

Pinniped phylogeny and a new hypothesis for their origin and dispersal

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Abstract

The relationships and the zoogeography of the three extant pinniped families, Otariidae (sea lions and fur seals), Odobenidae (one extant species, the walrus), and Phocidae (true seals), have been contentious. Here, we address these topics in a molecular study that includes all extant species of true seals and sea lions, four fur seals and the walrus. Contrary to prevailing morphological views the analyses conclusively showed monophyletic Pinnipedia with a basal split between Otarioidea (Otariidae + Odobenidae) and Phocidae. The northern fur seal was the sister to all remaining otariids and neither sea lions nor arctocephaline fur seals were recognized as monophyletic entities. The basal Phocidae split between Monachinae (monk seals and southern true seals) and Phocinae (northern true seals) was strongly supported. The phylogeny of the Phocinae suggests that the ancestors of *Cystophora* (hooded seal) and the Phocini (e.g. harp seal, ringed seal) adapted to Arctic conditions and ice-breeding before 12 MYA (million years ago) as supported by the white natal coat of these lineages. The origin of the endemic Caspian and Baikal seals was dated well before the onset of major Pleistocene glaciations. The current findings, together with recent advances in pinniped paleontology, allow the proposal of a new hypothesis for pinniped origin and early dispersal. The hypothesis posits that pinnipeds originated on the North American continent with early otarioid and otariid divergences taking place in the northeast Pacific and those of the phocids in coastal areas of southeast N America for later dispersal to colder environments in the N Atlantic and the Arctic Basin, and in Antarctic waters.

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1. Introduction

The topic of pinniped biogeography was probably first addressed by Sclater (1897), who postulated origin of the group in southern oceans. This view, which had been seconded by von Boetticher (1934), was formally questioned by Davies (1958), who advocated pinniped origin in the Holarctic. Based on the working hypothesis that “The pinnipeds are, and always have been, generally tied to a cold-water environment”, Davies concluded that the pinni-

peds had originated in the Arctic Basin, with the otarioids subsequently colonizing the N Pacific and the phocids the N Atlantic, before dispersing to other areas.

Davies (1958) had assumed monophyletic Pinnipedia in his study. That notion was gradually replaced, however, by a morphologically based view that favored pinniped diphyly with the otarioids sharing ancestry with the ursids and the phocids with the mustelids. This phylogenetic understanding also led to a revised pinniped biogeography, the essence of which was that early otarioid evolution had taken place in coastal areas of the N Pacific and that of the phocids in European waters.

Sarich (1969) challenged the notion of pinniped diphyly in an immunological study that unequivocally showed mono-

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phyletic Pinnipedia. This phylogeny has been recognized in essentially all later molecular analyses, irrespective of whether they have been based on nuclear data (de Jong and Goodman, 1982; Arnason and Widgren, 1986), complete mitochondrial (mt) genes (Arnason et al., 1995; Ledje and Arnason, 1996a,b) or, more recently, on complete mt genomes (Arnason et al., 2002; Arnason and Janke, 2002; Davis et al., 2004; Delisle and Strobeck, 2005). The molecular recognition of pinniped monophyly gradually led to reconsideration of the morphological understanding favoring pinniped diphyly. However, these newer morphological studies (e.g. Wyss and Flynn, 1993; Berta and Wyss, 1994) did not support the traditionally accepted sister group relationship between Otariidae and Odobenidae (=Otarioidea), but rather advocated a sister group relationship between Phocidae and Odobenidae (=Phocomorpha) to the exclusion of Otariidae. This latter relationship was assumed as the basis of a recent proposal for pinniped biogeography (Deméré et al., 2002). More recently, Fyler et al. (2005) addressed some aspects of Monachinae biogeography. Some conclusions of this paper are inconsistent, however, with recent advances in phocid paleontology (e.g. Koretsky, 2001; Koretsky and Holec, 2002; Koretsky and Sanders, 2002).

In the current study, we reconsider pinniped evolution and biogeography using more extensive molecular data than previously available, and by taking into account paleontological evidence that has previously not been placed in a phylogenetic context of this kind. The analyses include 21 newly sequenced and 10 previously published pinniped mt genomes. The sampling includes all recent species of true seals and sea lions, four fur seals and the walrus. The analysis followed the now common practice of joining the sequences of 12 mitochondrial (mt) protein-coding genes of each species into one long sequence. This approach, introduced by Arnason and Johnsson (1992), expanded on by Janke et al. (1994) and extensively discussed by Paton and Baker (2006), rests on the demonstration that, while individual genes may yield different trees, longer genes and in particular the concatenated sequences of all genes result in trees that show consistency with well-supported non-molecular hypotheses.

The initial phase of the study aimed at establishing pinniped relationships. Thereafter the phylogenetic results, in conjunction with molecular datings and new paleontological and climatological findings, were used to elaborate the new hypothesis for pinniped biogeography.

2. Materials and methods

Table 1 lists the 39 species included in the study and the accession numbers of their complete mt genomes (when applicable). The accession numbers of the new genomes are shown in bold. The mt genome of the ringed seal, *Phoca hispida*, was sequenced using cloned restriction fragments from enriched mtDNA preparations. The preparation of enriched mtDNA followed the procedure briefly described in Arnason et al. (1991). Remaining genomes were PCR

Table 1
Taxa included in the phylogenetic analyses

Pinnipedia
Odobenidae, walruses, one recent species
<i>Odobenus rosmarus</i> , walrus (AJ428576)
Otariidae, sea lions, fur seals
Callorhinae
<i>Callorhinus ursinus</i> , northern fur seal (AM181016)
Otariinae/Arctocephalinae
<i>Otaria byronia</i> , southern sea lion ^a
<i>Eumetopias jubatus</i> , northern sea lion (AJ428578)
<i>Zalophus californianus</i> , Californian sea lion (AM181017)
<i>Arctocephalus pusillus</i> , South African fur seal (AM181018)
<i>Phocarcos hookeri</i> , Hooker's sea lion (AM181019)
<i>Neophoca cinerea</i> , Australian sea lion (AM181020)
<i>Arctocephalus townsendi</i> , Guadalupe fur seal (AM181021)
<i>A. forsteri</i> , New Zealand fur seal (AF513820)
<i>A. australis</i> , South American fur seal ^a
Phocidae, true seals
Monachinae, monk seals and southern true seals
Monachini
<i>Monachus monachus</i> , Mediterranean monk seal ^a
<i>M. schauinslandi</i> , Hawaiian monk seal (AM181022)
Miroungini
<i>Mirounga leonina</i> , southern elephant seal (AM181023)
<i>M. angustirostris</i> , northern elephant seal ^a
Lobodontini
<i>Ommatophoca rossi</i> , Ross seal ^a
<i>Lobodon carcinophagus</i> , crabeater seal (AM181024)
<i>Leptonychotes weddelli</i> , Weddell seal (AM181025)
<i>Hydrurga leptonyx</i> , leopard seal (AM181026)
Phocinae, northern true seals
Erignathini
<i>Erignathus barbatus</i> , bearded seal (AM181027)
Cystophorini
<i>Cystophora cristata</i> , hooded seal (AM181028)
Phocini
Histriophocina
<i>Histriophoca fasciata</i> , ribbon seal (AM181029)
<i>Pagophilus groenlandicus</i> , harp seal (AM181030)
Phocina
<i>Phoca largha</i> , largha seal (AM181031)
<i>P. vitulina</i> , harbor seal, Icelandic specimen (X63726)
<i>P. vitulina</i> , harbor seal, Baltic Sea specimen (AM181032)
<i>P. caspica</i> , Caspian seal (AM181033)
<i>P. sibirica</i> , Baikal seal (AM181034)
<i>P. sibirica</i> , Baikal seal (AM181035)
<i>P. hispida</i> , ringed seal, Baltic Sea specimen (AM181036)
<i>Halichoerus grypus</i> (<i>Phoca grypa</i>), grey seal (X72004)
<i>Ursus americanus</i> , black bear (NC003426)
<i>U. maritimus</i> , polar bear (AJ428577)
<i>Mustela vison</i> , American mink ^a
<i>Gulo gulo</i> , wolverine ^a
<i>Vulpes vulpes</i> , red fox (AM181037)
<i>Canis familiaris</i> , dog (NC002008.4)
<i>Felis catus</i> , cat (U20753)
<i>Acinonyx jubatus</i> , cheetah (AY463959)
<i>Equus asinus</i> , donkey (X97337)
<i>Rhinoceros unicornis</i> , Indian rhinoceros (X97336)

