Colonization of the Southern Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence phylogenetic and Bayesian biogeographical analysis

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Fur seals and sea lions (Carnivora: Otariidae) evolved in the North Pacific and later dispersed throughout the Southern Hemisphere. However, the timing and number of dispersals into the Southern Hemisphere still remain poorly understood. To determine the biogeographical patterns of dispersal within fur seals and sea lions, we conducted cladistic analyses using combined evidence incorporating morphological and molecular data. The phylogeny produced in this study was then incorporated into Bayesian biogeographical analyses to reconstruct ancestral points of origin and dispersal patterns for otariid clades. Combined evidence analyses supported *Callorhinus* as the earliest diverging extant otariid, and a strongly supported northern sea lion clade (*Zalophus*, *Eumetopias*, and *Proterozetes*) as the sister group to a southern clade comprising the remainder of Otariidae. Fossil data constrained the timing and location of this dispersal as occurring between 6 and 7 Mya during a period of unusually cool sea surface temperatures and high productivity in the eastern equatorial Pacific, far older than suggested by prior studies. Our study indicates that the distribution of fur seals and sea lions is tightly linked to sea surface temperature and productivity, and suggests that otariids may be vulnerable to future anthropogenic climate change.

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INTRODUCTION

The Otariidae (fur seals and sea lions) is represented by 14 species found throughout the antitropical North Pacific and Southern Hemisphere (Berta & Churchill, 2012). The evolution of this group remains unclear, with no consensus on phylogenetic relationships between morphological and molecular phylogenies. Morphological phylogenies (Fig. 1) recognize two to three major clades,

a monophyletic Otariinae (sea lions; Berta & Deméré, 1986; Barnes, Ray & Koretsky, 2006) and a monophyletic *Arctocephalus* (southern fur seals; Berta & Deméré, 1986), with the northern fur seal *Callorhinus* as either the sister taxon to *Arctocephalus*, forming a monophyletic Arctocephalinae (Berta & Deméré, 1986), or as the earliest diverging lineage of crown Otariidae (Berta & Wyss, 1994).

By contrast, genotype-based phylogenies of Otariidae recover Otariinae, Arctocephalinae, and *Arctocephalus* as paraphyletic (Wynen *et al*., 2001; Árnason *et al*., 2006;

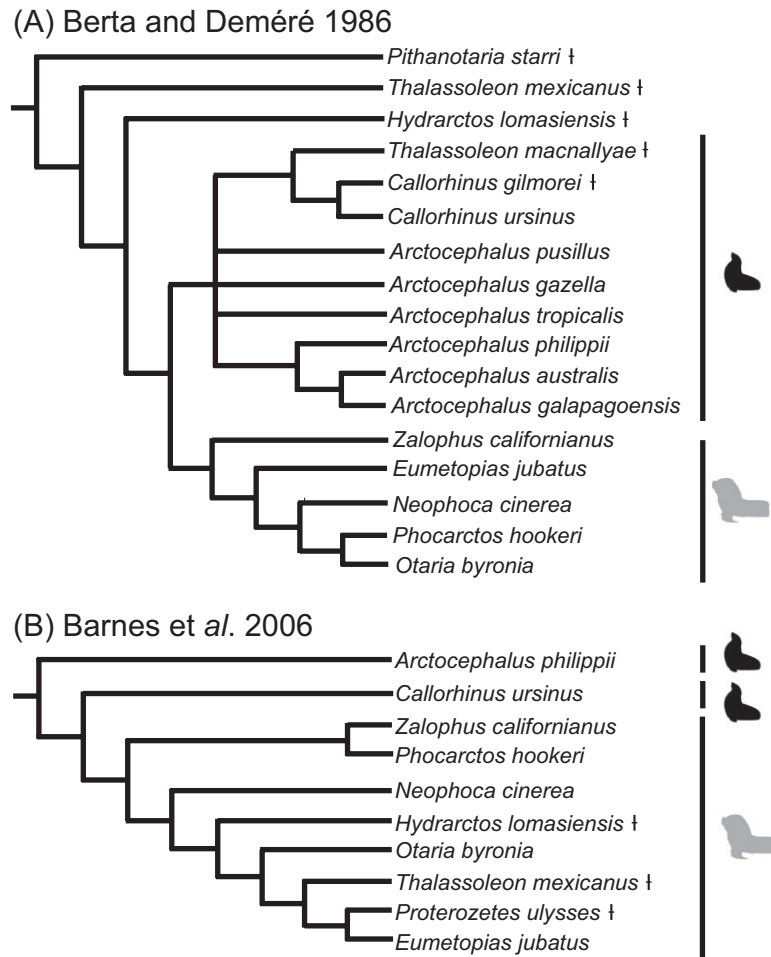*Corresponding author. E-mail: mchurch3@uwyo.edu

Figure 1. Results of prior analyses of otariid phylogeny using morphological data. Fur seal icons in black represent members of Arctocephalinae and sea lion icons in grey represent members of Otariinae. Extinct taxa are annotated with †.

Higdon *et al*., 2007; Yonezawa, Kohno & Hasegawa, 2009). Using genotype data, three main clades are recognized (Fig. 2). *Callorhinus* is recovered as the earliest diverging lineage within Otariidae. The next diverging lineage consists of a northern sea lion (NSL) clade composed of *Eumetopias* and *Zalophus*. Southern Hemisphere otariids are found as the monophyletic sister group to this clade. Within the Southern Hemisphere, *Otaria* is either found to be embedded within *Arctocephalus* (Wynen *et al*., 2001; Árnason *et al*., 2006), the earliest diverging lineage of southern otariid (Higdon *et al*., 2007), or unresolved within the southern clade (Yonezawa *et al*., 2009). *Phocarctos* and *Neophoca* are recovered as embedded within the *Arctocephalus* clade (Yonezawa *et al*., 2009), although most molecular phylogenies are unable to resolve the phylogenetic position of *Neophoca* within Otariidae (Wynen *et al*., 2001; Árnason *et al*., 2006; Higdon *et al*., 2007).

Disagreement on the phylogeny of Otariidae has led to markedly different interpretations of biogeography

in the group. Biogeographical studies agree on a North Pacific origin of the family (Repenning, Ray & Grigorescu, 1979; Deméré, Berta & Adams, 2003; Yonezawa *et al*., 2009) and on Pleistocene cross-hemispheric dispersals of *Zalophus* and *Arctocephalus philippii* (Deméré *et al*., 2003; Yonezawa *et al*., 2009). The number and direction of earlier cross-hemispheric dispersals are still debated, with prior studies suggesting two (Deméré *et al*., 2003; Koretsky & Barnes, 2006), or one (Yonezawa *et al*., 2009) Pliocene or older trans-hemispheric dispersals. Koretsky & Barnes (2006) argued for a North Pacific origin for *Arctocephalus* and Otariinae, with subsequent dispersal into the southeastern Pacific during the Pliocene. Deméré *et al*. (2003), using a different phylogeny to interpret pinniped biogeography, also identified separate dispersals of Arctocephalinae and Otariinae into the Southern Hemisphere, although were uncertain on the ancestral area of origin for the *Hydrarctos* lineage. Yonezawa *et al*. (2009) supported a monophyletic southern otariid claim, and argued instead for a single dispersal into
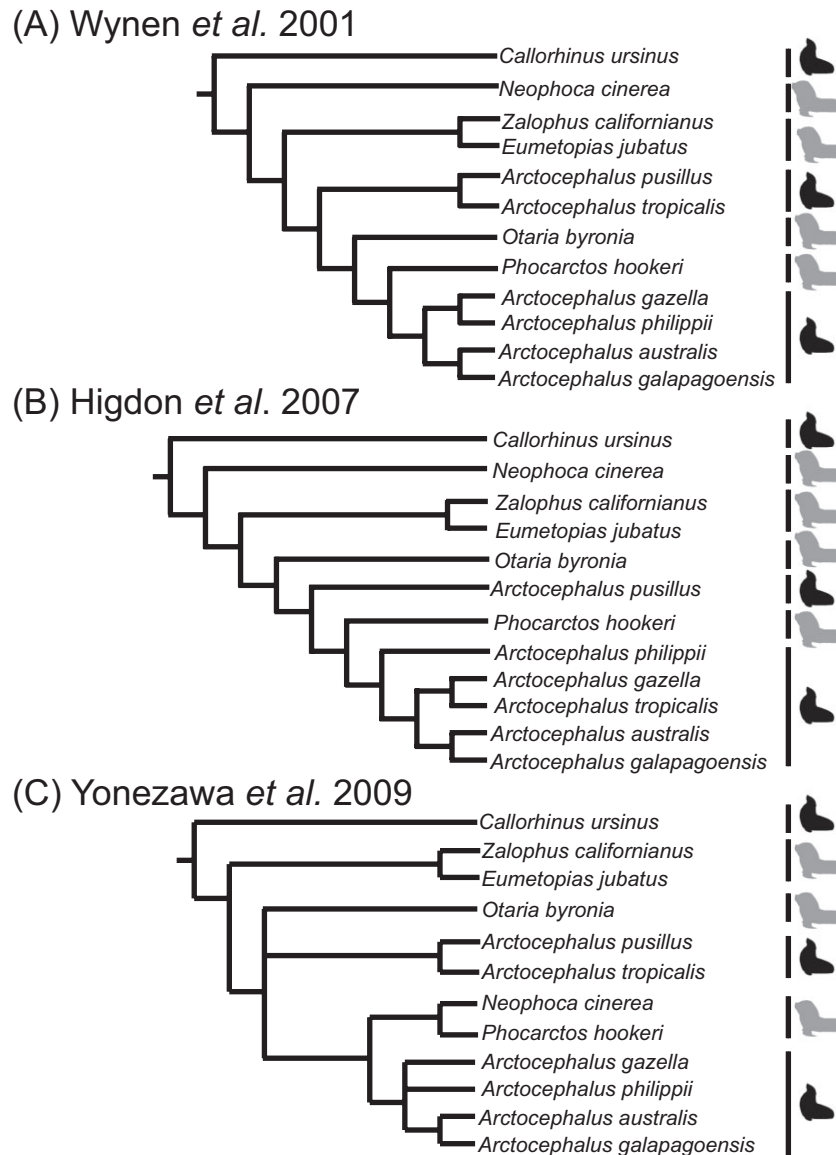
(A) Wynen *et al.* 2001

Callorhinus ursinus
Neophoca cinerea
Zalophus californianus
Eumetopias jubatus
Arctocephalus pusillus
Arctocephalus tropicalis
Otaria byronia
Phocarctos hookeri
Arctocephalus gazella
Arctocephalus philippii
Arctocephalus australis
Arctocephalus galapagoensis

(B) Higdon *et al*. 2007

Callorhinus ursinus
Neophoca cinerea
Zalophus californianus
Eumetopias jubatus
Otaria byronia
Arctocephalus pusillus
Phocarctos hookeri
Arctocephalus philippii
Arctocephalus gazella
Arctocephalus tropicalis
Arctocephalus australis
Arctocephalus galapagoensis

(C) Yonezawa *et al.* 2009

Callorhinus ursinus
Zalophus californianus
Eumetopias jubatus
Otaria byronia
Arctocephalus pusillus
Arctocephalus tropicalis
Neophoca cinerea
Phocarctos hookeri
Arctocephalus gazella
Arctocephalus philippii
Arctocephalus australis
Arctocephalus galapagoensis

Figure 2. Results of prior analyses of otariid phylogeny using molecular data. Fur seal icons in black represent members of Arctocephalinae and sea lion icons in grey represent members of Otariinae.

the Southern Hemisphere during the Pliocene. The timing of these dispersals as well as their directions are still poorly understood, making it difficult to determine what oceanographical or climatic events facilitated southward dispersal of Otariidae.

Increased knowledge of the biogeographical history of Otariidae is important as it will provide further information on how changes in climate may influence the evolution of the clade as well as the marine environment. Extant otariids are largely confined to cold upwelling regions today, and knowledge of the number and direction of trans-hemispheric dispersals that occurred in otariid evolution may provide insight into changes in coastal productivity, climate, and current patterns through time. Similarly, knowledge of how changes in climate have influenced otariid distribution in the past may provide insights into how anthropogenic climate change may affect future distribution. Marine mammal global distribution is strongly related to ocean temperature (Learmonth *et al*., 2006), and mass mortality events for pinnipeds have frequently been attributed to changes in sea surface temperate (SST) and regional productivity (Trillmich & Limberger, 1985; Trillmich *et al*., 1991). Although the full impact of anthropogenic climate change on pinniped populations is unknown, many species are likely to see reductions in range or population size (Learmonth *et al*., 2006).

In this study, we combined previously published genetic data from mitochondrial and nuclear genes with a new morphological data set for extant and extinct otariids, representing the largest combined evidence (morphological, behavioural, and molecular) phylogenetic analysis to date. The phylogeny produced by the combined (total) evidence analysis was used to interpret the biogeographical history of the group, using Bayesian ancestral character state reconstruction. Bayesian biogeographical reconstruction can incorporate uncertainty, allowing improved reconstruction of the biogeographical history of clades (Ksepka & Thomas, 2012). Although previous studies have employed phylogenies to examine otariid biogeography (Deméré *et al*., 2003; Koretsky & Barnes, 2006; Yonezawa *et al*., 2009), none has attempted to reconstruct ancestral points of origin using Bayesian methods.

MATERIAL AND METHODS

TAXONOMIC SAMPLING

For the purpose of this study, we followed the species level taxonomy of Berta & Churchill (2012) and all recent species recognized by that study were included as operational taxonomic units (OTUs). Also included within this analysis were nearly all described and valid fossil otariid taxa, including *Pithanotaria starri*, *Thalassoleon mexicanus*, *Thalassoleon macnallyae*, *Thalassoleon inouei*, *Callorhinus gilmorei*, *Hydrarctos lomasiensis*, *Neophoca palatina*, and *Proterozetes ulysses*.

