

A PHYLOGENETIC PERSPECTIVE ON THE EVOLUTION OF REPRODUCTIVE BEHAVIOR IN PAGOPHILIC SEALS OF THE NORTHWEST ATLANTIC AS INDICATED BY MITOCHONDRIAL DNA SEQUENCES

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The ice-breeding (pagophilic) habits and relatively short lactation periods of several species of "true" seals (Phocidae) of the Northwest Atlantic, including the harp seal (*Pagophilus*), bearded seal (*Erignathus*), and hooded seal (*Cystophora*), usually are assumed to have evolved in parallel. Current taxonomy regards *Pagophilus* and ringed seals (*Pusa*) along with harbor seals (*Phoca vitulina*) as subgenera of *Phoca*, unites *Phoca* (sensu lato) together with gray seals (*Halichoerus*) and *Erignathus* in the subfamily Phocinae, and places *Cystophora* with elephant seals (*Mirounga*) in a separate subfamily, Cystophorinae. Cladistic analysis of variation in the DNA sequence of the mitochondrial cytochrome *b* gene identifies three clades among northern seals: *Phoca-Pusa-Halichoerus*, *Cystophora-Pagophilus*, and *Erignathus*. *Erignathus* is the sister group to the other species examined. Each clade may be regarded as a tribe of the subfamily Phocinae (the Phocini, Cystophorini, and Erignathini, respectively). The phylogeny suggests that the ice-breeding habit and associated brief lactation are ancestral characters for the Phocinae and that instances of fast-ice or terrestrial breeding are convergences on the ancestral condition in other phocid subfamilies.

Key words: reproductive behavior, lactation, pagophilic, mitochondrial DNA, cytochrome *b*, Phocidae, molecular phylogeny

"True" seals (Phocidae) of the Northwest Atlantic, harbor seals (*Phoca vitulina*), harp seals (*Phoca* [*Pagophilus*] *groenlandica*), ringed seals (*Phoca* [*Pusa*] *hispida*), gray seals (*Halichoerus grypus*), bearded seals (*Erignathus barbatus*), and hooded seals (*Cystophora cristata*), exhibit a variety of reproductive patterns associated with different breeding substrates (Bonner, 1984; Bowen, 1991; Kovacs and Lavigne, 1985; Oftedal et al., 1987). Terrestrial-breeding species have relatively long lactation (24 days in *Phoca vitulina*—Muelbert, 1991), whereas species that breed on pack ice have brief but intense lactation. For example, *Cystophora* has the briefest lactation known

for any mammal (4 days—Bowen et al., 1985), but the milk is of high quality (Oftedal et al., 1987) and the young spend a large part of the day nursing (Perry and Stenson, 1992). Typically, patterns of lactation have been explained in adaptive terms, with reference to the ecology of individual species. Those species that give birth on stable substrates have extended lactation, whereas those that give birth on unstable pack ice have briefer lactation that permits young to achieve nutritional independence before the ice shifts or melts.

We believe that a preferable approach to the use of adaptive scenarios for separate species is to generate hypotheses about the

evolution of morphological and behavioral features based on well-resolved phylogenies (Brooks and McLennan, 1991). The essence of this approach is that similar character states shared among a group of species may be more concisely explained as an evolutionary inheritance from their common ancestor, rather than as the result of similar ecological constraints acting on each species individually. For example, de Muizon (1982) used a cladistic phylogeny of temperate and Antarctic seals to explain their origin and biogeographic dispersal. Miller (1991) showed that the similar patterns of reversed sexual dimorphism in these same species are best interpreted as the result of common ancestry, once their monophyletic origin is realized.

Variation in breeding behavior of phocid seals is difficult to explain in light of their current classification. The Phocidae usually are considered to consist of three subfamilies: northern seals (Phocinae), southern seals including Antarctic Weddell seals (*Leptonychotes*) and temperate monk seals (*Monachus*; Monachinae), and elephant seals (*Mirounga*) together with hooded seals (Cystophorinae). Seals of the Northwest Atlantic, with the exception of the hooded seal, are in the Phocinae. *Histiophoca* (which occurs outside the Northwest Atlantic), *Pusa*, and *Pagophilus* often are regarded as subgenera of *Phoca* (sensu lato); however, there is no general agreement as to their phylogenetic relationships (Wilson and Reeder, 1993). *Erignathus* and *Halichoerus* are morphologically distinctive genera (King, 1983). Hooded seals and elephant seals have been classified as the Cystophorinae on the basis of their distinctive incisor count (2/1 in both genera) and such superficial characters as their large size and prominent proboscis. However, King (1966) regarded the Cystophorinae as artificial and described several anatomical features that suggested *Mirounga* should be in the Monachinae and *Cystophora* in the Phocinae. This conclusion was supported by subsequent phenetic and cladistic anal-