Table 1 (continued)

Pinnipeds are arranged according to a scheme that is essentially consistent with the current phylogenetic findings. Traditional Otariinae (sea lions) and traditional Arctocephalinae (fur seals other than *Callorhinus*) have been grouped under Otariinae/Arctocephalinae. Accession numbers (when applicable) are shown in parenthesis. Numbers in bold refer to new sequences.

^a Data collected from individual genes reported by Davis et al. (2004). Tissue samples of *C. ursinus* were provided by Drs. Link E. Olson and Gordon H. Jarrell, Univ. of Alaska Museum, specimen UAM 52179 (AF 19825); DNA sample of *P. hookeri* was provided by Dr. C. Scott Baker, Ecology and Evolution Section, Univ. of Auckland, NZ, that of *A. townsendi* by Dr. Brent S. Stewart, Department of Chemistry, Portland State University, Portland, Oregon, and that of *N. cinerea* by Dr. Terry Bertozzi, Evolutionary Biol. Unit, South Australian Museum, Adelaide, Australia. The British Antarctic Survey provided samples of Antarctic phocids.

amplified, typically in 2–4 kb large fragments using Ex-Taq DNA polymerase and conserved primers that were constructed on the basis of various caniform mt sequences established in our laboratory. The PCR-products were purified by ultra-filtration (Millipore) and sequenced employing an ABI or a LICOR-4000L system. It should be observed that the highly heteroplasmic repeated parts of the pinniped control regions (e.g. Arnason and Johnsson, 1992) of specimens other than the ringed seal do not represent a particular clone but rather a majority rule consensus. The current sampling includes two complete mt genomes of two species with highly different distribution, the pelagic harbor seal, *Phoca vitulina*, and the Baikal seal, *Phoca sibirica*, endemic to Lake Baikal.

The phylogenetic analyses were carried out on the concatenated amino acid, aa, and nucleotide, nt, (1st plus 2nd codon positions) sequences of the 12 heavy strand encoded protein-coding genes. The light strand encoded NADH6 gene was not included as it deviates markedly in nt and aa composition from the other genes. In addition Phocina relationships were examined in nt analyses that included the 12 protein-coding mt genes, the 12S and 16S rRNA genes, and the control regions less their repeated parts (14,336 nt excluding gaps).

Phylogenetic analyses were performed using the TREE-PUZZLE (Strimmer and von Haeseler, 1996), PHYLIP (Felsenstein, 1993), MOLPHY (Adachi and Hasegawa, 1996), and PAUP (Swofford, 2002) packages. The mtREV-24 model of aa sequence evolution (Adachi and Hasegawa, 1996) and the TN-93 model of nt evolution (Tamura and Nei, 1993) were used for distance and likelihood analyses. Divergence times were estimated (aa data set) according to Sanderson (2002) using the “r8s” version of the 1.70 program package, applying the penalized likelihood method and a smoothing value of 32. The divergence between caniforms and feliforms set at 52 million years ago, MYA, (Flynn and Galiano, 1982) was used as a reference for calibration. The age of the oldest phocid fossils (Koretsky and Sanders, 2002) served as an intra-pinniped check of the utility of the caniform/feliform calibration point set at 52 MYA.

3. Results and discussion

3.1. Pinniped phylogeny

The carnivore tree was rooted with two perissodactyls (the Indian rhino and the donkey), a group that has been shown to be closely related to the carnivores (Xu et al., 1996). The sampling includes two feliforms, the domestic cat and the cheetah, that were used to establish the split between the feliforms and the caniforms. Basal caniform relationships were recently examined using mitogenomic data (Delisle and Strobeck, 2005). These relationships are therefore not addressed here.

Fig. 1 shows the phylogenetic tree identified in maximum-likelihood analysis of the concatenated aa sequences of 12 mt protein-coding genes (3601 aa). The analyses conclusively supported the sister group relationship between Otariidae and Odobenidae (= Otarioidea). As evident in Table 2 the alternative grouping of Phocidae and Odobenidae (= Phocomorpha) on a common branch [b] is incompatible with the maximum-likelihood tree [a] whether rate homogeneity is assumed or not.

3.1.1. Otariid relationships

Within the Otariidae there is a maximally supported basal split between the northern fur seal, *Callorhinus ursinus*, and a branch that contains the five sea lions and the four *Arctocephalus* species. The position of *Callorhinus* among the Otariidae (see Table 2c and d) corroborates morphological suggestions for a closer relationship between *Arctocephalus* and sea lions (Otariinae) than between the traditional fur seal genera *Arctocephalus* and *Callorhinus* (Repenning et al., 1971; Repenning and Tedford, 1977; Brunner, 2003). Neither traditional Otariinae nor *Arctocephalus* were identified as monophyletic entities. The finding is in agreement with morphological studies (Repenning et al., 1971; Repenning and Tedford, 1977) that have questioned the subdivision of the Otariidae into sea lions and fur seals and more recent conclusions based on comprehensive analyses of otariid skull morphometry (Brunner, 2003). On the basis of the abundant underfur layer of their pelage, *Callorhinus* and *Arctocephalus* have commonly been grouped together to the exclusion of the Otariinae. The separate position of *Callorhinus* among the Otariidae (Fig. 1; Table 2c and d) and the lack of support for monophyletic *Arctocephalus* and Otariinae (Table 2e) are consistent with the questioning (e.g. Repenning et al., 1971; Repenning and Tedford, 1977) of using pelage as a phylogenetic marker for separating sea lions and fur seals.

