

Chapter 3

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Source: Bulletin of the American Museum of Natural History, 2003(279) : 32-76

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0090\(2003\)279<0032:C>2.0.CO;2](https://doi.org/10.1206/0003-0090(2003)279<0032:C>2.0.CO;2)

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Chapter 3

Pinnipedimorph Evolutionary Biogeography

THOMAS A. DEMÉRÉ,¹ ANNALISA BERTA,² AND PETER J. ADAM^{2,3}

ABSTRACT

Previous hypotheses for the origin and diversification of pinnipeds have followed a narrative approach based mostly on dispersalist (i.e., center of origin) explanations. Using an analytical approach, we present a testable hypothesis to explain the evolutionary biogeography of pinnipedimorphs (fur seals, sea lions, walruses, seals, and their fossil relatives) based on both dispersal and vicariant events in the context of a species-level phylogenetic framework. This integrated hypothesis considers many lines of evidence, including physical and ecologic factors controlling modern pinniped distributions, past geologic events related to opening and closing of seaways, paleoceanographic models, the improving pinniped fossil record, and pinniped phylogenetic analyses based on both morphologic and molecular data sets. Oceanic biogeographic regions and faunal provinces are defined and oceanic circulation patterns discussed with reference to the distribution of extant and fossil species. Paleobiogeographic hypotheses for each of the major pinniped lineages are presented using area cladograms and paleogeographic maps showing oceanographic and tectonic changes during successive intervals of the Cenozoic.

Our biogeographic hypothesis supports an eastern North Pacific origin for pinnipedimorphs during the late Oligocene coincident with initiation of glaciation in Antarctica. During the early Miocene, pinnipedimorphs remained restricted to the eastern North Pacific, where they began to diversify. Otariids (fur seals and sea lions) are first known from the late Miocene in the North Pacific, where they remained restricted until the late Pliocene. A transequatorial dispersal into the western South Pacific at this time preceded the rapid diversification of this group that occurred during the Pleistocene in the Southern Ocean. Odobenids (walruses) evolved in the North Pacific during the late early Miocene and underwent dramatic diversification in the late Miocene with later members of the odobenine lineage dispersing into the North Atlantic, most likely via an Arctic route. Extinct archaic phocoids, the desmatophocids, known only from the early to late Miocene, were confined to the eastern and western North Pacific. Phocids, although postulated here to have a North Pacific origin, are first known as fossils from the middle Miocene in the eastern and western North Atlantic region, as well as the Paratethys. Both monachine and phocine seals are distinct lineages beginning in the middle Miocene in the eastern and western provinces of the North Atlantic. During the late Miocene, phocids underwent a dramatic diversification. The early biogeographic history of phocine seals is centered in the Arctic and North Atlantic. Subsequent dispersal of phocines into the Paratethys and Pacific occurred during the Pleistocene. In contrast, monachine seals have a southern hemisphere center of diversity, especially the lobodontines of the Southern Ocean. Southern dispersal of this clade most likely occurred through the Neogene Central American Seaway prior to its closure in the mid-Pliocene. The pagophilic nature of extant phocine and lobodontine seals is largely a function of Pleistocene glacioeustatic events.

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INTRODUCTION

Pinnipedimorphs are a monophyletic group of neritic marine arctoid carnivorans confined largely to the continental shelf areas of the world's oceans. They have a fossil record extending back at least to the late Oligocene (27–25 Ma). This record now includes specimens from all ocean basins except the Indian Ocean. Pinnipedimorphs include 33–36 living species (Rice, 1998) and at least 51 named fossil species. Basal pinnipedimorphs include species of the extinct taxon *Enaliarctos* and its relatives known from the North Pacific (Mitchell and Tedford, 1973). All other pinnipedimorphs can be placed in the more exclusive Pinnipedia clade, which includes three major taxa: (1) the Otariidae (fur seals, sea lions, and their extinct relatives), (2) the Odobenidae (walruses and their extinct relatives), and (3) the Phocoidea (Phocidae [true or earless seals] plus the extinct desmatophocids).

Proposals for the geographic origin and diversification of pinnipeds have largely been written as narrative accounts rather than as analytical models. This is a consequence of the fact that attempts to explain pinniped biogeographic distributions have been predominantly based on analysis of historical factors (i.e., temporal and geographic occurrence in the fossil record) and/or geologic and climatic factors (i.e., tectonic events, glacial/interglacial oscillations, oceanic currents, and formation of migration/dispersal routes and/or barriers) without regard to explicit phylogenetic hypotheses as the basis for constraining and testing historic biogeographic hypotheses. However, with recent advances in pinniped systematics, including well-supported phylogenies for fossil taxa based on morphology and for extant taxa using both morphologic and molecular data, it is now possible to offer a more comprehensive view of pinniped historical biogeography. Such a view is also enhanced by new discoveries of fossil pinnipedimorphs including discoveries in the eastern and western North Pacific, eastern South Pacific, and Paratethys regions. Detailed studies of present ocean circulation patterns, including both wind-driven circulation and thermohaline circulation, provide

a model for analyzing the relationship between pinniped distributions and ancient ocean circulation patterns. In addition, recent advances in plate tectonic theory have provided more refined ways of viewing events related to the opening and closing of oceanic basins, the development of possible dispersal corridors or barriers, and the possible fragmentation of species ranges. The application of cladistic methodology to analyzing biogeographic questions has been a major advance that provides an empirical approach for evaluating the role of both dispersal and vicariance in pinnipedimorph evolutionary history.

In this paper, we reexamine the historical biogeography of pinnipedimorphs in light of an improved resolution of their phylogenetic relationships, recent fossil discoveries providing revised distributional data, and new information regarding the nature and timing of paleogeographic and paleoceanographic events. We propose a framework for interpreting the historical biogeography of pinnipeds that is based on current ecologic, geologic, climatic, and historical factors, as well as hypotheses of pinniped phylogenetic relationships at a higher level of resolution (species level) than has been previously possible. We intend this model to stimulate others to compare pinniped historical biogeographic patterns with those from other marine organisms to develop broader, larger scale integrative and testable biogeographic hypotheses for the marine biota of the world ocean.

PREVIOUS WORK

The earliest attempts to explain pinniped biogeography were narrative accounts. Sclater (1897) proposed marine zoogeographic regions based on the distributions of marine mammals and generated lists of species characteristic of each region. He suggested that otariids and certain phocids originated in the Southern Ocean and dispersed into the Northern Hemisphere. Von Boetticher (1934) reexamined Sclater's regions, specifically with regard to the distribution of pinnipeds. Davies (1958a) presented the first thorough review of pinniped zoogeography, relying on

fossils, geology, and pinniped distributions to formulate an hypothesis of an Arctic Ocean center of origin. Scheffer (1958), in a monographic work on pinniped biology and systematics, included discussions on evolution and biogeography and also proposed a Northern Hemisphere origin for the group. These early studies assumed a static continental configuration and relied on the periodic opening and closing of hypothetical land bridges and marine straits to explain the present geographic distribution of pinnipeds. In more recent decades, an understanding of continental drift in the context of plate tectonic theory challenged the dominant view held early in the 20th century that the position of continents and ocean basins was fixed and that phantom land bridges were responsible for limiting dispersal. We now realize that just as continents have separated, collided, or drifted further apart, so too have ocean basins and their constituent marine biotas. In fact, an inverse relationship of interchange, termed complementarity by Hallam (1974), often exists between terrestrial and marine environments and their biotas. A classic case of complementarity occurred during formation of the Isthmus of Panama in the mid-Pliocene. Elevation of the isthmus created a corridor for terrestrial interchange between North and South America, but it also created a barrier to marine interchange between the tropical eastern Pacific Ocean and the Caribbean Sea. The relevance of complementarity to pinniped biogeography is obvious and will be discussed later.

Historical biogeography examines general patterns of occurrence of species and explains them in terms of evolutionary and geologic history. The role of historical biogeography in understanding the distribution of organisms has involved both dispersal and vicariant models. In the context of pinniped distributions, dispersal biogeographers have traditionally been interested in where pinnipeds originated (center of origin) and how and when they dispersed from that center. On the other hand, vicariant biogeographers have emphasized that the geographical pattern of pinnipeds is the result of common, past events (geologic and/or climatic) in earth history, with changes in configuration of ocean basins, land bridges, and straits

fragmenting or juxtapositioning species ranges. This latter approach also offers a means for testing biogeographic hypotheses using the premise that the same processes that caused a particular pinniped distribution also caused a similar distribution in other marine organisms.

As expected, much of the previous biogeographic history of pinnipeds has been discussed within a dispersalist framework. Davies (1958a) proposed a center of origin for pinnipeds in the Arctic Basin based, in part, on fossil evidence at that time for the earliest pinnipeds and their assumed primitive physiological adaptations to cold water. He went on to propose that the ancestors of otariids and walruses dispersed south into the North Pacific and were isolated there by emergence of an Aleutian land bridge, while phocids diversified in the Arctic and gradually dispersed south into the North Atlantic, following an advancing cold water boundary. This idea was further explored by him (Davies, 1958b), especially the effects that the expansion and contraction of sea ice during the Pleistocene had on the present day distribution of northern pinnipeds. In a classic treatment of pinniped biogeography based on an improved knowledge of fossil pinnipeds, Renning et al. (1979) suggested that "otaroid" pinnipeds (a paraphyletic grouping of sea lions, fur seals, walruses, their fossil relatives, and the extinct desmatophocids) evolved in Neogene temperate waters of the North Pacific from an arctoid (ursid) stock and that phocid pinnipeds (true seals) evolved in the North Atlantic from a different arctoid (mustelid) ancestry. This hypothesis, which assumes a diphyletic Pinnipedia, is based in large part on the published biogeographic pattern of fossil pinnipeds at that time, with phocids only known from deposits in the Atlantic Ocean basin and Paratethys region until the late Miocene (eastern South Pacific) and Pleistocene (North Pacific and Arctic Ocean), and otariids only known from the North Pacific basin until the late Pliocene (eastern South Pacific) and Pleistocene (South Atlantic and Southern Ocean). This diphyletic view is still advocated by some workers to interpret past patterns of geographical distribution (e.g., Bonner, 1990; Knox, 1994). In contrast, few attempts have

been made to explain the biogeographic distribution of various pinniped lineages based upon well-corroborated hypotheses of phylogenetic relationships; these include Muizon (1982) and Bininda-Emonds and Russell (1996) for phocids, Kohno et al. (1995a) for odobenids, and Berta and Deméré (1986) for otariids. See further comments about these phylogenetic hypotheses in the section Phylogeny and Biogeography.

BIOGEOGRAPHY OF EXTANT PINNIPEDS

In describing the distribution of extant pinnipeds, it is useful to recognize nine oceanic biogeographic regions (fig. 3.1) including the (1) Arctic Ocean region, (2) North Atlantic Ocean region, (3) Mid-Atlantic Ocean region, (4) South Atlantic Ocean region, (5) North Pacific Ocean region, (6) Mid-Pacific Ocean region, (7) South Pacific Ocean region, (8) Indian Ocean region, and (9) Southern Ocean region. We have subdivided each region into provinces (e.g., eastern North Pacific province, Paratethys province) for a total of 26 provinces summarized in table 3.1 and illustrated in figure 3.1. The following discussion describes the pinniped assemblages characteristic of each region (based primarily on King, 1983b; Riedman, 1990; and Rice, 1998) and concludes with an overview of general biogeographic patterns. The haul-out distributions of species are emphasized. Some pinnipeds (i.e., *Mirounga* spp., *Callorhinus ursinus*) have more pelagic habits and are often found outside the ranges described here. Figure 3.2 summarizes the major oceanic currents and areas of coastal upwelling that are discussed.

The Arctic Ocean region covers the entire Arctic Basin and includes the Beaufort Sea/Chukchi Sea province (1a) adjacent to western Canada and Alaska, the East Siberian Sea/Laptev Sea province (1b) adjacent to eastern Russia, and the Greenland Sea/Barents Sea/Kara Sea province (1c) adjacent to western Russia, Greenland, and Elsmere Island. This region roughly corresponds to the extreme northern portions of the Atlantic–Arctic and Pacific–Arctic ocean zones of Scheffer (1958) and the northern portion of the Arctatlantis pinniped region of Davies

(1958a; modified from Sclater, 1897). The greatest flow of marine water into the Arctic Ocean comes from the Atlantic via the Norwegian Current (a northeastern extension of the Gulf Stream; fig. 3.2), which splits into the North Cape and the Spitsbergen Currents. Marine water also enters from the Bering Strait and crosses the Arctic as the Trans-Arctic Current. The anticyclonic Beaufort Gyre system circulates surface waters in the western Canadian Arctic. The East Greenland Current carries the major flow of marine water out of the Arctic and into the North Atlantic.

Permanent sea ice in the Arctic Ocean and its fringe of seasonally changing pack ice and fast ice is a major factor controlling the distribution of pinnipeds in the region. The Arctic Ocean supports a pinniped assemblage consisting of six phocids and one odobenid. Otariids are, and have always been, entirely absent from the region. Two subspecies of *Odobenus* occur in the Arctic Ocean and display a disjunct distribution. *Odobenus rosmarus rosmarus* occurs in the Greenland Sea/Barents Sea/Kara Sea province and is distinct and apparently reproductively isolated from *O. r. divergens* from the Beaufort Sea/Chukchi Sea and East Siberian Sea/Laptev Sea provinces. Populations of *Erignathus barbatus* have a similar disjunct, but more circum-Arctic, distribution and some workers (King, 1983b) have assigned these to subspecies (*E. b. barbatus* in the Greenland Sea/Barents Sea/Kara Sea province and *E. b. nauticus* in the Beaufort Sea/Chukchi Sea and East Siberian Sea/Laptev Sea provinces). *Pusa hispida* is probably the most characteristic pinniped of the Arctic Ocean and is found throughout the region wherever there is open water. This taxon appears to be undergoing allopatric speciation with several distinct populations recognized and assigned by some workers to subspecies rank (Rice, 1998). The majority of these purported subspecies occur in the subarctic portions of the North Pacific and North Atlantic regions. *Pagophilus groenlandica* occurs in the open sea of the Greenland Sea/Barents Sea/Kara Sea province and extends its range into the subarctic North Atlantic (Hudson Bay/Baffin Bay province). *Histiophoca fasciata* is restricted to the Beaufort Sea/Chukchi Sea

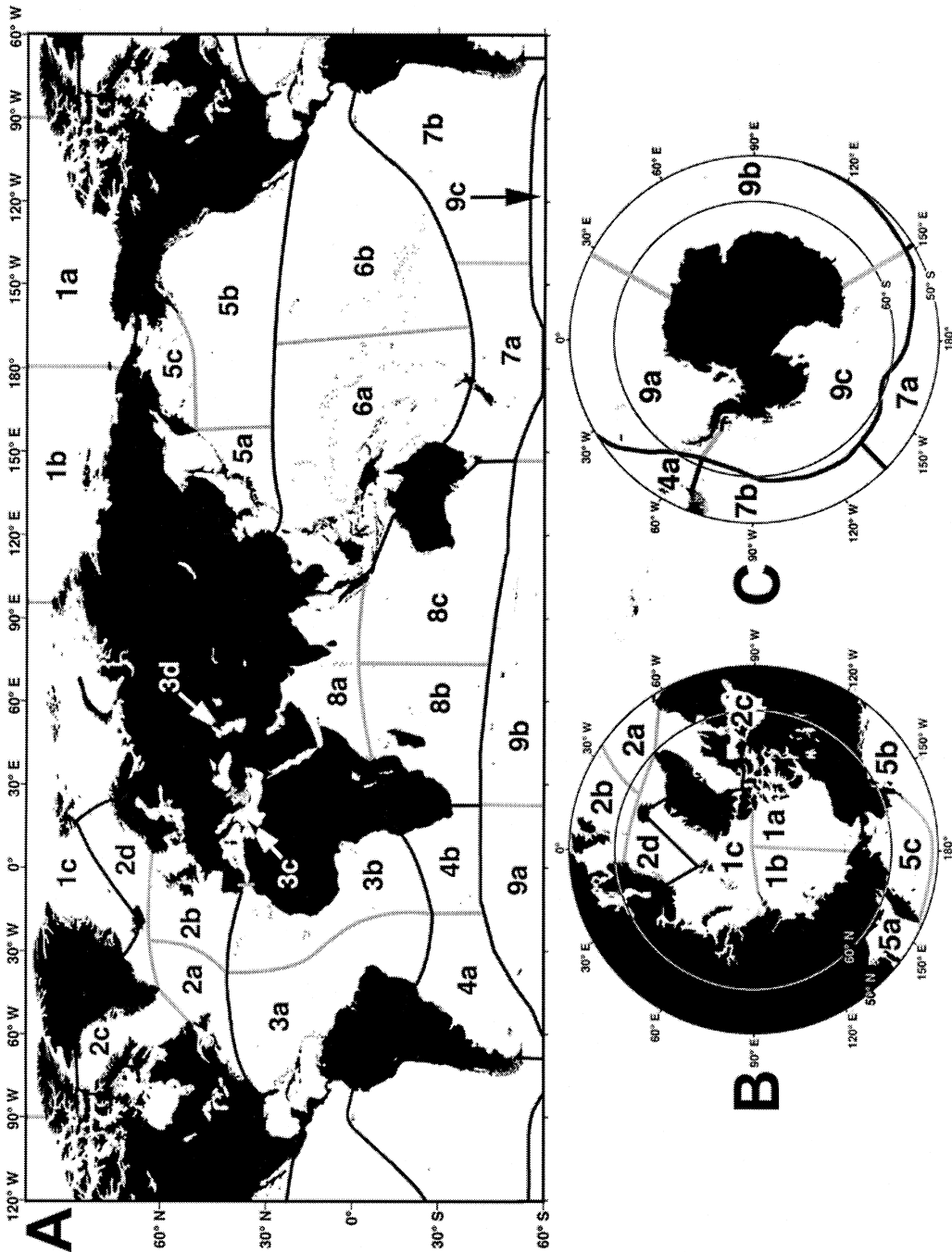


Fig. 3.1. Distribution of oceanic biogeographic regions (black lines) and provinces (gray lines) listed in table 3.1. A, World map; B, North Polar Region map; C, South Polar Region map.

