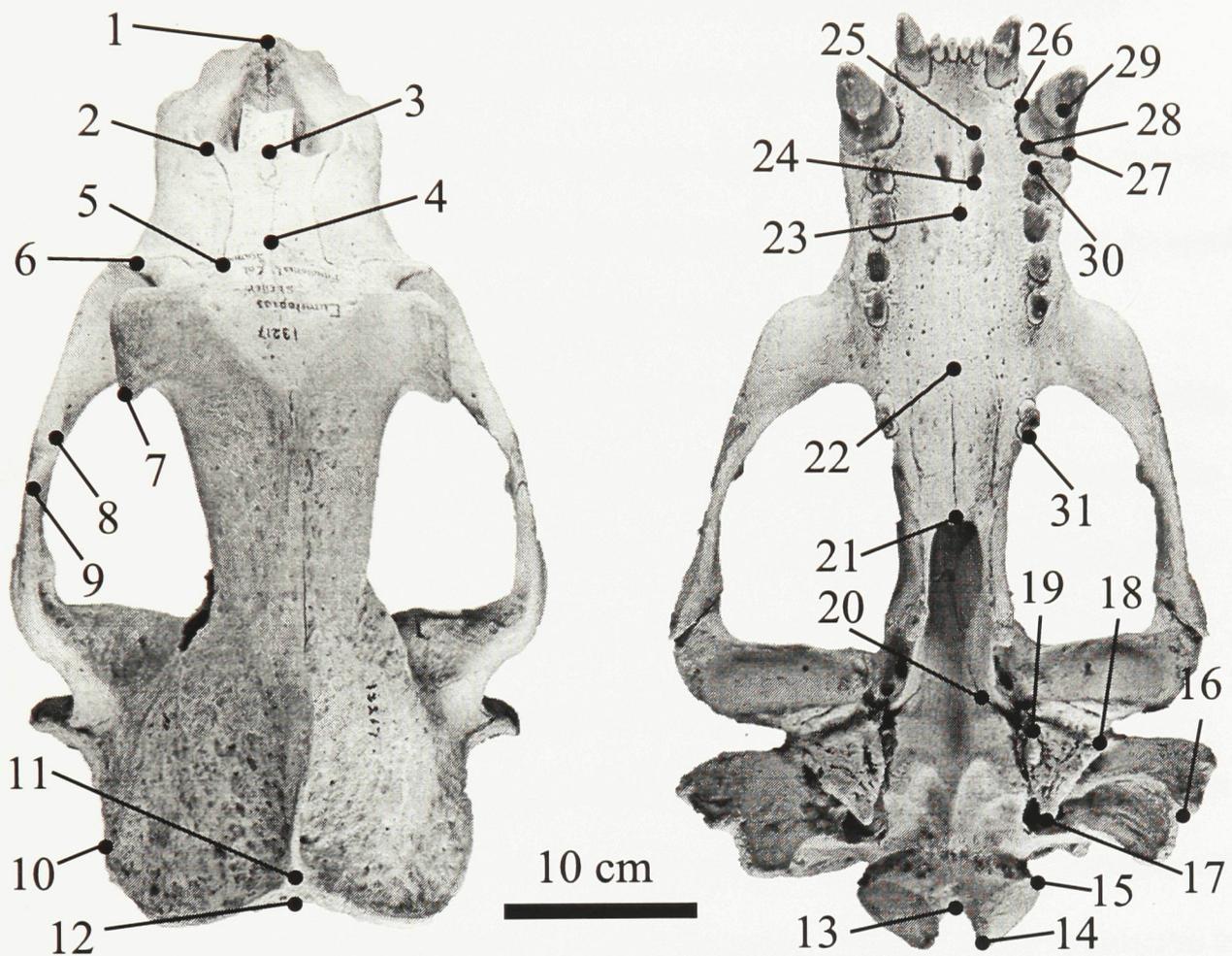


Figure 2: Dorsal (1-12) and ventral (13-31) landmarks used in this study, placed on example specimen of *Eumetopias jubatus*. Landmark descriptions can be found in Table 2.

(Claude, 2008). A full listing of the specific code used in this study can be found in Appendix 3.

The first set of analyses was intended to identify patterns of shape dimorphism present within each species and the region(s) of the skull (as indicated by landmarks) in which dimorphism was most concentrated. Combined matrices including landmark coordinate sets for males and females were arrayed using the *Abind* package for each species, in dorsal and ventral views. Generalized least-squares Procrustes analysis (GPA) was then performed using the *Shapes* package on each of these arrayed matrices in order to minimize the effect of absolute size differences while also aligning the combined coordinate sets. The mean skull shapes of males and females within each species were then determined by extracting the results of the GPA and plotting, using code from 'Calibrate' and 'Morphometrics with R', based on the mean position of each landmark. The mean shapes of male and female skulls were then superimposed over one another, with the resulting vectors between corresponding landmarks in males and females showing shape differences. For better visualization of the regions of dimorphism, the lengths of the vectors were multiplied by a factor of three.

The second set of analyses was designed to determine the primary morphological landmarks effecting dimorphism. Similar to the first set of analyses, landmark coordinate sets were normalized using a GPA, via 'Shapes', and aligned into arrayed matrices, via 'Abind'. These data were then analysed using principle component analysis (PCA) in order to identify the main

morphological drivers of dimorphism, and to visualize trends, using code from the MASS and Car packages, both within and across species. The results of these analyses were evaluated using 95% confidence intervals, and the principle component loadings were assessed to determine the variables most closely associated with dimorphism.

The final set of analyses was designed to determine the magnitude of dimorphism seen within each species, and quantitatively determine which pinniped taxa showed significant dimorphism. Using the landmarks identified in analyses one and two as controlling the majority of dimorphism, six landmarks were chosen for each of dorsal and ventral views of pinniped taxa. Coordinate data from these landmarks were used to perform a discriminant function analysis for each species in order to maximize group separation and test which intraspecific groupings (male vs. female) are significantly different from others.