The branch containing the Guadalupe, S. American and NZ fur seals and the Australian and Hooker's sea lions was strongly supported in all analyses. The joining of the three arctocephalids was also strongly supported but the relationship between this branch and the Australian and Hooker's sea lions was poorly resolved. The S African fur seal was the favored sister to the branch containing the three other arctocephalids and the Australian and Hooker's sea lions.

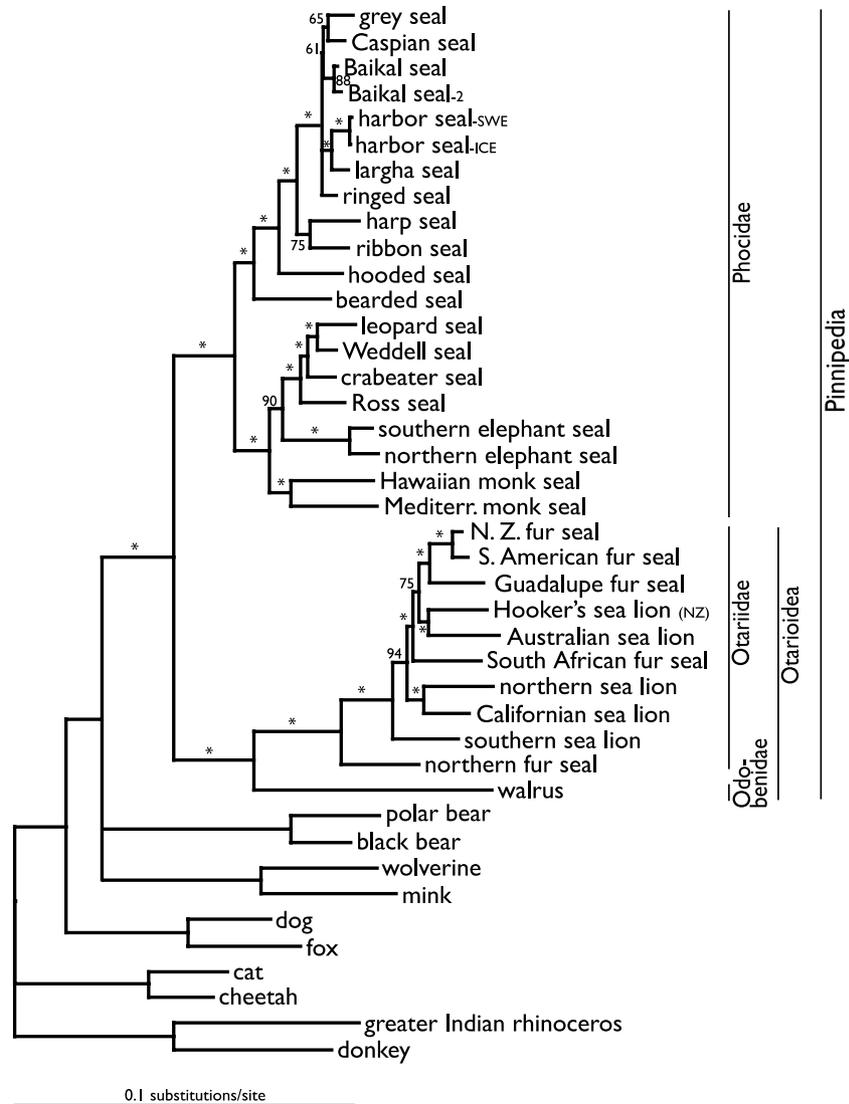


Fig. 1. Pinniped phylogenetic relationships based on maximum-likelihood analysis of the amino acid (aa) sequences of twelve mitochondrial protein-coding genes (3601 aa). Branches receiving 97% support or more are marked with *. Figures at other pinniped nodes indicate % support values. For details of some particular relationships at the generic level or higher see the text and Table 2. Two species, the harbor and the Baikal seals, with highly different pattern of distribution, are represented by two mt genomes each. The two harbor seals, one from Iceland and one from the Baltic Sea differed at four nucleotide positions. The corresponding difference between the two Baikal seals was 41. The limited difference between the two harbor seals may suggest post-glacial dispersal from a common core population.

The relationship between *Eumetopias/Zalophus*, *Otaria*, and remaining sea lions and the four *Arctocephalus* species was not conclusively resolved. Maximum-likelihood (ML) aa analysis with rate homogeneity (see Fig. 1) placed *Otaria byronia* (southern sea lion) as the sister group of the latter, while rate heterogeneity instead placed *Eumetopias/Zalophus* in that position, Table 2f and g.

3.1.2. Phocid relationships

Within the Phocidae the branches of both Monachinae (monk seals + southern true seals) and Phocinae (northern true seals) received maximum support. The basal Monachinae divergence between Monachini (monk seals) and Miroungini/Lobodontini was strongly supported and the split between Miroungini (elephant seals) and Lobodontini

(*Ommatophoca*, Ross seal; *Lobodon*, crabeater seal; *Leptonychotes*, Weddell seal and *Hydrurga*, leopard seal) received maximum support. *Ommatophoca* was identified as the sister group of the three other Lobodontini genera of which *Leptonychotes* and *Hydrurga* joined on a common branch. Various Monachinae relationships were examined in recent mitogenomic analyses (Davis et al., 2004). Our findings are consistent with these results and we do not, therefore, dwell on this particular topic. The deep split between the two *Monachus* species, the Hawaiian and the Mediterranean monk seals in Fig. 1 is nevertheless noteworthy in comparison to the lesser depth of Lobodontini divergences.

Mirounga (elephant seals) and *Cystophora* (hooded seal) have sometimes been grouped together in the subfamily Cystophorinae; a morphological hypothesis challenged by

Table 2
Analysis of specific pinniped relationships

Tree	$\Delta\ln L_{\text{hom}}$	SE	pSH_{hom}	$\Delta\ln L_{\text{het}}$	SE	pSH_{het}	Steps	SD
a—Best tree as in Fig. 1	<−36,870>		1.000	+4	±15	0.961	<4489>	
b—Phocomorpha	+117	±25	0.018	+68	±22	0.004	+37	±8
c— <i>Curs/Acep</i> sister to monophyletic Otariinae	+198	±35	0.000	+116	±28	0.000	+52	±8
d— <i>Acep/Curs</i> , Otariinae paraphyletic	+162	±29	0.004	+95	±27	0.001	+50	±9
e— <i>Arctocephalus</i> and Otariinae monophyletic	+55	±19	0.230	+35	±17	0.291	+17	±5
f— <i>Zcall/Ejub</i> sister to remaining Otariinae/ <i>Acep</i>	+5	±16	0.930	+2	±10	0.945	+3	±5
g— <i>Ejub</i> sister to remaining Otariinae/ <i>Acep</i>	+2	±22	0.866	<−34,335>		1.000	+0	±6
h— <i>Crcil/Mirounga</i> sister to Lobodontini	+233	±41	0.000	+178	±35	0.000	+53	±10
i— <i>Crcil/Mirounga</i> sister to Phocinae	+210	±42	0.000	+154	±35	0.000	+50	±10
j— <i>Crcil/Mirounga</i> sister to other Phocidae	+214	±42	0.000	+158	±34	0.000	+50	±10