TABLE 3.1

Oceanic Regions and Provinces (see also fig. 3.1)

1. Arctic Ocean region
1a. Beaufort Sea/ Chukchi Sea province
1b. East Siberian Sea/ Laptev Sea province
1c. Greenland Sea/ Barents Sea/ Kara Sea province
2. North Atlantic Ocean region
2a. western NAO province
2b. eastern NAO province
2c. Hudson Bay/ Baffin Bay province
2d. Denmark Strait/ Norwegian Sea province
3. Mid-Atlantic Ocean region
3a. western MAO province
3b. eastern MAO province
3c. Mediterranean Sea province
3d. Paratethys province
4. South Atlantic Ocean region
4a. western SAO province
4b. eastern SAO province
5. North Pacific Ocean region
5a. western NPO province
5b. eastern NPO province
5c. subarctic NPO province
6. Mid-Pacific Ocean region
6a. western MPO province
6b. eastern MPO province
7. South Pacific Ocean region
7a. western SPO province
7b. eastern SPO province
8. Indian Ocean region
8a. northern IO province
8b. western IO province
8c. eastern IO province
9. Southern Ocean region
9a. Atlantic SO province
9b. Indian SO province
9c. Pacific SO province

province of the Arctic and the adjacent subarctic North Pacific (Bering Sea and Okhotsk Sea). *Cystophora cristata* occurs in the western portion of the Greenland Sea/Barents Sea/Kara Sea province and the adjacent Hudson Bay/Baffin Bay province of the subarctic North Atlantic. Although primarily a North Atlantic species, *Halichoerus grypus* follows the Norwegian Current into the Greenland Sea/Barents Sea/Kara Sea province.

The North Atlantic Ocean region includes the northern portion of the Atlantic from about 70°N to about 35°N in the western province (2a) and to about 40°N in the eastern province (2b; includes the North Sea and

Baltic Sea). The subarctic portion of this region is divided between the Hudson Bay/Baffin Bay province (2c) and the Denmark Strait/Norwegian Sea province (2d). This region roughly corresponds to the southern portion of the Atlantic–Arctic ocean zone of Scheffer (1958) and the southern portion of the Arctatlantis pinniped region of Davies (1958a; modified from Sclater, 1897), who used the 20°C SST (sea surface temperature) isotherm as the southern regional boundary. The western boundary current is the warm Gulf Stream and its northeastern extension, the Norwegian Current, while the Canary Current is the eastern boundary current. Cold, south-flowing countercurrents include the Labrador Current in the western North Atlantic and the East Greenland Current in the central North Atlantic.

This region supports a diverse assemblage of pinnipeds, including five phocines and one odobenid. Otariids are entirely absent from the region. *Odobenus rosmarus rosmarus* occurs throughout the Hudson Bay/Baffin Bay province, as well as the western portion of the Denmark Strait/Norwegian Sea province. A trans-Arctic, allopatric distribution occurs in subspecies of *Phoca vitulina*, which can be further divided into eastern and western subspecies. *P. v. concolor* occupies the western North Atlantic and Hudson Bay/Baffin Bay provinces, while *P. v. vitulina* occurs in the eastern North Atlantic and Denmark Strait/Norwegian Sea provinces. *Halichoerus grypus* also has two distinct North Atlantic populations, one resident in the western North Atlantic and Hudson Bay/Baffin Bay provinces and another in the eastern North Atlantic and Denmark Strait/Norwegian Sea provinces. As mentioned, *Erignathus barbatus* and *Pusa hispida*, although primarily residents of the Arctic Ocean, do extend their ranges into the Hudson Bay/Baffin Bay and Denmark Strait/Norwegian Sea provinces. Disjunct populations of *P. hispida* also occur in the Baltic Sea and adjacent freshwater lakes in Finland (Lake Simaa) and Russia (Lake Ladoga). *Pagophilus groenlandica* is characteristic of the Hudson Bay/Baffin Bay, Denmark Strait/Norwegian Sea, and Greenland Sea/Barents Sea/Kara Sea provinces, but extends its range into the western North

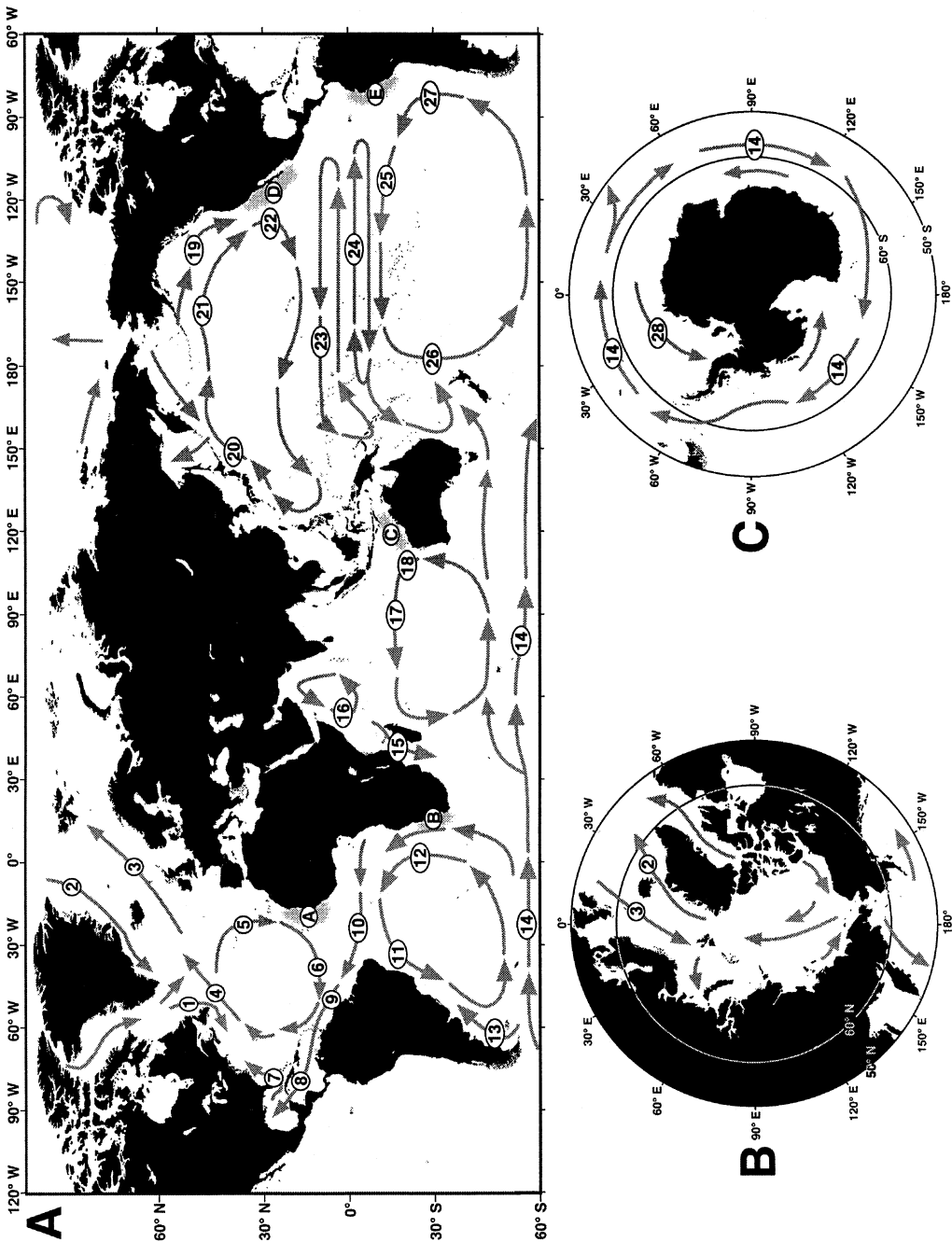


Fig. 3.2. Generalized distribution of ocean surface circulation patterns. A, World map; B, North Polar Region map; C, South Polar Region map. Letters refer to areas of upwelling and numbers refer to currents: 1, Labrador; 2, East Greenland; 3, Norwegian; 4, Gulf Stream; 5, Canary; 6, North Equatorial; 7, Florida; 8, Caribbean; 9, Guyana; 10, South Equatorial; 11, Brazil; 12, Benguela; 13, Falkland; 14, West Wind Drift; 15, Agulhas; 16, North Equatorial; 17, South Equatorial; 18, West Australian; 19, Alaskan; 20, Kuroshio; 21, North Pacific; 22, California; 23, North Equatorial; 24, Equatorial Counter; 25, South Equatorial; 26, East Australian; 27, Peru; 28, East Wind Drift.

Atlantic province along the Labrador Current.

The Mid-Atlantic Ocean Region encompasses the tropical and subtropical portions of the North and South Atlantic and includes the Caribbean Sea and Gulf of Mexico in the west (western Mid-Atlantic province; 3a) and the West African and Iberian coastlines in the east (eastern Mid-Atlantic province; 3b), as well as the Mediterranean Sea (3c) and remnants of the Paratethys Sea (3d; Black, Caspian, and Aral seas). This region corresponds with the Mesatlantis pinniped region of Davies (1958a; modified from Sclater, 1897), who placed its northern and southern boundaries at the 20°C SST isotherm. Ocean circulation in this region is dominated by the North and South Atlantic gyres (fig. 3.2). The South Equatorial Current (a northern segment of the South Atlantic Gyre) joins with the North Equatorial Current in the western equatorial Atlantic and flows westward before splitting into the Antilles Current that flows north of the West Indies and the Caribbean Current that flows west through the Yucatan Channel into the Gulf of Mexico. The Florida Current is the western boundary current that flows north along the east coast of North America to eventually become the Gulf Stream as it moves out to sea at Cape Hatteras.

Pinnipeds are rare in this warm water region and only include species of *Monachus*. The former range of the historically extinct *Monachus tropicalis* included the Gulf of Mexico and the Caribbean Sea between the Yucatan Peninsula and the Bahama Islands and has recently been extended south to the French Antilles (Debrot, 2000). Populations of *Zalophus californianus* in the western Mid-Atlantic province are the result of human introduction, and are not considered here (Rice, 1998). *M. monachus* is characteristic of the Mediterranean Sea, but is also known from the Azores, Canary Islands, and Moroccan coast in the eastern mid-Atlantic province and from the Black Sea in the Paratethys province. This province also supports the lacustrine endemic phocine *Pusa caspica*, which is only found in the Caspian Sea. *Pusa sibirica* is another lacustrine endemic known only from Lake Baikal in eastern Russia (not part of the Paratethys). It is interesting to

note that the region of coastal upwelling off West Africa caused by the Northeast Trade Winds (A in fig. 3.2A) is not associated with a pinniped fauna.

The South Atlantic Ocean region includes the southern portion of the Atlantic from about 60°S to about 35°S in the western province (4a) and from about 45°S to about 20°S in the eastern province (4b). This region is generally equivalent to the Temperate South Atlantic ocean zone of Scheffer (1958). Its northern boundary roughly corresponds with the 20°C SST isotherm and, as such, it includes part of the northern portion of the Notopelagia pinniped region of Davies (1958a; modified from Sclater, 1897) who used the 20°C isotherm as the southern boundary. The western boundary current is the warm Brazil Current, which eventually merges with the West Wind Drift that moves eastward across the South Atlantic. The eastern boundary current is the cold Benguela Current. In the western South Atlantic, an important countercurrent is the cold Falkland Current, which flows north along the coast of Argentina to almost 30°N. Southeast Trade Winds blowing across southwestern Africa create an area of strong upwelling off the coast of Namibia (B in fig. 3.2A). The western province (4a) supports a pinniped assemblage that includes two otariids and one phocid, while the eastern province supports only a single otariid. The otariine *Otaria byronia* ranges in the west from Cape Horn to Uruguay and from Tierra del Fuego to the Falkland Islands. Although not as widespread, the range of the arctocephaline *Arctocephalus australis* is generally sympatric with *Otaria*. The southernmost part of this region is also occupied by the monachine phocid *Mirounga leonina*, which occurs at Tierra del Fuego, the Falkland Islands, and Gough Island. *Arctocephalus pusillus pusillus* is the only resident pinniped in the eastern South Atlantic province and ranges from South Africa (Port Elizabeth) northward along the coast to Namibia.

The North Pacific Ocean region includes the northern portion of the Pacific from about 60°N to about 30°N in the western province (5a; includes the Sea of Okhotsk) and to about 25°N in the eastern province (5b; includes the Gulf of Alaska). The Bering Sea constitutes the subarctic portion of this re-

gion (5c). This region roughly corresponds to the Temperate North Pacific oceanic zone of Scheffer (1958) and the Arctirenia pinniped province of Davies (1958a, modified from Sclater, 1897) who used the 20°C isotherm as the southern boundary. The western boundary current is the warm Kuroshio Current, which becomes the North Pacific Current as it flows eastward south of the Aleutian Archipelago. The eastern boundary current is the cold California Current, which eventually merges with the North Equatorial Current to complete the North Pacific Gyre. The Oyashio Current and Alaskan Current are important south-flowing cold currents in the western and eastern North Pacific, respectively. Northeast Trade Winds blowing across western North America create an area of strong upwelling off the coast of California and Baja California (D in fig. 3.2).

This region supports a varied pinniped assemblage of four otariids, one odobenid, and two phocids. *Callorhinus ursinus* is probably the most abundant otariid of this region. This migratory species ranges from the Bering Sea (Pribilof Islands) south along both shores of the North Pacific to at least Honshu (30°N) in the western Pacific and southern California (32°N) in the eastern Pacific. The otariine *Eumetopias jubata* is generally sympatric with *C. ursinus*, the two species often sharing breeding sites in the Pribilof Islands and Aleutian Archipelago. *Zalophus californianus* is a common species in the temperate portion of this region, with three disjunct subspecies recognized. *Z. c. californianus* represents the largest population and occupies the eastern North Pacific from British Columbia (49°N) to Mexico (23°N). Populations in the western North Pacific are known from the Sea of Japan. This subspecies, *Z. c. japonicus*, may be extinct. The third subspecies, *Z. c. wollebacki* does not occur in this region, but is confined to the Galapagos Islands in the eastern South Pacific (7b). *Arctocephalus townsendi*, the only arctocephaline otariid in this region, is confined to the southern subtropical portion of the eastern North Pacific province. Although this species is typically found at Isla Guadalupe (29°N), its breeding range appears to be extending north to include the California Channel Islands (34°N). *Odobenus rosmarus*

divergens occurs in the Bering Sea, primarily in winter as individuals move south at the front of the advancing pack ice. As discussed already, the common phocine *Phoca vitulina* has disjunct subspecies occurring in the northern hemisphere. *P. v. richardsi* ranges from the Bering Sea south along the North American coast to Isla Cedros in Baja California (28°N). *P. v. stejnegeri* ranges from the Commander Islands (58°N) to Hokaido (4°N). The monachine *Mirounga angustirostris* only occurs in the eastern North Pacific province between about San Francisco, California (38°N) and Bahia Magdalena, Baja California Sur (24°N).

The Mid-Pacific Ocean region encompasses the tropical and equatorial Pacific including the Philippine Sea and Coral Sea in the west (6a) and the Hawaiian Islands, and west coast of Mexico and Central America in the east (6b). Because of a robust eastern boundary current (Peru Current) bringing cold water almost to the Equator coupled with strong coastal upwelling off Peru and Ecuador (E in fig. 3.2), the Galapagos Islands are not included in this region and are instead placed in the South Pacific Ocean region. The western boundary current is the East Australian Current, which brings warm surface water as far south as New Zealand (35°S). The North Equatorial Current and South Equatorial Current transport equatorial surface water to the west, while the intervening Equatorial Counter Current carries surface water to the east.

Monachus schauinslandi is the only phocid species that occurs in this warm-water region. Its range is restricted to the Hawaiian Islands (30° to 20°N), mainly the northwestern islands in the archipelago. It is noteworthy that the western Mid-Atlantic phocid *M. tropicalis* is not known from the western side of the Panamanian Isthmus. The otariine *Phocarctos hookeri* is historically known from New Zealand's North Island in the western province of the Mid-Pacific region, but is now known only from the western South Pacific province. The arctocephaline *Arctocephalus forsteri* is also known from the shores of the North Island of New Zealand.

The South Pacific Ocean region includes the southern portion of the Pacific from

about 50°S to about 30°S in the western province (7a; includes the Tasman Sea) and from about 60°S to about 6°S in the eastern province (7b). The Antarctic Convergence is taken as the region's southern boundary. This region roughly corresponds to the Temperate South Pacific oceanic zone of Scheffer (1958) and the eastern South Pacific portion of the Notopelagia pinniped province of Davies (1958a, modified from Sclater, 1897). The western boundary current is the warm East Australian Current, which eventually merges with the West Wind Drift that moves eastward across the South Pacific. The eastern boundary current is the cold Peru Current that carries surface waters north along the west coast of South America. The Southeast Trade Winds blowing across western South America create an area of strong coastal upwelling off the coast of Peru and Ecuador (E in fig. 3.2A).

This region supports a diverse pinniped assemblage of eight otariids and one phocid. As discussed above, the Galapagos Islands are included in this region because of northward displacement of the 20°C isotherm by the Peru Current and strong coastal upwelling off the west coast of Ecuador and Peru.

The Galapagos islands are home to the endemic otariine *Zalophus californianus wollebacki* and the arctocephaline *Arctocephalus galapagoensis*. The otariine *Otaria byronia* is very common along the west coast of South America from Cape Horn and Tierra del Fuego (55°S) to Isla Lobos de Tierra off Peru (6°S). The arctocephaline *Arctocephalus australis* is broadly sympatric with *Otaria* and is joined by the insular endemic *A. philippi* in the Isla Juan Fernandez group (33°S) and Isla San Felix group (26°S) off Peru. Three other otariids have very restricted ranges in the western South Pacific province. These include the otariine *Phocarctos hookeri* in the seas south of New Zealand around Campbell Island and the Auckland Islands (known archaeologically from the North Island; 6a); *Arctocephalus forsteri* is broadly sympatric with *P. hookeri*, but also occurs along the shores of New Zealand (North and South Islands; 6a, 7a), with a disjunct population also occurring off the south coast of Western and South Australia. *Arctocephalus pusillus doriferus* inhabits the shores of New

South Wales and Victoria and occurs throughout the Bass Strait between Tasmania and Australia. The circum-Antarctic *Mirounga leonina* is found in the subantarctic islands south of New Zealand (Campbell Island and the Auckland Islands).

The Indian Ocean region is divided into a northern province (8a) extending north from about 15°S to the Red Sea, Arabian Sea, and Bay of Bengal, a western province (8b) extending along the eastern shore of Africa from about 50°S to 15°S, and an eastern province (8c) extending along the western shore of Australia from about 50°S to 15°S. The southern boundary of this region is placed at the Antarctic Convergence. The western boundary current is the warm Agulhas Current that flows south along eastern Africa west of Madagascar. The eastern boundary current is the cold West Australian Current. The Southeast Trade Winds blowing off the Australian continent create strong upwelling off the north coast of Western Australia (C in fig. 3.2A). *Neophoca cinerea* occurs in this area of coastal upwelling, extending its range south and east along the southern coast of Western and South Australia, where it is broadly sympatric with *Arctocephalus forsteri*. *Arctocephalus tropicalis* occurs in the extreme southern portion of this region in the seas around the subantarctic islands of Prince Edward Island, Crozet Island, Marion Island, Amsterdam Island, and St. Paul Island (9b). Although *Arctocephalus gazella* is confined primarily to the Southern Ocean south of the Antarctic Convergence, it maintains breeding colonies on Prince Edward Island just north of the convergence in the subantarctic southern Indian Ocean.