Three taxa were selected as outgroups; the basal pinnipedimorphs *Enaliarctos emlongi* and *Pteronarctos goedertae*, and the modern walrus, *Odobenus rosmarus*. *Enaliarctos emlongi* and *Pt. goedertae* were chosen as outgroup taxa for the combined evidence and morphological analysis on the basis of the completeness of material available, and because all prior phylogenetic studies have agreed that they occupy a relatively basal position within pinnipedimorph phylogeny (Barnes, 1989; Berta & Wyss, 1994). *Odobenus* was used as an outgroup for analysis of molecular data as there is strong evidence that *Odobenus* is, amongst extant pinnipeds, the sister taxon to Otariidae (Flynn & Nedbal, 1998; Bininda-Emonds, Gittleman & Purvis, 1999; Sato *et al*., 2004, 2006; Delisle & Strobeck, 2005; Flynn *et al*., 2005; Árnason *et al*., 2006; Fulton & Strobeck, 2010). *Odobenus* was excluded from all morphological and combined evidence analyses because the highly derived nature of the walrus skull means that there are relatively few characters to directly link the modern walrus with basal pinnipedimorphs or otariids included within this study (Deméré, 1994; Kohno, 2006; Boessenecker & Churchill, 2013). Inclusion of *Odobenus* within the morphological phylogeny provided here either results in an unresolved basal polytomy in the combined evidence analysis with Otariidae and *Pteronarctos*, or placement of this taxon as the sister group to *Otaria*. Incorporation of a large number of fossil odobenid taxa with characters linking *Odobenus* to basal pinnipedimorphs was beyond the scope of this study (see Deméré, 1994, Kohno, 2006, and Boessenecker & Churchill, 2013).

CHARACTER SAMPLING

We examined 229 specimens for the purpose of this study (Appendix 1), representing all modern species and most fossil taxa. The morphological study incorporated 107 characters; 27 of these characters are new, whereas the rest are modified from previous characters used in other studies of pinniped evolution (Kellogg, 1922; Lyons, 1937; Sivertsen, 1954; Mitchell, 1968; Repenning, Peterson & Hubbs, 1971; Stirling & Warneke, 1971; Mitchell & Tedford, 1973; Morejohn, 1975; Repenning & Tedford, 1977; Muizon, 1978; King, 1983a, 1983b; Berta & Deméré, 1986; Berta & Wyss, 1994; Deméré, 1994; Bininda-Emonds & Russell, 1996; Adam & Berta, 2002; Brunner, 2004; Barnes *et al*., 2006; Boessenecker & Churchill, 2013). Also included within the morphological characters data set are two behavioural characters. Complete lists of characters as well as the morphological matrix used in this study are included on Morphobank (Project #529; http://www.morphobank.org/), as well as in Appendices 2 and 3. All applicable cranial characters are fully illustrated on this matrix.

Whenever possible, coding of taxa was based on adult male specimens. Otariidae possess strong sexual dimorphism, with features considered diagnostic of different genera enhanced in males. The only exception to this coding practice was the Miocene *Pithanotaria*, in which all described material may be referable to female or juvenile individuals (Repenning & Tedford, 1977; Barnes *et al*., 2006).

For taxa that were polymorphic for a given morphological character, we coded the taxa using the scaled character coding method (Wiens, 1999), in which taxa that were polymorphic for a given character state were coded as possessing an intermediate character state (state name 'Polymorphic') between the two character states. All polymorphic characters were run as ordered in the phylogenetic analysis, with penalties applied for character state transitions that skip the polymorphic character state. This method is more accurate and preserves greater phylogenetic signal than more traditional methods such as coding a taxon for both character states or only coding a taxon for the more common state. This method retains less phylogenetic information than the frequency bins method of coding for polymorphism (Wiens, 1999); however, given the small sample sizes available for some taxa (e.g. *Arctoc. philippii*, *Arctophoca tropicalis*) in Northern Hemisphere collections, we believe that this method

may be better suited for an analysis where the true frequency of occurrence for a given character state for a specific taxon cannot be determined.

For the combined and molecular analyses, whole published mitochondrial DNA sequences of *cytochrome b* (1212 bp) and *d-loop* (1480 bp) were gathered from GenBank (Appendix 4) for all recent taxa as well as *Odobenus*. These mitochondrial sequences were chosen as they are the only genes sampled for every taxon of interest. We also sampled published whole and partial nuclear genes (Appendix 4), including the *interphotoreceptor retinoid binding protein 3* (*IRBP*) with 1188 bp, *growth hormone receptor* (*GHR*) with 648 bp, and the *feline sarcoma* oncogene (*FES*) with 398 bp. Nuclear sequence data are more limited for otariid taxa than mitochondrial genes; for this study we were only able to gather all nuclear genes for *Odobenus*, *Zalophus californianus*, *Eumetopias*, *Otaria*, and *Arctophoca australis*. For *Callorhinus*, only *IRBP* and *FES* were available. Where possible, for species complexes containing multiple subspecies, gene sequences from the nominate subspecies were chosen, unless more complete gene sequences were available for other subspecies. All gene sequences were aligned using ClustalX (Larkin, 2007) and default settings. The matrix used for the combined evidence analysis is available in the document section of the Morphobank account for this project.

PHYLOGENETIC METHODOLOGY

Mitochondrial and nuclear sequence data were analysed separately. For mitochondrial DNA, *cytochrome b* and *d-loop* gene sequences were combined. For nuclear DNA, *IRBP*, *GHR*, and *FES* gene sequences were combined. For all analyses, molecular data were partitioned by gene. Models of nucleotide evolution were selected using jModeltest (Posada, 2008), with GTR + I + G (general time reversible model with separate gamma distributions and a separate proportion of invariant sites for each gene) selected as the model for all gene sequences. Bayesian analysis was implemented at 10 000 000 generations, with four chains and a sample frequency of 1000 for all molecular data. The first 5000 states were discarded in every analysis. Two runs were generated for each type of DNA, with the consensus used to generate the most probable tree.

Genetic and morphological data were analysed separately as well as combined. Two separate analyses of morphological and combined evidence data were performed, one analysis including all fossil taxa and a second in which we excluded poorly known fossil taxa, limiting our analysis to taxa with 50% or more of the cells for the morphological matrix coded (e.g. *T. mexicanus*, *T. macnallyae*, *Hydrarctos*, and *Proterozetes*). This was carried out to test the impact of incomplete fossil taxa on the phylogeny. Morphological and combined evidence analyses were performed using the program TNT (Goloboff, Farris & Nixon, 2008) under the maximum parsimony criteria. Genetic sequence data were analysed using Bayesian inference in MrBayes 3.11 (Huelsenbeck & Ronquist, 2001).

Analyses of morphological data in TNT were performed using 10 000 replicates with sectorial and tree-fusing options checked. We tested alternative character weighting schemes, testing equal and implied weighting (weights = K) and varying K from 2–6. A K value of 3 was selected for the morphological analyses and a K value of 5 was selected for the combined evidence analyses. These K values produce maximal support values without decreasing resolution(see Results). Bootstrap support values were calculated using symmetric resampling with 10 000 replicates. Combined evidence analyses performed under the maximum parsimony criteria were performed in TNT, using 1000 replicates, but otherwise with the same parameters as those used in the morphological analysis. Bootstrap support values were calculated using symmetric resampling with 1000 replicates.

BIOGEOGRAPHICAL RECONSTRUCTION

Reconstruction of the biogeographical history of Otariidae was performed using both the combined evidence and molecular scaffold trees generated by this study. Ancestral area reconstruction was performed under both a parsimony criterion using MESQUITE 2.72 (Maddison & Maddison, 2011), as well as a Bayesian binary Markov chain Monte Carlo (mcmc) using RASP (Yu, Harris, & He, 2011). RASP also determines whether different biogeographical events represent dispersal (colonization of a new region by a member of a clade previously absent from that area) or vicariance (former contiguous populations separated by dispersal barriers, leading to speciation). Parsimony ancestral character state reconstruction has been found to be fairly conservative compared with Bayesian and likelihood approaches (Lamm & Redelings, 2009); agreement between Bayesian and parsimony analyses of biogeography can thus be used as evidence of high support for a given biogeographical scenario (Ksepka & Thomas, 2012). Taxa were coded for the biogeographical analyses using the biogeographical provinces of Deméré *et al*. (2003; Appendix 5), with taxa coded for five different regions (North Pacific, South Pacific, South Atlantic, Indian Ocean, and Southern Ocean).

Parsimony analysis of biogeography was performed by tracing the range distribution of taxa over the tree using the 'reconstruct ancestral states' option and parsimony ancestral states. Bayesian mcmc analysis was performed using 50 000 cycles and ten chains, with a sample frequency of 100 and a burn-in of 100 states.

In addition to the biogeographical analysis, we also reconstructed the relative ancestral maximum SST tolerances for different clades within Otariidae. This was implemented using the same phylogeny used for the biogeographical analysis, with ~maximum SST tolerances traced as continuous characters in MESQUITE. SST data was gathered from the NOAA Earth System Research Laboratory website (http://www.esrl.noaa.gov/psd/map/clim/sst.shtml). Only summer temperatures were used, with SST data gathered from areas with breeding colonies that would be exposed to the warmest SST for that species.

RESULTS

PHYLOGENETIC ANALYSES

Morphology
For the analysis of morphology, three equally most parsimonious trees were recovered for the analysis incorporating all (ALL) fossil taxa [retention index (RI) = 0.65, consistency index (CI) = 0.47, tree length = 27.60; Fig. 3A]. For the analysis with fragmentary fossil taxa excluded (EX), one most parsimonious tree was recovered (RI = 0.68, CI = 0.49, tree length = 34.68; Fig. 3B). Variation in the K value for implied weighting affected the resolution of crown otariids, with resolution decreasing with an increase of K past 3. Results for analyses where K = 3 are discussed below, as this appeared to have been the weighting scheme that produced the maximal amount of resolution and support in the trees.

Relationships of most fossil taxa to crown Otariidae were poorly supported. In the ALL analysis, *Pithanotaria* was identified as the earliest diverging otariid lineage, but with poor support [bootstrap (bs) = 42]. Both analyses recovered *Thalassoleon* as paraphyletic. Within the ALL analysis, *Thalassoleon* formed a paraphyletic grade of basal stem otariid taxa, which formed a series of successive sister taxa to the remaining otariids. *Callorhinus gilmorei*, *Hydrarctos*, and *N. palatina* were identified as successive sister taxa to crown Otariidae, but with little support. Within the EX analysis, *T. mexicanus* was identified as the earliest diverging otariid lineage, sister to a clade composed of *T. macnallyae* and the remainder of Otariidae. *Hydrarctos* was recovered as the sister taxon to crown Otariidae.

Relationships amongst crown Otariidae recovered in both analyses were the same, only differing in bootstrap support. Most of these relationships were poorly supported. *Callorhinus ursinus* was recovered as the earliest diverging lineage of crown Otariidae, but with poor support (both analyses = bs < 20). A southern fur seal clade was found with poor support in both analyses and *Arctophoca* was paraphyletic, with *Arctophoca*

gazella as the earliest diverging lineage and sister taxon to a clade comprising *Arctocephalus* and the remainder of *Arctophoca*. *Arctophoca australis* and *Arctop. tropicalis* were successive sister groups to a clade comprising *Arctoc. philippii* and *Arctophoca galapagoensis*. Within Otariinae, a monophyletic *Zalophus* was marginally to poorly supported (ALL bs = 56, EX bs = 42) and identified as the earliest diverging lineage. The next diverging lineage was a clade consisting of *Proterozetes* and *Eumetopias*, with marginal support (ALL bs = 63, EX BS = 65). This clade formed the sister group to a monophyletic southern sea lion clade (SSL) with poor support in both analyses (both analyses = bs < 20). *Phocarctos* and *Otaria* were recovered as sister taxa within this clade with poor support (ALL bs = 37, EX bs = 40).

Molecules
Mitochondrial DNA produced a well-resolved tree (Fig. 4A) that recovered *Callorhinus* as outside a highly supported [posterior probability (pp) = 1.00)] clade comprising all other extant Otariidae. *Neophoca* was recovered as the earliest diverging lineage within this clade, but with poor support (pp = 0.62). High support (pp = 1.00) was found for the NSL clade, with *Zalophus* recovered as monophyletic with high support (pp = 0.98). Within *Zalophus*, *Zalophus japonicus* and *Zalophus wollebaeki* were recovered as sister taxa with strong support (pp = 1.00). Poor support (pp = 0.79) was recovered for an *Arctop. tropicalis* and *Arctocephalus* clade, which was in turn the sister group to a poorly supported clade (pp = 0.67) comprising *Otaria* and the remainder of *Arctophoca*. High support (pp = 1.00) was found for a clade comprising *Arctoc. philippii*, *Arctop. gazella*, *Arctop. australis*, and *Arctop. galapagoensis*. *Arctophoca philippii* was recovered as the earliest diverging lineage within this clade, with *Arctop. gazella* poorly supported (pp = 0.82) as sister taxon to a strongly supported clade (pp = 1.00) comprising *Arctop. australis* and *Arctop. galapagoensis*.

Nuclear DNA produced a poorly resolved tree (Fig. 4B), but recovered a monophyletic but poorly supported NSL clade (pp = 0.88) and a strongly supported southern otariid clade (pp = 0.97). Within the latter clade, *Otaria* was found as the sister taxon to *Arctop. australis* with moderate support (pp = 0.93), rendering southern fur seals and *Arctophoca* paraphyletic.