Arctocephalus (Acep): fur seals other than *Callorhinus ursinus (Curs)*, northern fur seal. Otariinae: sea lions. *Zalophus californianus (Zcal)*: California sea lion. *Eumetopias jubatus (Ejub)*: northern sea lion. *Cystophora cristata (Ccri)*: hooded seal. *Mirounga*: elephant seals. The Phocomorpha hypothesis, tree b, postulates a sister group relationship between Odobenidae (walruses) and Phocidae (true seals) to the exclusion of Otariidae (sea lions and fur seals). Trees c–g refer to relationships within the otariids and trees h–j to the relationship between *Cystophora/Mirounga* and remaining phocids. In tree c *Acep* and *Curs* are the basal sister group to monophyletic Otariinae. In tree d Otariinae is paraphyletic with *Callorhinus* on a terminal branch together with the four *Arctocephalus* species. Trees a–e and h–j refer to maximum-likelihood (ML) analysis of amino acid sequences, while trees f (neighbor joining) and g (Maximum parsimony) were based on nucleotide analysis of 1st and 2nd codon positions. The ML analysis was based on rate homogeneity (hom) as well as rate heterogeneity (het) with eight categories of variable sites and gamma distributed rates. L denotes the differences in the log likelihood and pSH the probability according to the Shimodaira–Hasegawa test. In the MP analysis steps give the number of additional mutations (steps) of alternative topologies relative to best tree and their standard deviations.

King (1966) but still favored in some studies (e.g. Koretsky, 2001). The joining of *Mirounga/Cystophora* on a common branch is incompatible with the current results, Table 2h–j. de Muizon (1982) joined the hooded, ribbon and harp seals in the Cystophorini as the sister group to the harbor, grey and ringed seals. That arrangement is incongruent with the mitogenomic findings and, as also noted by the author, his proposal was in contrast to previous cytogenetic evidence (Arnason, 1972). Cystophorini as defined by de Muizon (1982) would, in cytogenetic context, require that the $2n = 32$ Phocini karyotype had arisen at two different occasions. The same karyological problem arises with the tree (Koretsky, 2001) in which the bearded seal (*Erignathus barbatus*) with $2n = 34$ chromosomes resides among the Phocini, which have $2n = 32$ chromosomes. The pronounced karyological uniformity in marine mammals in general (Fay et al., 1967; Arnason, 1972, 1974, 1977, 1982) makes both these propositions implausible.

The basal Phocinae divergence between *Erignathus* and *Cystophora/Phocini* was strongly supported, as was also that between *Cystophora* and Phocini. The basal split within the Phocini was between the ribbon and harp seals (Histriophocina) and a branch (Phocina) that contains the remaining Phocini species, i.e. the harbor, largha, ringed, grey, Caspian, and Baikal seals. Within the Phocina a sister group relationship between the harbor and largha seals received maximum support and a sister group relationship between the grey and Caspian seals was also generally recognized (albeit with inconclusive support), but other relationships were poorly resolved. Phocina relationships were examined further in nt analyses that included all codon positions of the twelve protein-coding mt genes, the 12S and 16S rRNA genes, and the control regions less their repeated parts. In spite of the size of this extended data set (14,336 nt excluding gaps) the relationships within the

group remained inconclusively resolved even though there was again a general preference for a basal split between the largha/harbor seals and the remaining Phocina species and for the sister group relationship between the grey and Caspian seals to the exclusion of the Baikal seal. The limited resolution in this part of the tree suggests extensive diversification within a limited period of time.

The similar cranial (Burns and Fay, 1970) and postcranial (King, 1966) morphology of the Phocini has traditionally been taken as suggesting recent divergences. However, the current analyses suggest that Phocini in general diverged much earlier than commonly conceived. The morphological conservatism within the Phocini is apparent when compared to the morphological differentiation within the Lobodontini. As evident in Fig. 1 the depths of the divergences within the Phocini are similar to those of the four Lobodontini species, each of which is included in a separate genus. Also the molecular difference between the two monk seals exceeds that of many pinniped genera. These two cases exemplify well the limited agreement that may exist between morphologically based taxonomic levels and molecular distinction.

The position of the grey seal, genus *Halichoerus*, amidst species belonging to genus *Phoca* is problematic in the context of systematic nomenclature (see also Chapskii, 1955a, and McLaren, 1975). Arnason et al. (1995) drew attention to this inconsistency and suggested that the name *Halichoerus* should be abolished and the grey seal placed under the generic name *Phoca*. If so, the scientific name of the grey seal should be *Phoca grypa*.

3.2. The area of pinniped origin

In the current study, we have used molecular estimates of the ages of different pinniped divergences as an auxiliary

to paleontology and phylogeny in the examination of pinniped evolution and zoogeography. The calibration point applied was the divergence between feliform and caniform carnivores set at 52 MYA (Flynn and Galiano, 1982). As previously demonstrated (Arnason et al., 2000) the age of this calibration point (F/C-52) is consistent with three paleontologically well-established non-carnivoran calibration points, viz. A/C-60, the divergence between ruminant artiodactyls and cetaceans 60 MYA (Arnason et al., 1996), E/R-50, the divergence between equids and rhinocerotids 50 MYA (Arnason et al., 1998), and O/M-35, the divergence between odontocetes and mysticetes 35 MYA (Arnason et al., 2004) (originally placed at 33 MYA in Arnason et al., 2000). The minimum fossil-based age of the divergence between Feliformia and Caniformia is 43 MY based on a position of the extinct Viverravidae outside rather than within the Feliformia (Wesley-Hunt and Flynn, 2005). This minimum age does not refute a divergence 52 MYA, however, and we have therefore maintained F/C-52 as a calibration point due to its agreement with the three previously established non-carnivoran calibration points.

Fig. 2 shows the estimated times of pinniped divergences applying F/C-52 to the aa data set of twelve mt protein-coding genes. The estimates suggest that the basal pinniped split between Phocidae and Otarioidea took place ≈ 33 MYA. This dating exceeds by ≈ 5 MY the age (≈ 28 MY) of the oldest phocid fossil, the “Oligocene seal” from late Oligocene formations near Charleston, South Carolina, USA (Koretsky and Sanders, 2002). The Enaliarctinae (Mitchell and Tedford, 1973) from late Oligocene sites in Oregon, USA, constitute the earliest otarioid lineage so far described. The age of the oldest known *Enaliarctos* fossils is 25–27 MY (Berta, 1991). Thus, provided the molecular estimate of the divergence between Otarioidea and Phocidae is reasonably accurate, the ages of these fossils allow ≈ 5 MY for the establishment of morphological characteristics that permit their identification as belonging to either Otarioidea or Phocidae.