The Southern Ocean region encompasses the southern portions of the Atlantic (9a), Indian (9b), and Pacific (9c) oceans. As used here, the Southern Ocean includes areas only south of the Antarctic Convergence. This region roughly corresponds to the Antarctic ocean zone of Scheffer (1958) and the southern portion of the Notopelagia pinniped province of Davies (1958a, modified from Sclater, 1897). The West Wind Drift (the surface portion of the Antarctic Circumpolar Current) carries surface water in an easterly direction in the Southern Ocean. This surface current carries the southerly flow of the

South Atlantic, South Pacific, and South Indian Ocean gyres and gives rise to the cold north-flowing eastern boundary currents in each ocean (Benguela, Peru, and West Australian currents, respectively). The Antarctic Convergence is a major oceanographic boundary where the colder and saltier Antarctic surface waters sink beneath the northerly, warmer subantarctic surface waters. South of the Antarctic Convergence is the Antarctic Divergence, an area of upwelling and high primary productivity at the boundary between the east-flowing West Wind Drift and the west-flowing East Wind Drift.

Pinnipeds of the Southern Ocean include a diverse assemblage of monachine phocids and a single species of arctocephaline otariid. The range of *Arctocephalus gazella*, the sole otariid, includes remote subantarctic islands in the Atlantic Southern Ocean province (South Georgia, South Sandwich, South Orkney, South Shetland, and Bouvet islands) and Indian Southern Ocean province (Marion, McDonald, Heard, and Kerguelen islands). *Leptonychotes weddelli*, the most southerly ranging pinniped, is circumpolar south of the Antarctic Convergence and remains closely associated with fast ice near the shore of the Antarctic continent. Breeding colonies also occur on subantarctic islands including South Shetlands, South Georgia, and South Orkney islands. *Ommatophoca rossi* is also probably circumpolar, but is most often associated with pack ice in the Pacific Southern Ocean province (Ross Sea) and Atlantic Southern Ocean province (King Haakon VII Sea). The circumpolar *Lobodon carcinophagus* is the most abundant pinniped in the world. It is pelagic in habit and found throughout the year associated with pack ice. The largest populations are recorded from the Pacific Southern Ocean province (Amundsen Sea and Ross Sea). *Hydrurga leptonyx* is a circumpolar lobodontine that occurs in association with the outer fringes of the pack ice. This species is reported to migrate northward in winter, reaching the subantarctic islands of South Sandwich and South Orkney south of the Antarctic Convergence, as well as islands north of the convergence (Auckland, Macquarie, Campbell, Heard, and St. Paul islands). *Mirounga leonina* occurs on both sides of the Antarctic Convergence and is

known to reach the Antarctic Continent during the austral summer. The subantarctic islands in the Atlantic Southern Ocean province (South Georgia, South Orkney, and South Sandwich islands) support populations of this circumpolar species.

Having reviewed the modern distribution of pinnipeds, it is now possible to offer some general comments on the emerging biogeographic patterns. Pinnipeds generally occupy cool temperate to polar regions in the continental shelf areas of the world's oceans. Species of *Monachus* are a notable exception, and are confined to the tropics (3a and 6b) and Mediterranean Sea (3c). Unlike cetaceans, there are no cosmopolitan pinniped species. Distributional patterns include insular endemism (e.g., *Arctocephalus philippii*, *A. galapagoensis*, *Phocartos hookeri*, *Monachus schauinslandi*), coastal endemism (e.g., *A. pusillus pusillus*, *Neophoca cinerea*), lacustrine endemism (e.g., *Pusa caspica* and *P. sibirica*), sympatry (e.g., *A. australis* and *Otaria bryonia*, *Erignathus barbatus* and *Odobenus rosmarus*, *Callorhinus ursinus* and *Eumetopias jubata*, *Neophoca cinerea*, and *A. forsteri*), allopatry (e.g., *M. monachus*, *A. pusillus pusillus*), and antitropicality (e.g., *Mirounga leonina* and *M. angustirostris*, *A. townsendi* and *Arctocephalus* spp.). Within an ocean basin, pinnipeds generally have an asymmetric distribution extending to lower latitudes on the eastern shores of the oceans than on the western shores. This pattern is the combined result of the polar origin of eastern boundary currents (e.g., California Current, Peru Current, Benguela Current) and the trade wind-induced location of areas of strong coastal upwelling (e.g., western North America, South America, Africa). Pinnipeds are entirely missing from the northern and central Indian Ocean and the entire Malaysian Archipelago as well as most Polynesian islands (*A. forsteri* is known from the Cook Islands). Otariids, although entirely absent from the North Atlantic, typically occur at high latitudes and, as a group, display a gross pattern of antitropicality. The otariine *Eumetopias* occurs around the margins of the North Pacific (5a–c), while *Zalophus* occurs in the temperate western North Pacific (5a) and temperate eastern North Pacific (5b), as well as in the Galapagos Archipelago in the

tropical eastern Pacific (7b). The remaining otarines are confined to the southern hemisphere and include *Otaria*, with a coastal South American distribution (4a and 7b), *Neophoca*, with a coastal Australian distribution (8c), and *Phocarcos*, with a coastal New Zealand distribution (6a and 7a). Phocine phocids are confined to the Northern Hemisphere and except for a few species, are restricted to the Arctic and subarctic portions of this region. In contrast, monachine phocids (except *Mirounga angustirostris* and species of *Monachus*) are confined to the Southern Hemisphere, with the majority of species restricted to the Southern Ocean south of the Antarctic Convergence.

With few exceptions (e.g., *Callorhinus*, *Mirounga* spp., *Hydrurga*, *Ommatophoca*, *Lobodon*), pinnipeds have limited migrations. All, however, are amphibious and show a distinct pattern of marine feeding and terrestrial/sea ice breeding. Many species have elaborate breeding behaviors that involve establishment and defense of terrestrial territories by males, and generally extreme sexual dimorphism.

PHYSICAL AND ECOLOGIC FACTORS AFFECTING DISTRIBUTIONS—PAST AND PRESENT

Factors influencing the distribution of pinnipeds may be grouped as follows: (1) physical, including habitat and the type of haul-out substrate (e.g., ice), temperature, salinity, ocean current patterns, and water depth; and (2) ecologic, including the distribution and abundance of prey, predators, and competitors. Although one or more factors may exert greater influence on a particular distribution, usually a combination of factors influences observed distribution patterns.

Since all phocid seals must give birth to their pups on land or ice, their distributions during the breeding seasons are determined by the availability of suitable habitats. For ice-breeding seals, especially those inhabiting pack ice (e.g., *Hydrurga*, *Lobodon*, *Cystophora*, *Pagophilus*, and *Histriophoca*), the instability of the drifting ice floes from one season to the next affects their distribution. For land-breeding species, such as the South Farallon Island populations of *Mirounga an-*

gustirostris and central California's populations of *Phoca vitulina*, it has been suggested that the availability of, and access to, high quality breeding habitat may limit their distribution (Sydeman and Allen, 1999). With threats on neonates by terrestrial predators an important limiting factor, many pinnipeds choose isolated islands and/or rugged rocky mainland shores for birthing sites. The geographic distribution of such sites plays a direct role in determining the distribution of many species of pinnipeds, especially those of the Southern Ocean (e.g., *Arctocephalus tropicalis*, *A. gazella*, *Phocarcos hookeri*, and *Mirounga leonina*). In another study that examined the role of competition as an influence, the hypothesis that haul-out space is a contested resource was confirmed by comparing the number of agonistic interactions among harbor seals in northern California when this resource was limited (Neumann, 1999).

An important ecologic variable influencing the distribution of pinnipeds is food. The global distribution patterns of pinnipeds reveal that species diversity is higher in areas of coastal upwelling near continental margins where ocean circulation patterns bring nutrient-rich bottom water to the surface. Although several fur seals live in tropical or subtropical latitudes, ocean waters in these areas are often cold and rich in nutrients because of upwelling (Riedman, 1990). The diet of pinnipeds ranges from zooplankton (e.g., amphipods and euphausiids) to cephalopods (e.g., squid and octopus) and from schooling fish (e.g., sardines and anchovies) to penguins and (occasionally) other pinnipeds. Zooplankton such as krill, but also cephalopods (particularly squid), are typically concentrated in well-defined layers during daylight. These "deep scattering layers" migrate vertically to shallower areas at night in temperate areas and during the warmer months in high latitudes, and a correspondence has been found between pinniped distributions and that of krill and squid. It has been further suggested that the change in daily behavior of many common deep scattering layer species is likely the basis for marked differences in maximum depths between day and night dives seen in *Mirounga angustirostris* (Stewart and De Long, 1993), *Arcto-*

cephalus gazella (Croxall et al., 1994), and *Lobodon* (Lowry et al., 1988). In addition to the effects of water depth on prey availability, there are seasonal and regional changes in the distribution of pinnipeds and their prey. For example, both *Halichoerus grypus* and *Phoca vitulina* exhibit seasonal dispersal from breeding and moulting sites. These seasonal changes in movement patterns often appear related to changes in foraging areas (see references cited in Bowen and Siniff, 1999). Furthermore, there is good evidence that the foraging ranges of males and females differ among species, as evidenced in species of *Mirounga* (Stewart and De Long, 1993; Slip et al., 1994).

Changes in pinniped distributions have also been correlated with periods of warm sea surface temperatures associated with El Niño conditions that cause a 3–12°C increase in ocean temperature in the eastern Pacific. The 1982–1983 El Niño was a time of food shortage and increased rate of mortality, especially for temperate and tropical pinnipeds (e.g., *Arctocephalus galapagoensis*, *Monachus* sp., Año Nuevo Island population of *Mirounga angustirostris*; Trillmich et al., 1991). Some pinniped populations, however, increased during the 1983 and 1992 (and 1997–1998) El Niños due to a general northward migration from southern California breeding grounds, the latter associated with poor food availability (references cited in Sydeman and Allen, 1999).

In addition to short term climatic fluctuations such as El Niño events, long-term climatic changes such as decreased ice-associated habitat, and changes in prey availability affect pinnipeds—particularly those living in the Arctic (e.g., *Histiophoca*, *Pagophilus*, *Cystophora*, *Erignathus*, and *Odobenus*; Tynan and De Master, 1997; Bowen and Siniff, 1999). For example, declines in *Pusa hispida* density have been linked with the severity of ice conditions in the Beaufort Sea in 1974–1975 and 1982–1985 (Stirling et al., 1977; Harwood and Stirling, 1992). For pinnipeds inhabiting the Arctic, climatic change is likely to affect their prey availability. For example, the distribution of Arctic cod, an important prey item for *Pagophilus*, *Cystophora*, *Erignathus*, and *Pusa hispida*, varies

with ice conditions (references cited in Tynan and De Master, 1997).

The role of predation in influencing the distribution of pinnipeds has been examined in some pinniped populations, most notably *Mirounga angustirostris*. For example, predation by white sharks on juveniles and subadults has increased with time and may be limiting the size of the South Farallon Island population (Pyle et al., 1996). The long-term effect of this interaction may be one of limiting recruitment.

Since physical and ecologic factors affect the distribution of extant pinnipeds, it is likely that these factors also affected the distribution of pinnipeds in the past. It has been proposed that a key factor in the initial radiation of pinnipeds (and other marine mammals) was the onset of glaciation in the late Oligocene and the resulting development of a thermally stratified world ocean with cold bottom water, strong surface circulation gyres, and long-range thermohaline circulation. This restructured oceanic condition coupled with the development of extensive areas of coastal upwelling changed the location of primary marine productivity in the world's oceans from the equatorial region to high latitudes (Fordyce, 1980). It has also been postulated that the apparent decline in marine mammal diversity at various intervals during the Tertiary reflects oscillations in the strength of oceanic thermal gradients, with decreases in the thermal gradient correlated with decreased upwelling and primary productivity and thus limited dispersal and speciation in marine mammals (Lipps and Mitchell, 1976). The applicability of this general hypothesis as an explanation for fluctuations in marine mammal diversity through time is currently being re-examined (by PJA). The distribution of pinnipeds, however, cannot be explained solely in terms of changing food resources. Several large-scale physical factors (e.g., opening and closing of seaways, glacial and interglacial climatic events, and changes in ocean circulation patterns) have played an important role in previous explanations of fossil and modern pinniped biogeographic distributions. Below we review the major seaways that have been invoked as dispersal corridors used by pinnipeds and other marine mammals.

The Central American Seaway separating

North and South America allowed free exchange of marine waters between the equatorial Pacific and Atlantic oceans for most of the Cenozoic (see below). By the early late Miocene (11 Ma), however, tectonic activity in the region had resulted in progressive uplift of the Panama Sill and restriction of trans-oceanic circulation (Hallam, 1994). Duque-Caro (1990) further suggests that a strong eastern boundary current in the North Pacific (California Current) was bringing cool surface waters to the region and increasing the circulation barrier through the seaway. Such a cool current so close to the Equator, and possibly converging on a strong north-flowing eastern boundary current in the South Pacific (Peru Current), would have also provided a path for north-south crossing of the tropics by temperate water organisms, including pinnipeds. Although in the latest Miocene (6.3 Ma), free east-west trans-oceanic circulation was reestablished for a while, this was lost by the mid-Pliocene (3.7–3.1 Ma) with final emergence of the Isthmus of Panama (Duque-Caro, 1990). The final closure of the seaway is correlated with strengthening of the western boundary current in the North Atlantic (Florida Current and Gulf Stream) and warming of surface waters in the region (Dowsett and Cronin, 1990). The importance of the Central American Seaway to pinniped paleobiogeography involves the potential use of this seaway as an east-west dispersal corridor between the Pacific and the Atlantic. For example, it has been suggested that odobenine walruses and monachine seals followed this route (Repenning et al., 1979), the latter dispersing from east to west through the portal and the former dispersing from west to east. The impact of closure of the seaway on pinniped distributions has already been mentioned with regard to the use of strong eastern boundary currents as cool water pathways for crossing the tropics. However, an additional impact from closure of the seaway is the possible fragmentation of species ranges and the resulting divergence/speciation of taxa (e.g., *Monachus tropicalis* and *M. schauinslandi*). Currently, there is no good fossil evidence from the tropical eastern Pacific or Caribbean areas to unequivocally support or refute or even provide a temporal constraint on the hy-

pothesized dispersal of pinnipeds through the Central American Seaway. Those fossils that are available occur outside the Panamanian region and provide only a minimum age for constraining possible dispersal events through the seaway. These include the important fossil monachine phocid assemblage from the Pisco Formation in coastal Peru (Muizon, 1981) and the diverse fossil pinniped (phocid and odobenid) assemblage from the Yorktown Formation and correlative deposits in coastal North Carolina and Florida (Ray, 1976; Morgan, 1994).

The history of the Mediterranean Sea represents another important marine geologic factor for pinniped evolution. The modern Mediterranean Sea is a remnant of the Mesozoic and early Cenozoic Tethys Sea that provided a direct connection between the Paleogene North Atlantic and Indian oceans. During the early Miocene, tectonic events related to the collision of the African and Eurasian lithospheric plates resulted in severing the marine connection between the Mediterranean Sea and the Indian Ocean, and the establishment of a north-south land corridor between the two continents in the Middle East. This tectonic event also resulted in isolation of a northern arm of the Tethys to form the Paratethys, a region of present-day Eastern Europe extending from Austria to Uzbekistan and occupied by the modern Black, Caspian, and Aral seas. The initial isolation of Paratethys was followed by a short-lived marine transgression during the middle Miocene (Rögl and Steiniger, 1984) and eventually by renewed isolation and brackish conditions in the late middle/early late Miocene (Sarmatian). A large-scale drying of the Mediterranean region occurred in the late Miocene (Messinian Salinity Crisis), resulting in hypersaline conditions in the Mediterranean basin and formation of a series of hypersaline Paratethys lakes. The connection between the Mediterranean basin and the Atlantic was reestablished by the early Pliocene, while Paratethys remained isolated. The Mediterranean reconnection with the Atlantic provided a potential corridor for dispersal of the endemic phocid assemblage out of the region. The full impact of the continued isolation of the Paratethys on phocine evolution and biogeography (e.g., *Pusa*),

however, is controversial, with some workers suggesting a Paratethyan origin for this lineage followed by dispersal into the Arctic basin and other workers proposing an Arctic origin followed by dispersal into Paratethys (see below).

The establishment of the Bering Strait, which provides a direct polar connection between the oceans of the Northern Hemisphere (North Pacific, Arctic, and North Atlantic), represents a third major geologic event having a significant influence on pinniped evolution. The Bering Strait opened as the result of plate tectonic interactions during the latest Miocene to earliest Pliocene (5.5–4.8 Ma; Marinovich, 2000). This opening was associated with an initial phase of trans-Arctic biotic interchange in which water flowing north to south through the strait facilitated dispersal of Atlantic and Arctic molluscs into the North Pacific region. Pinnipeds, particularly odobenine walruses, could have also participated in this interchange (see later discussion) but there is no direct fossil evidence in the Arctic basin to support this hypothesis. The flow of surface marine waters through the Bering Strait reversed during the mid-Pliocene (3.6 Ma), an event correlated with the elevation of the Isthmus of Panama, closure of the Central American Seaway, and reorganization of Northern Hemisphere ocean circulation (Haug and Tiedemann, 1998). The resulting south-to-north flow established the modern Arctic Ocean circulation pattern (Trans-Arctic Current) and facilitated the dispersal of Pacific molluscs into the Arctic and North Atlantic (Marinovich, 2000). Subsequent glacioeustatic oscillations during the late Pliocene and Pleistocene caused the cyclic exposure and submergence of the Bering Land Bridge, the closing and opening of the Bering Strait, and the periodic isolation of the North Pacific from the Arctic Ocean and North Atlantic. The importance of these glacioeustatic events to Pleistocene phocid and odobenid biogeography (see below) was discussed extensively by Davies (1958b).

The Southern Ocean, a circumpolar seaway connecting the southern portions of the Pacific, Atlantic, and Indian oceans, was an important marine corridor for east–west dispersal of fur seals, sea lions, and lobodontine

phocids. Unlike the preceding seaways, it has remained open throughout the Neogene. Prior to the mid-Oligocene, remnants of the Gondwana supercontinent prevented the free circumpolar circulation of ocean water. Opening of the Southern Ocean via northward continental drift of South America, Africa, and Australia in the mid-Oligocene is correlated with establishment of a circumpolar ocean current (West Wind Drift) and initiation of glaciation in east Antarctica. This event had a global impact on restructuring circulation systems of the world ocean and initiation of the glacial conditions of the Pleistocene. Although today the Southern Ocean is a major area of pinniped diversity, the fossil record from this region is too poorly known at present to provide any direct evidence of the biological events leading up to that diversity.

Having reviewed the physical, historical, and ecologic factors that have certainly played major roles in establishing the biogeographic pattern of modern pinnipeds, we now turn to the value of phylogeny in constraining and testing competing hypotheses proposed to explain this pattern.