RESULTS

Comparative Description of Fossil Material.—USNM 314290 (Fig. 3) is a small, partially deformed skull, lacking mandibles, originally referred to as a juvenile of *Enaliarctos emlongi* by Berta (1991). The skull is approximately 158 mm in total length; Reliable width measurements could not be obtained due to deformation, although the estimated reconstructed maximum skull width is 83.6 mm. The skull is dorsoventrally crushed, probably due to sediment compaction,

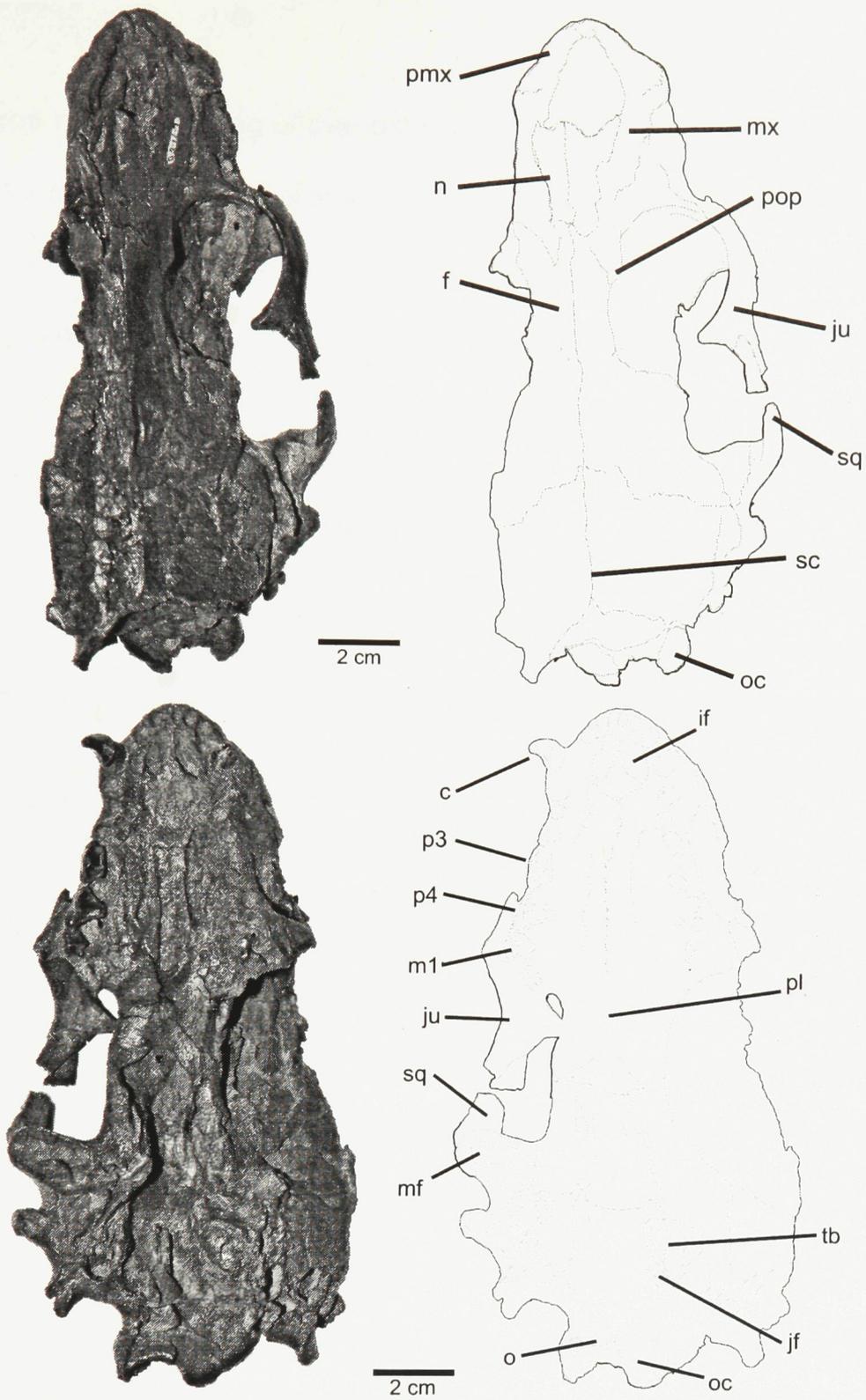


Figure 3: At top: dorsal views of USNM 314290, with photograph (left) and interpretive drawing displaying visible sutures (right). At bottom: ventral views of USNM 314290, with photograph (left) and interpretive drawing displaying visible sutures (right). Dashed lines indicate sutures. Scale bar = 2cm.

with some minor shearing of the rostrum in the mediolateral plane. Despite post-depositional deformation, most key morphological features are preserved and can be reliably characterized. Though there are certainly some features shared between this specimen and *E. barnesi*, the high amount of dental similarity between USNM 314290 and *E. emlongi*, and the nearly exclusive reliance on dental characteristics in differentiating *Enaliarctos* species, supports Berta's (1991) inclusion of this individual into *E. emlongi*. The rationale of that assignment will be explained in the following section.

USNM 314290 is morphologically similar to the skulls of other *Enaliarctos* species, particularly *E. emlongi*. Many of the teeth are missing from USNM 314290, although those that are preserved are in good condition. Due to the absence of the mandibles, only upper dentition can be described. With the exception of the canines, the dentition preserved in USNM 314290 is very similar to that of the *E. emlongi* holotype (USNM 250345). No incisors are preserved in USNM 314290, although the alveoli show that three incisors were present on each side of the premaxilla. The left and right canines are preserved, although the left canine has been fractured from the skull itself. The canines have a smaller transverse section than those of the *E. emlongi* holotype (USNM 250345) or referred snout (USNM 314540). Similarly, the canines of USNM 314290 have a smaller transverse section than those of either the holotype (USNM 314295) or referred skull (USNM 335375) of *E. barnesi*, while they are more similar to those of *Pacificotaria hadromma* (USNM 167648) or *Pinnarctidion rayi* (USNM 314325). The canines of USNM 314290 are similar to *E. emlongi* specimens in

being slightly recurved and possessing a vertical crest extending medially from the posterior to lingual face. Two of the four premolars (P3 and P4) are preserved, but only on the right side. Examination of the alveoli shows P1 to have been single rooted, with P2 being double rooted. There does not appear to be an embrasure pit between P2 and P3, while a shallow embrasure pit is present between P3 and P4. P3 is very similar in shape to that of *E. emlongi*, and unlike other *Enaliarctos* species, in possessing a well-developed crest-like metacone. P4 is triple rooted, with a large conical paracone separated from a relatively short metacone. In these respects, as well as with a lingual cingulum and similar wear patterns, the P4 of this specimen displays diagnostic characteristics of *E. emlongi*. Of the molars, only M1 is preserved, although it is present on both the left and right sides. Between P4 and M1 there is a deep embrasure pit, which is unlike *E. emlongi*, but similar to *E. barnesi*. M1 is double rooted, with a paracone and metacone of nearly equal height, a large parastyle, and a slightly sloped protocone. Unfortunately, M1 is not preserved in the holotype of *E. emlongi*, although the morphology of M1 in this specimen is different from that of *E. barnesi* in the relatively smaller size of the paracone. M2 is not preserved in this specimen, nor can the alveoli be identified, due to poor preservation. The palate is slightly arched dorsally, and the palatine sulci are shallow, while extending from a position medial of P4 to a position medial of P2. In these respects, the specimen is similar to *E. emlongi*. A spur-like process extends posteriorly from the maxilla in this specimen, which is not seen in the holotype of *E. emlongi*. However, a similar process is found in cf. *P. rayi* (of