The monophyly of the Pinnipedia and the occurrence of the earliest pinniped fossils on both the Atlantic (phocids) and Pacific (otarioids) coasts of N America strongly suggest that pinnipeds originated on this continent. Previous studies of pinniped origin, irrespective of whether they were based on their monophyly or diphyly, have generally assumed that pinnipeds originated on the shores of oceans or large bodies of water. We find it more plausible, however, that the initial adaptation to the aquatic environment took place in a more restricted (even genetically so) and less exposed habitat. We therefore postulate that the pinnipeds after an initial non-marine (lacustrine, riverine or estuarine) phase of evolution entered the marine environment, probably from the southern shores of N America with the ancestors of extant phocids taking an eastward route into Atlantic waters and those of the otarioids dispersing in a westward direction into the Pacific. The postulate that the pinnipeds did not originate on wide ocean shores inevitably raises the question whether the split between Phocidae and Otarioidea occurred before or at their entrance into the

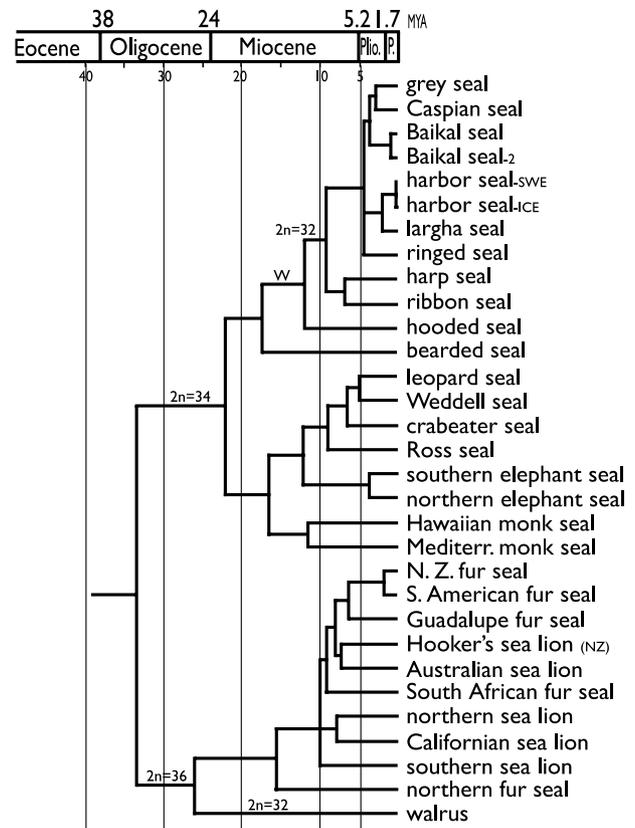


Fig. 2. Molecular estimates of pinniped divergences applying as a calibration point the divergence between feliform and caniform carnivores set at 52 million years ago (MYA). The tree includes the chromosome numbers of different lineages. The Phocini are characterized by the $2n = 32$ chromosomal synapomorphy relative to other true seals which have $2n = 34$. W signifies the white natal coat characterizing the Cystophorini/Phocini branch, as compared to the brown/greyish color of other phocids. The 33 MYA estimate of the divergence between Otarioidea and Phocidae exceeds by ≈ 5 MY the age of the oldest phocid fossils. One SD for estimates 5 MYA is about 10%. For the deepest divergences the corresponding percentages are 3–5%.

marine environment. The slow morphological evolution in pinniped lineages such as the Phocini and the Otariinae/Arctocephalinae complex is well established. If this morphological conservatism is related to the marine environment we find it likely that the initial morphological differentiation between Phocidae and Otarioidea took place before they entered this environment.

3.3. Otarioid zoogeography

The basal otarioid split between Odobenidae and Otariidae is in agreement with the traditional paleontological and morphological interpretation of early otarioid evolution (e.g. Mitchell, 1968, 1975; Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Repenning et al., 1979). The molecular estimate of the Otariidae/Odobenidae divergence placed it close to the age of the oldest enaliarctid fossils. The oldest typical odobenid fossils, the Imagotariinae (Mitchell, 1968), are about 14 MY old (Mitchell, 1968; Repenning and Tedford, 1977; Repenning et al., 1979). They are thus much younger than the molecular estimate of

the divergence between Odobenidae and Otariidae as are also the oldest otariid fossils. The absence of typical odobenid and otariid fossils in layers that contain a sequence of enaliarctid fossils may suggest that the pace of morphological evolution was slow in the lineages of early odobenids and otariids, making it difficult to paleontologically define their origins.

The Odobenidae diversified and flourished in the N Pacific in the Miocene with a few species also occurring in the N Atlantic. The single extant species, which probably evolved from sub-tropical/tropical ancestors, became isolated in the Atlantic well before the rise of Isthmus of Panama and gradually adapted to colder conditions in the N Atlantic and the Arctic, from where it presumably re-colonized the N Pacific in Pleistocene times (Repenning and Tedford, 1977; Repenning et al., 1979).

The basal split between *Callorhinus* and the other otariid species, dated to ≈ 16 MYA, corroborates the common understanding of early otariid evolution in the N Pacific. It is conceivable that the split between *Eumetopias/Zalophus*, *Otaria*, and the branch containing the remaining otariids took place in the same region with *Otaria* ancestors colonizing the W coast of S America for a later dispersal to the south Atlantic side of the continent with the ancestors of *Eumetopias* and *Zalophus* remaining in the northern Pacific. It is plausible that also the split between *Arctocephalus pusillus* and the branch containing the three other *Arctocephalus* species and *Phocarctos* and *Neophoca* took place in the northern Pacific with *A. pusillus* colonizing South Africa and the ancestors of *Phocarctos*, *Neophoca*, *Arctocephalus australis*, and *A. forsteri* colonizing the southern Pacific with *Arctocephalus townsendi* remaining in the N Pacific. The tree does not exclude alternative scenarios, however. Thus the split between *A. pusillus* and the remaining taxa may have taken place in southern oceans. This could make up a sequence of events ending with a secondary *Arctocephalus* dispersal (*A. townsendi*) into the NE Pacific. The paleontological record does not provide an answer to the question of otariid colonization of southern oceans, and considering the limited morphological distinction among extant *Arctocephalus* and Otariinae, even an extensive record might not provide an answer to this question.

Wynen et al. (2001) examined otariid relationships and biogeography in a molecular study (≈ 700 nt) that included all extant otariid species. Like the current study the findings were inconsistent with monophyly of both *Arctocephalus* and sea lions, but the basal position of *Neophoca* in the tree favored by Wynen et al. (2001) differs notably from that of the current study.

3.4. Phocid zoogeography

Previous phocid zoogeographical studies have in general concentrated on the relatively rich fossil history of phocids in Europe, notably the Paratethys region. However, these studies were undertaken prior to the introduction of phylogenies based on large data sets such as those of complete

mt genomes, and without considering the implications of the “Oligocene seal” from South Carolina (Koretsky and Sanders, 2002) for the interpretation of both pinniped origin and phocid evolution. The age of this fossil surpasses by 12–13 MY the mid Miocene age (≈ 15 MY) of *Devinophoca claytoni*, the oldest European phocid fossil hitherto described (Koretsky and Holec, 2002). The greatly different age of these two fossils strongly suggests that the early phase of phocid evolution took place in the Atlantic coastal areas of N America rather than in those of W Europe or the Paratethys region.