HISTORICAL REVIEW OF PINNIPEDIMORPH HIGHER LEVEL PHYLOGENY

As mentioned previously, the approach taken here differs from previous narrative accounts in that it explicitly employs a phylogenetic framework as a context from which to examine the history of pinnipedimorph diversification. This method forces the biogeographer to ask several questions. Is the group monophyletic? If so, what and where is its sister group? On both morphologic and molecular grounds pinnipedimorphs constitute a monophyletic group (Wyss, 1987; Flynn et al., 1988; Berta and Wyss, 1994; Vrana et al., 1993; Bininda-Emonds and Russell, 1996; Flynn and Nedbal, 1998). Although we have depicted a hypothesis that supports ursids as the sister group of pinnipedimorphs, it is acknowledged that the various arctoid carnivorans (including mustelids and procyonids in addition to ursids) are difficult to separate at their point of divergence. Other hypotheses support pinnipedimorphs

as either allied with mustelids (e.g., Bininda-Emonds and Russell, 1996) or as having an unresolved arctoid ancestry (e.g., Arnason and Widegren, 1986; Arnason and Ledje, 1993). Another as yet unresolved issue is the interrelationships among major pinnipedimorph groups. Most morphologic data supports a link between phocids and odobenids (Wyss, 1987; Wyss and Flynn, 1993; Berta and Wyss, 1994), whereas molecular data favors a more traditional link between odobenids and otariids (Vrana et al., 1993; Lento et al., 1995; Arnason et al., 1995). Resolution of this conflict will likely benefit most from more detailed exploration of morphologic and molecular data sets that offer both additional (e.g., fossil) taxa and characters. We follow here the morphologic data that support odobenid + phocid alliance (Phocomorpha clade) and phocids in turn allied with the extinct desmatophocids (Phocoidea clade).

METHODOLOGY

A complete species-level phylogeny for pinnipeds including fossil and extant taxa is, as yet, unavailable. We here use a composite tree (fig. 3.3) based on the basic topology of the generic-level phylogeny of Berta and Wyss (1994) but with the following substitutions: (1) we replaced Otariidae with the phylogeny of Bininda-Emonds et al. (1999) and our own work based on morphologic and molecular data, (2) we replaced phocid subfamilies with the consensus phylogeny obtained by Bininda-Emonds et al. (1999) and added fossil taxa based on Berta and Wyss (1994) and Muizon (1982), (3) we replaced Odobenidae with the phylogeny of Deméré and Berta (2001), and (4) we replaced Desmatophocidae with the phylogeny of Deméré and Berta (2002). These major clades are widely accepted as monophyletic and their combination into a single tree is supported by the robustness of basal nodes in the composite tree (an exception is the Phocoidea clade with 55% support). We next examine interrelationships of the various pinnipedimorph groups and use temporal and geologic evidence (figs. 3.3–3.7, table 3.2) to support or refute previous hypotheses of their origin, diversification, and dispersal.

PHYLOGENY AND BIOGEOGRAPHY: AN INTEGRATION

BASAL PINNIPEDIMORPHS: Basal pinnipedimorphs were amphibious carnivorans with shearing teeth, flexible spines, and flipper-like fore and hind limbs. They were likely coastal dwellers capable of more efficient terrestrial locomotion than extant pinnipeds (Berta and Ray, 1990). The basal taxon *Enaliarctos* is known from five species (Mitchell and Tedford, 1973; Berta, 1991) from the late Oligocene and early Miocene of California (27–25 Ma; figs. 3.3, 3.7). Another basal taxon is *Pinnarctidion* with two species described from the early Miocene, *P. bishopi* from California and *P. rayi* from Oregon. Although *Pinnarctidion* has previously been regarded as a member of the Phocoidea clade (Berta, 1994b; Berta and Wyss, 1994) this alliance is no longer supported (Deméré and Berta, 2002). *Pinnarctidion* is more likely a basal pinnipedimorph as proposed by Barnes (1979). A later diverging lineage, more closely allied with pinnipeds than with *Enaliarctos*, is represented by *Pteronarctos* and *Pacificotaria* from the early and middle Miocene (19–15 Ma) of coastal Oregon (Berta, 1994a; fig. 3.3).

When the hypothesis of pinnipedimorph monophyly is used to constrain the historical biogeography of the group, it is most parsimonious to consider that the common ancestor of all pinnipeds, including basal pinnipedimorphs, originated in the North Pacific rather than hypothesizing two separate areas of origin, one for otariids and odobenids in the North Pacific and another for phocids in the North Atlantic (Repenning et al., 1979). Among those supporting a single-origin hypothesis, Davies (1958a) has proposed an origin of pinnipeds in the Arctic basin followed by separate dispersals and subsequent diversification of phocids in the North Atlantic and otariids and odobenids in the North Pacific. The fossil record, however, does not provide any evidence for an Arctic origin, but instead favors a single origin in the North Pacific basin. The oldest known record (OKR; Walsh, 1998) for pinnipedimorphs is currently established by *Enaliarctos tedfordi* and *E. barnesi* (table 3.2) from the late Oligocene (Chattian) Yaquina Formation of

coastal Oregon (eastern North Pacific, 5b). Until an older OKR is discovered, the Oregon record provides both a minimum age for the origin of pinnipedimorphs and a likely region of origin. It should be mentioned that two partial femora assigned to the Phocidae by Koretsky and Sanders (1997) were purportedly collected from upper Oligocene deposits in South Carolina (western North Atlantic, 2a). However, these fragmentary specimens have not been formally described and their stratigraphic provenience may be in question. It would be of major significance to find late Oligocene phocid remains in this region.

PINNIPEDIA CLADE: The Pinnipedia includes three major monophyletic taxa: (1) the Otariidae, (2) the Odobenidae, and (3) the Phocoidea (Phocidae plus the extinct desmatophocids; Berta and Wyss, 1994).

Pinnipeds include animals that lost the well-developed carnassial teeth of basal pinnipedimorphs and evolved important middle ear aquatic adaptations (Repenning, 1972, 1976). The OKR of Pinnipedia is currently established by *Desmatophoca brachycephala* from the early Miocene (Aquitanian) Astoria Formation of Washington State (eastern North Pacific, 5b) suggesting that divergence of pinnipeds from basal pinnipedimorphs likely occurred sometime before 18 Ma, probably in the North Pacific Ocean Basin.

OTARIIDAE—FUR SEALS AND SEA LIONS: The monophyletic Otariidae or eared seals (Berta and Wyss, 1994; figs. 3.3, 3.4) includes animals with broad supraorbital processes of the frontals and generally homodont dentitions. Otariids swim with forelimb propulsion and have retained the ability to rotate the hind feet forward for quadrupedal “walking” during terrestrial locomotion. Extant otariids are often divided into two subgroups, the Otariinae (sea lions) and the Arctocephalinae (fur seals). Although prior systematic work based on morphology (Berta and Deméré, 1986) suggested that only the otariines were monophyletic, a more recent analysis (Bininda-Emonds et al., 1999) suggests that both subgroups are monophyletic (but see Lento et al., 1995, 1997 for a different view).

The most basal otariid is the poorly known *Pithanotaria starri* from the late Miocene

(Tortonian) Sisquoc Formation of California (eastern North Pacific, 5b; figs. 3.4, 3.7). This record also establishes the otariid OKR. Other basal otariids include “*Thalassoleon*” *mcnallyae* and “*Thalassoleon*” *inouei* from the late Miocene of California and early Pliocene of Japan, respectively (Repenning and Tedford, 1977; Kohn, 1992). The next diverging otariid lineage includes “*Thalassoleon*” *mexicanus* and the *Callorhinus* clade from the late Miocene and late Pliocene to Recent, respectively, of the western North Pacific (5b; Repenning and Tedford, 1977; Berta and Deméré, 1986) and *Hydrarctos lomasiensis* from the late Pliocene or early Pleistocene of the eastern South Pacific (7b; Muizon, 1978; Muizon and de Vries, 1985). The latter record establishes the OKR for southern hemisphere otariids.

The otariid crown clades, Otariinae and Arctocephalinae, share a rather recent common ancestry and do not contain any extinct genera. The OKR for this pairing is problematical, with all pre-Pleistocene records of dubious validity (see discussions in Miyazaki et al., 1995). Until more taxonomically diagnostic fossil material is found and described, only the late Pleistocene occurrences from Brazil (*Otaria byronia*; Drehmer and Ribeiro, 1998) and New Zealand (*Neophoca palatina*; King, 1983a) can be considered reliable. Within the extant Otariinae, five monotypic genera and species are recognized (table 3.2). Relationships among sea lions suggest that *Zalophus* is the basal taxon with *Eumetopias*, *Neophoca*, *Phocarctos*, and *Otaria* as sister taxa (Bininda-Emonds et al., 1999). It is noteworthy that the two basal otariines represent North Pacific Ocean endemics. The *Arctocephalus* clade consists of eight extant species whose interrelationships (fig. 3.4) suggest a division into three subgroups: (1) the “*pusillus*” species group consisting of *A. pusillus pusillus* and *A. pusillus doriferus*, (2) the “*gazella*” species group that includes *A. gazella* and *A. tropicalis*, and (3) the “*galapagoensis*” species group that includes *A. townsendi* as sister taxon to an unresolved clade containing *A. galapagoensis*, *A. australis*, *A. forsteri*, and *A. philippii* (Bininda-Emonds et al., 1999). Interestingly, the two basal arctocephaline groups represent Southern Hemisphere endemics.

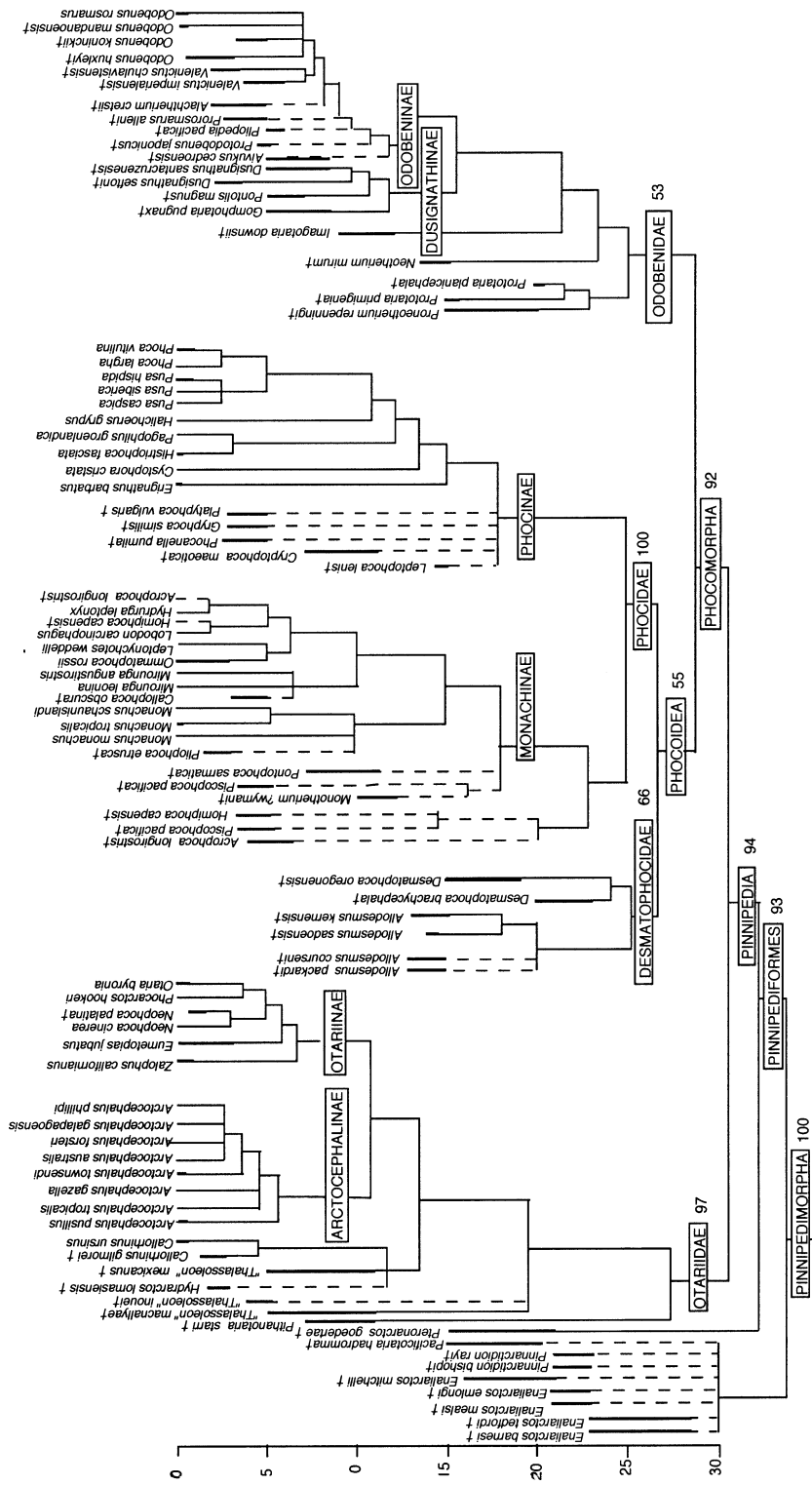


Fig. 3.3. Composite phylogeny depicting the relationships and chronologic ranges (m.y.) of extinct and living pinnipedimorphs (phylogeny based on Berta and Wyss, 1994; Bininda-Emonds et al., 1999; Deméré et al., 2001, 2002). Bootstrap frequencies resulting from bootstrap analyses (1000 replications) reported by Bininda-Emonds and Russell (1996). Thick lines show stratigraphic ranges of taxa, thin lines indicate phylogenetic relationships, and dashed lines indicate uncertain phylogenetic position of fossil taxa (note: alternate positions are shown for *Acrophoca*, *Homiphoca*, and *Piscophoca* fide Muizon, 1982). Branching points are not necessarily correlated with the time scale.

TABLE 3.2

Chronostratigraphy of Pinnipedimorphs

Numbers preceding taxonomic names refer to localities shown in figure 3.7.

A. LATE OLIGOCENE

LATE OLIGOCENE 29.3–23.3 Ma (CHATTIAN)

YAQUINA FM.; EASTERN NORTH PACIFIC, OREGON, USA (BERTA, 1991)

“Enaliarctidae”

(1) *Enaliarctos barnesi* Berta, 1991(2) *E. tedfordi* Berta, 1991**B. EARLY MIOCENE**

EARLY EARLY MIOCENE 23.3–21.5 Ma (AQUITANIAN)

NYE MUDSTONE, ASTORIA FM.; EASTERN NORTH PACIFIC, OREGON AND WASHINGTON, USA (BARNES, 1987)

“Enaliarctidae”

(3) *Enaliarctos emlongi* Berta, 1991(4) *Pinnarctidion rayi* Berta, 1994

Desmatophocidae

(5) *Desmatophoca brachycephala* Barnes, 1987

JEWITT SAND; EASTERN NORTH PACIFIC, CALIFORNIA, USA (MITCHELL AND TEDFORD, 1977)

“Enaliarctidae”

(11) *Enaliarctos mealsi* Mitchell and Tedford, 1973(12) *E. mitchelli* Barnes, 1979(13) *Pinnarctidion bishopi* Barnes, 1979

LATE EARLY MIOCENE 21.5–16.3 Ma (BURDIGALIAN)

ASTORIA FM.; EASTERN NORTH PACIFIC, OREGON, USA (BARNES, 1989; DEMÉRÉ AND BERTA, 2001)

“Enaliarctidae”

(6) *Pteronarctos goedertae* Barnes, 1989(7) *P. piersoni* Barnes, 1990(8) *Pacificotaria hadromma* Barnes, 1992

Desmatophocidae

(9) *Desmatophoca oregonensis* Condon, 1906

Odobenidae

(10) *Proneotherium repenningi* Barnes in Kohno et al., 1995

AKEYO FM.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)

“Enaliarctidae”

(14) gen. et sp. indet.

C. MIDDLE MIOCENE

EARLY MIDDLE MIOCENE 16.3–14.2 Ma (LANGHIAN)

CALVERT FM. AND CORRELATIVE UNITS; WESTERN NORTH ATLANTIC, MARYLAND AND VIRGINIA, USA (RAY, 1976, 1977)

Phocidae

Monachinae

(26) *Monotherium? wymani* (Leidy, 1853)

Phocinae

(24) *Leptophoca lenis* True, 1906(25) *Prophoca* sp. indet.

SHIMO FM.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)

Odobenidae

(32) *Prototaria primigena* Takeyama and Ozawa, 1984(33) *P. planicephala* Kohno, 1994

LATE MIDDLE MIOCENE 14.6–11 Ma (SERRAVALLIAN)

BISMANTOVA FM.; MEDITERRANEAN, ITALY (CIGALA AND PILLERI, 1985)

Phocidae

Monachinae

(29) cf. *Monotherium* sp. indet.