Combined evidence
For the combined evidence analysis, one most parsimonious tree was recovered in the ALL analysis (RI = 0.41, CI = 0.69, tree length = 89.15; Fig. 5A). A single most parsimonious tree was also recovered in the EX analysis (RI = 0.43, CI = 0.69, tree

(A) All taxa included
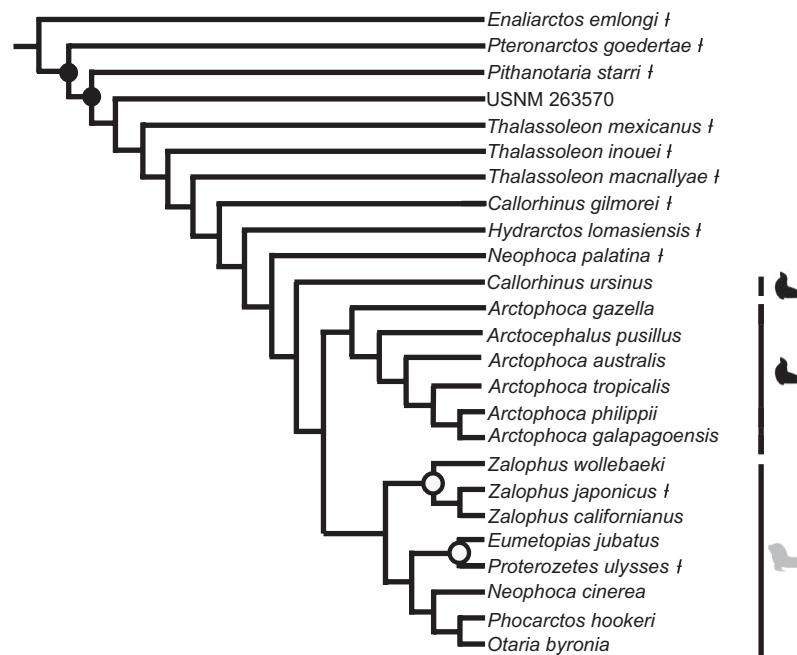
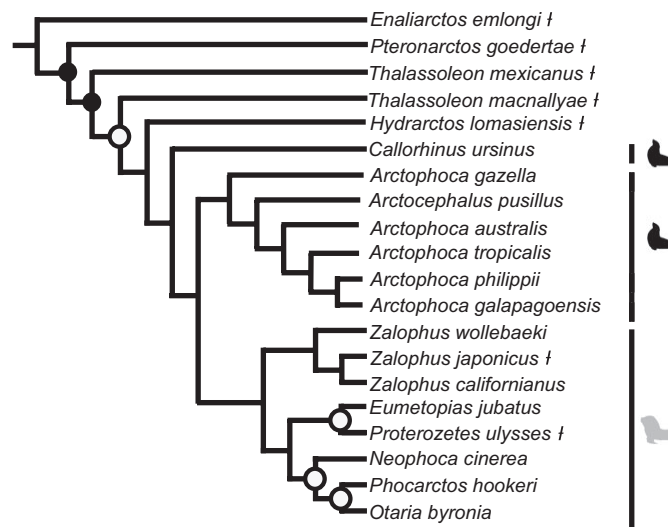**(B) All taxa with 50% or more of cells coded**

Figure 3. Results of maximum parsimony phylogenetic analysis of morphological characters. Fur seal icons in black represent members of Arctocephalinae and sea lion icons in grey represent members of Otariinae. Nodes with high support (bootstrap ≥ 70) are indicated by a black circle; nodes with moderate support (bootstrap = 50–70) are indicated by a white circle. Extinct taxa are annotated with †.

length = 87.41; Fig. 5B). The topologies of strict consensus trees were similar between the two analyses, although bootstrap support values are greater in the EX analysis (see below). Variation in the K value for implied weighting affected the bootstrap support of otariid clades, with maximal support found when K = 5.

Results for analyses where K = 5 are discussed below, as this appears to have been the weighting scheme that produced the maximal amount of resolution and support in the trees. The addition of molecular data to the morphological data set caused major changes in topology, and significantly increased support values.
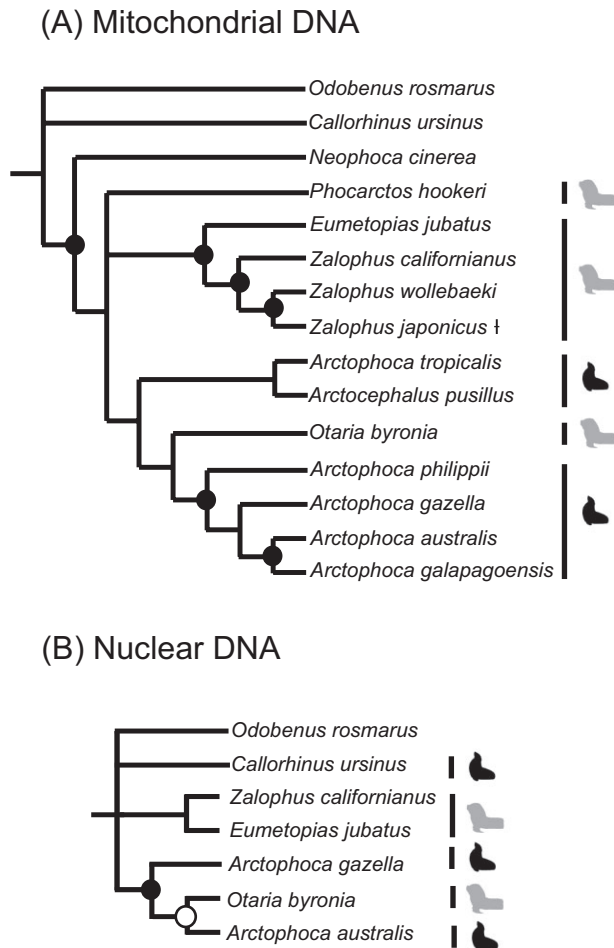
(A) Mitochondrial DNA

(B) Nuclear DNA

Figure 4. Results of Bayesian phylogenetic analysis of molecules. Mitochondrial DNA (A) includes *cytochrome b* and *d-loop* sequences. Nuclear DNA (B) includes *interphotoreceptor retinoid binding protein 3*, *growth hormone receptor*, and *feline sarcoma* oncogene gene sequences. Fur seal icons in black represent members of Arctocephalinae and sea lion icons in grey represent members of Otariinae. Nodes with high support (posterior probability ≥ 0.95) are indicated by a black circle; nodes with moderate support (posterior probability = 0.90–0.94) are indicated by a white circle. Extinct taxa are annotated with †.

Otariinae and Arctocephalinae were found to be paraphyletic, whereas monophyly was recovered for *Arctocephalus*. Four main clades of crown Otariidae were recognized: *Callorhinus* as the earliest diverging crown otariid lineage; *Neophoca cinerea* as the next diverging otariid lineage; a NSL clade consisting of *Zalophus*, *Proterozetes*, and *Eumetopias* with strong support (ALL bs = 70, EX bs = 73); and a southern clade. Within the southern clade, *Phocarctos* and *Otaria* were recovered as sister taxa, but with poor support (ALL bs = 41, EX bs = 46) and as the earliest diverging lineage of southern otariids. *Arctocephalus s.l.* was recovered

as monophyletic, with *Arctop. tropicalis* the sister taxon to *Arctocephalus pusillus* with moderate support (ALL bs = 58, EX bs = 60). The remaining southern fur seals formed a clade. The majority of fossil taxa were recovered as an assemblage of stem taxa, with *Thalassoleon* paraphyletic. The exceptions were *Proterozetes*, which was recovered within the NSL clade as the sister taxon to *Eumetopias*; and *Hydrarctos*, which was recovered as the sister taxon to *Arctocephalus s.l.* in the EX analysis, but recovered outside of crown Otariidae in the ALL analysis.

BIOGEOGRAPHY

For the Bayesian biogeographical analysis, seven dispersal events and five vicariance events were identified for the tree produced by the EX parsimony combined evidence analysis (Table 1; Fig. 6A), their likely dispersal routes illustrated in Figure 7. The North Pacific was identified as the point of origin for Otariidae. An initial early dispersal/vicariance event into the South Pacific was indicated, leading to the evolution of the southern fur seal and the *Phocarctos–Otaria* clade. Two other separate southward dispersal events were identified, *Neophoca* into the Indian Ocean and *Z. wollebaeki* to the Galapagos Islands. The South Pacific was recovered as the centre of origin for the *Phocarctos–Otaria* clade, the southern fur seal clade, and a clade composed of *Arctoc. philippii*, *Arctop. gazella*, *Arctop. australis*, and *Arctop. galapagoensis*. A dispersal/vicariance event was indicated, but the point of origin was poorly resolved for the clade containing *Arctop. tropicalis* and *Arctocephalus*. A dispersal/vicariance event was identified at the origin of the clade containing the remainder of *Arctophoca*, with separate dispersal/vicariance events associated with the colonization of the North Pacific by *Arctoc. philippii townsendi*, and colonization of the Southern Ocean by *Arctop. gazella*. The parsimony biogeographical analysis (Table 1; Fig. 6B) identified a similar pattern; both found strong support for a central role of the South Pacific in Otariidae biogeography. Reconstruction of ancestral maximal SST tolerance suggested ancestral tolerances of 16–18 °C for the common ancestor of Otariidae, 18–20 °C for the ancestors of the NSL clade, and 20–22 °C for the southern clade (Fig. 8).

DISCUSSION

PHYLOGENY OF OTARIIDAE

Comparisons of the results of the morphological, molecular, and combined evidence analyses
Overall, the only commonality amongst analyses using morphological, molecular, and combined evidence was monophyly of Otariidae and *Zalophus*. Phylogenetic
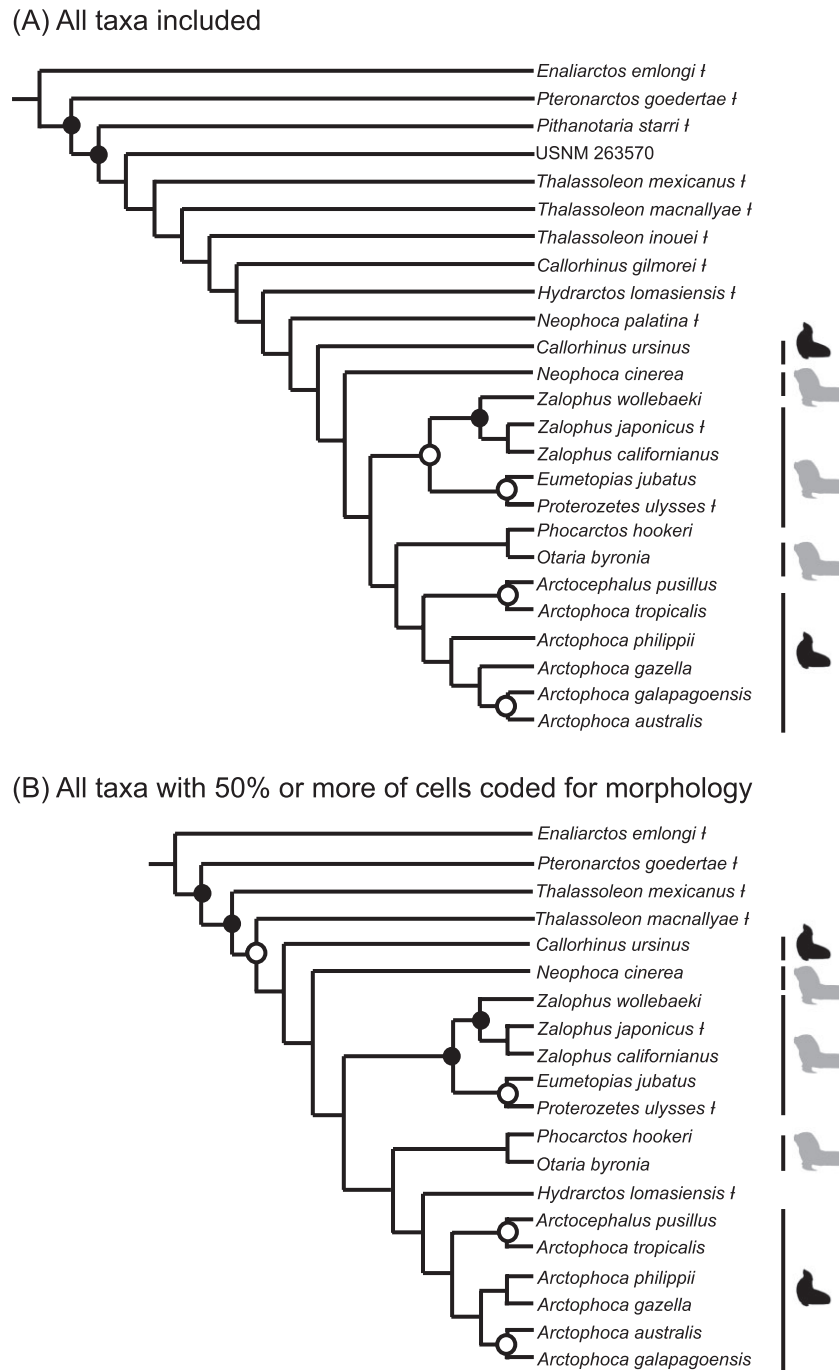
Figure 5. Results of maximum parsimony phylogenetic analysis of combined evidence. Fur seal icons in black represent members of Arctocephalinae and sea lion icons in grey represent members of Otariinae. Nodes with high support (bootstrap ≥ 70) are indicated by a black circle; nodes with moderate support (bootstrap = 50–70) are indicated by a white circle. Extinct taxa are annotated with †.

analyses based on molecular data support monophyly of a NSL clade and paraphyly of southern fur seals and Otariinae. This is consistent with most previous analyses of otariid relationships based on genetic data (Wynen *et al*., 2001; Árnason *et al*., 2006; Higdon *et al*., 2007; Yonezawa *et al*., 2009). A clade comprising *Arctoc. pusillus* and *Arctop. tropicalis* is also recovered in analyses of mitochondrial DNA, as well as a clade comprising the remainder of *Arctophoca* (Wynen *et al*., 2001; Yonezawa *et al*., 2009).