The molecular estimates placed the divergence between Monachinae and Phocinae at ≈ 22 MYA. This dating is congruent with the age (≈ 18 MY) of *Leptophoca lenis* (True, 1906; Koretsky, 2001), the oldest Phocinae fossil hitherto identified. The location of *Leptophoca* in SE USA also supports our hypothesis that early phocid evolution took place in southeastern N America and not in Europe.

The Monachinae divergence between Monachini and Miroungini/Lobodontini was dated to ≈ 16 MYA and that between Miroungini and Lobodontini to ≈ 13 MYA. Based on the estimate of the divergence between Monachini and Miroungini/Lobodontini we find it likely that this divergence, and probably also that between Miroungini and Lobodontini, took place in coastal areas of southern N America. On the basis of Peruvian fossil finds it has been argued (Repenning et al., 1979; de Muizon, 1982) that the most probable southward route of the Lobodontini was along the W coast of South America even though a southward colonization via the Atlantic was not excluded. However, in the absence of fossil data the current phylogenetic results do not allow speculations as to Lobodontini dispersal within the southern oceans and Antarctic waters. The northern elephant seal has usually been taken as a late colonist (from the south) of the NE Pacific. The molecular estimate, ≈ 4 MY, of the divergence between the northern and southern elephant seals may, however, allow an alternative explanation, namely that the divergence between the two species was the result of the rise of Isthmus of Panama and a coincident disruption of a *Mirounga* population that was ancestral to the two now living species.

The depth of the split between the Hawaiian and Mediterranean monk seals is of interest to the discussion of phocid zoogeography as this divergence has commonly been related to a Monachini colonization of the Caribbean and Hawaii via a westward route from Europe (Repenning et al., 1979; de Muizon, 1982). However, the age of the oldest Monachinae fossil, the Late/Middle Miocene (≈ 14.5 MY) *Monotherium wymani* from Virginia, exceeds the age of the oldest Monachinae fossils in Europe. In contrast to the hypothesis of a trans-Atlantic *Monachus* dispersal from Europe to America we therefore hypothesize that the split between the ancestors of the Hawaiian and Mediterranean monk seals, like other basal phocid divergences, took place in the coastal areas of southern North America. We cannot postulate whether the estimated time of the intra-*Monachus* divergence, ≈ 13 MYA, was coincident with an eastward

trans-Atlantic dispersal that gave rise to the Mediterranean monk seal or whether that dispersal occurred later or when the *Monachus* colonization of Hawaii took place. However, the scenario we propose appears to show greater compatibility with molecular data and the fossil record than the traditional hypothesis for *Monachus* dispersal.

The deepest Phocinae split, that between Erignathini and Cystophorini/Phocini, was dated to ≈ 17 MYA and that between Cystophorini and Phocini to ≈ 12 MYA (Fig. 2). *Erignathus* feeds largely on benthic invertebrates, while *Cystophora* and Phocini are primarily fish feeders. It is probable that the divergence between Erignathini and Cystophorini/Phocini was coincident with a northward and eastward Phocinae expansion in the N Atlantic and a shift towards more pelagic feeding behavior. The white natal coat of Cystophorini/Phocini (shed *in utero* in the hooded and harbor seals), as compared to the greyish/brown natal coat of *Erignathus* and all Monachinae seals, suggests that Cystophorini/Phocini had adapted to cold climate prior to their divergence. Deep sea drilling at the Lomonosov Ridge during the summer of 2004 has yielded evidence of Arctic glacial conditions in mid Miocene or even earlier (Prof. Jan Backman, personal communication). This makes it plausible that ice-breeding and the origination of the white natal coat of Cystophorini/Phocini was triggered by these conditions. Thus, this coat represents a derived state relative to the coat color of more basal phocid lineages. Of the two sister taxa, the largha and the harbor seal, the former has maintained a white natal coat. This suggests that the *in utero* shedding of the white natal coat in the harbor seal arose secondarily after the divergence of the two species. It is noteworthy that Chapskii (Chapskii, 1955a) and McLaren (McLaren, 1975) argued along the same lines in the absence of the currently available phylogenetic information. The presence of two pairs of mammary teats in *Erignathus* is another ancestral trait that separates *Erignathus* (albeit without zoogeographical implications) from all other northern phocids, which have only one pair of teats. The same kind of reduction has occurred in the Monachinae in which the Monachini have two pairs of teats as compared to only one pair in Miroungini and Lobodontini.

The dating estimates placed the divergence between Histriophocina and Phocina at ≈ 9 MYA. This implies that the $2n = 32$ chromosomal Phocini karyotype originated from the $2n = 34$ chromosomal karyotype sometime in the interval between 12 and 9 MYA. In the light of the slow karyological evolution in marine mammals (Arnason, 1972, 1982) it is likely that the $2n = 32$ karyotype arose in a small isolated population.

The earliest European Phocini fossils are 11–12 MY old from Sarmatian Paratethys. These fossils as well as several younger Paratethyan fossils have been assigned to a number of different genera (e.g. Koretsky, 2001). The position of these genera in the morphological tree (Koretsky, 2001) suggests that the descendants of Paratethyan phocids are not represented amidst extant Phocina. Compared to the limited morphological differentiation within the Phocini

(Burns and Fay, 1970) it is apparent that the pace of differentiation of the Paratethyan phocids was on a strikingly different scale, probably as the result of adaptation to different niches in a shrinking Paratethys. The deep (≈ 7 MY) divergence between the two extant Histriophocina species, the harp (north Atlantic, Arctic) and ribbon (north Pacific) seals, is notable. The molecular estimate of their divergence implies that they separated long before the opening up of the Bering Strait. It is probable that these two pelagic species established themselves in different parts of the Arctic basin and that the ribbon seal entered the north Pacific after the opening up of the Bering Strait.

The limited molecular resolution among the Phocina suggests that their basal radiations took place within a narrow temporal window. The molecular estimates place these events at ≈ 4.5 MYA. It is possible that the basal radiation of the Phocina was triggered by a geological change that altered the ecological conditions in the Arctic and the N Atlantic. The opening of the Bering Strait ≈ 5.4 MYA (Gladenkov et al., 2002) would be one such possibility. Another possible explanation would be the gradual rise of the Isthmus of Panama and the coincident change of circulation in the North Atlantic.

The presence of landlocked seals in the Caspian Sea and Lake Baikal has been an enigmatic zoogeographical question. A close relationship between these species and the ringed seal has been commonly assumed and the three species have frequently been included in a genus of their own, *Pusa*. The current phylogenetic findings are at variance with that proposal as they rather favor a position of the grey seal within “*Pusa*” as the sister group to the Caspian seal. The Baikal seal was in turn sister to the branch containing the Caspian and grey seals.