yses (Burns and Fay, 1970; de Muizon, 1982). However, Cystophorinae is still retained in many standard works (e.g., Hall, 1981; Stains, 1984; Wilson and Reeder, 1993). Perhaps for this reason, ice-breeding in the phocines has been hypothesized to have evolved at least twice in parallel (Bonner, 1984). For example, harp seals and hooded seals, which are placed in separate subfamilies, are both pack-ice breeders with shortened lactation periods (Bowen, 1991; Oftedal et al., 1987).

The purpose of the present study was to clarify phylogenetic relationships among phocid seal species of the Northwest Atlantic to provide a framework in which to understand the evolution of their reproductive behavior. There is a powerful new tool for this purpose, direct comparison of DNA sequences, made possible by enzymatic amplification of selected portions of the genome by the polymerase chain reaction (Saiki et al., 1988). We chose a portion of the mitochondrial cytochrome *b* gene that has been investigated extensively and found to be useful for clarifying systematic relationships of closely related species and genera of other vertebrate groups (Bartlett and Davidson, 1991a; Birt-Friesen et al., 1992; Bowen et al., 1993; Carr and Hughes, 1993; Carr and Marshall, 1991; Hedges et al., 1993; Irwin et al., 1991; Kocher et al., 1989; McVeigh et al., 1991; Zhang and Ryder, 1993).

MATERIALS AND METHODS

Muscle tissue was collected from one individual each of *Cystophora*, *Erignathus*, *Halichoerus*, *Phoca* [*Pagophilus*] *groenlandica*, *Phoca* [*Pusa*] *hispida*, and *Phoca* [*Phoca*] *vitulina*. Within *Phoca* (sensu lato), subgenus names will be used hereafter for clarity; unless otherwise qualified, *Phoca* will refer to *Phoca vitulina* only. All collections were made under permit to G. B. Stenson, Department of Fisheries and Oceans, St. John's, Newfoundland. Extraction of DNA by an acid guanidinium thiocyanate-phenol technique, symmetric and asymmetric amplification of DNA by the polymerase chain reaction, and single-stranded DNA sequencing

	L	A	M	H	Y	T	S	D	T	T*	T	A	F	S	S	V	T	H	I	C	20
Phoca	cta	gcc	ata	cac	tac	acc	tca	gac	aca	acc	aca	gcc	ttc	tca	tca	gta	acc	cac	atc	tgc	60
Pusa	
Halichoerus	
Pagophilus	..gt	..ttggtt	
Cystophorat	..t	..ttgatt	
Erignathustttgatt	
Martesatt	...	ggttt	
	R	D	V	N	Y	G	W	I	I	R	Y	L*	H	A	N	G	A	S	M	F	40
Phoca	cga	gac	gta	aac	tac	ggc	tga	atc	atc	cgt	tat	ctt	cac	gca	aat	gga	gct	tcc	ata	ttt	120
Pusatc	
Halichoerusc	
Pagophilusaacc	
Cystophorataacc	
Erignathust	..ttaa	..at	..ctt	..c	
Martest	..cta	..c	..a	..a	..t	..cgc	
	F	I	C	L	Y	M	H	V	G	R	G	L	Y	Y	G	S	Y	T	F	T*	60
Phoca	ttc	atc	tgc	cta	tac	atg	cat	gta	gga	cga	gga	ctg	tat	tac	ggc	tcc	tac	aca	ttc	aca	180
Pusagat	
Halichoerusgat	
Pagophilusta	..cc	..ctt	
Cystophoraga	..cc	..ctt	
Erignathusga	..ca	..ct	..tt	..t	..t	..t	
Martesg	..t	..c	..c	..c	..cc	..a	..c	..t	..a	..t	..t	..t	..t	..c	..c	
	E	T	W	N	I	G	I	I	L	L	F	T	V*	M	A	T	A	F	M	S	80
Phoca	gag	aca	tga	aac	atc	ggc	att	atc	ctc	tta	ttc	acc	gtc	ata	gct	aca	gca	ttc	atg	ggc	240
Pusa	..aac	..gt	...	
Halichoerusac	..gt	...	
Pagophilus	..atcc	..g	
Cystophoratc	
Erignathus	..aa	..cca	...	
Martes	..at	..tcag	..a	..taa	..t	

FIG. 1.—Variation in the DNA sequences of six phocid seals and *Martes americana* within a 240-base-pair region of the mitochondrial cytochrome *b* gene. In the last six sequences, nucleotides are identical to those in the first sequence except where indicated. The top line gives the inferred amino-acid sequence according to the International Union of Biochemists single-letter code; amino-acid residues that are variable among phocids are indicated by asterisks. Numbers adjacent to the first and second lines indicate position numbers in the protein and nucleotide sequences, respectively.