Berta, 1994A), *E. tedfordi* and *E. barnesi*, with the feature considered diagnostic to the latter by Berta (1991). The incisive foramina are similar to *E. emlongi* in being deep and separated by a narrow crest, but are unlike *E. emlongi*, or other *Enaliarctos* specimens, in being positioned much closer to the canines and incisors. This difference in position appears to be due to the narrow, rounded shape of the snout, which is in sharp contrast to the much wider and blunt, almost squared, shape seen in the holotype of *E. emlongi*. This difference in shape does not appear to be related to the deformation present in this skull. Another noted difference between the skull of USNM 314290 and *Enaliarctos* specimens are the low sagittal and lambdoidal crests, which are more pronounced in the *E. emlongi* holotype. The posterior end of the anteroventral process of the jugal attaches anterolaterally to M1 in USNM 314290, a feature shared with, and diagnostic of, *E. emlongi*. The middle ear and basicranial morphology of USNM 314290 was examined by x-ray computed microtomography (Fig. 4) for comparison with other pinnipedimorphs, and to assess the similarities and differences between this specimen and the *E. emlongi* holotype. The tympanic bulla had been previously removed from in the holotype of *E. emlongi* (as well as in most other USNM *Enaliarctos* specimens in which the bullae preserved) for examination of the internal structures, but was completely intact in this specimen. The morphology of the middle ear is very similar to that of *E. emlongi*, particularly in possessing a mediolaterally expanded pear-shaped promontory, a posteriorly oriented round window, a nearly circular epitympanic recess, a deep elliptical fossa for the tensor tympani, and a larger tympanic crest

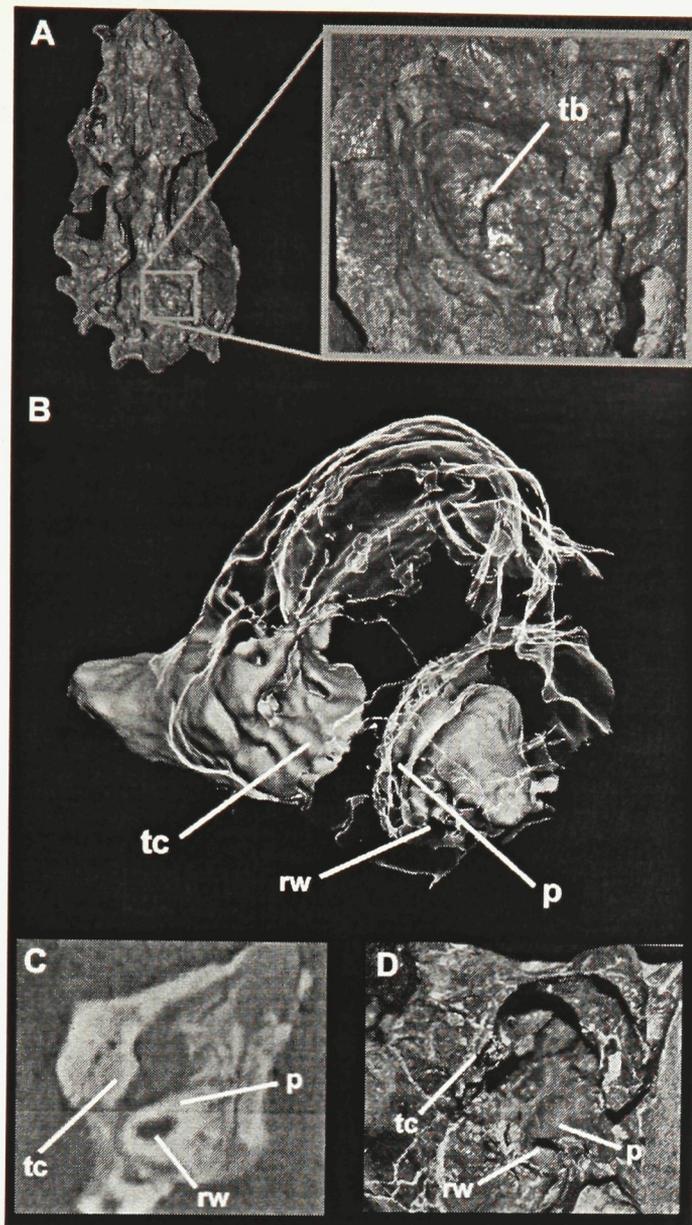


Figure 4: Views of middle ear structures of USNM 250345 (D) and USNM 314290 (A-C). A. Ventral view of skull and left tympanic bulla. B. 3-D reconstruction of left tympanic bulla and middle ear structures as obtained from micro-CT scans. C. Internal view of left tympanic bulla and middle ear structures from raw micro-CT image data. D. Photograph of right tympanic region with bulla removed, showing middle ear structures. All CT images are reflected from their original orientation. Of particular note in comparison are the extent of the shelf of the tympanic crest and the posterolateral orientation of the promontorium.

that projects into the tympanic cavity. The orientation of the round window and extent of the tympanic crest are of particular significance, as within *Enaliarctos* they are only present to these forms in *E. emlongi*. Despite some morphological differences, this specimen shares many diagnostic characters, such as in the canine, 3rd premolar, 4th premolar, jugal, and middle ear, with *E. emlongi*, supporting Berta's (1991) referral of this specimen.

Ontogenetic Status of Fossil Material.—The rationale for the assigned juvenile status of USNM 314290 by Berta (1991) was not specified, as the specimen was never given a full description, but was presumably related to the small size of the skull in relation to the much larger skull of the *E. emlongi* holotype. The sutures (Fig. 3b&d) of USNM 314290 exhibit a closed pattern consistent with those of full adult (sensu Brunner et al, 2004) modern pinnipeds (particularly otariids), including full closure of the occipito-parietal, squamosoparietal, interparietal, interfrontal, coronal, basisphenoid-presphenoid, and basioccipito-basisphenoid sutures, and probable full closures of the maxillary and premaxillary-maxillary sutures (the degree of closure in some regions is partially obscured by deformation and/or surface damage). Work by Brunner et al (2004) showed that among modern pinnipeds, the basisphenoid-presphenoid, interfrontal, maxillary, and premaxillary-maxillary sutures were the last to close, signalling physical maturity. Of note, fractures that appear on USNM 314290 do not appear to follow sutures preferentially, suggesting that the sutures are fully fused and thus did not offer obvious zones of weakness for fracture propagation.