Table 1. Ancestral area reconstructions for key clades recovered in the maximum parsimony combined evidence analysis. Topology used was that of the EX analysis, which excluded fossil taxa that had 50% or fewer of their cells coded in the morphological matrix

Clade	Parsimony	Bayesian	Bayesian probability (%)
Otariidae	NP	NP	99.68
Crown Otariidae	NP	NP	99.13
Neophoca cinerea + NSL + southern clade	NP	NP	88.85
NSL + southern clade	NP	NP	73.36
NSL	NP	NP	89.44
Zalophus	NP	NP	99.66
Southern clade	SP	SP	59.38
Phocarctos + *Otaria* clade	SP	SP	86.78
Arctocephalus s.l.	SP	SP	63.19
Arctocephalus pusillus + *Arctophoca tropicalis* clade	Equivocal	SP	34.96
Arctophoca s.s.	SP	SP	99.70

NP, North Pacific; NSL, northern sea lion; SP, South Pacific.

The morphological analyses in contrast recognized the monophyly of Otariinae and southern fur seals, a result not recovered in molecular analyses but consistent with past cladistic studies that used morphology (Deméré & Berta, 2005; Barnes *et al.*, 2006). Overall, the phylogeny based on morphological characters alone is poorly supported, and inconsistent with the results of molecular analyses, despite the large sample size of specimens examined compared with prior morphological studies (229), as well as employing the largest sampling of characters to date in a phylogenetic analysis of the group. Within Otariidae, only four clades received even moderate support; a clade comprising *T. macnallyae* and all later diverging otariids; a sister taxon relationship between *Eumetopias* and *Proterozetes*; a southern sea lion clade, and a sister taxon relationship between *Phocarctos* and *Otaria*.

There are several factors that appear to confound attempts to reconstruct the phylogeny for this clade using only morphological characters. Compared with other pinniped clades such as phocids, otariids show less variability in cranial shape (Jones & Goswami, 2010). Lack of morphological distinction within lineages is a result of a combination of frequent hybridization across species and genera (Berta & Churchill, 2012), relatively recent diversification (Yonezawa *et al.*, 2009), and lack of ecological specialization within lineages (Jones & Goswami, 2010). These factors contribute to absence of differentiation in morphology as well as extensive individual variability. When taxa did possess unique character states, such as the simplified dentition of *Arctop. gazella* or the elongated palate of *Otaria*, these were often autapomorphic features that were of limited use in identifying clades. A second confounding factor is the relative poor representation of

many taxa (i.e. *Arctop. tropicalis*, *Arctoc. philippii*) within osteological collections. Many extant taxa are rare, endangered, and restricted to relatively remote islands. This has prevented the collection of adequate comparative material for adult specimens of several taxa, especially *Arctoc. philippii* and most subantarctic taxa. This prevents rigorous quantification of polymorphism within characters, in addition to making it relatively difficult to gather large data sets of quantitative cranial measurements. Owing to these issues, our study was often forced to use qualitative characters and rely on less rigorous methods of coding polymorphism.

The phylogenetic analysis of the morphological data set resulted in a poorly supported phylogeny (Fig. 3) when compared with the mitochondrial DNA phylogeny (Fig. 4A). Unfortunately, although the molecular data produced a more robust tree, the amount of mitochondrial and nuclear DNA available for use in phylogenetic reconstruction was limited. The only gene sequence data that was available for nearly all extant otariids was *cytochrome b* and *d-loop*, and the phylogenetic signal present within this data set may instead reflect the mitochondrial gene tree and not the species tree (Maddison, 1997). This may explain the position and poor support for *N. cinerea* in the phylogeny, where it was found to be the sister taxon to a clade comprising northern sea lions and all other southern otariids, consistent with several prior molecular phylogenies (Wynen *et al.*, 2001; Higdon *et al.*, 2007). By contrast, the morphological analysis found *N. cinerea* to be the sister taxon to a *Phocarctos–Otaria* clade, whereas Yonezawa *et al.* (2009) considered *N. cinerea* to be the sister taxon to *Phocarctos* within a southern otariid clade. To address the issue of gene trees, we also included nuclear DNA; however, this was only

(A) Bayesian Ancestral Area Reconstruction
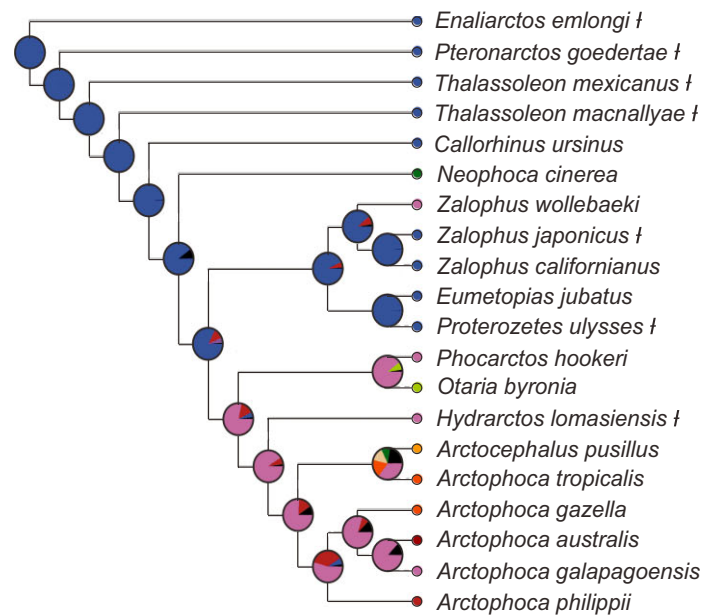
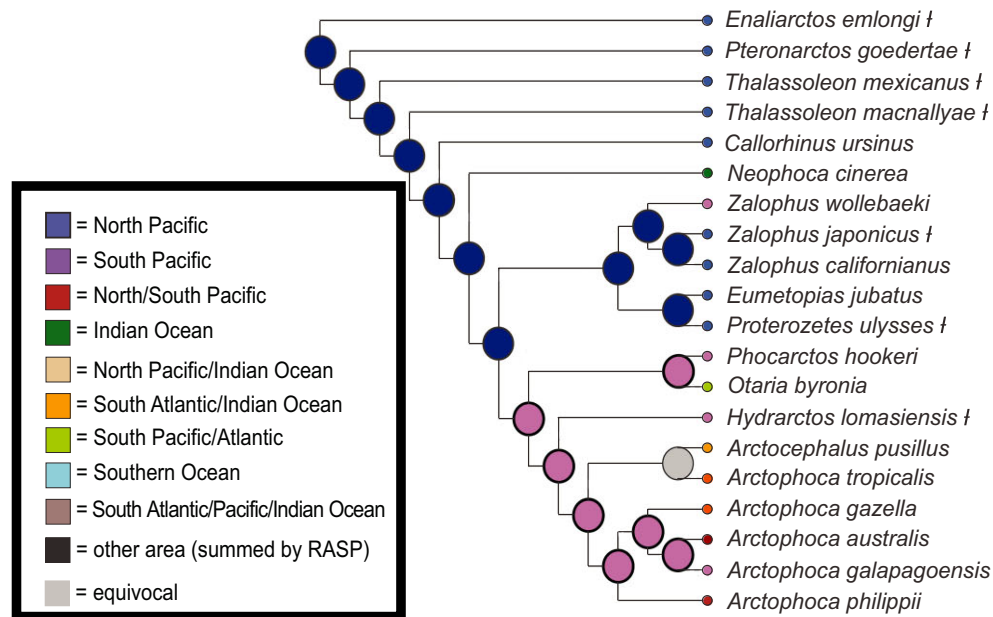## (B) Maximum Parsimony Ancestral Area Reconstruction

Figure 6. Results of Bayesian (A) and maximum parsimony (B) ancestral area reconstruction. Phylogeny used was the EX combined evidence phylogeny, which excludes fossil taxa with 50% or fewer cells coded for morphology. Key in lower left corner is for both A and B. Extinct taxa indicated by †. RASP in figure key refers to the program used for Bayesian ancestral character state reconstruction.

available for six of the 14 otariid taxa within this study. The nuclear DNA was able to confirm monophyly of northern sea lions and a southern clade of otariids, but cannot address the relationships of taxa with more controversial relationships, such as *Arctocephalus* or *Neophoca*.

The combination of morphological and molecular characters within the combined evidence analysis
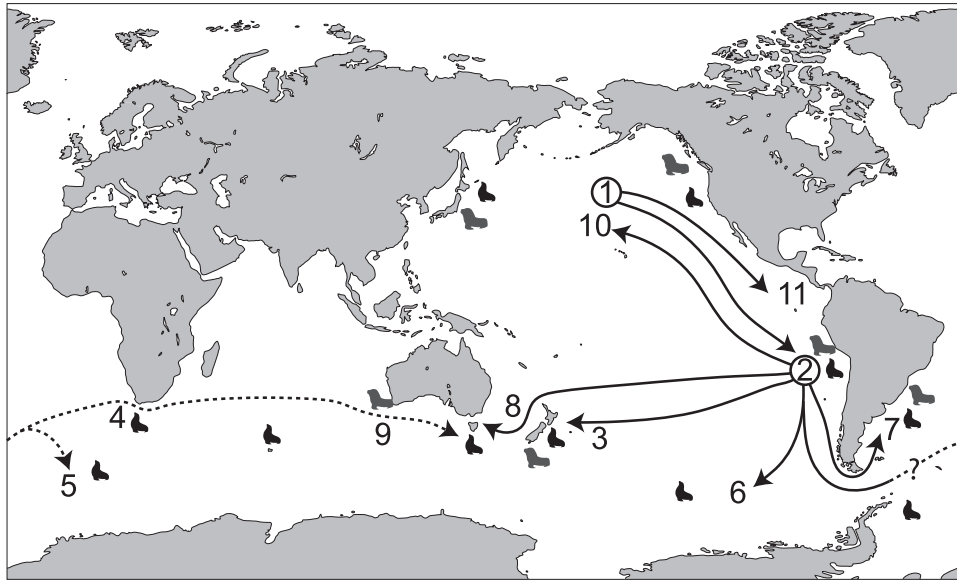
Figure 7. Pattern of otariid dispersal based upon Bayesian ancestral area reconstruction presented in Figure 6. Numbers in circles represent major centres of origin, and with directions of dispersals indicated by arrows. Less certain dispersal routes are indicated by black dashed lines. 1, origin of Otariidae in North Pacific; 2, origin of Southern Hemisphere clade in eastern South Pacific; 3, dispersal of ancestor of *Phocarctos* to New Zealand; 4, dispersal of ancestor of *Arctocephalus* to South Africa; 5, tentative dispersal of *Arctophoca tropicalis* to Southern Ocean; 6, dispersal of *Arctophoca gazella* to Southern Ocean; 7, dispersal of *Otaria* and *Arctophoca australis* to Atlantic coastline of South America; 8, dispersal of *Arctop. australis* to New Zealand and Australia; 9, tentative dispersal of *Arctocephalus* to Australia from South Africa; 10, dispersal of *Arctocephalus philippii* to the west coast of North America; 11, dispersal of *Zalophus* to the Galapagos. Historic presence of sea lions (grey silhouettes) and fur seals (black silhouettes) on map indicated. Dispersal of *Neophoca* into Indian Ocean not shown.

produced a tree that had superior support and resolution compared with trees produced by either data types alone. For the EX analysis, which excluded fossil taxa that had 50% or fewer of their cells coded in the morphological matrix, only six clades were identified with moderate to strong support using morphology. Six clades were also identified in the analysis that only used mitochondrial DNA. By contrast, eight clades were found with moderate to strong support in the combined evidence tree. A southern fur seal clade, sister clade to *Hydractos* was recovered in the EX; a novel clade unrecovered in either the morphological or molecular analyses. In addition, whereas the overall topology shares more similarities with the molecular results, including monophyly of northern sea lions, *Arctophoca s.s.*, and a sister taxon relationship between *Arctop. tropicalis* and *Arctop. gazella*, the overall topology shows greater resolution, with the NSL clade sister to a clade comprising all southern otariids with the exception of *Neophoca*. Finally, a *Phocarctos–Otaria* clade is recovered, consistent with our morphological results but not identified in prior molecular analyses (Wynen *et al.*, 2001; Árnason *et al.*, 2006; Higdon *et al.*, 2007; Yonezawa *et al.*, 2009). These findings support previous studies that have found combined evidence

approaches to phylogeny to be superior to methods only relying on either molecules or morphology (Kluge, 1989; Nixon & Carpenter, 1996; Queiroz & Gatesy, 2006; Hermsen & Hendricks, 2008). Owing to the superior resolution and support values, the remaining portion of this discussion will focus on using the EX combined evidence analysis to interpret the phylogenetic history of Otariidae.

Phylogenetic relationships within Otariidae
The topology recovered in the combined evidence analysis shares features of both previous morphological-based phylogenies as well as phylogenies based on genetic data, with a number of novel synapomorphies identified for different clades (Appendix 6). For the purpose of this discussion, we will focus on the results relevant in the discussion of the biogeography of Otariidae, and characters relevant to the northern sea lion clade, the southern otariid clade, and the southern fur seal clade.