EARLY SARMATIAN DEPOSITS; CENTRAL PARATETHYS, AUSTRIA (GRIGORESCU, 1977)

Phocidae

(30) “*Phoca*” *vindobonensis* Toulou, 1898

Monachinae

(31) *Pristiphoca vetusa* (Zapfe, 1937)

TABLE 3.2
(Continued)

LATE MIDDLE MIOCENE 14.6-11 Ma (SERRAVALLIAN) (Continued)
BERCHEM FM.; EASTERN NORTH ATLANTIC, BELGIUM (DOLLO, 1909; RAY, 1977)
Phocidae
Phocinae
(27) <i>Leptophoca proxima</i> (Van Beneden, 1876)
(28) <i>Prophoca rousseaui</i> Van Beneden, 1876
CHOPTANK FM.; WESTERN NORTH ATLANTIC, MARYLAND, USA (RAY, 1976, 1977)
Phocidae
Monachinae
(23) gen. et sp. indet.
ROUND MOUNTAIN SILT, MONTEREY AND TOPANGA FMS.; EASTERN NORTH PACIFIC, CALIFORNIA, USA (BARNES, 1988)
Desmatophocidae
(15) <i>Allodesmus kernensis</i> Kellogg, 1931
(16) <i>A. courseni</i> (Downs, 1956)
(17) <i>A. packardi</i> Barnes, 1972
(18) aff. <i>Desmatophoca</i> n. sp.
Odobenidae
(19) <i>Neotherium mirum</i> Kellogg, 1931
(20) <i>Pelagiartcos thomasi</i> Barnes, 1988
ROSARITO BEACH FM., EASTERN NORTH PACIFIC, BAJA CALIFORNIA, MEXICO (DEMÉRÉ ET AL., 1984)
Desmatophocidae
(21) <i>Allodesmus</i> sp. indet.
Odobenidae
(22) cf. <i>Neotherium</i> sp. indet.
TSURUSHI AND AOKI FMS.; WESTERN NORTH PACIFIC (MIYAZAKI ET AL., 1995)
Desmatophocidae
(34) <i>Allodesmus sinanoensis</i> (Nagao, 1941)
(35) <i>A. sadoensis</i> Barnes and Hirota, 1995
(36) <i>A. megallos</i> Hirota, 1995
EOLON FM.; WESTERN NORTH PACIFIC, RUSSIA (DUBROVO, 1981)
Odobenidae
(37) <i>Kamtschatarctos sinelnikova</i> Dubrovo, 1981
D. LATE MIOCENE
EARLY LATE MIOCENE 10.4-6.7 Ma (TORTONIAN)
MIDDLE SARMATIAN SANDSTONES; EASTERN PARATETHYS, EASTERN EUROPE (GRIGORESCU, 1977; KORETSKY AND RAY, 1994)
Phocidae
Monachinae
(72) <i>Pontophoca sarmatica</i> Alekseev, 1924
Phocinae
(73) <i>Cryptophoca maeotica</i> (Nordmann, 1860)
(74) " <i>Pusa</i> " <i>pontica</i> (Eichwald, 1853)
DIEST FM.; EASTERN NORTH ATLANTIC, BELGIUM (DOLLO, 1909; RAY, 1977)
Phocidae
Monachinae
(68) <i>Monotherium aberratum</i> Van Beneden, 1876
(69) <i>M. affine</i> Van Beneden, 1876
(70) <i>M. delognei</i> Van Beneden, 1876
Phocinae
(71) gen. et sp. indet.
ST. MARY'S FM.; WESTERN NORTH ATLANTIC, MARYLAND AND VIRGINIA, USA (RAY, 1977)
Phocidae
Monachinae
(61) <i>Monotherium aberratum</i> Van Beneden, 1876

TABLE 3.2
(Continued)

EARLY LATE MIOCENE 10.4-6.7 Ma (TORTONIAN) (Continued)	
SANTA MARGARITA FM.; EASTERN NORTH PACIFIC, CENTRAL CALIFORNIA, USA (REPENNING AND TEDFORD, 1977)	
Otariidae	(41) <i>Pithanotaria starri</i> Kellogg, 1925
Desmatophocidae	(42) <i>Allodesmus</i> sp. indet.
	(43) gen. et sp. indet.
Odobenidae	(44) <i>Imagotaria downsi</i> Mitchell, 1968
MONTEREY FM.; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (BARNES ET AL., 1985)	
Otariidae	(45) <i>Pithanotaria starri</i> Kellogg, 1925
	(46) gen. et sp. indet.
Desmatophocidae	(47) <i>Allodesmus</i> ? sp. indet.
Odobenidae	(48) <i>Imagotaria downsi</i> Mitchell, 1968
	(49) cf. <i>Pontolis</i> sp. indet.
AOSO AND KOETOI FMS.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)	
Odobenidae	(75) <i>Imagotaria</i> sp. cf. <i>I. downsi</i> Mitchell, 1968
PARANÁ FM.; WESTERN SOUTH ATLANTIC, ARGENTINA (MUIZON AND BOND, 1982)	
Phocidae	
Monachinae	(67) <i>Properiptychus argentinus</i> (Ameghino, 1893)
LATE LATE MIOCENE 6.7-5.2 Ma (MESSINIAN)	
EASTOVER FM.; WESTERN NORTH ATLANTIC, MARYLAND AND VIRGINIA, USA (RAY, 1977)	
Phocidae	
Monachinae	(62) ? <i>Monotherium wymani</i> (Leidy, 1853)
EMPIRE FM.; EASTERN NORTH PACIFIC, OREGON, USA (THIS REPORT)	
Odobenidae	(38) <i>Imagotaria</i> n. sp. 1
	(39) <i>Imagotaria</i> n. sp. 2
Dusignathinae	(40) <i>Pontolis magnus</i> (True, 1905)
PURISIMA AND ETCHEGOIN FMS; EASTERN NORTH PACIFIC, CENTRAL CALIFORNIA, USA (REPENNING AND TEDFORD, 1977; BARNES AND PERRY, 1989)	
Otariidae	(50) <i>Thalassoleon macnallyae</i> Repenning and Tedford, 1977
Odobenidae	
Dusignathinae	(51) <i>Dusignathus santacruzensis</i> Kellogg, 1927
	(52) <i>Gomphotaria</i> sp. indet.
Odobeninae	(53) <i>Pliopedia pacifica</i> Kellogg, 1921
	(54) odobenine new sp.
CAPISTRANO AND SAN MATEO FMS; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (BARNES ET AL., 1981; BARNES AND RASCHKE, 1991)	
Otariidae	(55) <i>Thalassoleon</i> sp. indet.
Odobenidae	
Dusignathinae	(56) <i>Gomphotaria pugnax</i> Barnes and Raschke, 1991
	(57) gen. et sp. indet.

TABLE 3.2
(Continued)

LATE LATE MIOCENE 6.7-5.2 Ma (MESSINIAN) (Continued)
ALMEJAS FM.; EASTERN NORTH PACIFIC, BAJA CALIFORNIA, MEXICO (REPPENING AND TEDFORD, 1977)
Otariidae
(58) <i>Thalassoleon mexicanus</i> Repenning and Tedford, 1977
Odobenidae
Dusignathinae
(59) <i>Dusignathus santacruzensis</i> Kellogg, 1927
Odobeninae
(60) <i>Aivukus cedrosensis</i> Repenning and Tedford, 1977
AOSO AND KOETOI FMS; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)
Otariidae
(76) gen. et sp. indet.
PISCO FM.; EASTERN SOUTH PACIFIC, PERU (MUIZON AND DEVRIES, 1985)
Phocidae
Monachinae
(63) <i>Acrophoca</i> new sp.
(64) <i>A.</i> sp. indet.
(65) gen. et sp. indet.
(66) gen. et sp. indet.
E. PLIOCENE
LATEST MIOCENE-EARLY PLIOCENE
BLACK ROCK FM.; WESTERN SOUTH PACIFIC, AUSTRALASIA (FORDYCE AND FLANNERY, 1983)
Phocidae
Monachinae
(117) gen. et sp. indet.
EARLY PLIOCENE 5.2-3.4 Ma (ZANCLIAN)
LOWER PLIOCENE MONTPELLIER SANDS, MEDITERRANEAN, FRANCE (MUIZON, 1982)
Phocidae
Monachinae
(99) <i>Pristiphoca occitana</i> Gervais, 1859
KATTENDIJK AND LILLO FMS; EASTERN NORTH ATLANTIC, BELGIUM (RAY, 1977)
Odobenidae
Odobeninae
(100) <i>Alachtherium cretsii</i> du Bus, 1867
(101) <i>Odobenus konincki</i> (Van Beneden, 1871)
Phocidae
Monachinae
(102) <i>Callophoca obscura</i> Van Beneden, 1876
Phocinae
(103) <i>Gryphoca similis</i> Van Beneden, 1876
(104) " <i>Phoca</i> " <i>vitulinoides</i> Van Beneden, 1871
(105) <i>Phocanella pumila</i> Van Beneden, 1876
(106) <i>Platyphoca vulgaris</i> Van Beneden, 1876
YORKTOWN FM.; WESTERN NORTH ATLANTIC, VIRGINIA AND NORTH CAROLINA, USA (RAY, 1977)
Odobenidae
Odobeninae
(83) <i>Prorosmarus alleni</i> Berry and Gregory, 1906
Phocidae
Monachinae
(84) <i>Callophoca obscura</i> Van Beneden, 1877
(85) <i>Homiphoca</i> sp. cf. <i>H. capensis</i> (Hendey and Repenning, 1972)
(86) <i>Pliophoca etrusca</i> Tavanii, 1941
Phocinae
(87) <i>Gryphoca</i> sp. indet.
(88) <i>Phocanella pumila</i> Van Beneden, 1877
(89) <i>Platyphoca</i> sp. indet.

TABLE 3.2
(Continued)

EARLY PLIOCENE 5.2-3.4 Ma (ZANCLIAN) (Continued)
UPPER BONE VALLEY FM.; WESTERN NORTH ATLANTIC, FLORIDA, USA (MORGAN, 1994)
Odobenidae
Odobeninae
(90) <i>Odobenus huxleyi</i> (Lankester, 1865)
Phocidae
Monachinae
(91) <i>Callophoca obscura</i> Van Beneden, 1877
Phocinae
(92) <i>Phocanella pumila</i> Van Beneden, 1877
VARSWATER FM.; EASTERN SOUTH ATLANTIC, SOUTH AFRICA (MUIZON AND HENDEY, 1980)
Phocidae
Monachinae
(108) <i>Homiphoca capensis</i> (Hendey and Repenning, 1972)
SAN MATEO FM.; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (BARNES ET AL., 1981)
Otariidae
(77) <i>Thalassoleon?</i> sp. indet.
Odobenidae
Dusignathinae
(78) gen. et sp. indet.
IMPERIAL FM.; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (MITCHELL, 1961)
Odobenidae
Odobeninae
(79) <i>Valenictus imperialensis</i> Mitchell, 1961
TAMUGIGAWA AND JOSHITA FMS.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)
Odobenidae
Odobeninae
(109) <i>Protodobenus japonicus</i> Horikawa, 1995
(110) <i>Alachtherium</i> sp.
(111) <i>Odobenini</i> gen. et sp. indet.
NISHIYAMA AND SENHATA FMS.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)
Odobenidae
Odobeninae
(112) <i>Odobenus</i> sp.
Otariidae
(113) <i>Thalassoleon inouei</i> Kohno, 1992
(114) <i>Eumetopias</i> sp. aff. <i>E. jubatus</i> (Schreber, 1776)
PISCO FM.; EASTERN SOUTH PACIFIC, PERU (MUIZON, 1981)
Phocidae
Monachinae
(95) <i>Acrophoca longirostris</i> Muizon, 1981
(96) <i>Piscophoca pacifica</i> Muizon, 1981
(97) new gen. et sp.
(98) new gen. et sp.
LATE PLIOCENE 3.4-1.64 Ma (PIACENZIAN)
PIACENZIAN SANDSTONES; MEDITERRANEAN, ITALY (MUIZON, 1982)
Phocidae
Monachinae
(107) <i>Pliophoca etrusca</i> Tavani, 1942
TAMIAMI FM.; WESTERN NORTH ATLANTIC, FLORIDA, USA (MORGAN, 1994)
Odobenidae
Odobeninae
(93) <i>Odobenus huxleyi</i> (Lankester, 1865)
Phocidae
Monachinae
(94) <i>Callophoca obscura</i> Van Beneden, 1877

TABLE 3.2
(Continued)

LATE PLIOCENE 3.4-1.64 Ma (PIACENZIAN) (Continued)
SAN DIEGO FM; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (DEMÉRÉ, 1994a)
Otariidae
(80) <i>Callorhinus gilmorei</i> Berta and Deméré, 1986
Odobenidae
Dusignathinae
(81) <i>Dusignathus seftoni</i> Deméré, 1994
Odobeninae
(82) <i>Valenictus chulavistensis</i> Deméré, 1994
NISHIYAMA AND SENHATA FMS; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)
Odobenidae
Odobeninae
(115) <i>Odobenus</i> sp.
Otariidae
(116) <i>Callorhinus gilmorei</i> Berta and Deméré, 1986
TANGAHOE FM.; WESTERN SOUTH PACIFIC, AUSTRALASIA (MCKEE, 1987; 1994)
Phocidae
Monachinae
(118) <i>Ommatophoca rossi</i> Gray, 1844
Phocidae indet.
(119) Phocidae sp. A
(120) Phocidae sp. B
(121) Phocidae sp. C
F. PLEISTOCENE
EARLY PLEISTOCENE 1.64-0.79 Ma
RED CRAG AND MERKSEM SANDS; WESTERN NORTH ATLANTIC, WESTERN EUROPE
(DOLLO, 1909; VAN DER FEEN 1968; RAY, 1977)
Odobenidae
Odobeninae
(148) <i>Alachtherium antwerpiensis</i> Hasse, 1909
(149) <i>Odobenus huxleyi</i> (Lankester, 1865)
PORT ORFORD FM.; EASTERN NORTH PACIFIC, OREGON, USA (BARNES AND MITCHELL, 1975)
Otariidae
(125) <i>Eumetopias</i> new sp.
Phocidae
Phocinae
(126) <i>Phoca</i> sp. cf. <i>P. vitulina</i> Linnaeus, 1758
SHIMONOHORO FM.; WESTERN NORTH PACIFIC, JAPAN (MIYAZAKI ET AL., 1995)
Otariidae
(156) <i>Eumetopias</i> sp.
(157) <i>Zalophus</i> sp.
Odobenidae
Odobeninae
(155) <i>Odobenus</i> sp.
UNKNOWN FORMATION; EASTERN SOUTH PACIFIC, PERU (MUIZON AND DE VRIES, 1985)
Otariidae
(146) <i>Hydrarctos lomasiensis</i> (Muizon and de Vries, 1985)
LATE PLEISTOCENE 790-10 Ka
NORTH SEA FLOOR; EASTERN NORTH ATLANTIC, WESTERN EUROPE (VAN BREE AND ERDBRINK, 1987)
Odobenidae
Odobeninae
(150) <i>Odobenus rosmarus</i> (Linnaeus, 1758)
Phocidae
Phocinae
(151) <i>Erignathus barbatus</i> (Erxleben, 1777)
(152) <i>Halichoerus grypus</i> (Fabricius, 1791)
(153) <i>Phoca vitulina</i> Linnaeus, 1758

TABLE 3.2
(Continued)

LATE PLEISTOCENE 790-10 Ka (Continued)

CHAMPLAIN SEA; WESTERN NORTH ATLANTIC, CANADA (HARINGTON 1977, 1984, 1988)

Odobenidae

Odobeninae

- (137) *Odobenus rosmarus* (Linnaeus, 1758)

Phocidae

Phocinae

- (138) *Erignathus barbatus* (Erxleben, 1777)
(139) *Pagophilus groenlandica* (Erxleben, 1777)
(140) *Phoca vitulina* Linnaeus, 1758
(141) *Pusa hispida* (Schreber, 1775)

KEMPSVILLE FM. AND CORRELATIVE DEPOSITS, WESTERN NORTH ATLANTIC, VIRGINIA, USA (RAY ET AL. 1968; McDONALD AND RAY 1992)

Odobenidae

- (142) *Odobenus rosmarus* (Linnaeus, 1758)

Phocidae

Phocinae

- (143) *Halichoerus grypus* (Fabricius, 1791)
(144) *Phoca* sp. indet.

NEARSHORE MARINE SEDIMENTS; WESTERN NORTH ATLANTIC, FLORIDA, USA (MORGAN, 1994)

Phocidae

Monachinae

- (145) *Monachus tropicalis* (Gray, 1850)

GUBIK FM.; ARCTIC OCEAN, ALASKA, USA (REPENNING 1983)

Phocidae

Phocinae

- (122) *Histiophoca fasciata* (Zimmermann, 1783)
(123) *Phoca vitulina* Linnaeus, 1758
(124) *Pusa* sp. indet.

SANGAMON INTERGLACIAL DEPOSITS; EASTERN NORTH PACIFIC, ALASKA TO CENTRAL CALIFORNIA, USA (KURTÉN AND ANDERSON 1980)

Odobenidae

Odobeninae

- (127) *Odobenus rosmarus* (Linnaeus, 1758)

Otariidae

- (128) *Callorhinus ursinus* (Linnaeus, 1758)
(129) *Eumetopias jubata* (Schreber, 1776)
(130) *Arctocephalus townsendi* Merriam, 1897

Phocinae

- (131) *Erignathus barbatus* (Erxleben, 1777)
(132) *Pusa hispida* (Schreber, 1775)

SAN PEDRO SAND; EASTERN NORTH PACIFIC, SOUTHERN CALIFORNIA, USA (MILLER, 1971)

Otariidae

- (133) *Eumetopias* sp. indet.
(134) *Zalophus* sp. indet.

Phocidae

Monachinae

- (135) *Mirounga* sp. indet.

Phocinae

- (136) *Phoca* sp. cf. *P. vitulina* Linnaeus, 1758
-

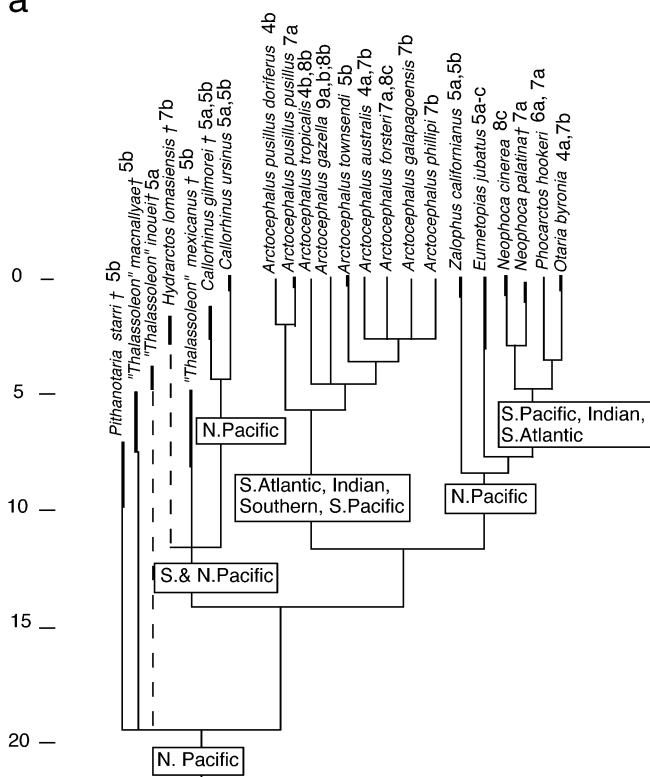
TABLE 3.2
(Continued)

LATE PLEISTOCENE 790-10 Ka (Continued)
MANDANO FM. AND CORRELATIVE DEPOSITS; WESTERN NORTH ATLANTIC, JAPAN (MIYAZAKI ET AL., 1995)
Otariidae
(158) <i>Callorhinus ursinus</i> (Linnaeus, 1758)
(159) <i>Eumetopias ojiyaensis</i> (Horikawa, 1981)
(160) <i>E. watasei</i> Matsumoto, 1925
(161) <i>Zalophus californianus</i> (Lesson, 1828)
Odobenidae
Odobeninae
(162) <i>Odobenus mandanoensis</i> Tomida, 1989
Phocidae
Phocinae
(163) <i>Phoca</i> sp. cf. <i>P. vitulina</i> Linnaeus, 1758
(164) <i>Phoca</i> sp. cf. <i>P. largha</i>
NUKUMARIAN AND CASTLECLIFFIAN AGE DEPOSITS; WESTERN SOUTH PACIFIC, AUSTRALASIA
Otariidae
(165) <i>Neophoca cinerea</i> (Péron, 1816)
(166) <i>N. palatina</i> King, 1983
Phocidae
Monachinae
(167) cf. <i>Mirounga</i> sp. indet.
Phocidae indet.
(168) gen. et sp. indet.
CHUI FM.; WESTERN SOUTH ATLANTIC, BRAZIL (DREHMER AND RIBEIRO, 1998)
Otariidae
(147) <i>Otaria byronia</i> (Blainville, 1820)
EASTERN SOUTH ATLANTIC, SOUTH AFRICA (REPENNING AND TEDFORD, 1977)
Otariidae
(154) <i>Arctocephalus pusillus</i> (Schreber, 1776)