Given that the skull sutures of USNM 314290 are closed (particularly those that fuse later in life), the status of USNM 314290 as a juvenile can be rejected. This specimen more likely represents an adult individual.

Sexual Size Dimorphism in Skulls of Modern Pinnipeds.—The comparisons of average skull size in the measured pinniped species, both as species averages and sex-based values, are shown in Table 3. Additionally, the table shows the results of the t-test of these averages. From the t-test, all three otariid taxa show significant difference between male and female skull length and indicate that adult males are larger than females in these taxa. The phocids, with the exceptions of *Cystophora* and *Halichoerus*, show little to no statistical difference between male and females. In *Cystophora* and *Halichoerus*, males have significantly greater average skull lengths than females.

Degree of Skull Shape Differences and Regions of Sexual Dimorphism.—Results of the GPA and landmark vector maps for each species, in dorsal and ventral views, can be seen in Figure 5. In this figure, female landmark maps were superimposed upon those of males, with vectors displayed showing the landmark displacement required to transform the female condition into that of the male. Comparisons here are qualitative, and vectors have been magnified to allow easier visualization. In the dorsal superimpositions, dimorphism was detectable in the three otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*), and in two of the phocid taxa (*Cystophora* and *Halichoerus*). The dimorphism in the otariid

Table 3: Comparative skull measurements, averages, and T-test results for each modern pinniped species.

Family	Taxon	Avg. Skull Length (mm)	Std. Dev. (mm)	Average Skull Length (Male) (mm)	Std. Dev. (Male) (mm)	Average Skull Length (Fem.) (mm)	Std. Dev. (Fem.) (mm)	Skull Length Difference (%)	Rel. Std. Dev. (%)	T-test (p value)
Otariidae	<i>Arctocephalus</i>	206.89	30.80	244.33	9.29	188.17	14.86	29.85	14.89	3.65E-04
Otariidae	<i>Callorhinus</i>	215.65	29.07	243.30	8.51	188.00	3.56	29.41	13.48	2.44E-10
Otariidae	<i>Eumetopias</i>	355.85	41.49	395.90	5.24	315.80	6.56	25.36	11.66	2.62E-16
Phocidae	<i>Leptonychotes</i>	255.25	19.02	255.25	24.78	255.25	15.17	0.00	7.45	1.00E+00
Phocidae	<i>Hydrurga</i>	384.90	22.11	386.67	7.57	384.14	26.68	0.66	5.74	8.24E-01
Phocidae	<i>Cystophora</i>	250.70	19.83	265.30	14.51	236.10	12.10	12.37	7.91	1.29E-04
Phocidae	<i>Halichoerus</i>	273.00	26.28	296.90	7.98	252.08	15.98	17.78	9.63	2.82E-05
Phocidae	<i>Erignathus</i>	224.09	10.95	227.53	7.41	220.65	13.31	3.12	4.89	2.62E-01
Phocidae	<i>Pusa</i>	181.27	11.95	182.95	12.25	179.58	12.04	1.88	6.59	5.42E-01
Phocidae	<i>Monachus</i>	259.55	19.37	254.50	23.74	264.60	13.11	-3.82	7.46	2.58E-01

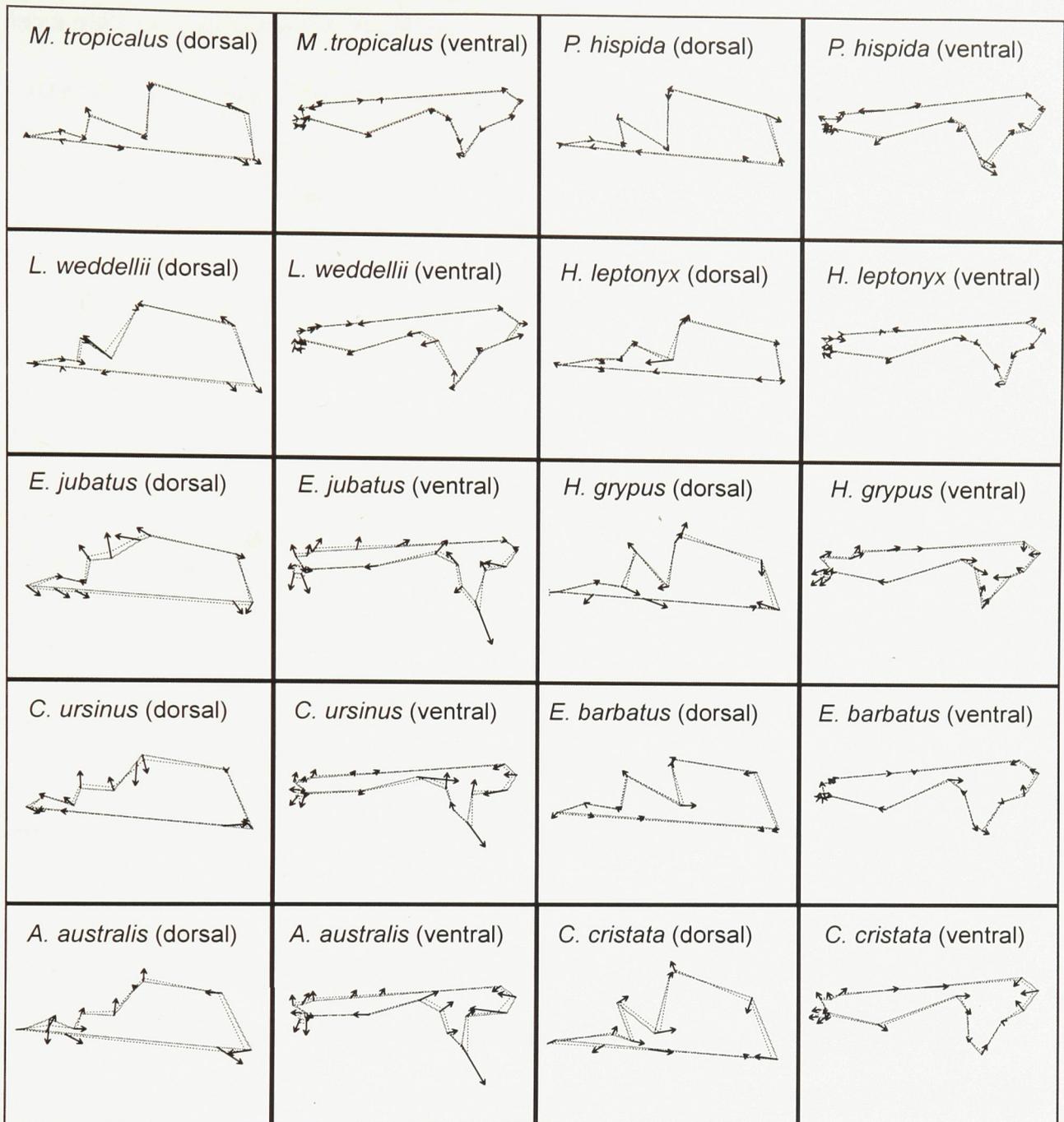


Figure 5: Dorsal and ventral inter-landmark comparison of sampled modern pinniped taxa. Landmark coordinate polygons represent one side of sampled skull, and were non-mirrored. Vectors represent distortion on each landmark required to transform female position into male position. Vectors magnified three times for ease of visualization.