The combined evidence analysis confirmed the existence of a NSL clade comprising *Eumetopias*, *Proterozetes*, and *Zalophus*. A NSL clade has been recovered in nearly all previous genotype-based analyses (Wynen *et al.*, 2001; Árnason *et al.*, 2006;
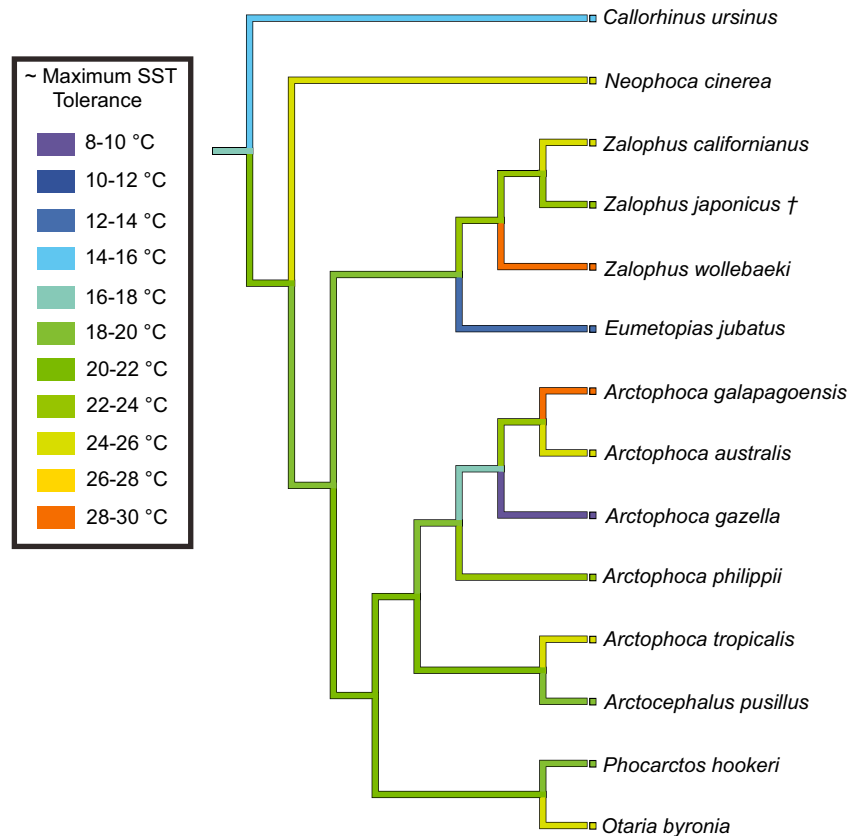
Figure 8. Ancestral maximal sea surface temperature (SST) tolerance for Otariidae. Phylogeny used was the EX combined evidence phylogeny, which excludes fossil taxa with 50% or fewer cells coded for morphology. Fossil taxa are excluded. Extinct taxa are annotated with †.

Higdon *et al.*, 2007; Yonezawa *et al.*, 2009), but not in prior morphological phylogenetic analyses. Berta & Deméré (1986) found *Zalophus* and *Eumetopias* to be successive sister taxa to a SSL clade. Barnes *et al.* (2006) recovered *Zalophus* as the sister taxon to *Phocarctos*, and the earliest diverging lineage within Otariinae. *Eumetopias* and *Proterozetes* were recovered as sister taxa, the clade in turn the sister group to *Otaria* and embedded well within Otariinae.

The NSL clade is in turn the sister group to a 'southern clade' consisting of *Phocarctos*, *Otaria*, *Arctocephalus*, and *Arctophoca*. This confirms Otariinae as being paraphyletic, with sea lions evolving at least twice and possibly three times. Monophyly of 'Otariinae' was recovered by Berta & Deméré (1986), but paraphyly is consistent with all prior genetic analyses (Wynen *et al.*, 2001; Árnason *et al.*, 2006; Higdon *et al.*, 2007; Yonezawa *et al.*, 2009). Synapomorphies for this clade identified by Berta & Deméré (1986) include: possession of a single-rooted M^1; a straight upper tooth row; robust humerus; more convoluted neopallium; sparse underfur; and sucking louse specificity (characters 19, 27, 28, 31, 35, and 37 of Berta & Deméré, 1986). Rooting

of the M^1 is variable across Otariidae, and we do not find this feature a useful synapomorphy for 'Otariinae'. A double-rooted M^1 is present in some individuals of *Eumetopias*, *Zalophus*, *Neophoca*, and *Phocarctos*, whereas a single-rooted M^1 was observed within many members of *Arctophoca*. A double-rooted M^1 has also been found to occur within a small proportion of *Callorhinus* (Boessenecker, 2011). A straight upper tooth row is observed in *Callorhinus*, *T. mexicanus*, and *Pithanotaria*, besides 'Otariinae', and is here interpreted as the ancestral condition for Otariidae. We did not include presence of a robust humerus or sparse underfur as characters within this analysis because of concerns over allometry.

The presence or absence of thick underfur is a good example of a morphological feature that is potentially influenced by allometry. Marine mammals must maintain a constant body temperature, which is more difficult to do in a cold, fluid environment. Pinnipeds rely on blubber and fur for insulation. Fur traps pockets of air within the integument, and is a superior insulator compared with blubber. However, when diving at depth this air layer is expelled, reducing the

effectiveness of the integument for insulation (Iverson, 2008; Liwanag *et al*., 2012). Blubber thus is a much more effective insulator for many marine mammals. The efficiency of blubber, however, varies by the size of the animal, with larger taxa having thicker layers of blubber and better insulation against cold oceanic temperatures (Iverson, 2008). At smaller body sizes, as present within fur seals, the blubber layer by itself is not efficient enough for insulation, and must be supplemented with fur to provide adequate insulation. At a large body size, such as that achieved by sea lions, blubber may be more effective, and may also improve diving ability.

We also did not incorporate characters related to the neopallium within this study, owing to difficulty in coding this character for fossil taxa as well as lack of comparative data for this study. Sucking louse specificity (Kim, Repenning & Morejohn, 1975) as a character was also not incorporated in this study, although the evolutionary patterns of parasites are often similar to those of their hosts. However, sympatry of sea lions and fur seals in many areas provides opportunities for transfer of lice between unrelated species. In addition, differences in morphology between sucking lice specialized for sea lions vs. fur seals may reflect adaptations for different integuments, and not phylogeny. Rigorous phylogenetic analysis of pinniped lice is still lacking, and the taxonomic identity of lice for many species (e.g. *Arctophoca*) remains poorly known (Kim *et al*., 1975). For the above reasons, we excluded this character from our analysis.

Barnes *et al*. (2006) also recognized a monophyletic 'Otariinae' and recognized the following characters as synapomorphies (characters 7, 13, 17, 19, and 40 of Barnes *et al*., 2006): a straight upper tooth row; enlarged I³; lateral extremity of supraorbital process of the frontal (SOP) hooked; posterior portion of sagittal crest elevated compared with the anterior portion; and enlarged antorbital processes. We discuss the possession of a straight upper tooth row above. We did not include cross-sectional shape of the I³ because we believe the shape to be more influenced by biomechanics than phylogeny. We interpret the shape of the I³ to be related to body size. A large otariid has a larger skull and dentition than a smaller taxon. A larger I³ would necessitate allometric changes in cross-sectional shape, as it would be exposed to greater mechanical stress and increased risk of fracture, which could be mediated by having a circular cross-sectional shape vs. the narrow oval shape retained by small taxa. As interpreted here, development of incisors with a circular cross-section occurred four times within Otariidae, within *T. mexicanus*, the NSL clade, *Neophoca*, and the *Phocarctos–Otaria* clade. The derived condition associated with the formation of a hook on the lateral extremity of the SOP appears to be equivalent to character

32 of this study (frontal: SOP shape). We observed a similar shape to the supraorbital process of the frontal as characterizing the SFL clade, to be absent for *Eumetopias* and *Otaria*, and to be variably present within *Callorhinus*.

We disagree with the characterization of the sagittal crest as presented within Barnes *et al*. (2006). At least two characters in our analysis seem to be relevant to the character state described for character 17 of Barnes *et al*. (2006). In character 53 of this study, shape of sagittal crest, the overall shape of the sagittal crest is convex in *Zalophus* and *Eumetopias*, whereas low and increasing in height posteriorly in *Otaria* and *Phocarctos*, and a low ridge in *Neophoca*. In character 54, sagittal crest location, the sagittal crest is largely developed in the posterior portion (braincase) of the skull in *Eumetopias*, *Otaria*, *Phocarctos*, and *Neophoca*. Within *Zalophus*, the sagittal crest originates in the orbital region of the skull and extends to the braincase. In either case, characteristics of the sagittal crest cannot be used as a synapomorphies for 'Otariinae'.

Within the southern clade, *Hydrarctos* is recovered as the sister taxon to a southern fur seal clade, although with poor support. Previous phylogenetic studies have placed this taxon as outside of crown Otariidae (Berta & Deméré, 1986) or as the sister taxon to a clade composed of *T. mexicanus*, *Otaria*, *Eumetopias*, and *Proterozetes* (Barnes *et al*., 2006). The results of our study are consistent with the original classification by Muizon (1978), who considered *Hydrarctos* a subgenus of *Arctocephalus s.l.*

A southern fur seal clade (*Arctocephalus s.l.*) was recovered in the combined evidence analysis, a novel finding of this study. This also confirms the paraphyly of 'Arctocephalinae', with *Callorhinus* recovered as the earliest diverging crown otariid. The previous morphological analysis for Otariidae (Berta & Deméré, 1986) was not able to resolve the position of members of this clade, with *Arctocephalus*, *Arctop. gazella*, *Arctop. tropicalis*, and a clade composed of *Arctop. australis*, *Arctop. galapagoensis*, and *Arctoc. philippii* as part of an unresolved polytomy with a clade composed of *Callorhinus* and *T. macnallyae*. Prior genetic analyses have recovered this clade as paraphyletic, with *Neophoca* and *Phocarctos* (Árnason *et al*., 2006; Yonezawa *et al*., 2009), *Phocarctos* and *Otaria* (Wynen *et al*., 2001), or *Phocarctos* (Higdon *et al*., 2007) embedded within the southern fur seal clade.

COLONIZATION OF THE SOUTHERN HEMISPHERE

Using a combination of fossil data, ancestral character state reconstruction, and palaeoclimatic proxies, it is possible to constrain the time of dispersal of Otariidae into the Southern Hemisphere (Fig. 9). The oldest known
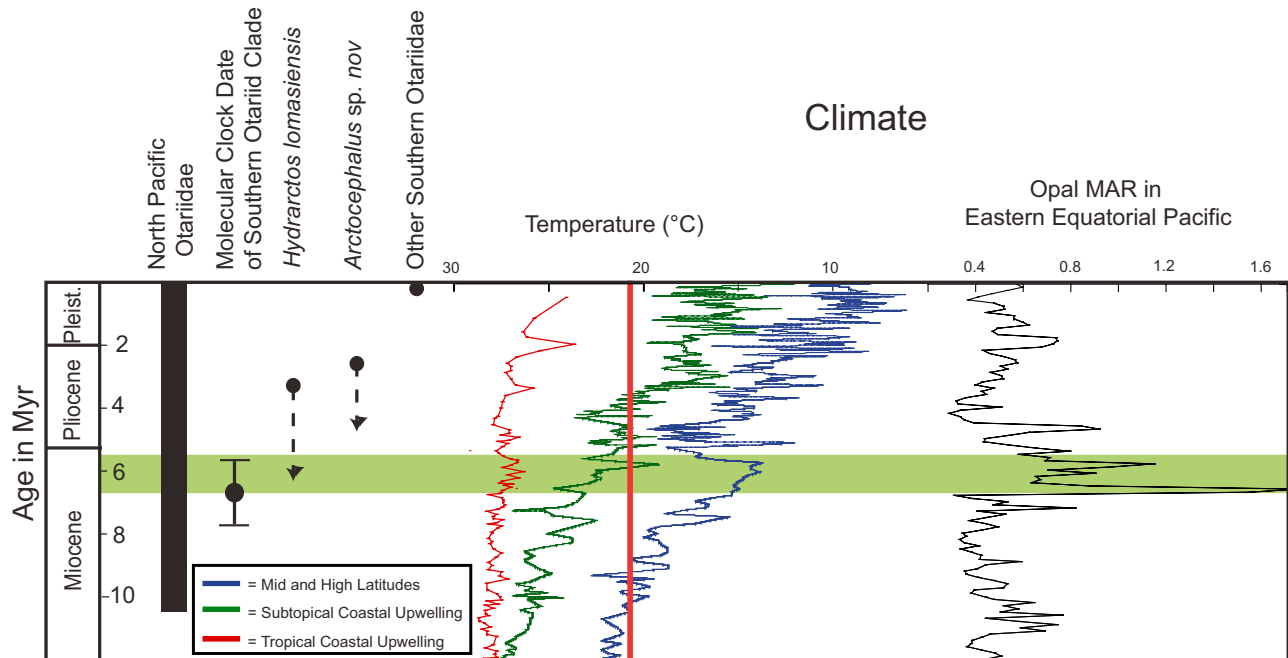
Figure 9. Timing of dispersal of Otariidae into the Southern Hemisphere, as constrained by molecular clock (Yonezawa *et al.*, 2009), fossil, and climatic data. Youngest ages of fossil taxa *Hydrarctos lomasiensis* (Muizon, 1978; Pilleri, 1990; Ehret *et al.*, 2012) and *Arctocephalus* sp. nov. (Avery & Klein, 2011) indicated by circles, with possible oldest ages indicated by the dashed lines. Temperature data from Fedorov *et al.* (2013) and Rousselle *et al.* (2013) based on Ocean Deep-drilling Program sites 1021 (high latitude), 1010 (subtropical), and U1338 (tropical). Opal mass accumulation rates (MAR) from Farrell *et al.* (1995). Vertical red line indicates maximum sea surface temperature (SST) temperature tolerance reconstructed for ancestor of southern clade. Green horizontal bar indicates the most likely time period of dispersal into the Southern Hemisphere from the North Pacific, when subtropical SSTs were depressed and equatorial productivity was high.

otariid fossils date to the early late Miocene in the North Pacific (Deméré *et al.*, 2003), although molecular clock divergence dates place the divergence between Otariidae and Odobenidae in the early Miocene (Yonezawa *et al.*, 2009). In the Southern Hemisphere, most otariid fossils are of Pleistocene age (Table 2), with only *Hydrarctos* and *Arctocephalus* sp. nov. known from older sediments (the Pisco Formation of Peru and Varswater Formation of South Africa, respectively). The youngest possible age for *Hydrarctos* is ~3.9 Myr (Muizon & DeVries, 1985), but this taxon may be as old as 6.59 Myr (Pilleri, 1990; Ehret *et al.*, 2012). The age range for *Arctocephalus* sp. nov. is from 2.7–5 Myr (Avery & Klein, 2011). This provides evidence that otariids were present in the eastern North Pacific and South Atlantic no later than 3.9 Mya, which postdates the split between the northern sea lions and the southern clade (~6.7 Mya; Yonezawa *et al.*, 2009). *Hydrarctos* was found in our phylogeny to be the sister group to southern fur seals (*Arctocephalus* + *Arctophoca*), strongly supporting an eastern South Pacific place of origin for this clade.