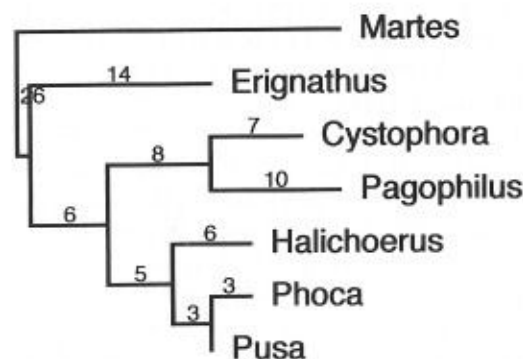


FIG. 2.—Cladogram of the mitochondrial cytochrome *b* sequences of six species of phocid seals and *Martes americana*.

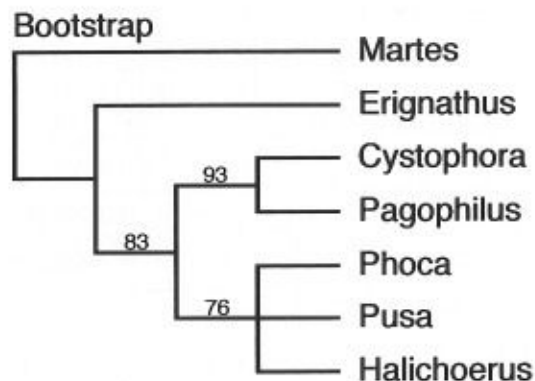


FIG. 3.—Bootstrap analysis of phylogenetic relationships among six species of phocid seals. Numbers on each branch indicate the percent occurrence of that group in 5,000 bootstrap replicates.

TABLE 1.—Sequence differences among six species of phocids and *Martes americana*. The estimated sequence differences (number of pairwise differences/240) are given in the upper one-half matrix. Numbers of nucleotide changes are given in the lower one-half matrix.

Taxon	Taxon						
	<i>Phoca</i>	<i>Pusa</i>	<i>Halichoerus</i>	<i>Pagophilus</i>	<i>Cystophora</i>	<i>Erignathus</i>	<i>Martes</i>
<i>Phoca</i>	0	0.013	0.033	0.083	0.079	0.108	0.175
<i>Pusa</i>	3	0	0.038	0.087	0.083	0.096	0.163
<i>Halichoerus</i>	8	9	0	0.104	0.100	0.108	0.175
<i>Pagophilus</i>	20	21	25	0	0.071	0.121	0.196
<i>Cystophora</i>	19	20	24	17	0	0.117	0.183
<i>Erignathus</i>	26	23	26	29	28	0	0.167
<i>Martes</i>	42	39	42	47	44	40	0

ing northern phocid taxa share six synapomorphies with respect to *Erignathus* and are grouped in 83% of bootstrap replications.

The genotypes of the seals differ from one another by 1.3–12.1%; *Martes* differs from the various species of seals by 16.3–19.6% (Table 1). To compare genetic differentiation among species of seals with that in another mammalian group, we calculated a UPGMA tree from the uncorrected sequence differences and included data from a group of ungulate species, *Odocoileus*, *Alces*, and *Bos* (Fig. 4). The topology of the UPGMA tree is identical to one of the two minimum-length parsimony trees

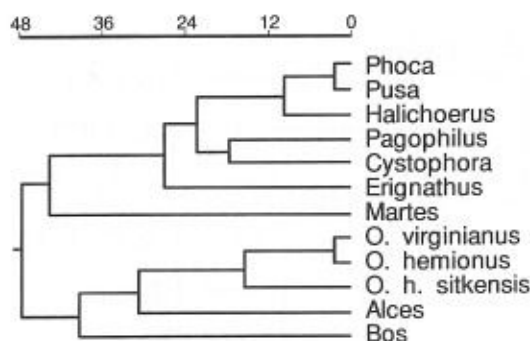


FIG. 4.—Phenogram (unweighted pair-group method using arithmetic averages) of relationships among six species of phocid seals, *Martes americana*, and five artiodactyl taxa, based on uncorrected, pairwise sequence differences from Table 1 and additional data from Carr and Hughes (1993) and Anderson et al. (1982).