taxa was concentrated in the landmarks in the rostral region, showing lateral expansion in males. The two dimorphic phocids were not as consistent in shape dimorphism, with *Cystophora* showing lateral expansion of the rostrum and jugal, and relative lengthening of the skull, whereas *Halichoerus* showed some lateral expansion of the rostrum and jugal, but less relative skull lengthening. The other phocid taxa showed little to no detectable dimorphic patterns. In the ventral superimpositions, strong dimorphism was detectable in the three otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*), and weaker dimorphism in three of the phocid taxa (*Cystophora*, *Halichoerus*, and *Leptonychotes*). The dimorphism in the otariid taxa was consistently concentrated in the landmarks of the basicranium and mastoid, showing considerable lateral expansion of the region in males, and in the rostral region showing lateral expansion in males. The three phocid taxa showed less consistent shape dimorphism. *Cystophora* showed a relative lengthening of the skull in males, concentrated around a larger palate, with some widening of the basicranium. *Halichoerus* showed a similar lengthening of the palate, but also showed some relative narrowing of the basicranium in males. *Leptonychotes* showed a somewhat opposite signal, with the palate shortening in males. All other phocid taxa showed little to no detectable dimorphic patterns.

Principle Component Analysis of Sexual Dimorphism.—Results of the summary PCA incorporating all 10 species, performed in order to visualize larger scale trends in dimorphism, can be seen for dorsal and ventral landmarks in

Figure 6, with similar plots isolated for each individual species in Appendix 4. Individual specimens were shown to hold the same relative positions within their species in both the single species analysis and larger all-species summary analysis.

In the analysis of dorsal landmark sets, three distinct groups were identified. The first group comprises the three otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*), and all show separation between male and female morphospaces. The second group is the largest, and includes the phocids *Pusa*, *Monachus*, *Erignathus*, *Halichoerus*, *Hydrurga*, and *Leptonychotes*, although the latter is separated from the majority of the group. Within this phocid group, *Halichoerus* shows some evidence of dimorphism, although it is less pronounced than seen among the otariids. *Pusa*, *Monachus*, *Hydrurga*, and *Erignathus* show little dimorphism, with extensive regions of overlap between male and female confidence intervals. *Leptonychotes*, positioned somewhat separate from the rest of the group, shows no evidence of dimorphism. The third distinct group is positioned a considerable distance from all other morphospaces and contains only one taxon, *Cystophora*, which shows evidence of dimorphism. The otariids and phocids are primarily separated in morphospace along the PC-I axis, with otariids positioned positively and phocids negatively. Along the PC-II axis, the otariid taxa cluster close to the zero position, while the phocids are distributed across negative and positive positions (with most species in mid to low positive positions, and *Cystophora* positioned negatively).