Unlike otariids, phocids (earless seals) have a rich Southern Hemisphere fossil record that extends to the middle Miocene (~12–14 Mya; Cozzuol, 2001; Deméré

et al., 2003). Although otariids were present in the North Pacific during this time, there is no evidence of Otariidae from the Miocene of the eastern South Pacific (Valenzuela-Toro *et al.*, 2013), suggesting a comparatively late dispersal across the equator for this clade. The early appearance of phocids in the Southern Hemisphere when compared to Otariidae probably relates to differences in ecology. Extant Otariidae are confined to regions with high upwelling and cool water temperatures, usually less than 24 °C (Deméré *et al.*, 2003). By contrast, phocids are found in a much wider variety of environments, including tropical oligotrophic waters.

Comparisons of dispersal patterns in other taxa (Lindberg, 1991; Burridge, 2002), as well as geography (Parrish, Serra & Grant, 1989), indicate that this dispersal probably took place along the eastern margin of the Pacific (Fig. 7). Fossil evidence indicates the presence of otariids in the eastern Pacific before the advent of Late Pliocene global cooling at ~3 Mya (Fedorov *et al.*, 2013). Prior to this (3–5 Mya) was a stage in earth climate history known as the Pliocene warm period (Ravelo, Dekens & McCarthy, 2006), when SST temperatures in tropical and subtropical waters were above

Table 2. Age and locality data for Southern Hemisphere fossil otariids

Taxon	Material	Locality	Epoch	Age
Arctocephalus sp. nov. (Avery & Klein, 2011)	Femur	Varswater Fm., South Africa	Pliocene	5–2.7 Myr
Hydrarctos lomasiensis (Muizon, 1978)	Skull, mandible, postcrania	Pisco Fm., Peru	Early Pliocene – late Pleistocene	< 6.59 Myr (Muizon & DeVries, 1985; Pilleri, 1990; Ehret et al., 2012)
Hydrarctos lomasiensis (Pilleri, 1990)	Skull	Pisco Fm., Peru	Pliocene	–
Otariidae indet. (Fleming, 1953)	Vertebrae	Butler Shell Conglomerate, New Zealand	Early Pleistocene	–
Neophoca palatina (King, 1983a)	Skull	Unnamed unit, New Zealand	Late Pleistocene	0.45–0.25 Myr
cf. *Otaria byronia* (Valenzuela-Toro et al., 2013)	Mandibles	Estratos de Caldera, Chile	Late Pleistocene	105 Kyr
Otariidae indet. (Valenzuela-Toro et al., 2013)	Postcrania	Estratos de Caldera, Chile	Late Pleistocene	105 Kyr
Arctocephalus pusillus (Avery & Klein, 2011)	Mandibles, postcrania	Numerous localities, South Africa	Late Pleistocene	330–1 Kyr
cf. *Otaria byronia* (Drehmer & Ribeiro, 1998)	Partial skull	Chui Fm., Brazil	Late Pleistocene	–
Neophoca cinerea (McCoy, 1877; Gill, 1968)	Skull, mandible	Unnamed unit, Australia	Late Pleistocene	–
Arctophoca sp. (Oliveira & Drehmer, 1997)	Postcrania	Unnamed unit, Brazil	Late Pleistocene	–

Fm., Formation.

the reconstructed tolerance (~20–22 °C) of ancestors of the southern clade (Fedorov *et al*., 2013; Rousselle *et al*., 2013), and equatorial productivity was suppressed (Farrell *et al*., 1995; Fig. 9). This would have made trans-hemispheric dispersal of otariids difficult. Similar conditions were also present in the equatorial eastern Pacific prior to ~7 Mya (Fedorov *et al*., 2013; Rousselle *et al*., 2013), which explains the absence of Otariidae from older fossil deposits in South America.

From approximately 6–7 Mya however, subtropical SST dropped to within the reconstructed maximal tolerance of otariids (Fig. 9; Fedorov *et al*., 2013; Rousselle *et al*., 2013), and productivity greatly increased in the equatorial eastern Pacific (Farrell *et al*., 1995). Cooling of subtropical and tropical waters and enhanced productivity would have facilitated dispersal of Otariidae across the equator. Timing of these climatic events is also correlated with the prior molecular clock estimates of the age of the southern otariid clade (5.7–7.7 Myr; Yonezawa *et al*., 2009) and the maximum possible age of the fossil otariid *Hydrarctos* (Ehret *et al*., 2012). This provides strong evidence that the initial dispersal of the Otariidae across the equator occurred between 6 and 7 Mya, far earlier than suggested by previous studies (Muizon & DeVries, 1985; Deméré *et al*., 2003).

Our biogeographical analysis suggests that from the Miocene to the present, trans-equatorial dispersal was an infrequent event for the Otariidae, and may have only been possible during periods of high productivity and reduced tropical and subtropical SSTs. This also supports palaeoclimate data and climate model simulations of a nearly constant presence of an equatorial band of warm, low-productivity water throughout the latter half of the Neogene in the Pacific (Wara, Ravelo & Delaney, 2005; Brierley & Fedorov, 2010; Fedorov *et al*., 2013; Rousselle *et al*., 2013). Furthermore, this study establishes the strong influence of SST and productivity on otariid distribution. Future changes in SST and productivity will possibly lead to radical shifts in otariid distributions, most severely impacting those populations at low latitudes.

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APPENDIX 1

LIST OF SPECIMENS EXAMINED FOR THIS STUDY
ABBREVIATIONS FOR MUSEUM COLLECTIONS
USED IN THIS STUDY

AIM, Auckland War Memorial Museum, Auckland, NZ; AMNH, American Museum of Natural History, New York City, NY, USA; BMNH, British Museum of Natural History, London, UK; CAS, California Academy of Sciences, San Francisco, CA, USA; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; DMNS, Denver Museum of Nature and Science, Denver, CO, USA; HM, National Museum of Japanese History, Chiba, Japan; HMH, Historical Museum of Hokkaido, Sapporo, Japan; HUM, Hokkaido University Museum, Sapporo, Japan; HUMZ, Hokkaido University Fisheries Department, Hakodate, Japan; KUZ, Kyoto University Museum, Kyoto, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; NSMT, National Museum of Nature and Science, Tokyo, Japan; SCMNH, Santa Cruz Museum of Natural History, Santa Cruz, CA, USA; SDNHM, San Diego Natural History Museum, San Diego, CA, USA; UAM, University of Alaska, Fairbanks, AK, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; UWBM, University of Washington Burke Museum, Seattle, WA, USA.

Enaliarctos emlongi: USNM 250345, 314540, 314290.

Pteronarctos goedertae: USNM 250320, 335432, 250323, 206274, 250282, 335695, LACM 123883.

Odobenus rosmarus: AMNH 29903, 73303, 73302, CM 15337, CAS 261, HUMZ Z58, UAM 12085, USNM 22014, 21101, 200226, UWBM 80659.

Arctocephalus pusillus: AMNH 81701, 81707, 81705, 81706, BMNH 1925-1-2-68, 1925-1-2-66, 1953-4-9-1, 1925-1-2-268, 1220 A, 1887-5-6-1, 1968-9-26-12, 1889-2-20-1, 1960-1-29-1, 1960-1-29-4, USNM 484928.

Arctophoca gazella: BMNH 1962-6-14-7, 1958-7-8-14, 1960-8-10-6, 1960-8-10-26, 1960-8-10-20, USNM 39226.

Arctophoca tropicalis: BMNH 1957-8-1-1, 1957-8-1-2, 1957-4-23-23, 1957-4-23-11, 1955-3-14-2.

Arctophoca philippii: AMNH 76844, BMNH 1883-11-8-1, CAS 27097, USNM 83618.

Arctophoca australis: AMNH 254569, 254565, 205917, BMNH 1876-2-15-4, 1872-6-25-1, 1868-9-26-8, 1968-9-26-2, 1968-9-26-4, 1950-11-14-1, 84-978, 84-972, 84-923, 84-921, 84-912, NSMT – M 24898, USNM 396921, 550479, 550480, 396062, 23331, 504895, 239140.

Arctophoca galapagoensis: AMNH 100341, BMNH 1977-19-91-1, CAS 1186, 1184.

Callorhinus ursinus: BMNH 1893-1-28-2, 1950-3-29-8, 1878-5-10-2, HUM 15111, 15198, 15026, 15911, 15768, 15813, 15317, 15820, 15565, 15919, 15797, 15804, 15405, KUZ 15794, 15788, 15784, 15782, 15780, 15779, 15768, 15766, 15762, 15759, 15758, 15755, UWBM 12550, 18335, 18336.

Zalophus californianus: BMNH 1966-10-24-2, 1968-6-10-1, CAS 23301, 22246, 22203, 22166, 22165, UWBM 34995, 315180, 32518, 27289, 34942, 34980, 34947, 39428, 34941, 34943.

Zalophus wollebaeki: AMNH 99465, 99464, 99462, 99461, 99463, 63946, CAS 1182, 7216, 13289, 1192, 1183.

Zalophus japonicus: BMNH 1873-3-12-1, 1896-5-19-2, HM-97R 22541, FN1 984, 2-97R 22541, 2-97R-980909, 2-97R 980815, 2-97R 60000, 2-FN1 980604, HMH 55953-1, 55953-5, 55953-6, 55953-2, 55953-7, 55953-4, 55953-3.

Eumetopias jubatus: BMNH 1992-272, 1950-3-29-11, 1950-7-21-4, KUZ 75K11, 75K10, 75K9, 75K8, 75K6, 75K5, 75K4, 75K4, 75K3, 75K2, 75K1, UWBM 19896, 51177, 39483, 20152, 51178, 32571, 6780.

Neophoca cinerea: BMNH 1968-9-26-30, 1968-9-26-25, 1968-9-26-1-3, 1925-10-8-23, 1897-10-10-5, USNM 571463, 504729.

Phocarctos hookeri: USNM 489526, 344985, 484531, 344982, 344981, 344980, BMNH 336-b, 1876-2-16-9, 1851-7-18-48.

Otaria byronia: AMNH 77910, 77920, 205919, 77918, 77917, 73120, BMNH WS 479, 1886-12-13-1, 335-m, USNM 550142, 550307, 550227, 484912, 95063, 153568, 153567.

Pithanotaria starri: USNM 11056, UCMP 219377.

Thalassoleon mexicanus: NMNS-PV 15411 (cast of IGCU 902), SDNHM 68313, 65172, 61563.

Thalassoleon macnallyae: UCMP 219696, 219675, 219482, 219426, 112809, 128379, SCMNH 9975.1.

cf. *Thalassoleon macnallyae*: USNM 263570.

Thalassoleon inouei: NMNS-PV 19656 (cast of CBMPV 807).

Proterozetes ulysses: USNM 187108, 187109, UCMP 219377.

Callorhinus gilmorei: SDNHM 25176, 25531, 26239, 25554, 25535.

Neophoca palatina: AIM Mamm 175.1.

APPENDIX 2

MORPHOLOGICAL AND BEHAVIOURAL CHARACTERS USED IN THE MORPHOLOGICAL AND COMBINED EVIDENCE PHYLOGENETIC ANALYSIS

All characters that include the character state 'Polymorphic' are considered ordered.