(Fig. 2). The magnitude of the differences among *Phoca*, *Pusa*, and *Halichoerus* is on the same order as that between species and subspecies within *Odocoileus*. The differences between those three species of seals and the *Pagophilus*-*Cystophora* pair are slightly greater than the maximum difference between the species of *Odocoileus*. All of the seals examined are more similar to each other than are different cervid genera in the same subfamily. *Martes* is about as different from the phocids as is *Bos* from the deer, where the latter belong to separate families within the same suborder.

After completion of our analysis of northern phocids, DNA sequences from two monachine species (*Leptonychotes* and *Monachus*) became available (Árnason et al., 1993). With *Martes* as the outgroup and all substitutions weighted equally, inclusion of these species gives two minimum-length trees of length = 112 (consistency index = 0.72). As before, the trees are identical except for the relative positions of *Halichoerus* and *Pusa* (Fig. 5). As before, *Pagophilus*-*Cystophora* and *Pusa*-*Phoca*-*Halichoerus* form two separate clades, which occur in 91 and 92% of 5,000 bootstrap replications, respectively, and all of these species occur as a more inclusive clade, which occurs in 70% of bootstrap replications (Fig. 6). The two monachines share four synapomorphies, but do not occur as sister taxa in a majority of bootstrap replications. Although *Erignathus* appears to be the sister species

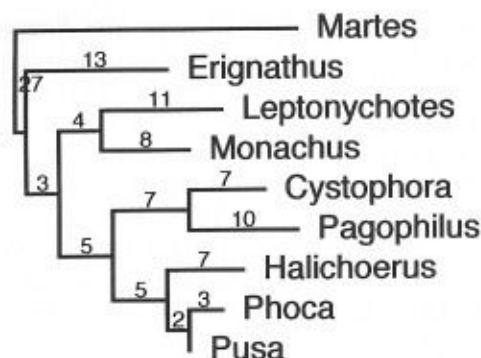


FIG. 5.—Cladogram of the mitochondrial cytochrome *b* sequences of six species of phocine seals, two species of monachine seals, and *Martes americana*.

to all other phocids examined, including both monachine species and the remaining northern species (Fig. 5), the relative branching order of these groups is not reliably resolved by the bootstrap (Fig. 6).

Although the outgroup species was chosen on the assumption that the Phocidae are derived from mustelid carnivores (de Muizon, 1982; Sarich, 1969; Tedford, 1976), use of alternative species from other families of terrestrial carnivores as outgroups does not materially affect the analysis of phocine relationships (results not shown). A parsimony and bootstrap analysis of cytochrome *b* sequences from phocids, mustelids (S. A. Hicks and S. M. Carr, pers. obser.), ursids and procyonids (Zhang and Ryder, 1993), and canids and felids (S. E. Bartlett and W. S. Davidson, pers. obser.) gives no strongly corroborated indication that phocids are more closely related to any one or another family of terrestrial carnivores, an ambiguity that is consistent with the morphological analysis of Wyss (1989).

DISCUSSION

Cladistic analysis of the molecular data suggests that seals of the Northwest Atlantic comprise two well-defined clades, one including only *Erignathus* and the other including the remaining phocines. The latter clade comprises two distinct subclades, one

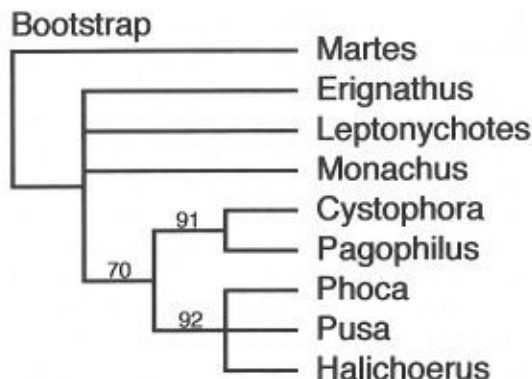


FIG. 6.—Bootstrap analysis of phylogenetic relationships among six phocine and two monachine seals. Numbers on each branch indicate the percent occurrence of that group in 5,000 bootstrap replicates.