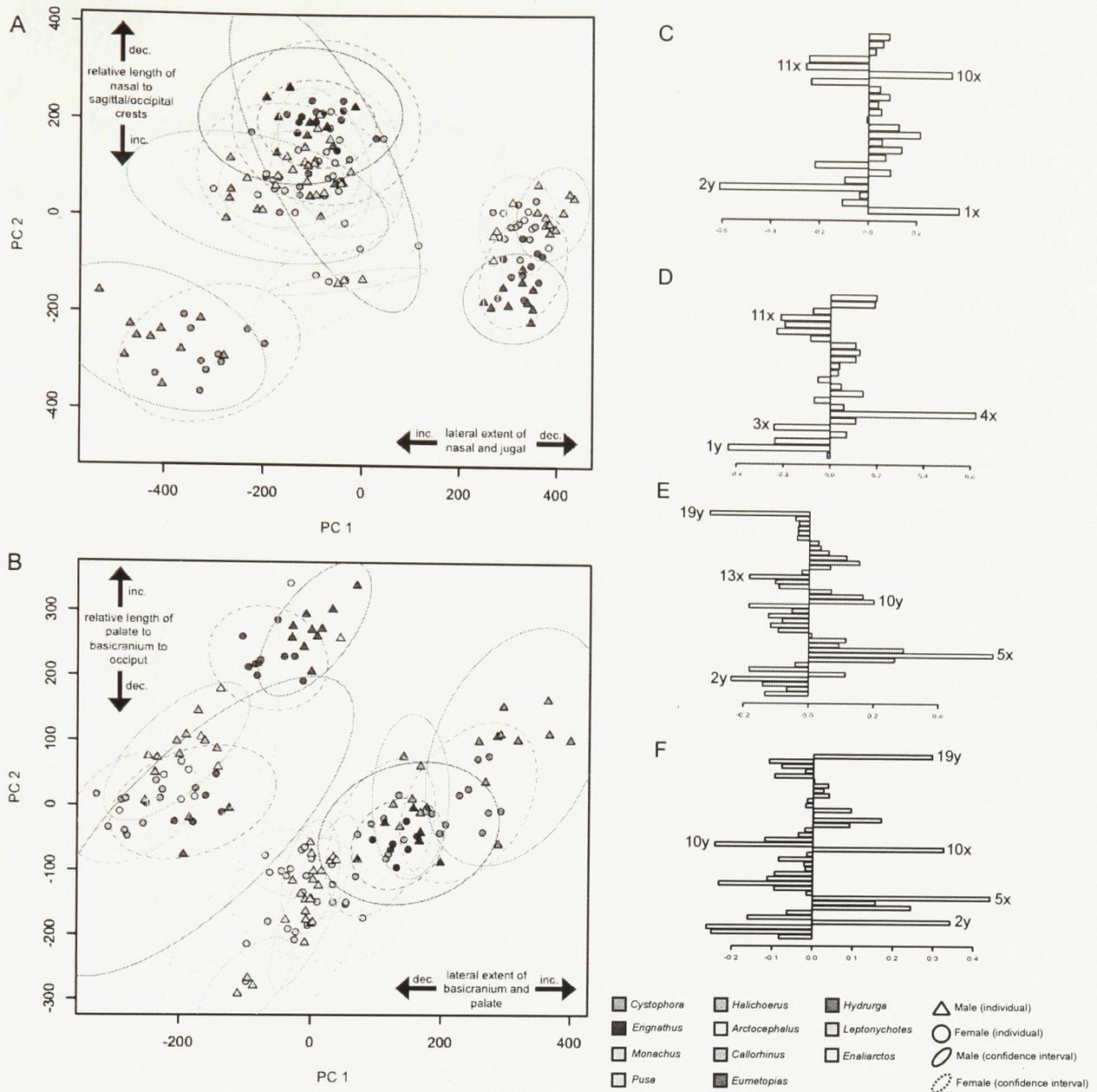


Figure 6: Results of summary PCA of landmarks incorporating sampled modern and fossil species. A, Dorsal results with intraspecific male and female confidence intervals; B, Ventral results with intra-specific male and female confidence intervals; C, loading plot for dorsal principal component I; D, loading plot for dorsal principal component II. E, loading plot for ventral principal component I; D, loading plot for ventral principal component II. Confidence intervals set at 95%. Loading plots labeled with landmark variables controlling majority of variation. Individual symbol legend at bottom of figure.

Examination of the principle component loadings show that PC-I represents primarily the lateral extent of the nasal and jugal, with lateral extent increasing negatively along the axis, and PC-II represents primarily the relative length of the nasal to sagittal/occipital crests, with length increasing negatively along the axis. The species plotted according to these morphological factors, and did not group strictly according to closest phylogenetic relation. Changes along PC-I were responsible for most dimorphism, with males of dimorphic taxa generally plotting more negatively along PC-I than females. PC-II had considerably less influence on intra-specific dimorphism, and instead appeared to be responsible for inter-specific separation among the phocids.

The male and female individuals of the fossil taxon *Enaliarctos emlongi* plot within otariids, and most closely to *Eumetopias*. Their relative positions from one another are similar to those seen in the sample modern taxa.

In the analysis of ventral landmark sets, two distinct groups were identified. The first group is composed of *Arctocephalus*, *Callorhinus*, *Eumetopias*, and *Hydrurga*. Within this group all show sexual dimorphism with separation between male and female morphospaces. However, the male confidence intervals of *Arctocephalus* and *Hydrurga* are much larger than their female counterparts and fall beyond their species-level confidence interval. The second group contains *Pusa*, *Monachus*, *Erignathus*, *Halichoerus*, *Leptonychotes*, and *Cystophora*. Among this group, both *Halichoerus* and *Cystophora* show evidence of dimorphism, although with more overlap in morphospace between males and females than was present among otariids.

Leptonychotes shows some weak evidence of dimorphism. *Pusa*, *Monachus*, and *Erignathus* show little dimorphism, with extensive regions of overlap between males and females. Both of the larger groups appear to be influenced jointly by PC-I and PC-II, and follow a similar trend in the distribution of taxa within each group. The first group is distributed along PC-I from moderately negative to low positive positions, and along PC-II from low negative to high positive positions. The larger group is distributed along PC-I from slightly negative to highly positive positions, and along PC-II from highly negative to moderately positive positions.

All dimorphic taxa, with the exception of *Hydrurga* and *Leptonychotes*, display a similar trend in dimorphism, with male morphospaces displaced from those of females through a positive shift along both PC-I and PC-II axes. In *Hydrurga* and *Leptonychotes* the pattern is reversed. Examination of the principle component loadings show that PC-I represents primarily the lateral extent of the basicranium and palate, with lateral extent increasing positively along the axis, and PC-II represents primarily the relative lengths of the palate to the basicranium and the basicranium to the occiput, with length increasing positively along the axis. The male and female specimens of the fossil, *E. emlongi* plot within the *Eumetopias* confidence interval.

Discriminant Function Analysis of Sexual Dimorphism.—Results of the discriminant function analysis, showing examples of dimorphic and non-dimorphic outcomes in dorsal and ventral views, can be seen in Figure 7. The total number of landmarks used for these comparisons were reduced to the six

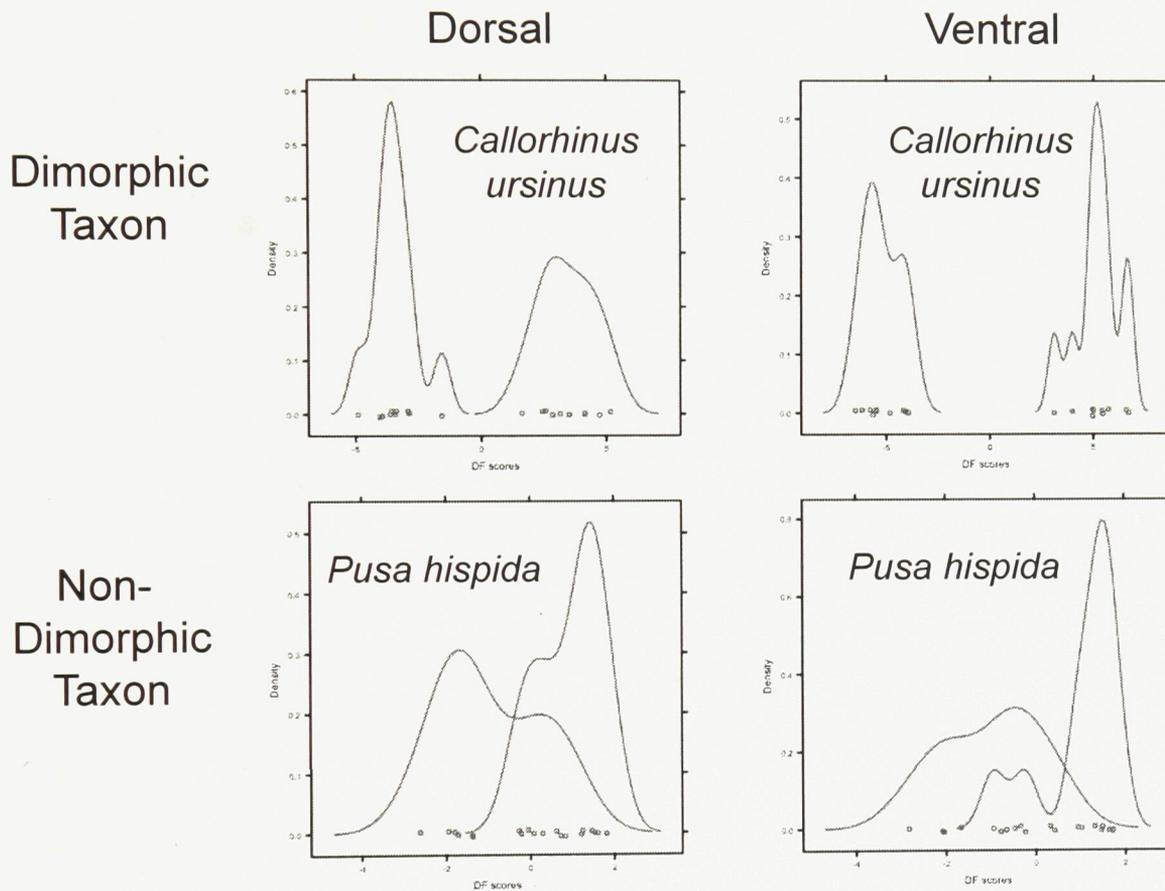


Figure 7: Results of discriminant function analysis of condensed landmarks, showing representative examples of dimorphic and non-dimorphic taxa in dorsal and ventral views.