McLaren (1960) reviewed hypotheses related to the origin of the Caspian and Baikal seals. The hypothesis favored at that time by W European and U.S. scientists was that the divergences between the three “*Pusa*” species were of a late (Pleistocene) date, while the opposite view, advocated by some East-European scientists (notably by Chapskii, 1955b), was that these divergences and the colonization (from the north) of the Paratethyan (Ponto-Caspian) basin had taken place close to the Miocene/Pliocene boundary. The current molecular estimates are distinctly incongruent to the proposal of a late “*Pusa*” dispersal in connection with Pleistocene glaciations. The “late” invasion hypothesis has also been dismissed in recent analyses of three mt genes (*cytb*, COI, and COII), which placed the isolation of the Caspian and Baikal seals in mid Pliocene or earlier (Palo and Väinölä, 2006). A Pliocene entrance into the Caspian basin from the northern seas is consistent with analyses of comparable molecular data of Arctic and Caspian invertebrates (Väinölä, 1995; Väinölä et al., 2001).

The limited resolution among the ringed, grey, Caspian, and Baikal seals does not allow the drawing of firm conclusions regarding the sequence of events leading to the isolation of seals in Lake Baikal. A colonization of Lake Baikal

via the eastern part of an extended Caspian Sea has been proposed (Chapksii, 1955b; McLaren, 1960). That scenario would not be refuted by the favored topology. Similarly, the current results as such would not refute a primary “Pusa” colonization of Lake Baikal and a subsequent colonization of the Caspian Sea. However, in the absence of geological evidence for these hypotheses the most plausible explanation to the presence of seals in Lake Baikal is an independent colonization of Lake Baikal from the Arctic Ocean via Lena/Yenisei.

With the exception of the monk seals, all extant phocids live in temperate to cold waters. In the light of the phocid tree and the N American location of all earliest phocid fossils we hypothesize that the early phase of phocid evolution took place in the relatively warm waters of the southeastern parts of this continent and that the basal phocid split between Monachinae and Phocinae occurred here prior to the phocid colonization of colder environments. We find it likely that the white natal coat of Cystophorini and Phocini is indicative of adaptation to such environments and ice-breeding. If so, our hypothesis including the molecular estimates is borne out by non-biological information, namely the recent (2004, summer) geochronological investigations of the Lomonosov Ridge, which have shown much colder conditions in the Arctic basin in Mid-Miocene times than previously acknowledged.

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References

- Adachi, J., Hasegawa, M., 1996. MOLPHY v. 2.3. Comput. Sci. Monogr. 28, 1.
- Arnason, U., 1972. The role of chromosomal rearrangement in mammalian speciation with special reference to Cetacea and Pinnipedia. *Hereditas* 70, 113–118.
- Arnason, U., 1974. Comparative chromosome studies in Pinnipedia. *Hereditas* 76, 179–226.
- Arnason, U., 1977. The relationship between the four principal pinniped karyotypes. *Hereditas* 87, 227–242.
- Arnason, U., 1982. Karyotype stability in marine mammals. *Cytogenet. Cell Genet.* 33, 274–276.
- Arnason, U., Widegren, B., 1986. Pinniped phylogeny enlightened by molecular hybridizations using highly repetitive DNA. *Mol. Biol. Evol.* 3, 356–365.
- Arnason, U., Gullberg, A., Widegren, B., 1991. The complete nucleotide sequence of the mitochondrial DNA of the fin whale. *J. Mol. Evol.* 33, 556–568.
- Arnason, U., Johnsson, E., 1992. The complete mitochondrial DNA sequence of the harbor seal, *Phoca vitulina*. *J. Mol. Evol.* 34, 493–505.
- Arnason, U., Bodin, K., Gullberg, A., Ledje, C., Mouchaty, S., 1995. A molecular view of pinniped relationships with particular emphasis on the true seals. *J. Mol. Evol.* 40, 78–85.
- Arnason, U., Gullberg, A., Janke, A., Xu, X., 1996. Pattern and timing of evolutionary divergences among hominoids based on analyses of complete mtDNAs. *J. Mol. Evol.* 43, 650–661.
- Arnason, U., Gullberg, A., Janke, A., 1998. Molecular timing of primate divergences as estimated by two nonprimate calibration points. *J. Mol. Evol.* 47, 718–727.
- Arnason, U., Gullberg, A., Gretarsdottir, S., Ursing, B., Janke, A., 2000. The mitochondrial genome of the sperm whale and a new molecular reference for estimating eutherian divergence dates. *J. Mol. Evol.* 50, 569–578.
- Arnason, U., Adegoke, J.A., Bodin, K., Born, E.W., Esa, Y.B., Gullberg, A., Nilsson, M., Short, R.V., Xu, X., Janke, A., 2002. Mammalian mitogenomic relationships and the root of the eutherian tree. *Proc. Natl. Acad. Sci. USA* 99, 8151–8156.
- Arnason, U., Janke, A., 2002. Mitogenomic analyses of eutherian relationships. *Cytogenet. Genome Res.* 96, 20–32.
- Arnason, U., Gullberg, A., Janke, A., 2004. Mitogenomic analyses provide new insights into cetacean origin and evolution. *Gene* 333C, 27–34.
- Berta, A., 1991. New *Enaliarctos* (Pinnipedimorpha) from the Oligocene and Miocene of Oregon and the role of “enaliarctids” in pinniped phylogeny. *Smithson. Contrib. Paleobiol.* 69, 1–33.
- Berta, A., Wyss, A.R., 1994. Pinniped phylogeny. *Proc. San Diego Soc. Nat. Hist.* 29, 33–56.
- Brunner, S., 2003. Fur seals and sea lions (Otariidae): identification of species and taxonomic review. *Systematics Biodiv.* 1, 339–439.
- Burns, J.J., Fay, F.H., 1970. Comparative morphology of the skull of the ribbon seal, *Histriophoca fasciata*, with remarks on systematics of Phocidae. *J. Zool. London* 161, 363–394.
- Chapksii, K.K., 1955a. An attempt at revision of the systematics and diagnostics of the subfamily Phocinae. *Akad. Nauk. SSSR Tr. Zool. Inst.* 17, 160–199.
- Chapksii, K.K., 1955b. On the problem of the history of development of the Caspian and Baikal seals. *Akad. Nauk. SSSR Tr. Zool. Inst.* 17, 200–216.
- Davies, J.L., 1958. The Pinnipedia: an essay in zoogeography. *Geogr. Rev.* 48, 474–493.
- Davis, C.S., Delisle, I., Stirling, I., Siniff, D.B., Strobeck, C., 2004. A phylogeny of extant Phocidae inferred from complete mitochondrial DNA coding regions. *Mol. Phylogenet. Evol.* 33, 363–377.
- de Jong, W.W., Goodman, M., 1982. Mammalian phylogeny studied by sequence analysis of the eye lens protein alpha-crystallin. *Z. f. Säugetierek.* 5, 257–276.
- Delisle, I., Strobeck, C., 2005. A phylogeny of the Caniformia (order Carnivora) based on 12 complete protein-coding mitochondrial genes. *Mol. Phylogenet. Evol.* 37, 192–201.
- Deméré, T.A., Berta, A., Adam, P.J., 2002. Pinnipedimorph evolutionary biogeography. *Bull. Am. Mus. Nat. Hist.* 279, 32–76.
- de Muizon, C., 1982. Phocid phylogeny and dispersal. *Ann. S. Afr. Mus.* 89, 175–213.
- Fay, F.H., Rausch, V.R., Feltz, E.T., 1967. Cytogenetic comparison of some pinnipeds (Mammalia: Eutheria). *Can. J. Zool.* 45, 773–778.
- Felsenstein, J., 1993. *Phylogenetic Inference Programs (PHYLIP)*, Univ. of Washington and University Herbarium, Univ. of California, Seattle.
- Flynn, J.J., Galiano, H., 1982. Phylogeny of Early Tertiary Carnivora, with a description of a new species of Protictis from the Middle Eocene of northwestern Wyoming. *Am. Mus. Novit.* 2725, 1–64.
- Fyler, C.A., Reeder, T.W., Berta, A., Antonelis, G., Aguilar, A., Androukaki, E., 2005. Historical biogeography and phylogeny of monachine seals (Pinnipedia: Phocidae) based on mitochondrial and nuclear DNA data. *J. Biogeogr.* 32, 1267–1279.
- Gladenkov, A.Y., Oleinik, A.E., Marincovich, L., Barinov, K.B., 2002. A refined age for the earliest opening of Bering Strait. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 183 (3–4), 321–328.