consisting of *Phoca*, *Pusa*, and *Halichoerus* and the second consisting of *Pagophilus* and *Cystophora*. Molecular differences between *Halichoerus* and *Pusa* or *Phoca* are somewhat greater than those between species of *Odocoileus*. The differences are not so large as the largest differences within *O. hemionus*, which may reflect parphyly of subspecies (Carr and Hughes, 1993). *Pagophilus* cannot be regarded as congeneric with *Phoca*; its closest relative is *Cystophora*, and the difference between the two species is great enough to justify placing them in separate genera. *Erignathus* is the sister group to all other northern seals examined; its relationship to monachine seals (represented by *Leptonychotes* and *Monachus*) is not yet resolved. The maximum genetic distance among seals of the Northwest Atlantic is somewhat less than that between cervid genera in the same subfamily.

The arrangement presented here is essentially identical to that of de Muizon (1982), who made a cladistic analysis of the skeletal and muscular morphology of phocid seals. De Muizon (1982) regarded the Phocidae as comprising only two subfamilies, the Monachinae and the Phocinae. The latter is defined by three synapomorphies involving the mastoid crest, the carotid fora-

men, and the carinus fossa. De Muizon (1982) further divided the Phocinae into three tribes, the Erignathini (containing *Erignathus* only), Phocini (comprising *Phoca* (sensu stricto), *Pusa*, and *Halichoerus*), and the Cystophorini (comprising *Pagophilus*, *Cystophora*, and *Histriophoca*). The latter two tribes are separated from the first by a single synapomorphy, a deep gluteal fossa on the ilium, which is shallow in *Erignathus* and the Monachinae. *Erignathus* is, thus, the sister species to the remaining Phocinae. The Phocini are defined by the manner of closing of the external cochlear foramen, and the Cystophorini by the degree of extension of the mesethmoid and the shape of the palatines. Within the Cystophorini, *Pagophilus* and *Histriophoca* are united by a synapomorphy of the premaxillary-maxillary suture. Within the Phocini, *Halichoerus* is apomorphic in respect to several features involving its greatly enlarged snout. *Phoca* and *Pusa* are regarded by de Muizon (1982) as sister genera. Following the convention of phyletic sequencing (Nelson, 1974), de Muizon (1982) arranged these taxa as three tribes, Erignathini, Cystophorini, and Phocini, rather than dividing the latter two as subtribes. Except for the separation of *Phoca* and *Pusa*, and the position of *Histriophoca* for which we have no molecular data, we concur with this arrangement for the Phocinae.

This analysis may clarify the pattern of cytogenetic evolution in phocid seals. Phocid seals are either $2n = 34$, as in the monachines, *Erignathus*, and *Cystophora*, or $2n = 32$, as in all other phocines, including *Pagophilus* (and *Histriophoca*; Árnason, 1974). Árnason (1974:203,184) describes the karyotype of *Pagophilus* as "identical" to that of the Phocini and that of *Cystophora* as "virtually identical" to that of *Mirounga*. The difference between the karyotypes is the fusion of a satellite and a telocentric element in the former into a single large metacentric element in the latter. Given the phylogeny proposed here, this fusion must have occurred after the diver-

gence of the Phocini-Cystophorini lineage from *Erignathus* (or possibly the monachines). We then must postulate either that the karyotypes of $2n = 32$ for *Pagophilus* (and presumably of *Histriophoca*) and the Phocini are the results of parallel fusions or that the karyotype of $2n = 34$ for *Cystophora* is the result of a revertant fission. We favor the latter hypothesis as more parsimonious. Árnason et al. (1993) also thought that parallel fusions are unlikely and suggested instead that *Cystophora* was an outgroup to all phocids with $2n = 32$, a conclusion that is not supported by the present analysis.

If the phylogeny presented here is correct, similarities between *Pagophilus* and *Phoca* [sensu stricto], hitherto regarded as congeneric, should now be regarded either as shared-ancestral characters or as instances of parallel evolution, rather than as the results of recent common ancestry. Similarities between *Pagophilus* and *Cystophora*, hitherto regarded as belonging to separate families, should now be regarded either as shared-derived characters or as shared-ancestral characters (if found also in other phocid taxa), rather than as the results of parallel evolution. This suggests a major reinterpretation of the evolution of breeding and lactation patterns in northern seals.