most responsible for variation in both dorsal and ventral (as indicated in the loading diagrams within Figure 6). Plots for each species can be seen in Appendix 5. Comparisons here are quantitative, and show the degree of sexual dimorphism (shape only) within each species. In the dorsal analyses, significant dimorphism was detectable in the three otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*), and in two of the phocid taxa (*Cystophora* and *Halichoerus*). The other phocid taxa showed no significant dimorphism. In the ventral analyses, significant dimorphism was detectable in the three otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*), and two of the phocid taxa (*Cystophora* and *Halichoerus*). All other phocid taxa showed no significant dimorphic patterns.

DISCUSSION

Fossil Material.—In most important diagnostic features, such as the middle ear and dentition, USNM 314290 is very similar to the holotype of *E. emlongi*, and is best referred to this taxon. The closed sutural patterns strongly support the referral of this specimen to mature adult status. That, combined with a number of notable morphological features that characterize females in modern pinnipeds (e.g., slender canines, low sagittal and lambdoidal crests, and narrower snout) (Howell, 1929; Brunner et al, 2004; Sanfelice et al, 2008), suggests that this specimen represents a female. We propose that the holotype represents a male of the species, with the species therefore showing a qualitatively similar pattern of SSD to those of modern otariids. This study

highlights certain issues related to the taxonomy of stem-pinnipeds, given that *Enaliarctos* is considered a 'meta-taxon', a taxon lacking unambiguous characters to support monophyly or paraphyly (Gauthier, 1986; Berta, 1991). A number of the *Enaliarctos* species share diagnostic characters, with the dental morphology seeming to provide the only traits that separate the species, and even those traits seem to have some overlap or individual variation. A number of the *Enaliarctos* species, such as *E. emlongi*, *E. barnesi*, and *E. tedfordi*, have overlapping or adjacent stratigraphic distributions within the late Oligocene to early Miocene Yaquina Formation of Oregon (Berta, 1991; Prothero et al, 2001). The overlying Nye mudstone and Astoria Formation contain stem-pinnipeds, such as *E. emlongi* and *P. rayi*, with the ranges of both taxa overlapping within or near the upper Nye (Berta, 1991; Berta, 1994A). This could suggest a closer relation between *Enaliarctos* and *Pinnarctidion* than is currently thought, given their stratigraphic and morphological similarities. However, additional work, including a comparison of the middle-ear regions of other taxa, is required before such an assessment can be reliably made. The 'meta-taxon' status of *Enaliarctos*, combined with the number of similarities with other time equivalent stem-pinnipeds, suggests that a major taxonomic revision of the group may be required. However, the close similarity of dental and middle ear morphology suggests that USNM 314290 should remain within *E. emlongi*, pending any future taxonomic revisions, but must be noted as representing an adult specimen, and most likely a female.

Identifying dimorphism in *Enaliarctos* has a number of implications for understanding pinniped evolution and for predicting the reproductive behaviour of early pinnipeds. Given the considerable size difference between USNM 314290 and USNM 250345, and the difference in snout and canine morphology, the dimorphism present in *Enaliarctos emlongi* can most closely be compared with that of a modern otariid (Howell, 1929; Cassini, 1999; Sanfelice, 2008). Additionally, in modern pinnipeds SSD is closely tied with reproductive ecology, with highly dimorphic species (generally otariids, but also odobenids and some phocids) using a land-based and highly polygynous harem system, and species showing little dimorphism (most phocids) reproducing in water with little to no polygyny (Cassini, 1999). Given the high degree of dimorphism present, a land-based and more polygynous breeding system is suggested for *E. emlongi*. Similarly, the fossil taxon *Desmatophoca*, currently classified as a sister clade to Phocidae, displays evidence of SSD according to a study of multiple mature individuals by Deméré & Berta (2003). Taken together, this suggests that the considerable degree of sexual dimorphism characteristic of otariids is in fact plesiomorphic in pinnipeds, that the sister clade of phocids also showed noticeable SSD, and that early fossil forms may have possessed a breeding system similar to modern otariids.

Modern Comparisons and Multivariate Analyses.—Comparisons of relative skull size in modern pinniped skulls (Table 3) show that all otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*) show detectable SSD, with two phocids

(*Cystophora* and *Halichoerus*) also showing SSD. Interestingly, these phocids (with the possible exception of *Cystophora*), are also known to breed on land in highly polygynous mating systems (Cassini, 1999).

The examination of intra-specific cranial shape differences showed that all examined otariid taxa, and the polygynous phocid taxa studied here, display cranial sexual-dimorphism. The otariid taxa (*Arctocephalus*, *Callorhinus*, and *Eumetopias*) showed similar patterns of shape dimorphism, with males showing lateral expansion of the rostrum in dorsal comparisons, and a combination of lateral basicranial and rostral expansion and palate elongation in ventral comparisons. These differences may be related to the role of land-based male-male combat in otariid mating systems, as the expanded rostrum accommodates larger canine teeth, and the expanded basicranium and mastoid provide more attachment area for neck musculature (Howell, 1929; Cassini, 1999; Brunner et al, 2004). *Cystophora* and *Halichoerus* both showed evidence of dimorphism, mostly seen dorsally in the lateral expansion of the nasal and jugal, and ventrally in the expansion of the palate both laterally and, in *Cystophora*, posteriorly. *Leptonychotes* appears to display some dimorphism, but this is potentially unreliable due to the small sample size and lower male-to-female ratio in available specimens. The pronounced expansion of the nasal and palate in *Cystophora* may be related to attachment and housing of the inflatable 'hood' used by males during reproductive displays (Cassini, 1999; Jones and Goswami, 2010; Naughton, 2012).