1. *Height of skull:* < 32% basal length of skull (0); > 32% or polymorphic for this trait (1).
2. *Dorsal surface of skull at forehead:* flat (0); slightly to strongly convex (1). (Modified from Repenning *et al.*, 1971; Brunner, 2004.)
3. *Rostrum: widest portion:* posterior to canines (0); at canines (1).
4. *Facial angle:* less than or equal to 65 (0); polymorphic (1); greater than 65 (2). (Modified from Repenning *et al.*, 1971; Berta & Deméré, 1986.)
5. *Premaxilla: prenarial process:* large, forming a half-circle in dorsal view, and giving a tapered appearance to the snout (0); reduced to a low ridge in dorsal view, enhances overall bluntness of snout (1). (Modified from Bininda-Emonds & Russell, 1996.)
6. *Premaxilla*: *depth of fossa between canine and incisor:* shallow or absent (0); deep (1). (Modified from Bininda-Emonds & Russell, 1996.)
7. *Premaxilla: contact with nasals:* contact limited to the lateral margins of the anterior half of nasals (0); contact between the premaxilla and nasal extends to midway along the lateral margins of the nasal, or greater (1); contact limited to anterior terminus of nasals with limited or no contact along the lateral margins (2).
8. *Premaxilla: lateral view:* gradual slope from nasal region to prenarial region (0); strongly concave (1); premaxilla mostly excluded from lateral view (2).
9. *Maxilla: fossa muscularis:* present (0); absent (1). (Modified from Berta & Wyss, 1994.)
10. *Maxilla: nasiolabialis fossa:* present and well developed (0); absent or poorly developed (1). (Modified from Mitchell & Tedford, 1973; Berta & Deméré, 1986; Berta & Wyss, 1994.)
11. *Maxilla: surface of posterodorsal portion:* flat (0); inflated (1); inflated due to development of canines (2).
12. *Maxillopalatine suture: anterior edge:* straight or M-shaped (0); polymorphic (1); rounded (2). (Modified from Bininda-Emonds & Russell, 1996.)
13. *Maxilla: diastema between upper P^4 and M^1:* absent (0); present (1); present and greatly elongated (2). (Modified from Barnes *et al.*, 2006.)
14. *Maxilla: diastema between upper M^1 and M^2:* absent (0); polymorphic (1); present (2). (Modified from Repenning *et al.*, 1971; Berta & Wyss, 1994.)

15. *Size of diastema between M^1 and M^2:* slight diastema (0); polymorphic (1); large diastema (2). (Modified from Mitchell & Tedford, 1973; Repenning & Tedford, 1977; Berta & Deméré, 1986.)

16. *Maxilla: visibility of infraorbital foramen in lateral view:* visible (0); not visible (1).

17. *Maxilla: embrasure pit between P^4 and M^1:* deep (0); shallow or absent (1). (Modified from Repenning *et al.*, 1971; Berta & Wyss, 1994; Barnes *et al.*, 2006.)

18. *Maxilla: palatine process:* terminates at last molar (0); extends past anterior margin of temporal fossa (1); extends to approximate level of postorbital process of zygomatic (2); extends past the level of the postorbital process of zygomatic (3). (Modified from Repenning *et al.*, 1971; Berta & Wyss, 1994.)

19. *Nasal–frontal suture:* transverse (0); V-shaped (1); W-shaped (2). (Modified from Berta & Deméré, 1986.)

20. *Nasals: anterior flaring:* lateral walls parallel and largely straight, with minor anterior flaring (0); lateral wall concave, with extreme flaring of the anterior portion of the nasals (1). (Modified from Sivertsen, 1954; Repenning *et al.*, 1971; Berta & Deméré, 1986; Barnes *et al.*, 2006.)

21. *Palate: surface:* flat to slightly concave (0); polymorphic (1); deeply concave (2). (Modified from Repenning *et al.*, 1971; Berta & Deméré, 1986; Deméré, 1994; Adam & Berta, 2002; Barnes *et al.*, 2006.)

22. *Palate: length:* long (53–60% basal length of skull) (0); short (45–52% basal length of skull) (1); extremely short (< 45% basal length of skull) (2); extremely long (> 60% basal length of skull) (3). (Modified from Deméré, 1994.)

23. *Palatine: shape of posterior edge:* arched or triangular (0); straight (1). (Modified from Bininda-Emonds & Russell, 1996.)

24. *Pterygoid: hamular processes:* minor dorsoventral development (0); enlarged, with extensive dorsoventral development (1); absent (2). (Modified from Barnes *et al.*, 2006.)

25. *Orbit: anterior margin:* indistinct ridge connecting antorbital process with zygomatic arch (0); low ridge connecting antorbital process with zygomatic arch (1); ridge developed into prominent anterior plate (2).

26. *Antorbital process:* indistinct but present (0); small ridge on frontal (1); well developed (2); prominent on frontal and maxilla (3); prominent only on maxilla (4); absent (5). (Modified from Berta & Deméré, 1986; Barnes *et al.*, 2006.)

27. *Construction of antorbital process:* from frontal and maxilla (0); from frontal only (1); from maxilla only (2). (Modified from Deméré, 1994.)

28. *Breadth of skull across antorbitals:* less than or equal to breadth of rostrum (0); greater than breadth of rostrum (1).

29. *Frontal–maxilla suture:* V-shaped (0); straight, transverse (1); Divergent, often with expansion of the frontal into maxilla as a lobe (2). (Modified from Deméré, 1994.)

30. *Constriction between braincase and orbital region in dorsal view:* narrowest constriction between braincase and supraorbital processes (0); narrowest constriction adjacent to anterior margin of braincase (1). (Modified from Repenning *et al.*, 1971.)

31. *Frontal: shape of intertemporal margin:* concave (0); straight (1).

32. *Frontal: supraorbital process (SOP) shape:* supraorbital ridge (0); completely absent (1); large; lateral margins expanded, giving SOP a more rectangular shape (2); polymorphic (3); large and triangular (4). (Modified from Berta & Deméré, 1986; Berta & Wyss, 1994; Barnes *et al.*, 2006.)

33. *Frontal: angle between SOP and anterior orbital margin:* greater than 60 (0); polymorphic (1); less than or equal to 60 (2).

34. *Frontal: anterior root of sagittal crest:* crest emerges from region of the SOP, either from one point or slightly bifid (0); anterior emergence of crest bifid, and preceded by prominent divergent crests that originate on the posterior portion of the SOP (1). (Modified from Barnes *et al.*, 2006.)

35. *Lacrimal:* distinct (0); fuses early in ontogeny to maxilla and frontal (1). (Modified from Mitchell & Tedford, 1973; Berta & Deméré, 1986; Berta & Wyss, 1994.)

36. *Orbital vacuities: position:* absent (0); present and anteriorly positioned (1); present and posteriorly positioned (2). (Modified from Berta & Wyss, 1994; Deméré, 1994; Barnes *et al.*, 2006.)

37. *Orbital vacuities: extent of bone reduction:* minor, small foramen or fissure (0); major, large foramen or greatly widened suture (1). (Modified from Bininda-Emonds & Russell, 1996.)

38. *Zygomatic arch: ventral view:* laterally bowed (0); unbowed or slightly medially bowed (1). (Modified from Barnes *et al.*, 2006.)

39. *Zygomatic arch: region posterior to postorbital process:* thin (0); polymorphic (1); thick (2). (Modified from Berta & Wyss, 1994.)

40. *Squamosal: mastoid and postglenoid process contact:* separated (0); polymorphic (1); closely appressed (2).

41. *Relationship of mastoid process with paraoccipital process:* close to paraoccipital process connected via low, discontinuous ridge (0); close to paraoccipital process connected via high, discontinuous ridge (1); distant from paraoccipital (2).

(Modified from Berta & Wyss, 1994; Barnes *et al*., 2006.)

42. *Basioccipital: shape:* trapezoidal (0); rectangular (1). (Modified from Repenning *et al*., 1971; Berta & Deméré, 1986.)

43. *Carotid canal:* broad, with no overlap by tympanic (0); polymorphic (1); tympanic bulla overlaps or partially overlaps the canal, excluding much of it from view on the ventral surface (2).

44. *Tympanic bulla: posterior projection:* absent or indistinct (0); short (1); long and well developed (2). (Modified from Mitchell, 1968; Barnes *et al*., 2006.)

45. *Tympanic bulla: angle between posterior and lateral margins:* greater than 90 (0); approximately 90 (1).

46. *Tympanic bullae: ventral surface:* bulbous (0); flat or concave (1). (Modified from Repenning *et al*., 1971.)

47. *Tympanic bulla: complex ornamentation:* absent from ventral surface (0); present on ventral surface (1). (Modified from Repenning *et al*., 1971; Berta & Deméré, 1986; Barnes *et al*., 2006.)

48. *Periotic: pit for tensor tympani:* present (0); absent (1). (Modified from Berta & Wyss, 1994.)

49. *Parietal: anterolateral corner of braincase:* forms a right angle (0); smoothly merges with orbital region (1). (Modified from Barnes *et al*., 2006.)

50. *Parietal: lateral protuberances:* absent (0); polymorphic (1); present (2).

51. *Occipital: exposure in dorsal view:* visible as a triangular wedge between nuchal crests (0); polymorphic (1); not visible or only present as a very small triangular wedge in dorsal view (2); visible as a rounded crescent (3).

52. *Sagittal crest:* present (0); absent (1); polymorphic (2); separate temporal ridges present (3). (Modified from Deméré, 1994; Bininda-Emonds & Russell, 1996.)

53. *Sagittal crest: shape:* low ridge (0); convex (1); low, increases in height posteriorly (2).

54. *Sagittal crest: location:* largely confined to braincase (0); emergence of sagittal crest in orbital region, extending to braincase (1). (Modified from Barnes *et al*., 2006.)

55. *Nuchal crests: shape in lateral view:* project from dorsal surface of the back of the sagittal crest anteroventrally over the top of the mastoid to the external auditory meatus (0); curved: traces the posterior margin of the skull onto the mastoid process (1). (Modified from Barnes *et al*., 2006.)

56. *Mandible: shape of ventral margin:* straight (0); sinuous (1). (Modified from Boessenecker & Churchill, 2013.)

57. *Mandible: genial tuberosity:* absent or weakly developed (0); large genial tuberosity (1). (Modified from Boessenecker & Churchill, 2013.)

58. *Mandible: development of digastric insertion:* transversely rounded (0); sharp crest (1). (Modified from Boessenecker & Churchill, 2013.)

59. *Mandible: angular process shape:* narrow (0); broad (1); reduced to low triangular ridge or bump (2); absent or indistinct (3). (Modified from Repenning *et al*., 1971; Berta & Deméré, 1986.)

60. *Mandible: medial shelf of angular process:* does not form medial shelf (0); forms small medial shelf (1). (Modified from Repenning *et al*., 1971; Berta & Deméré, 1986.)

61. *Mandible: base of coronoid process:* narrow (less than 42% of mandible length) (0); broad (greater than or equal to 42% of mandible length) (1). (Modified from Repenning *et al*., 1971; Repenning & Tedford, 1977; Berta & Deméré, 1986; Boessenecker & Churchill, 2013.)

62. *Length of masseteric fossa:* long (> 28% length of mandible) (0); short (< 28% length of mandible) (1). (Modified from Brunner, 2004.)

63. *Extension of upper tooth row:* extends to level of the maxillary base of the zygomatic arch (0); extends to level of anterior portion of temporal fossa (1); extends to or past level of middle of temporal fossa (2); well anterior to the level of the maxillary base of the zygomatic arch (3).

64. *Upper postcanine tooth row:* laterally concave (0); straight and parallel (1); laterally convex (2); postcanine tooth row kinked at approximately P^3 (3). (Modified from Repenning *et al*., 1971; Deméré, 1994; Barnes *et al*., 2006.)

65. *Postcanines: labial cingulum:* absent (0); polymorphic (1); present (2).

66. *Premolars: P^2–P^3 accessory cusps:* absent; a well-developed paracone and metacone instead (0); absent or small cusps present (1); well-developed cusps present (2). (Modified from Kellogg, 1922; Repenning *et al*., 1971; Repenning & Tedford, 1977; Berta & Deméré, 1986; Barnes *et al*., 2006.)

67. *Upper P^3: rooting:* double-rooted (0); single-rooted (1). (Modified from Berta & Wyss, 1994.)

68. *Upper P^3–P^4: crowns:* three cusps (0); two cusps, paracone emphasized (1); one cusp (2); peg-like crown (3); complex labial cusps (4). (Modified from Deméré, 1994.)

69. *Protocone:* present and well developed (0); present but vestigial, often worn away (1); absent (2). (Modified from Berta & Wyss, 1994.)

70. *Upper P^4: protocone shelf:* present (0); absent (1). (Modified from Berta & Wyss, 1994.)

71. *Upper P^4: rooting:* three-rooted (0); three-rooted with posterior root bilobed (1); double-rooted (2); single-rooted (3). (Modified from Berta & Wyss, 1994.)

72. *Molar wear:* unworn or slight wear (0); molars heavily worn, reduced to flat button (1). (Modified from Repenning *et al*., 1971.)

73. *Upper M¹:* present (0); absent (1). (Modified from Berta & Wyss, 1994.)

74. *Upper M¹: rooting:* triple-rooted (0); double-rooted (1); polymorphic (2); single-rooted (3). (Modified from Repenning *et al*., 1971; Berta & Deméré, 1986; Berta & Wyss, 1994.)

75. *Upper M²:* present (0); polymorphic (1); absent (2). (Modified from Berta & Wyss, 1994; Barnes *et al*., 2006.)

76. *Lower tooth row length:* long (> 40% of length of mandible) (0); polymorphic (1); short (< 40% of length of mandible) (2). (Modified from Berta & Deméré, 1986; Berta & Wyss, 1994.)

77. *Lower P¹: crown size:* smaller than crowns of P²⁻⁴ (0); similar in size to P²⁻⁴ (1).

78. *Lower P¹: root width:* root or alveolus is same diameter as P²⁻⁴ (0); root or alveolus smaller in diameter than P²⁻⁴ (1).

79. *Lower P²: rooting:* double (0); double or bilobate (1); polymorphic (2); single (3). (Modified from Berta & Deméré, 1986.)

80. *Lower P³⁻⁴: rooting:* double (0); single (1). (Modified from Berta & Deméré, 1986.)

81. *Lower M¹⁻²: trigonid and talonid:* present (0); suppressed (1). (Modified from Berta & Wyss, 1994.)