By combining phylogenetic and stratigraphic data, it seems clear that otariids evolved in the eastern North Pacific sometime before 11 Ma with basal taxa occurring in the eastern and western parts of that region by the late Miocene. Using the phylogeny, it is most parsimonious to assume that divergence of *Thalassoleon* + *Callorhinus* and otariine + arctocephaline clades also occurred in the North Pacific. Stratigraphic data (i.e., OKR for *Thalassoleon mexicanus*) suggest that this divergence occurred prior to 6 Ma (late Miocene). The divergence of the otariine and arctocephaline clades is poorly constrained by stratigraphic data. Species of the arctocephaline clade are known in the fossil record only from the Pleistocene, with poorly documented records from the eastern South Atlantic (4b; *A. pusillus*) and the eastern North Pacific (5b; *A. townsendi*; see Re-

penning and Tedford, 1977). It seems likely that initial divergence of this clade involved a single transequatorial dispersal event from the North Pacific into the Southern Hemisphere crossing into the eastern South Pacific (7b; fig. 3.4) via eastern boundary currents (i.e., California and Peru currents). *Hydrarcotos lomasiensis* from the late Pliocene/early Pleistocene of Peru (7b) provides a possible minimum age for this Southern Hemisphere dispersal event, since it predates all described fossil occurrences of *Arctocephalus*. Once in the Southern Hemisphere, speciation of the *Arctocephalus* clade occurred, with six of the currently recognized species diversifying in high latitudes. High species diversity of this clade likely reflects rapid speciation during the Pleistocene. Dispersal of *A. pusillus pusillus* in the eastern South Atlantic (4b) and *A. pusillus doriferus* in the western South Pa-

a



b

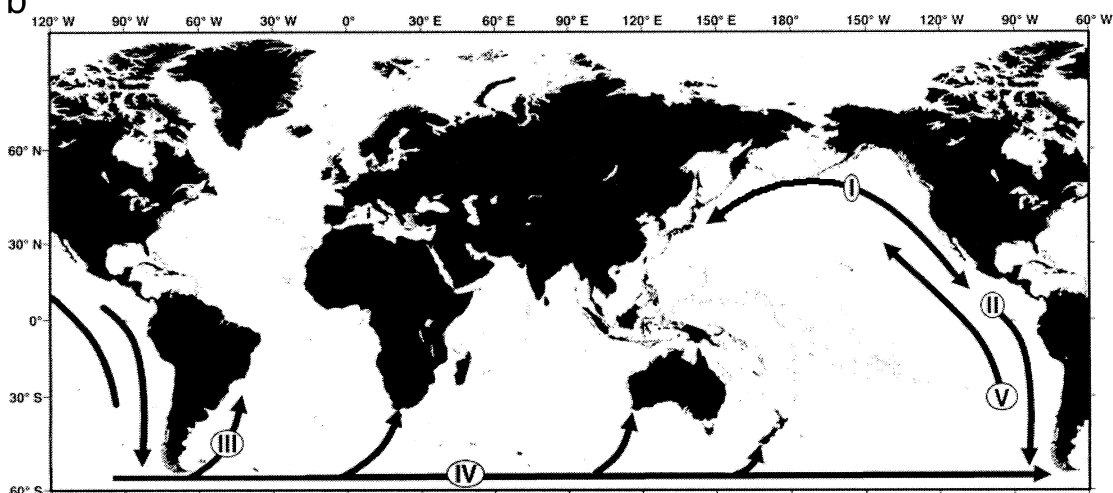


Fig. 3.4. Area cladogram of otariids and summary of principal dispersal/vicariant events hypothesized to explain their distribution around the world. (I) Earliest otariids in North Pacific before 11 Ma; *Thalassoleon* + *Callorhinus* and divergence of arctocephaline + otariine clades and establishment of circum-North Pacific range by early Pliocene; (II) transequatorial dispersal from North Pacific into the Southern Hemisphere crossing the eastern South Pacific; earliest fossil otariid in Southern Hemisphere 2–3 Ma; (III) speciation of *Arctocephalus* clade and dispersal into eastern South Atlantic; (IV) continued diversification and dispersal into southern Indian Ocean and western South Pacific following West Wind Drift; (V) Pleistocene reinvasion of the Northern Hemisphere by dispersal or vicariance (glacial-interglacial oscillation).

cific (7a) followed the West Wind Drift. A later divergence following this same dispersal route is hypothesized to account for the present day distributions of *A. tropicalis* in the Atlantic and Indian Southern Ocean (9a,b), *A. gazella* in the Atlantic and Indian Southern Ocean (9a,b), and *A. forsteri* in the waters off New Zealand and southern Australia (7a). Evolution of the *A. australis*–*A. philippi*–*A. galapagoensis* clade likely occurred in the eastern South Pacific (7b), with expansion of the *A. australis* range along the eastern shore of South America (4a) possibly following the cold Falkland Current. The modern geographic range of *A. townsendi* in the temperate eastern North Pacific off Baja California (5b) is anomalous relative to other species of *Arctocephalus*, and suggests a south-to-north transequatorial dispersal event during a Pleistocene glacial period when strong eastern boundary currents and coastal upwelling would provide an oceanographic “corridor” for crossing the tropics. However, the hypothesized phylogenetic position of *A. townsendi* outside the *A. australis*–*A. philippi*–*A. galapagoensis* clade does not provide any supporting evidence for a possible divergence from known eastern South Pacific arctocephaline taxa. The phylogeny, however, does provide possible evidence for south-to-north divergence of *A. galapagoensis* from an *A. australis*–*A. philippi* clade. This divergence could have been either by south-to-north dispersal to the Galapagos Archipelago or by a vicariant event related to Pleistocene glacial-interglacial oscillations, fragmentation of an ancestral home range, and allopatric speciation in the Galapagos Archipelago.

The historical biogeography of sea lions is similar to that of fur seals and also suffers from a limited fossil record. As mentioned, basal sea lions *Zalophus* and *Eumetopias* are known from the Pleistocene (and possibly Pliocene) of the western and eastern North Pacific (Miyazaki et al., 1995). Except for modern populations of *Zalophus* in waters of the Galapagos Archipelago (7b), otariines are presently, and have probably always been, confined to temperate, high latitudes. We propose that otariines reached the Southern Hemisphere via a single transequatorial dispersal event in the eastern Pacific Ocean,

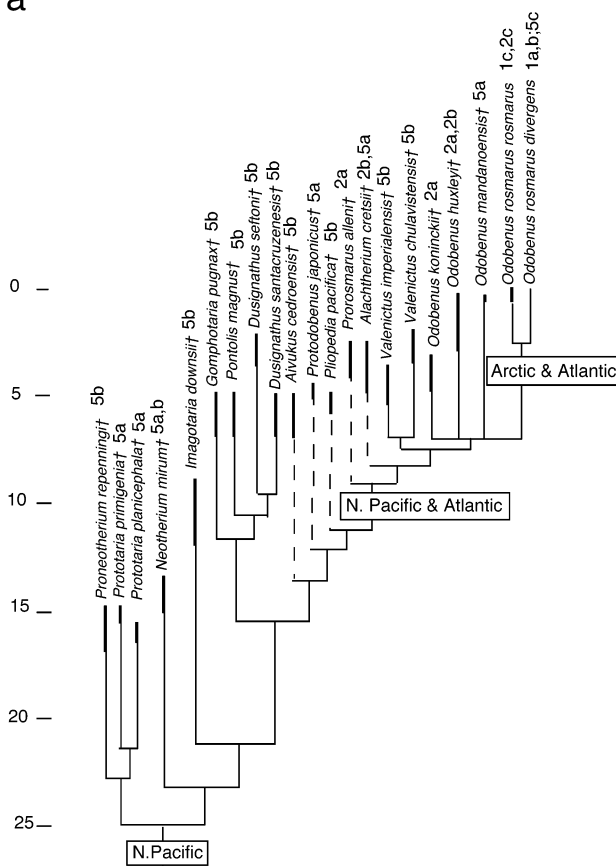
perhaps coincident with the arctocephaline dispersal event discussed previously. Speciation in the *Neophoca*–*Phocarctos*–*Otaria* clade most likely occurred during the Pleistocene in the Southern Hemisphere via the West Wind Drift, either preceding or following the Southern Ocean dispersal of otariines (i.e., speciation then dispersal or range expansion then allopatric speciation). These events were likely synchronous with fur seal dispersal events. In support of this claim, we note the broadly sympatric distributions of *Otaria bryonia* and *Arctocephalus australis* in the eastern South Pacific and western South Atlantic, of *Neophoca cinerea* and *Arctocephalus forsteri* in waters off southern Australia, and of *Phocarctos hookeri* and *Arctocephalus forsteri* in waters south of New Zealand.

PHOCOMORPHA CLADE: Phocomorpha include two major monophyletic taxa: (1) the Odobenidae and (2) the Phocoidea (Phocidae plus the extinct Desmatophocidae; Berta and Wyss, 1994). Phocomorphs include animals with enlarged auditory ossicles (Berta and Wyss, 1994). The OKR of Phocomorpha is currently established by *Desmatophoca brachycephala* from the early Miocene (Aquitian) Astoria Formation of Washington State (eastern North Pacific, 5b), suggesting that evolution of phocomorphs likely occurred sometime prior to 18 Ma, probably in the North Pacific Ocean Basin (fig. 3.5, table 3.2).

ODOBENIDAE—WALRUSES: The monophyletic Odobenidae or walrus clade (Deméré, 1994b; Kohno et al., 1995a; figs. 3.3, 3.5) includes a single extant species *Odobenus rosmarus*, and at least 20 fossil species arranged in 14 genera. Living *Odobenus* swims primarily with hindlimb propulsion and, like all odobenids, has retained the ability to rotate the hind feet forward for quadrupedal “walking” during terrestrial locomotion.

The most basal odobenid taxa comprise the *Prototaria*–*Proneotherium* clade from late early and/or early middle Miocene deposits of the western and eastern North Pacific (5a, 5b; Kohno et al., 1995a). The odobenid OKR is currently established by *Proneotherium repenningi* from the late early Miocene (Burdigalian) Astoria Formation of the eastern North Pacific (5b). Although

a



b

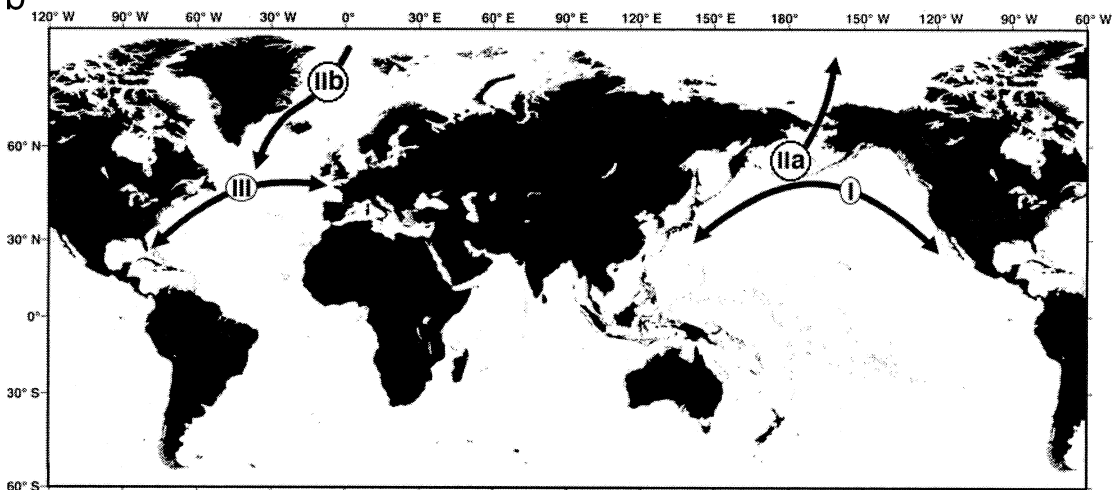


Fig. 3.5. Area cladogram of odobenids and summary of principal dispersal/vicariant events hypothesized to explain their distribution around the world. (I) Earliest odobenids in North Pacific before 18 Ma; evolution and divergence of dusignathines and odobenines also in North Pacific; dusignathines North Pacific endemics; (II) diversification and dispersal of odobenines following a northern Arctic Ocean route (IIa) through the open Bering Strait 4–5 Ma from the Pacific into the Atlantic (IIb); continued diversification and dispersal of odobenines to both shores of the North Atlantic (III).

Kohn et al. (1995a) assign this taxon to the early middle Miocene, the geologic age of *Proneotherium* is probably older because of its apparent occurrence near the base of the long-ranging Astoria Formation (Deméré and Berta, 2001). Other basal odobenids include *Neotherium mirum* (middle Miocene; eastern North Pacific) and *Imagotaria downsii* (late Miocene; eastern North Pacific) as successive sister taxa. Later diverging walruses can be grouped into two monophyletic groups (figs. 3.3, 3.5). The Dusignathinae includes the extinct genera *Dusignathus*, *Gomphotaria*, and *Pontolis*. The dusignathine OKR is established by *Dusignathus santacruzensis*, *Gomphotaria pugnax*, and *Pontolis magnus* from late late Miocene (Messinian) deposits of the eastern North Pacific (5b). The Odobeninae includes, in addition to the modern walrus *Odobenus*, the extinct genera *Aivikus*, *Protodobenus*, *Pliopedia*, *Alachtherium*, *Prorosmarus*, and *Valenictus* (Deméré, 1994b; figs. 3.3, 3.5). The latter five taxa comprise the Odobenini crown clade, the OKR of which is established by *Protodobenus japonicus* from the early Pliocene (Zanclian) Tamugigwa Formation of Japan (5a; western North Pacific).

Phylogenetic and stratigraphic data suggest that odobenids first evolved in the North Pacific region sometime before 18 Ma (late early Miocene) with basal taxa being confined to the eastern and western parts of this region during the middle Miocene. The fossil record reveals that basal odobenids ranged as far south as northern Baja California, Mexico in the eastern North Pacific region during the middle Miocene (based on undescribed material aff. *Neotherium* sp.; Barnes, 1998; fig. 3.5). Using the phylogeny it is most parsimonious to assume that divergence of the dusignathine and odobenine clades also occurred in the eastern North Pacific. Stratigraphic data (i.e., OKRs of *Gomphotaria pugnax* and *Aivikus cedrosensis*) suggest that this divergence occurred prior to 6 Ma (late Miocene). The fossil record further suggests that dusignathines remained endemic to the eastern North Pacific region throughout their evolutionary history. In contrast, odobenines underwent dramatic diversification during the late Miocene with later members of this lineage dispersing from the North Pa-

cific into the eastern and western North Atlantic by early Pliocene time (fig. 3.5). It has been proposed that members of the odobenine lineage first entered the Caribbean from the Pacific via the Central American Seaway between 5 and 8 Ma (Repenning et al., 1979) and then dispersed northward into the North Atlantic, where the Odobenini clade is postulated to have evolved. According to this hypothesis, odobenids became extirpated from the Pacific in the Pliocene, and then less than one million years ago the modern genus *Odobenus* returned to the North Pacific through the Arctic Ocean (Repenning and Tedford, 1977; Repenning et al., 1979). A late Miocene southern dispersal route is supported by the occurrence of the basal odobenine *Aivikus* from Baja California, Mexico. However, a new and improving record of fossil walruses from Japan and California supports an alternative hypothesis involving a northern, east-to-west dispersal route during the early Pliocene. Rather than being extirpated from the North Pacific during the Pliocene, odobenids continued to diversify in that region into the Pleistocene (Tomida, 1989; Kohn et al., 1995b). In fact, using the phylogeny (fig. 3.5), it is most parsimonious to assume that evolution of the Odobenini clade actually occurred in the North Pacific. The OKR of *Protodobenus japonicus* further suggests that this divergence happened prior to 4.5 Ma (early Pliocene). The discovery of *Alachtherium* in the early Pliocene of Japan (Kohn et al., 1998) supports the hypothesis. This taxon was formerly considered to be a North Atlantic endemic odobenine from the late Pliocene and Pleistocene of western Europe (Ray, 1976; Deméré, 1994b). Its earlier occurrence in the North Pacific, however, suggests that *Alachtherium* more likely evolved in that ocean region before dispersing into the North Atlantic during the early Pliocene. The timing of this event is important because the potential for biotic exchange through the Central American Seaway had been dramatically reduced by the early Pliocene (Duque-Caro, 1990) making it less likely that odobenines would use this warm water route. At the same time, however, geologic events in the Arctic Ocean had established a wide open Bering Strait and high global sea levels combined with ice-free,

trans-Arctic circulation, which in turn, provided a suitable northern dispersal route between the North Pacific and North Atlantic regions (Marincovich, 2000). The timing for this event is also coincident with dispersal of Pacific mollusks (e.g., *Mya arenaria*) into the Atlantic and their appearance in such odobenine-producing deposits as the Scaldian sands of Belgium (2b; eastern North Atlantic) and the Yorktown Formation of North Carolina, USA (2a; western North Atlantic; Vermij, 1991).

The historical biogeography of the modern genus *Odobenus* is more difficult to determine because of a limited fossil record and imprecise biochronologic control. The paucity of complete skulls and dentitions makes it impossible to resolve phylogenetic relationships at this time among the various proposed fossil species of this genus (fig. 3.5), and the strong possibility exists that several of these taxa are conspecific. Kohno et al. (1995b) concluded on the basis of stratigraphic and geographic occurrences of Pleistocene *Odobenus* that the genus evolved in the North Pacific, dispersed into the Arctic Ocean, and eventually the North Atlantic, probably during one of the early interglacial events of the latest Pliocene or Pleistocene. During the Pleistocene, there was possibly a single circum-arctic species of *Odobenus* that extended its range into near temperate latitudes in both the Pacific and Atlantic during interglacial periods. The two extant subspecies of *Odobenus rosmarus* may represent the product of range fragmentation and allopatric speciation during a glacial period of maximum Arctic sea ice volume.

PHOCOIDEA CLADE: Phocoidea includes two monophyletic taxa: (1) the extinct Desmatophocidae and (2) the extant Phocidae (true or earless seals; Berta and Wyss, 1994). Phocoids include animals with a mortised squamosal/jugal contact and posterior termination of nasals posterior to contact between the frontal and maxilla bones (Berta and Wyss, 1994). The OKR of Phocoidea is currently established by *Desmatophoca brachycephala* from the early Miocene (Aquitania) Astoria Formation of Washington State (eastern North Pacific, 5b), suggesting that divergence of phocoids from odobenids likely oc-

curred sometime before 18 Ma, probably in the North Pacific Ocean Basin.