The principle component analyses of shape dimorphism in dorsal view confirmed the results of the landmark superimposition, showing *Arctocephalus*, *Callorhinus*, *Eumetopias*, *Cystophora*, and *Halichoerus* as dimorphic. These results provide additional evidence of a relation between the dimorphism of *Cystophora* and the display 'hood' of males, as they plotted away from other taxa due to their expanded nasal and surrounding structures. The principle component analysis of dimorphism in ventral cranial shape supports the results of the landmark superimposition, showing *Arctocephalus*, *Callorhinus*, *Eumetopias*, *Cystophora*, *Hydrurga*, and *Halichoerus* as dimorphic in shape. The species plotted according to the aforementioned morphological factors controlling each PC axis, and did not group strictly according to closest phylogenetic relation (such as in the closer association of *Pusa* and *Monachus* to each other than to more phylogenetically related phocids). Changes along both PC axes contributed to dimorphism, with males of dimorphic taxa generally plotting more positively along both axes than females. Both *Hydrurga* and *Leptonychotes* showed a reversed pattern, with females generally plotting more positively along the PC axes. This may represent dimorphism in which the females are larger and showing the otherwise 'male' traits, which is supported by observational records of females generally being larger within these species (Nowak et al, 2003; Naughton, 2012). The confidence intervals of males belonging to *Hydrurga* and *Arctocephalus* expand beyond the confidence intervals of their respective taxa, which is most likely due to the limitations of available specimens and bias from the resultant low male to female ratio present in samples of these taxa. Fossil

individuals of *Enaliarctos emlongi* were plotted into the dorsal and ventral morphometric analyses. In dorsal, the male and female individuals of *E. emlongi* plotted generally within otariids, closest to the morphospace of *Callorhinus*, but the distance between the two in morphospace along PC-1 was larger than seen in any of the modern taxa. This is most likely related to the rostrum of the female skull, which although fully intact, was deformed during fossilization and as a result would distort the dorsal landmark signals. Along PC-2, the fossil forms are fairly consistent to *Callorhinus*, with the male showing a more positive position than the female. In ventral, the male and female individuals of *E. emlongi* plotted within otariids, and closest to *Eumetopias*, with the distance between the two in morphospace similar to that seen in modern taxa. Along PC-1, the fossils plotted along a similar pattern to modern otariids, with the male showing a more positive position, related to the greater lateral extent of the palate and basicranium. However, along PC-2 the fossils showed the opposite pattern to that seen in modern forms, with the female showing a greater relative length of palate to basicranial length. This may be related to the diagenetic distortion seen in the female skull, but this cannot be confirmed. The distortion in the basicranial region is less than in the rostral area, supporting the explanation for the unusual placement on PC-2, and providing additional support for the pattern seen along PC-1. The precise positions of the male and female of this fossil taxon relative to one another may not be overly informative, as they each represent only one data point, but their general positioning within otariids does suggest that modern

otariids may represent a good model for predicting ancestral pinniped reproductive strategies.

The discriminant function analysis supported the results of the GPA and PCA in providing quantitative evidence of the degree of sexual shape dimorphism in skulls of males and females of each species. In both dorsal and ventral, the same five taxa (*Arctocephalus*, *Callorhinus*, *Eumetopias*, *Cystophora* and *Halichoerus*) were identified as dimorphic, with *Callorhinus* and *Eumetopias* showing the greatest degree of dimorphism. Non-dimorphic taxa, particularly *Pusa* and *Monachus*, showed greatly overlapping male and female ranges, and non-significant values when tested for difference.

Cranial diversity (both size and shape) in modern pinnipeds is closely related to sexual dimorphism in otariids, and in some phocid lineages, and also appears closely tied to reproductive strategy. Otariids breed on land using a harem-based system in which males fight for control of females, whereas most phocids breed in water and use a female-choice driven system in which males and females mate in pairs or in small groups (Cassini, 1999). However, some phocids utilize a different strategy for mating, with *Halichoerus* mating on land and using a polygynous system, and *Cystophora* mating in water but with males using an elaborate morphological display to attract females (Cassini, 1999). From this we can see that more dimorphic species are associated with land-based polygynous systems, whereas taxa showing little to no cranial dimorphism also exhibit water-based mating and low levels of polygyny. That the fossil forms fell within the otariid dimorphic morphospace suggests that size and shape

dimorphism is a plesiomorphic condition in pinnipeds, continued in otariids, and lost in early phocids, having been secondarily re-selected for in some lineages. This is further supported by the presence of SSD in *Desmatophoca*, within the pinniped crown-group and sister-clade to Phocidae. Overall, this study confirms a link between cranial dimorphism and reproductive strategy, and suggests a deep-time origin is the most parsimonious explanation for modern patterns of pinniped reproduction.

CONCLUSION

The purpose of this study was to investigate sexual dimorphism in the cranial morphology of pinnipeds, and to determine how early sexual dimorphism appeared in the evolutionary history of pinnipeds. Through this multi-proxy approach using modern and fossil specimens, a deep-time (possibly late Oligocene, given fossil specimen ages) origin for SSD in pinnipeds seems most parsimonious. The explanation of why otariids continued to use a highly-polygynous mating system with its associated high degree of SSD, while phocids switched to a weakly-polygynous to near-monogamous system (with some later reversions to high-polygyny) is unclear, but may relate to ecology and biogeography. The most morphologically basal pinniped fossil is *Puijila darwini*, found in lake deposits in the Arctic, and Rybczynski et al (2009) suggested the possibility of an arctic origin for pinnipeds, with the ancestor of otariids evolving and moving southwest into the Pacific Ocean, whereas phocids evolve and

remained in polar regions while also spreading into the Atlantic Ocean. Interestingly, modern otariids are abundant in equatorial and southern ocean regions, but are not found in the north Atlantic or Arctic oceans (Nowak et al, 2003). Phocids, by contrast, are widespread from temperate to polar waters. There is some evidence to suggest a link between ocean productivity (via upwelling zones) and the location of otariid breeding colonies (Black et al, 2011). Given that polar to sub-polar waters are known to be more productive than tropical to sub-tropical regions (Black et al, 2011), it is possible that one of the pressures maintaining otariid reproductive strategy is food availability. As early otariids dispersed, their colonies would require large amounts of nutrients, and would therefore concentrate together near upwelling zones, whereas phocids, in the more nutrient-rich waters of the polar regions, would be less restricted by food availability and could spread out their population. This could allow for a non harem-based system to develop, and consequently less pressure to maintain the considerable size and shape disparity between males and females. Thus, there is a possible link between the evolution of sexual dimorphism, reproductive behaviour, and biogeography. Further studies could illuminate the evolutionary trends of all pinnipeds, and give us further insight into the evolution of sexual selection and animal mating systems.

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