Among phocids, terrestrial parturition has been regarded as the ancestral condition, as is still seen in the three temperate- or tropical-zone species of *Monachus*. The conventional interpretation of the evolution of the pagophilic habit in northern seals is stated by Bonner (1984:255): "Phocid seals have adopted an ice-breeding habit at least twice, and probably more often, in their evolutionary history. . . ." Bonner (1984) and others have argued that the ice habitat provides both advantages and disadvantages to breeding seals. Although ice affords an unlimited homogeneous environment for parturition and allows for immediate access to deep water, it is an extremely unstable, cold substrate on which to care for young. The solution to the problem of life on the

ice has been to shorten the lactation period following the shift from stable terrestrial breeding to breeding on unstable pack ice, so as to reduce the time of the offspring's dependence on the mother. Implicit in this hypothesis is the phylogenetic assumption that the pagophilic habit of *Pagophilus* is a derived character within Phocinae whereas that of *Cystophora* is a homoplasious character within another evolutionary lineage, Cystophorinae. That is, harp seals and hooded seals have evolved parallel solutions to similar problems.

Given the phylogeny presented here, the pagophilic habit in the Cystophorini (including *Pagophilus* and *Cystophora*) is explained more parsimoniously as a shared condition that evolved in their common ancestor. Further, given that *Erignathus*, the sister group to all other northern phocids, also breeds on pack ice and has a short lactation period (12–18 days—Burns, 1981b), it is most parsimonious to hypothesize that the ice-breeding habit, and consequently shortened lactation, is in fact the shared ancestral condition for the Phocinae as a whole. Terrestrial breeding in the various species of Phocini may have evolved once or several times, depending on the ultimate resolution of their phylogenetic relationships. For example, various populations of *Halichoerus* use either land, fast ice (ice attached to land), or pack ice as breeding substrates at different times and in different parts of their range (Mansfield and Beck, 1977). *Pusa* breeds on fast ice (King, 1983). Among the four extant species of *Phoca* [sensu stricto], one (*Phoca vitulina*) breeds on land, two (*P. caspica* and *P. sibirica*) breed on fast ice, and one (*P. largha*) breeds on pack ice (King, 1983). If *Halichoerus* was indeed the sister group to all species of *Phoca* [sensu stricto] as well as *Pusa* (cf. Figs. 2 and 4), this would suggest that the variety of substrate preferences found in extant species has evolved from ecologically variable behavior in their common ancestor, with a trend toward an increasingly stable substrate (pack ice to fast

ice to land). If, conversely, *Pusa* or *Phoca largha* were the sister to the remaining species of Phocini including *Halichoerus*, a more complicated pattern of reversion and secondary convergence in substrate preference must have occurred. The evolution of pagophilic behavior cannot be understood without a completely resolved phylogeny of the Phocini. Referring to unpublished sequence data on *Pusa*, Árnason et al. (1993: 329) state “the mtDNA difference between the harbor and ringed seals is not distinctly less than that between either of these species and the gray seal. Thus the mtDNA data do not suggest that there is a generic distinction between the gray and harbor seals, unless a generic distinction is also applied to the ringed seal.” A proper cladistic assessment of this argument must await publication of the data.

The phylogeny proposed in the present paper should help us to understand other aspects of the evolution of reproductive behavior in phocid seals. In some cases, apparent inconsistencies between substrate preferences and between lactation patterns in seals may be resolved. It generally is believed that extended lactation is typical of the monachines, not only for terrestrial-breeding temperate or tropical species (including *Monachus*), but also for Antarctic species that breed on fast ice (including *Leptonychotes*—Bonner, 1984). If the southern monachines are indeed a strictly monophyletic sister group to the northern phocines as suggested by de Muizon (1982), this would suggest that terrestrial breeding and prolonged lactation (Bonner, 1984) are shared ancestral characters for the Phocidae as a group that reflect their terrestrial fissiped ancestry. Terrestrial breeding and prolonged lactation in monachine seals therefore would not require special ecological explanations. Instances of prolonged lactation in northern seals would then be regarded as secondary convergence(s) on this ancestral condition, which would require specific, possibly separate, ecological explanation(s). Some anomalies

exist. For example, *Histiophoca*, which according to de Muizon's (1982) analysis is the sister species of *Pagophilus* within the Cystophorini, is a pack-ice breeder, but is thought to have a relatively long lactation period (3–4 weeks—Burns, 1981a). However, data on the lactation periods of many species of seals are poor, and in many cases, the length of lactation appears to have been overestimated (Bowen, 1991). A more complete understanding of the evolution of reproductive patterns in phocids will require accurate data on the duration of lactation and further molecular investigation of the phylogenetic relationships among the Phocini and the other phocines as well as between phocines and monachines.

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