82. *Lower M¹: metaconid:* reduced (0); absent (1). (Modified from Berta & Wyss, 1994.)

83. *Lower M²:* present (0); absent (1). (Modified from Berta & Deméré, 1986; Berta & Wyss, 1994.)

84. *Vertebral foramen:* proportionally same size as in terrestrial carnivores (0); enlarged (1). (Modified from Repenning & Tedford, 1977; Berta & Deméré, 1986.)

85. *Cervical vertebrae: size:* larger than thoracic and lumbar, spinal canal less than one-half diameter of centrum (0); smaller than thoracic and lumbar, with spinal canal nearly as large as centrum (1). (Modified from Berta & Wyss, 1994.)

86. *Lumbar vertebrae: transverse processes:* long (0); short (1). (Modified from Berta & Wyss, 1994.)

87. *Scapula: secondary spine:* absent (0); present (1). (Modified from Berta & Wyss, 1994.)

88. *Humerus: supinator ridge:* well developed (0); absent or poorly developed (1). (Modified from Berta & Wyss, 1994.)

89. *Radius: position of pronator teres process:* positioned on the distal 60% of the radius (0); positioned on the proximal 40% of the radius (1).

90. *Femur: fovea for teres femoris ligament:* present and well developed (0); strongly reduced or absent (1). (Modified from Berta & Wyss, 1994.)

91. *Tibia and fibula:* unfused (0); polymorphic (1); fused proximally (2). (Modified from Lyons, 1937; Repenning & Tedford, 1977; Berta & Wyss, 1994.)

92. *Calcaneum: secondary shelf of sustentaculum:* absent or developed as a thin groove (0); developed as narrow shelf (1); developed as wide shelf (2). (Modified from Muizon, 1978; Berta & Deméré, 1986.)

93. *Baculum: apex:* transversely narrow (0); transversely narrow, resembles a figure of eight in anterior view (1); broad with keels (2); broad with keels, with further expansion laterally (3). (Modified from Morejohn, 1975; Repenning & Tedford, 1977; Berta & Deméré, 1986; Berta & Wyss, 1994.)

94. *Postcruciate sulcus:* absent (0); present (1). (Modified from Repenning & Tedford, 1977 and Berta & Deméré, 1986.)

95. *Pseudosylvian sulcus:* weakly present or absent (0); present, deep (1); strongly developed (2); reduced or absent (3). (Modified from Berta & Wyss, 1994.)

96. *Posterior ectosylvian gyrus:* broad and convoluted (0); narrow and unconvoluted (1). (Modified from Repenning & Tedford, 1977; Berta & Deméré, 1986.)

97. *Head tuft in males:* absent (0); present in the form of a crown (1); present in form of small tuft (2). (Modified from Repenning *et al*., 1971.)

98. *Mane:* absent (0); present in males (1); present in males and exaggerated (2).

99. *Tooth pigmentation:* absent (0); present (1).

100. *Coloration: sexual dimorphism in contrast:* absent (0); male has bolder patterns or darker coloration than female (1).

101. *Coloration: sexual dimorphism in colour:* absent (0); females grey dorsally (1).

102. *Coloration: facial pattern:* absent (0); face pale (1).

103. *Coloration: contrast between dorsal and ventral surfaces:* absent or slight (0); strongly contrasting (1).

104. *Coloration: contrast between nape and crown in males* absent (0); present (1).

105. *Body size:* small taxa (< 300 kg) (0); large taxa (> 300 kg) (1). (Modified from Repenning *et al*., 1971.)

106. *Haul out site preference:* beach-type environments (0); polymorphic (1); rocky, boulder-type environments (2).

107. *Thigomatism:* weak (0); strong (1). (Modified from Stirling & Warneke, 1971; Berta & Deméré, 1986.)

APPENDIX 3

MORPHOLOGICAL CHARACTER MATRIX USED IN THIS STUDY

Character state A represents taxa that are polymorphic for state 0 and 1.

Taxon	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–107
Enaliarctos emlongi	0000000000	0000?000A0	0000000000	00?000?000	0000000000	0000100000	0100000000	0001000000	000??0?0?0	0??71????	????0??
Pteronarctos goedertae	0000001000	0000?01100	0100000021	10?1010100	1020000000	0001000000	0000000000	100100?00?	000??0??0??	???????	????0??
Arctocephalus pusillus	0?11011111	0011101210	0100112121	1401111120	1021101101	2020100110	1013121211	3001020021	1111011111	2200000111	0000111
Arctophoca gazella	0010010011	0202211211	0100112121	1401111110	1111000100	2020100100	0113011221	3102000021	1111011111	2200000110	0000000
Arctophoca tropicalis	0110011111	0101111211	0100112121	1400111100	1021000100	0020000000	0013111221	3001001021	1111011111	2200002110	0110020
Arctophoca philippii	0110011011	0010?11220	0100112011	1400111120	1021100100	0020000110	0113011221	3002000121	1111011111	2200000110	0001020
Arctophoca australis	0010011111	0001101211	0100112121	1400111120	1011100100	0020100110	0013111211	3002010021	1111011111	2200000110	0000020
Arctophoca galapagoensis	0010011111	0002101221	0100112011	1401111120	1121100100	0020000110	0013111221	3001001021	1111011111	2200000110	0000020
Callorhinus ursinus	0002000111	1000?11211	0200002021	1300111110	1101101100	0000000001	0001011211	3001121021	1111011111	0211011110	0001000
Zalophus californianus	0010000101	000??11210	0100112120	0301111110	1121100110	2011000011	0001211211	3002220021	1111011111	2220000110	0001101
Zalophus wollebaeki	0010001011	?001011210	0100112120	1401111110	1121100100	1011000001	0001211211	3003020021	1111011111	2220000110	0001101
Zalophus japonicus	0010001011	0002211210	0100112121	0301111120	1121100110	2011000001	1001211221	3002110021	1111?11111	2220000110	0001021
Eumetopias jubatus	0110111011	011??11211	0000112120	0211111110	1121011110	2010000000	1111011221	3001200121	1111011111	1230000110	0000121
Neophoca cinerea	0110011011	000??01211	0000110021	1400111100	1121000110	2000111001	0011221211	3002101021	1111?11111	2230000111	10A1101
Phocarctos hookeri	0110000011	0001201210	1000112111	1400111121	1102000111	2020011000	1011211211	3002101021	1111?11111	2230000111	10A0101
Otaria byronia	1010001011	0102111311	2311212121	0211111122	1022111122	2020011111	1001221221	3008121021	??1101100?	2230000211	0000101
Pithanotaria starri	?00000?0??	??1????11??	0?0???11??	?4?0?11??	??????????	7000?000??	??1010022?	2001002700	111??????	0???????	????0??
Hydrarctos lomasiensis	?010011011	0000?01221	0?00112111	1401111120	112?1??700	00?0100010	0?112211221	2002020021	1110011101	?1??????	???????
Thalassoleon mexicanus	0010001011	0200?11220	0000112121	0200111120	1021000100	0120100000	1?11010221	2001002000	??10011101	0017?0????	????1??
Thalassoleon macnallyae	?0???????	?202?12??	0??????21	14?0?????0	1101101700	0000000001	0?1?01????	2??20?2010	??10011101	10?0?????	????0??
USNM 263570	?0?000????	?00??012??	0?0???????	???111110?	1?????1??	?????????	??11??0??1	2?0107???	?????????	?????????	???70??
Thalassoleon inouei	??????????	??????????	??????????	?????????0	100110112?	?????110??	0??21???0	????2?000	111??????	?????????	???70??
Proterozetes ulysses	?100110011	0022?01220	0100111120	0401111100	1?21001110	2020000000	0?11211???	30?21?7121	?11??71?	?????????	????1??
Callorhinus gilmorei	???00????	??00??1???	??????????	14??????0	01??????	?????00000	0?10011221	2001027010	1111011110?	11??????	????0??
Neophoca palatina	?110???11	0?0???1?20	0?0?112121	1??1?11??0	1101100100	00?017????	??01?71???	2?012?????	?????????	?????????	????1??

APPENDIX 4

GENBANK ACCESSION NUMBERS FOR MITOCHONDRIAL GENE SEQUENCES USED IN THIS STUDY

| Taxon | Mitochondrial genes | | Nuclear genes | | |
	Cytochrome b	*D-loop*	*IRBP*	*FES*	*GHR*
Odobenus rosmarus	AJ428576	AJ428576	DQ205892	GU931105	GU931129
Arctocephalus pusillus	AM181018	AM181018	–	–	–
Arctophoca gazella	X82292	AF384380	DQ205891	–	DQ205814
Arctophoca tropicalis	AF380887	AF384385	–	–	–
Arctophoca philippii townsendi	AM181021	AM181021	–	–	–
Arctophoca australis australis	AY377329	AF384402	DQ205887	DQ205776	DQ205810
Arctophoca galapagoensis	AF380900	AF384386	–	–	–
Callorhinus ursinus	AM181016	AM181016	AB188516	–	–
Zalophus californianus	AM181017	AM181017	AY750612	GU931102	GU931126
Zalophus wollebaeki	AM422152	AM945178	–	–	–
Zalophus japonicus†	–	AB262364	–	–	–
Eumetopias jubatus	AJ428578	AJ428578	DQ205890	DQ205779	DQ205813
Neophoca cinerea	AM181019	AM181019	–	–	–
Phocarctos hookeri	AM181020	AM181020	–	–	–
Otaria byronia	AY377328	AF384423	DQ205889	DQ205778	DQ205812

FES, *feline sarcoma* oncogene; *GHR*, *growth hormone receptor*; *IRBP*, *interphotoreceptor retinoid binding protein 3*.
†indicates extinct taxa.

APPENDIX 5

DISTRIBUTION OF FUR SEALS AND SEA LIONS AS CODED FOR BIOGEOGRAPHICAL ANALYSIS

Taxon	Distribution
Enaliarctos emlongi†	North Pacific
Pteronarctos goedertae†	North Pacific
Arctocephalus pusillus	South Atlantic; Indian Ocean
Arctophoca gazella	Southern Ocean
Arctophoca tropicalis	Southern Ocean
Arctophoca philippii	North Pacific; South Pacific
Arctophoca australis	South Pacific; South Atlantic; Indian Ocean
Arctophoca galapagoensis	South Pacific
Callorhinus ursinus	North Pacific
Zalophus californianus	North Pacific
Zalophus wollebaeki	South Pacific
Zalophus japonicus†	North Pacific
Eumetopias jubatus	North Pacific
Neophoca cinerea	Indian Ocean
Phocarctos hookeri	South Pacific
Otaria byronia	South Pacific; South Atlantic
Thalassoleon mexicanus†	North Pacific
Thalassoleon macnallyae†	North Pacific
Hydrarctos lomasiensis†	South Pacific
Proterozetes ulysses†	North Pacific

†indicates extinct taxa.

APPENDIX 6

LIST OF UNEQUIVOCAL SYNAPOMORPHIES FOR MAJOR
CLADES RECOVERED IN THE COMBINED EVIDENCE
PHYLOGENETIC ANALYSIS

Topology used was that of the analysis with fragmentary fossil taxa excluded, which excluded fossil taxa that had 50% or fewer of their cells coded in the morphological matrix. Numbers refer to characters in character list (Appendix 2), whereas numbers in parentheses refer to state number.

*Crown Otariidae (Callorhinus
ursinus + Neophoca cinerea + northern sea lion
clade + southern otariid clade)*
67(1): single rooted P^3; 71(3): single-rooted P^4; 79(3): single-rooted P_2; 80(1): single-rooted P_4; 89(1): pronator teres insertion positioned on the proximal 40% of the radius; 92(2): secondary shelf of the sustentaculum of the calcaneum developed as a wide shelf.

*Northern sea lion clade (Eumetopias +
Proterozetes + Zalophus)*
30(0): narrowest constriction of cranium in dorsal view located midway between braincase and supraorbital processes of the frontal; 53(1): sagittal crest convex in lateral view; 77(0): P_1 crowns small than $P_{2–4}$ crowns.

Eumetopias and Proterozetes clade
5(1): prenarial process reduced to low ridge in dorsal view; 13(2): greatly elongated diastema between P^4 and M^1; 78(1): P_1 root alveolus smaller in diameter than $P_{2–4}$ root alveoli.

Zalophus
6(0): shallow fossa between upper canines and incisors; 54(1): emergence of sagittal crest in orbital region, extending to braincase; 93(3): baculum broad with keels.

*Southern otariid clade (Otaria + Phocarctos +
Arctocephalus + Arctophoca)*
53(2): low sagittal crest, which increases in height posteriorly.

Phocarctos and Otaria clade
6(0): shallow fossa between upper canines and incisors; 21(1&2): tendency for a deeply concave palate; 40(1&2): tendency for the mastoid processes and postglenoid processes of the squamosal to be widely separated from each other; 44(2): a well-developed posterior projection of the tympanic bullae; 61(1): coronoid process of the mandible with a broad base.

Hydrarctos + southern fur seal clade
49(0): anterolateral corner of braincase forms a right angle; 51(0): occipital in dorsal view visible as a triangular wedge.

Southern fur seal clade (Arctocephalus + Arctophoca)
58(1): digastrics insertion forms a sharp crest on the mandible; 64(3): upper postcanine tooth row kinked at the position of P^3; 65(1&2): tendency for postcanine labial cingulum to be absent; 93(0): transversely narrow baculum.

Arctocephalus pusillus + Arctophoca tropicalis clade
8(1): premaxilla strongly concave in lateral view; 74(1): double-rooted M^1.

*Arctophoca sensu stricto (Arctophoca gazella,
Arctophoca philippii, Arctophoca australis,
and Arctophoca galapagoensis)*
62(1): short masseteric fossa; 105(0): small body size.