- Janke, A., Feldmaier-Fuchs, G., Thomas, W.K., von Haeseler, A., Paabo, S., 1994. The marsupial mitochondrial genome and the evolution of placental mammals. *Genetics* 137, 243–256.
- King, J.E., 1966. Relationship of the hooded and elephant seals (genera *Cystophora* and *Mirounga*). *J. Zool.* 158, 385–398.
- Koretsky, I.A., 2001. Morphology and systematics of Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the north Atlantic region. *Geologica Hung. Ser. Palaeontologica Fasc.* 54, 1–109.
- Koretsky, I.A., Holec, P., 2002. A primitive seal (Mammalia: Phocidae) from the early middle Miocene of central Paratethys. *Smithson. Contrib. Paleobiol.* 93, 163–178.
- Koretsky, I., Sanders, A.E., 2002. Paleontology of the Late Oligocene Ashley and Chandler Bridge formations of South Carolina, 1: Paleogene pinniped remains; the oldest known seal (Carnivora: Phocidae). *Smithson. Contrib. Paleobiol.* 93, 179–183.
- Ledje, C., Arnason, U., 1996a. Phylogenetic analyses of complete cytochrome *b* sequences of the order Carnivora with particular emphasis on the Caniformia. *J. Mol. Evol.* 42, 135–144.
- Ledje, C., Arnason, U., 1996b. Phylogenetic relationships within caniform carnivores based on the analyses of the mitochondrial 12S rRNA gene. *J. Mol. Evol.* 43, 641–649.
- McLaren, I.A., 1960. On the origin of the Caspian and Baikal seals and the paleoclimatological implication. *Am. J. Sci.* 258, 47–65.
- McLaren, I.A., 1975. A speculative overview of phocid evolution. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* 169, 43–48.
- Mitchell, E.D., 1968. The Mio-Pliocene pinniped Imagotaria. *J. Fish. Res. Board Can.* 25, 1843–1900.
- Mitchell, E.D., 1975. Parallelism and convergence in the evolution of Otariidae and Phocidae. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* 169, 12–26.
- Mitchell, E.D., Tedford, R.H., 1973. The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bull. Am. Mus. Nat. Hist.* 151, 201–284.
- Palo, U., Väinölä, R., 2006. The enigma of the landlocked Baikal and Caspian seals addressed through phylogeny of phocine mitochondrial sequences. *Biol. J. Linn. Soc.* 88, 61–72.
- Paton, T.A., Baker, A.J., 2006. Sequences from 14 mitochondrial genes provide a well-supported phylogeny of the Charadriiform birds congruent with the nuclear RAG-1 tree. *Mol. Phylogenet. Evol.* 3, 668–687.
- Repenning, C.A., Peterson, R.S., Hubbs, C.L., 1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. *Antarctic Res. Ser.* 18, 1–34.
- Repenning, C.A., Tedford, R.H., 1977. Otarioid seals of the Neogene. *U. S. Geol. Surv. Prof. Pap.* 992, 1–93.
- Repenning, C.A., Ray, C.E., Grigorescu, D., 1979. Pinniped biogeography. In: Gray, J., Boucot, A.J. (Eds.), *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Oregon State University Press, pp. 357–369.
- Sanderson, J., 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* 19, 101–109.
- Sarich, V.M., 1969. Pinniped phylogeny. *Syst. Zool.* 18, 416–422.
- Slater, P.L., 1897. On the distribution of marine mammals. *Proc. Zool. Soc. London*, 349–359.
- Strimmer, K., von Haeseler, A., 1996. Quartet puzzling: a quartet maximum-likelihood method for reconstructing tree topologies. *Mol. Biol. Evol.* 13, 964–969.
- Swofford, D.L., 2002. PAUP*, Version 4. Sinauer Ass., Sunderland, Massachusetts.
- Tamura, K., Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10, 512–526.
- True, W., 1906. Description of a new genus and species of fossil seal from the Miocene of Maryland. *Proc. U. S. Natl. Mus.* 30, 835–840.
- von Boetticher, H., 1934. Die geographische Verbreitung der Robben. *Z. f. Säugetiere* 9, 359–368.
- Väinölä, R., 1995. Origin and recent endemic divergence of a Caspian *Mysis* species flock with affinities to the “glacial relict” crustaceans in boreal lakes. *Evolution* 49, 1215–1223.
- Väinölä, R., Vainio, J.K., Palo, J.U., 2001. Phylogeography of “glacial relict” *Gammaracanthus* (Crustacea, Amphipoda) from boreal lakes and the Caspian and White seas. *Can. J. Fish. Aquat. Sci.* 58, 2247–2257.
- Wesley-Hunt, G.D., Flynn, J.J., 2005. Phylogeny of the Carnivora: basal relationships among the Carnivoramorpha, and assessment of the position of “Miadoidea” relative to Carnivora. *J. Syst. Paleontol.* 3, 1–28.
- Wynen, L.P., Goldsworthy, S.D., Insley, S.J., Adams, M., Bickham, J.W., Francis, J., Gallo, J.P., Hoelzel, A.R., Majluf, P., White, R.W.G., Slade, R., 2001. Phylogenetic relationships within the family Otariidae (Carnivora). *Mol. Phylogenet. Evol.* 21, 270–284.
- Wyss, A.R., Flynn, J.J., 1993. A phylogenetic analysis and definition of the Carnivora. In: Szalay, F.S., Novacek, M.J., McKenna, M.C. (Eds.), *Mammal Phylogeny 2, Placentals*. Springer-Verlag, New York, Berlin, Heidelberg, pp. 32–52.
- Xu, X., Janke, A., Arnason, U., 1996. The complete mitochondrial DNA sequence of the greater Indian rhinoceros, *Rhinoceros unicornis*, and the phylogenetic relationship among Carnivora, Perissodactyla and Artiodactyla (+ Cetacea). *Mol. Biol. Evol.* 13, 1167–1173.