DESMATOPHOCIDS—EXTINCT PHOCID RELATIVES: An extinct family of archaic phocoids, the desmatophocids were animals with enlarged paroccipital processes and bulbous crowned postcanine teeth (Deméré and Berta, 2002). Desmatophocids probably swam with forelimb propulsion and retained the ability to rotate the pes forward for quadrupedal “walking” during terrestrial locomotion. The Desmatophocidae includes two genera, *Desmatophoca* and *Allodesmus*, which together contain at least six described species from the early and middle Miocene (fig. 3.3). The OKR of Desmatophocidae is currently established by *Desmatophoca brachycephala* from the early Miocene (Aquitania) Astoria Formation of Washington, USA (eastern North Pacific, 5b), suggesting that divergence of desmatophocids from phocoids likely occurred sometime before 18 Ma, probably in the North Pacific Ocean Basin. The OKR of Desmatophocidae is the same age as for the Phocoidea clade. The youngest known record (YKR; Walsh, 1998) of Desmatophocidae is based on unpublished specimens of *Allodesmus* from the late Miocene (Tortonian) Montesano Formation of Washington, USA (Bigelow, 1994).

The basal taxon *Desmatophoca* evolved in the eastern North Pacific region in the early Miocene and, based on current paleontological evidence, was endemic to that region. However, its sister taxon, *Allodesmus*, underwent an important diversification during the middle Miocene that eventually involved dispersal to the western North Pacific (Barnes and Hirota, 1995). In the eastern North Pacific, *Allodesmus* extended its range during the late middle Miocene southward into Baja California, Mexico (Barnes, 1998).

PHOCIDAE—SEALS: The monophyletic Phocidae (Wyss, 1988) includes seals with inflated auditory bullae, no alisphenoid canal, and derived tarsal morphology (Muizon, 1982). Phocids swim with hind limb propulsion and have lost the ability to rotate the pes forward. Consequently, terrestrial locomotion for phocids does not involve quadrupedal “walking”. Traditionally, extant phocids have been divided into two to four major subgroups; monachines (monk seals), lobo-

dontines (Antarctic seals), cystophorines (hooded and elephant seals), and phocines (remaining Northern Hemisphere seals). The consensus phylogeny for extant phocids (Bininda-Emonds et al., 1999) supports monophyly of the Monachinae, Lobodontini, and Phocinae (figs. 3.3, 3.6). The Cystophorinae, however, is not recognized as a monophyletic group (King, 1966) and its members are instead divided among Monachinae and Phocinae. The Monachinae clade includes *Monachus* (monk seals), *Mirounga* (elephant seals), and the Lobodontini (Antarctic seals). Bininda-Emonds et al. (1999) support the *Monachus* species group as monophyletic (contrary to Wyss, 1988) and position *M. monachus* as the basal taxon (figs. 3.3, 3.6). The next diverging monachine lineage includes *Mirounga* and the Lobodontini clade, which in turn includes the monotypic taxa *Leptonychotes*, *Ommatophoca*, *Lobodon*, and *Hydrurga* (Wyss, 1988; Bininda-Emonds et al., 1999). The relationships of several fossil monachines to extant taxa were discussed by Muizon (1982) but are poorly supported (as shown by alternate topologies in figs. 3.3 and 3.6). The positions of other fossil taxa are, as yet, unresolved.

The Phocinae clade includes sister taxa *Erignathus*, *Cystophora*, and the tribe Phocini (Wyss, 1988). The Phocini (fig. 3.3) is further divided into *Histriophoca* + *Pagophilus*, *Halichoerus*, and *Pusa* + *Phoca* (Bininda-Emonds et al., 1999). The latter crown clade includes two sister groups: (1) *Pusa caspica* + *Pusa siberica* + *Pusa hispida* and (2) *Phoca largha* + *Phoca vitulina*. The relationships of fossil phocines to one another and to extant taxa are, as yet, unresolved, as indicated by their position as a polytomy at the base of the phocine clade (figs. 3.3, 3.6). The need for detailed taxonomic studies and rigorous phylogenetic hypotheses of relationships for these fossil taxa is critical to a better understanding of the historical biogeography of the phocine clade.

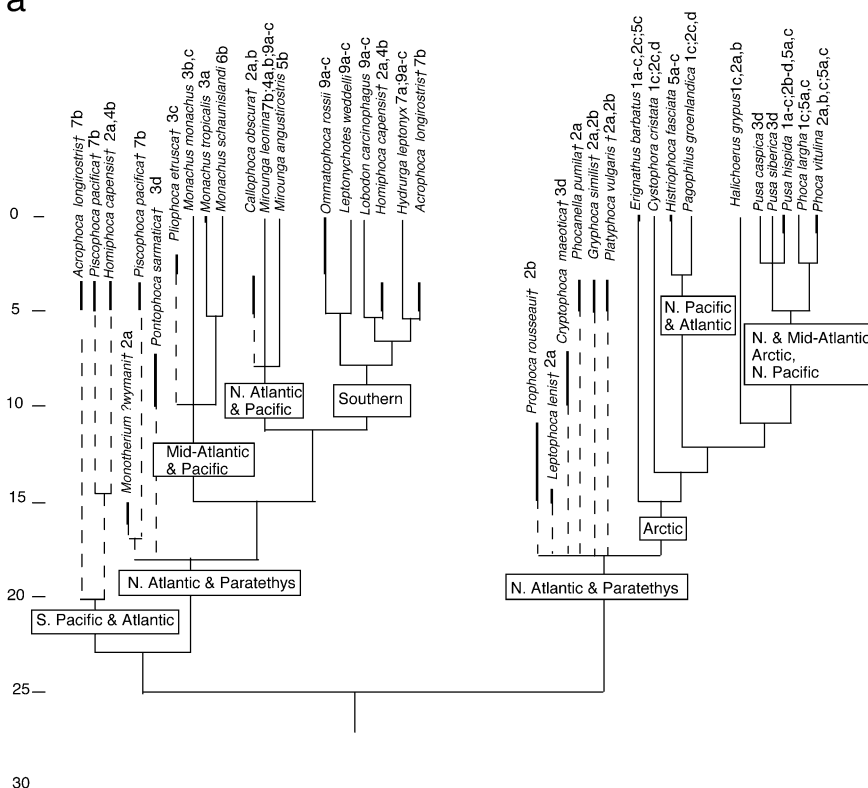
The OKR of phocids is currently established by *Leptophoca lenis* from the middle Miocene (Langhian) Calvert Formation of Maryland, USA (western North Atlantic; 2a). As noted by Ray (1977), the Calvert phocids are assigned to the Phocinae and Monachinae, suggesting that divergence of the two

clades occurred sometime prior to the middle Miocene. An older, poorly documented record of phocids from the late Oligocene (Chattian) of the western North Atlantic (South Carolina) has been proposed by Korytsky and Sanders (1997) but awaits description and scientific scrutiny. Overall, our knowledge of fossil phocids is severely limited due to a paucity of detailed morphologic descriptions of taxa and rigorous analyses of character evolution and phylogenetic relationships. The studies of Muizon (1981, 1982) and Muizon and Hendey (1980) are notable exceptions.

On the basis of phylogenetic data, it is most parsimonious to assume that phocids evolved in the North Pacific during the early Miocene (fig. 3.6), with divergence of the basal phocid taxa (i.e., phocids and desmaphocids) occurring sometime before 18 Ma. Phylogenetic and stratigraphic data, however, also suggest that divergence of the phocine and monachine clades likely occurred in the North Atlantic sometime before 16 Ma. These two closely timed events require long-distance dispersal of some currently unknown basal phocid from the North Pacific into the North Atlantic, either northward through the Arctic Ocean or southward through the Central American Seaway. As discussed by Costa (1993) and Bininda-Emonds and Russell (1996), a southern route is more likely because of the lack of an early Miocene marine corridor through Beringia and the presence of a wide-open Central American Seaway at the same time. It is admitted that the absence of basal phocid fossils in the North Pacific and Caribbean is a weakness of this hypothesis.

Combining the phylogenies of Bininda-Emonds et al. (1999) for extant monachines and Muizon (1982) for fossil monachines suggests that it is most parsimonious to assume that monachines evolved in the North Atlantic, possibly in the western part of that ocean basin based on the monachine OKR as currently established by *Monotherium? wymani* from the middle Miocene (Langhian) Calvert Formation (Ray, 1976). Other early monachine fossil taxa, including *Monotherium aberratum* from the late Miocene (Tortonian) of the eastern and western North Atlantic (Ray, 1976), *Pristiphoca vetusta* from

a



b

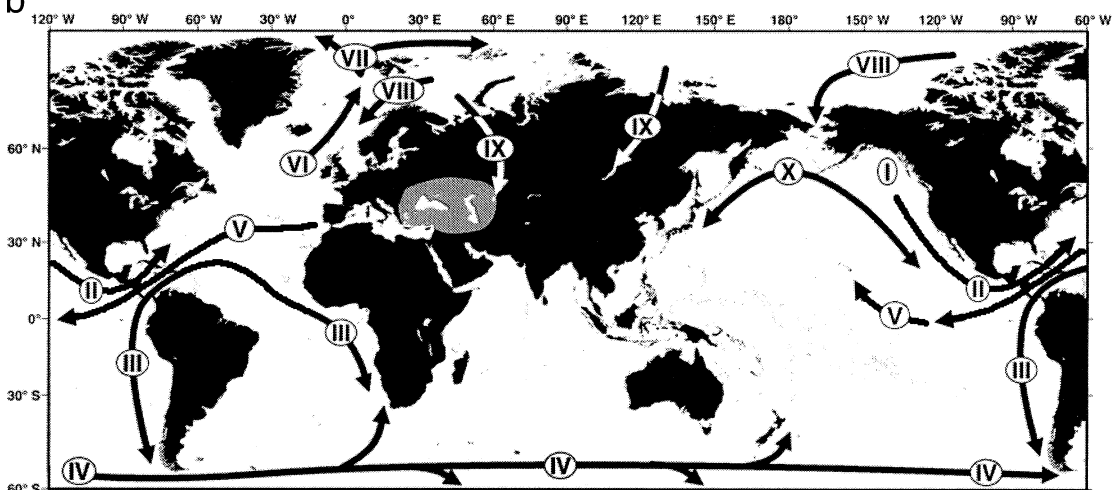


Fig. 3.6. Area cladogram of phocids and summary of principal dispersal/vicariant events hypothesized to explain their distribution around the world. Rough outline of Paratethys shaded gray. (I) Earliest phocids in North Pacific with divergence of basal phocoids (phocids and desmatophocids) before 18 Ma; (II) following dispersal of presently unknown basal phocid from the North Pacific into North Atlantic via a southern route (i.e., Central American Seaway) divergence of monachines and phocines in the North Atlantic; earliest record of both clades 15 Ma; (III) dispersal of monachine relatives southward into the eastern South Pacific and/or South Atlantic in the early middle Miocene; (IV)

the middle Miocene (Badenian = Serravalian) of Central Paratethys (Muizon, 1982), and *Pontophoca sarmatica* from the late Miocene (Sarmatian = Tortonian) of Eastern Paratethys (Grigorescu, 1977), suggest a trans-Atlantic dispersal event in the middle and late Miocene that also involved invasion of the Paratethys. A separate invasion (perhaps post-Messinian) of the Mediterranean Tethys is documented by the occurrence of "*Pristiphoca*" *occitana* in the early Pliocene of southern France and *Pliophoca etrusca* in the late Pliocene of northern Italy. Muizon (1982) proposed that these Pliocene Mediterranean monachines were probably ancestral to the *Monachus* species clade. Muizon further suggests that *Monachus* evolved in the Mediterranean, expanded its range to include Mauritania in the eastern North Atlantic, and then dispersed east to west across the equatorial Atlantic via the North Equatorial Current to reach the Caribbean. Presumably, allopatric speciation in the Caribbean resulted in the evolution of the modern *M. tropicalis*. There is no consensus on the timing of the subsequent dispersal of *Monachus* from the Caribbean through the Central American Seaway and into the central North Pacific (*M. schauinslandi*), but it must have occurred prior to the mid-Pliocene closure of this corridor. Repenning and Ray (1977) suggest that the divergence and dispersal of *M. schauinslandi* likely occurred prior to 14.5 Ma, while Muizon (1982) suggested that these events occurred just prior to 4.0–3.5 Ma. Regardless of when the divergence and east-to-west dispersal occurred, the fact that they did occur is supported by *Monachus* phylogeny, which places the Mediterranean *Monachus mona-*

chus in a basal position to the *M. tropicalis* + *M. schauinslandi* clade.

The monachine crown clade of *Mirounga* plus Lobodontini also has a North Atlantic origin based on the occurrence of early diverging fossil members from the eastern and western shores of this ocean basin (Ray, 1976). The OKR for this clade is established by *Monotherium aberratum*, *M. affine*, and *M. delognei* from the late Miocene (Tortonian) Diest Formation and St. Mary's Formation of Belgium and Maryland, respectively (Ray, 1976), suggesting that the divergence of the *Mirounga* and lobodontine clades occurred sometime before 11 Ma in the North Atlantic. Muizon (1982) proposes that species of *Monotherium* are allied with the lobodontine seals, and that this group evolved in the North Atlantic prior to its dispersal into the Southern Hemisphere. Whether this dispersal occurred solely through the Central American Seaway and then south along the Pacific coast of South America, or involved at least some period of migration south along the Atlantic coast of Africa via the eastern boundary currents is controversial. Clearly, there was at least some dispersal of phocids through the Central American Seaway, as is evidenced by the well-studied monachine fauna from the late Miocene (Messinian) to early Pliocene (Zanclean) Pisco Formation of Peru (Muizon, 1981). The Pliocene fauna includes two well-documented monachine phocids, *Acrophoca longirostris* and *Piscophoca pacifica*. The former taxon Muizon (1982) allies with the extant *Lobodon-Hydrurga* clade. The OKR for southern lobodontines is established by undescribed fossils from the late Miocene portion of the Pisco Formation (Muizon and de

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diversification and dispersal of lobodontines southward into colder waters of the Southern Ocean; (V) dispersal of *Monachus* from the Mediterranean into the Caribbean and continuing on to the Hawaiian islands through the Central American seaway; (VI) dispersal of basal phocines from North Atlantic into the Arctic; *Erignathus* extends range into the Bering Sea; (VII) diversification of phocines; (VIII) range expansion of *Histriophoca* and *Pagophilus* clade followed by range fragmentation (i.e., glacial/interglacial oscillations) and allopatric speciation; *Histriophoca* enters the North Pacific and *Pagophilus* enters the North Atlantic; *Halichoerus* disperses southward from the Arctic into the North Atlantic; (IX) vicariance during the Pleistocene (i.e., glacial/interglacial oscillations) resulting in speciation with *Pusa hispida* entering the circum-Arctic, *Pusa caspica* entering the Caspian Sea, and *Pusa siberica* entering Lake Baikal; (X) vicariance and divergence of *Phoca vitulina* and *Phoca largha* in the North Pacific.

Vries, 1985) suggesting that dispersal occurred sometime before 7 Ma. From Peru it is suggested that lobodontines radiated into high southern latitudes, initially along the Pacific shore of South America and then throughout the Southern Ocean via the West Wind Drift. This Southern Ocean diversification and dispersal included the evolution and establishment of *Homiphoca capensis* known from the early Pliocene (Zanclean) Varswater Formation of South Africa (Muizon and Hendey, 1980). An alternative hypothesis holds that while one group of ancestral lobodontines dispersed through the Central American Seaway, a second group dispersed south along the eastern shore of Africa to become *H. capensis*. The reported, but undocumented occurrence of *Homiphoca* in the early Pliocene (Zanclean) Yorktown Formation of North Carolina (Ray, 1976) complicates the historical biogeography of this taxon, but may be explained by a hypothesis involving a south-to-north return of *Homiphoca* via the Benguela eastern boundary current, followed by an east-to-west crossing of the Atlantic via the South Equatorial Current, and finally a south-to-north dispersal via the Florida or Gulf Stream western boundary current. This elaborate ad hoc hypothesis underscores the critical need for the collection and detailed study of the fossil phocid faunas of the Atlantic, Mediterranean, and Paratethyan Neogene.

The historical biogeography of the *Mirounga* clade is similar to that of lobodontines and also suffers from a limited and poorly documented fossil record. The OKR for this clade is established by *Callophoca obscura* from the early Pliocene (Zanclean) Yorktown Formation of North Carolina (western North Atlantic; 2a). The trans-Atlantic distribution of this taxon as discussed by Ray (1976) and Muizon (1982) suggests that *C. obscura* may actually have evolved in the eastern North Atlantic sometime before 4.5 Ma and dispersed east to west across the equatorial Atlantic via the North Equatorial Current, continuing northward along the eastern shore of North America. Some members of this dispersing lineage could have passed through the Central American Seaway at this time (late Miocene or earliest Pliocene) to establish the lineage in the eastern South Pacific. Subsequent speciation in the Pacific resulted

in the evolution of *Mirounga* (*M. leonina*) and its dispersal in the subantarctic Southern Ocean via the West Wind Drift. The occurrence of *Mirounga* (*M. angustirostris*) in the eastern North Pacific suggests a transequatorial dispersal event and allopatric speciation, possibly coincident with the Pleistocene dispersal and speciation events proposed for the *Arctocephalus townsendi* lineage. Obvious weaknesses of this hypothesis include the lack of *Callophoca* or related fossil taxa in the pinniped-rich Neogene deposits of the Pisco Formation of Peru and the lack of fossils of *Mirounga* in rocks older than the late Pleistocene.

Although both the monachine and phocine seals had their origin in the relatively warm Neogene North Atlantic, only monachines were diverse enough to include one thermophilic lineage that remained in relatively warm Quaternary seas and at least two more thermophobic lineages that dispersed to the south and have their greatest modern diversity in the high latitudes of the Southern Hemisphere. In contrast, phocines remained in the Northern Hemisphere, moving progressively farther north as Pleistocene climates cooled so that today they have their greatest diversity in arctic and subarctic regions. As discussed earlier, the phocine OKR is currently established by *Leptophoca lenis* from the middle Miocene (Langhian) Calvert Formation of Maryland, USA (western North Atlantic region; 2a). At about this same time, however, fossil seals are also present in the Central Paratethys (Koretsky and Holec, 2002) documenting a trans-Atlantic phocine distribution and posing the question of a western versus eastern North Atlantic origin for the group. Species closely related to the western North Atlantic phocines are recorded from the late middle Miocene (Serravallian) Berchem Formation of Belgium (eastern North Atlantic; 2b), while the poorly documented but coeval (early Sarmatian) "*Phoca*" *vindobonensis* shows continued occupation of the Central Paratethys (Grigorescu, 1977). The latest well-documented Paratethyan phocines, *Cryptophoca maeotica* and "*Pusa*" *pontica*, are known from the late Miocene (middle Sarmatian = Tortonian) of the Eastern Paratethys and coincide with the major period of isolation and hyposalinity

proposed for this inland waterway (Koretsky and Ray, 1994). As described by Repenning et al. (1979), the Pliocene phocine record is more diverse than that for the late Miocene and consists of a somewhat cosmopolitan trans-Atlantic fauna (table 3.2) known from the Yorktown and Upper Bone Valley formations of the western North Atlantic (2a) and the Kattendijk and Lillo formations of the eastern North Atlantic (2b). These authors suggest that an apparent asymmetry in Pliocene phocid dominance documented in these two regions (i.e., monachine dominance in the western North Atlantic and phocine dominance in the eastern North Atlantic) may be an initial indication of the modern temperature preferences of these two groups, with the center of monachine diversification in the warmer western North Atlantic and the center of phocine diversification in the cooler eastern North Atlantic. The timing of this apparent temperature dichotomy is synchronous with closure of the Central American Seaway and the proposed northward deflection of the North Equatorial Current and strengthening of the warm Gulf Stream. Unfortunately, rigorous phylogenetic analyses of Miocene and Pliocene fossil phocines are lacking, making it impossible to reliably employ evolutionary relationships in evaluating historical biogeographic patterns at this time. Phylogenies for extant phocines, however, are available (Bininda-Emonds et al., 1999), and provide a means for constraining discussion of higher phocine biogeography.

It has been proposed that the biogeography of modern phocine seals is the product of two rather recent dispersal events, one involving dispersal of the *Pusa-Phoca* lineage into the Arctic from a Paratethyan refugium and another involving the northward dispersal of the remaining phocine lineages into the Arctic from a North Atlantic center of origin followed by glacioeustatic-forced diversification in the Arctic and invasion of the North Pacific (see Repenning et al., 1979). This dual dispersal hypothesis is countered by a single dispersal hypothesis that involves the dispersal of phocines into the Arctic from a North Atlantic center of origin followed by glacioeustatic-forced diversification in the Arctic and radial invasion of the North Pa-

cific, Caspian Sea, and Lake Baikal (see Davies, 1958b). Unfortunately, the fossil record of higher phocine seals is limited to Pleistocene occurrences and does not provide any useful evidence for testing these competing hypotheses except to show that phocids entered the North Pacific sometime before the early Pleistocene (Barnes and Mitchell, 1975). The phylogeny, however, does provide a means for testing these biogeographic hypotheses (e.g., see Hoberg and Adams, 1992) and lends strong support to the single dispersal hypothesis. Basal taxa such as *Erignathus* and *Cystophora* appear to have originated in the Arctic during the Pleistocene, with *Erignathus* extending its range into the Bering Sea (5c) and North Atlantic (2c) and *Cystophora* dispersing into the North Atlantic (2c,d). This pattern could also be explained by a North Atlantic origin followed by dispersal and diversification in the Arctic and, for *Erignathus*, invasion of the Bering Sea. *Histiophoca fasciata* and its sister taxon *Pagophilus groenlandica* apparently represent the products of glacioeustatic-forced allopatric speciation during the Pleistocene with the evolution of *Histiophoca* in the North Pacific (5a,c) and *Pagophilus* in the North Atlantic (2c,d). *Halichoerus* represents southward dispersal from the Arctic (1c) into the temperate North Atlantic (2a,b). Phylogenetic and biogeographic evidence suggests that divergence of the *Pusa-Phoca* lineage from *Halichoerus* likely occurred in the Greenland Sea/Barents Sea portion of the Arctic, as did the subsequent divergence of *Pusa* from *Phoca*. Following divergence, the subarctic *Phoca vitulina* expanded its range during Pleistocene interglacial periods to include the circum-arctic shoreline and the North Pacific. Succeeding glacial/interglacial oscillations resulted in reduced gene flow between isolated populations and the formation of distinct subspecies. The closely related *Phoca largha* may be the descendant of one of the earliest *Phoca* populations to be isolated by glacial conditions. A similar hypothesis is proposed for evolution of the *Pusa* lineage. Following initial divergence, the ringed seal *Pusa hispida* expanded its range to include nearly the entire Arctic region and the subarctic portions of the Atlantic and Pacific. The Caspian seal *Pusa caspica*, found

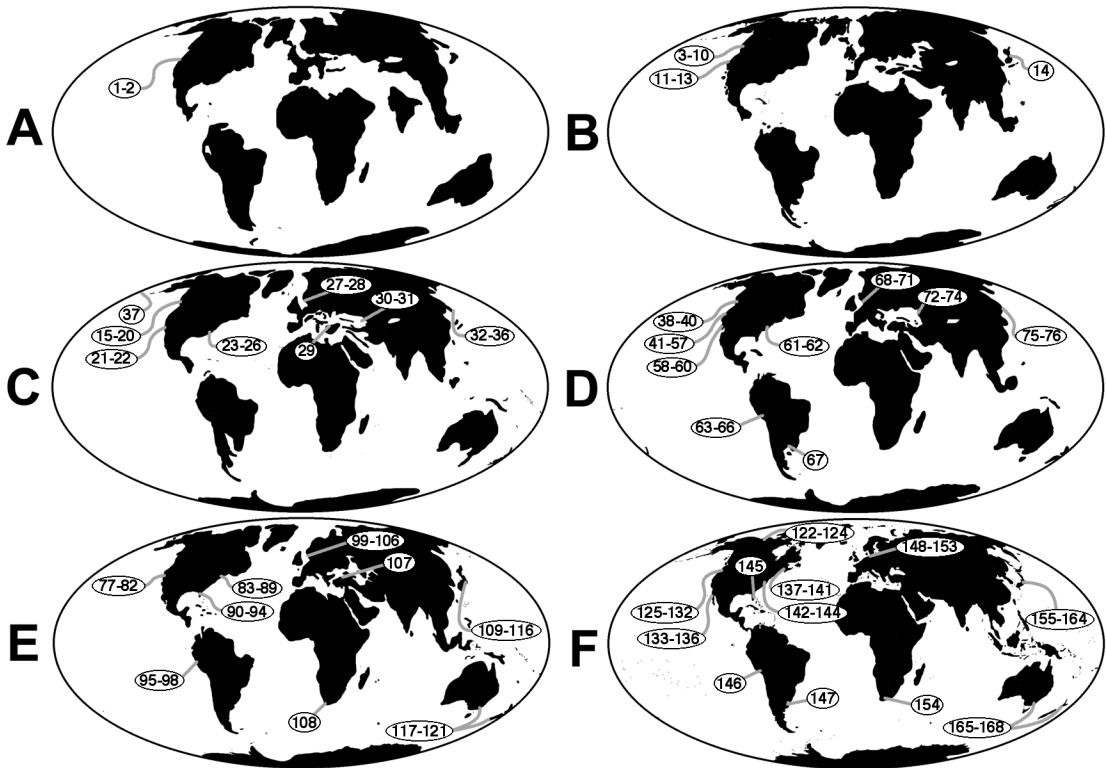


Fig. 3.7. Paleogeographic maps showing the distribution of pinnipedimorphs during time intervals: **A**, late Oligocene; **B**, early Miocene; **C**, middle Miocene; **D**, late Miocene; **E**, Pliocene; **F**, Pleistocene (see table 3.4; base maps from Smith et al., 1994).

only in the inland Caspian Sea far from other phocids, may represent the product of allopatric speciation in a peripheral population of *Pusa hispida*. As briefly discussed already, Davies (1958a) has suggested that *Pusa* entered the Paratethys from the Arctic during the Pleistocene by way of an ancestral Volga River drainage and became trapped in that drainage. Another landlocked species, *Pusa sibirica*, found only in Lake Baikal of eastern Siberia, is proposed to have had a similar history. In support of this view, Davies (1958a) noted the modern occurrence of isolated populations of *Pusa hispida* in freshwater lakes in Russia (Lake Ladoga) and Finland (Lake Simaa). The alternative hypothesis for the evolution of the *Pusa* lineage from Miocene Paratethyan phocines such as "*Pusa*" *pontica* proposes that the occurrence of *Pusa* and *Phoca* in the Arctic basin is the result of a south-to-north dispersal event from this landlocked refugium (McLaren,

1960; Grigorescu, 1977; and Repenning et al., 1979). There are several problems with this hypothesis, not the least of which is the presumed thermophilic nature of Miocene Paratethyan seals and the observed pagophilic nature of modern *Pusa caspica* and its sister taxa *P. sibirica* and *P. hispida*. Another weakness is the current lack of convincing anatomical evidence for the close phylogenetic relationship of Paratethyan fossil seals and modern *Pusa*.

DIVERSITY THROUGH TIME

In this final section we summarize pinnipedimorph diversity through time using paleogeographic maps (fig. 3.7) and a chronostratigraphic framework (table 3.2). The earliest pinnipedimorphs (*Enaliarctos* spp.) are known from latest Oligocene (Chattian) age sublittoral marine deposits in the eastern North Pacific region of Oregon and Wash-

ington (Berta, 1991; fig. 3.7A, table 3.2). Globally, during the Oligocene, northward movement of Australia and India resulted in initial opening of the Southern Ocean, establishment of a Circumantarctic Current, and development of steepening thermal gradients between subantarctic waters and those at temperate latitudes (Kennett, 1980). Progressive intensification of this current system produced a decoupling of the warm subtropical oceanic gyres from the cooling Southern Ocean circulation, and this led to initiation of glaciation in Antarctica. With establishment of the Circumantarctic Current (West Wind Drift), phytoplankton productivity increased, especially in the New Zealand–Campbell Plateau region of the Southern Ocean. This increased productivity has been correlated with the initial evolution of mysticete cetaceans in the early Oligocene of the southern hemisphere (Fordyce, 1977). The impact of this reorganization of ocean circulation on the late Oligocene evolution of pinnipeds in the Northern Hemisphere, although not precisely known, is likely to have been one of increased coastal food resources. In addition, a major global sea level rise in the late Oligocene (Haq et al., 1987) is likely to have greatly increased the area of neritic habitats in continental shelf regions.

During the early Miocene, pinnipedimorphs remained restricted to the eastern North Pacific, where they began to diversify (fig. 3.7B, table 3.2). This diversification included additional species of *Enaliarctos*, the basal pinnipedimorph *Pinnarctidion*, and the earliest desmatophocid (*Desmatophoca*). The earliest odobenids (*Proneotherium*) may have evolved in the late early Miocene (Burdigalian), but are clearly present by the early middle Miocene (Langhian). Basal phocids are likely to have diverged at this time and dispersed into the Atlantic via the wide open Central American Seaway. During the early Miocene, the Drake Passage opened, resulting in a stronger Circumantarctic Current and establishment of the general oceanic water masses of modern oceans (Wise et al., 1985). Oceanic productivity remained greatest in the equatorial regions in spite of the breakup of the Tethys Sea by collision of India and Africa with Eurasia and closure of the connection between the eastern Mediterranean and

the Indian Ocean. Paratethys began to be isolated from the Mediterranean Sea at this time, beginning its history as a series of separate hyposaline basins.

The earliest confirmed phocids are known from the early middle Miocene (Langhian) of the western North Atlantic and had established a circum-North Atlantic distribution by the late middle Miocene (Serravalian) that also included the Mediterranean Sea and Paratethys (fig. 3.7C, table 3.2). In the North Pacific, species of the basal pinniped taxa *Pteronarctos* and *Pacificotaria* were common in the early middle Miocene. *Desmatophoca* persisted during this period, while its sister taxon, *Allodesmus*, underwent an impressive radiation in the late middle Miocene with at least three species known from California and one from Japan (Repenning, 1976; Repenning et al., 1979; Barnes and Hirota, 1995). Species of the early diverging odobenid *Prototaria* are recorded from the western North Pacific in the early middle Miocene and probably overlapped temporally with *Proneotherium* (sister taxon) in the eastern North Pacific. The later diverging odobenid *Neotherium* is found in the eastern North Pacific in the late middle Miocene of California and Baja California. The basal pinnipedimorphs of the early Miocene, *Enaliarctos* and *Pinnarctidion*, were extinct by late middle Miocene time.

During the early middle Miocene, formation of a permanent ice cap in East Antarctica resulted in a sharp decline in bottom water temperatures, steepened latitudinal thermal gradients, and increased levels of upwelling and plankton productivity along continental margins (Woodruff and Savin, 1989). Ongoing tectonic activity and uplift of the Panama Sill resulted in intensified gyral circulation of surface waters, especially in the North Pacific. The Central American Seaway remained a dispersal corridor; however it was becoming more of a filter. Coastal upwelling intensified off the Peruvian coast at this time (Ibaraki, 1992), establishing the modern pattern of low latitude cold water in the northeastern South Pacific.

During the late Miocene, phocid and odobenid pinnipeds underwent a dramatic diversification (fig. 3.7D, table 3.2). Monachine phocids became common in the western

and eastern North Atlantic, while phocines radiated in Paratethys prior to the Messinian Salinity Crisis. Lobodontine monachines dispersed from the western North Atlantic through the Central American Seaway and south into the eastern South Pacific. There is currently no evidence that this dispersal extended into the North Pacific.

In the North Pacific, species of the generalized odobenid *Imagotaria* are found in both the western and eastern North Pacific. A major radiation produced two crown odobenid clades, the dusignathines and the odobenines, with at least two genera each (*Dusignathus* and *Gomphotaria*, *Aivukus* and *Pliopedia*, respectively). These taxa apparently remained in the eastern North Pacific. Otariid fur seals first appeared in the early late Miocene of the eastern North Pacific (*Pithanotaria*) and dispersed to the western North Pacific by the late late Miocene (*Thalassoleon*).

An ice cap formed in West Antarctica during the late Miocene and intensified a decline in bottom water temperatures and a steepening of latitudinal thermal gradients. The Southern Ocean experienced a major cooling event and worldwide sea levels were low (Warheit, 1992). Late Miocene collision of Africa with the Iberian Peninsula, closure of the western Mediterranean portal, and isolation of the Paratethys as a brackish inland sea mark the time of the Messinian Salinity Crisis. The flow of warm water from the Mediterranean to the North Atlantic was shut off, which intensified the cooling of the North Atlantic. A steeper thermal gradient in the upper part of the water column caused an increase in the speed of the anticyclonic North Atlantic Gyre. Steeper latitudinal and water column thermal gradients were probably associated with increased levels of upwelling, evidence for which is supplied by the rich Miocene and Pliocene phosphate deposits of eastern North America (Whitmore, 1994). Increased upwelling is in turn correlated with high phytoplankton productivity and higher productivity with cetacean diversification. A similar chain of events is postulated for the North Pacific except that here the increased productivity is reflected in the extensive siliceous (diatoms) deposits of California.

During the Pliocene, odobenines had a cir-

cum-North Pacific distribution that included *Valenictus* in the eastern North Pacific and *Protodobenus* and *Alachtherium* in the western North Pacific. Dispersal of this clade into the North Atlantic via the Arctic Ocean was complete at this time, having begun during the preceding late Miocene. The last of the dusignathine walruses is known from the late Pliocene of the eastern North Pacific. Pliocene otariids remained confined to the North Pacific and included *Thalassoleon* (western North Pacific) and *Callorhinus* (eastern North Pacific).

The center of monachine diversity had shifted to the western North Atlantic by the early Pliocene, while phocines became the dominant phocids in the eastern North Atlantic. The majority of these phocines appear to represent circum-North Atlantic endemics (Ray, 1976). In the Mediterranean, vicariant events in place during the Messinian Salinity Crisis drove speciation of the resident monachine lineages, which remained in complete isolation until at least the late Pliocene. The first monachine seals to reach the eastern South Atlantic (early Pliocene, South Africa) dispersed either directly from the North Atlantic or indirectly by way of the Central American Seaway and the eastern South Pacific. In the eastern South Pacific, lobodontine seals that had probably arrived during the late Miocene speciated to produce several genera and endemic species.

During the Pliocene between 3.7 and 3.1 Ma, the Central American Seaway finally closed with elevation of the Isthmus of Panama (Duque-Caro, 1990). Prior to this time, water flow through the seaway had been reduced substantially (Benson et al., 1991) and the North Atlantic Gyre had probably become well developed. With the seaway closed the Gulf Stream was strengthened and surface water temperatures in the western North Atlantic increased (Dowsett and Poore, 1991). In the North Pacific, closure of the seaway had a similar effect on strengthening of the anticyclonic circulation gyre, although in the North Pacific water temperatures decreased. Onset of Northern Hemisphere glaciation began 2.5 Ma (Barron and Baldauf, 1989) and was followed by a period of rapid global sea level fluctuations. These fluctuations extended through the Pleistocene

and were associated with intensified tectonic activity, polar glaciation, and decreasing water temperatures. This established the strong north–south thermal gradient of modern oceans. The late Pliocene and Pleistocene climatic deterioration was effective in creating barriers to marine mammal dispersal. High latitude taxa could not disperse across the equatorial region during interglacial periods and this resulted in the development of antitropical distributions for certain cetaceans and pinnipeds (Gaskin, 1982; fig. 3.7E, table 3.2).

During the early Pleistocene, fossil species of odobenine walrus occurred in the eastern North Atlantic and probably also in the western North Atlantic (fig. 3.7F, table 3.2). Their distribution was more southern than late Pleistocene occurrences of *Odobenus rosmarus* from the North Atlantic and North Pacific and probably reflected glacial maxima. Pleistocene otariids from the North and South Pacific are all assigned to modern genera, although their diversity is lower than for the modern fur seal and sea lion fauna. Remains of phocid seals are reported for the first time from the eastern North Pacific in the early Pleistocene and are referred to the modern taxon, *Phoca vitulina*. This dispersal event is postulated to have occurred via the Arctic Ocean (Repenning et al., 1979). North Pacific phocid diversity increased in the late Pleistocene to include additional phocines and a monachine seal. In the North Atlantic, phocine diversity began to approach its modern level, especially in late Pleistocene Lake Champlain of eastern Canada (Ray et al., 1982; Harington, 1988).

The Pleistocene continued warm and cold climatic fluctuations that began in the Pliocene. The global refrigeration of glacial periods established effective barriers to the dispersal of “relict Tethyan” marine mammal taxa such as *Monachus* (Gaskin, 1982). These taxa became confined to the tropics. Phocine seals at this time apparently adapted to the colder northern waters and began their impressive high-latitude adaptive radiation. This radiation was probably driven by the “speciation pump” of glacioeustatic oscillations and the related increase and decrease of sea ice volume and the cyclic expansion and fragmentation of species home ranges and re-

duced gene flow (Davies, 1958b). This phocine radiation is still very much underway (Ray, 1976). In the Southern Hemisphere, monachines diversified (in the absence of phocines) in the colder waters to produce the Antarctic lobodontine seal fauna of today. The antitropical distribution of species of *Arctocephalus* and *Mirounga* may be the result of Pleistocene fragmentation of formerly more cosmopolitan species ranges.

ACKNOWLEDGMENTS

Long term study of fossil pinnipeds by two of us (AB and TAD) has been supported by various grants from the National Science Foundation including BSR 8607061, BSR 9006535, DEB 9419802, and INT 9417088 to AB and DEB 9419803 to TAD. AB was first introduced to fossil carnivorans by Richard H. Tedford and is pleased to offer her contribution to this volume in his honor.

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