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# Pinniped Evolution

ANNALISA BERTA

The name Pinnipedia was first proposed for fin-footed carnivores more than a century ago. Pinnipeds—fur seals and sea lions, walruses and seals—are one of three major clades of modern marine mammals, having a fossil record going back at least to the late Oligocene (27–25 Ma—millions of years before present).
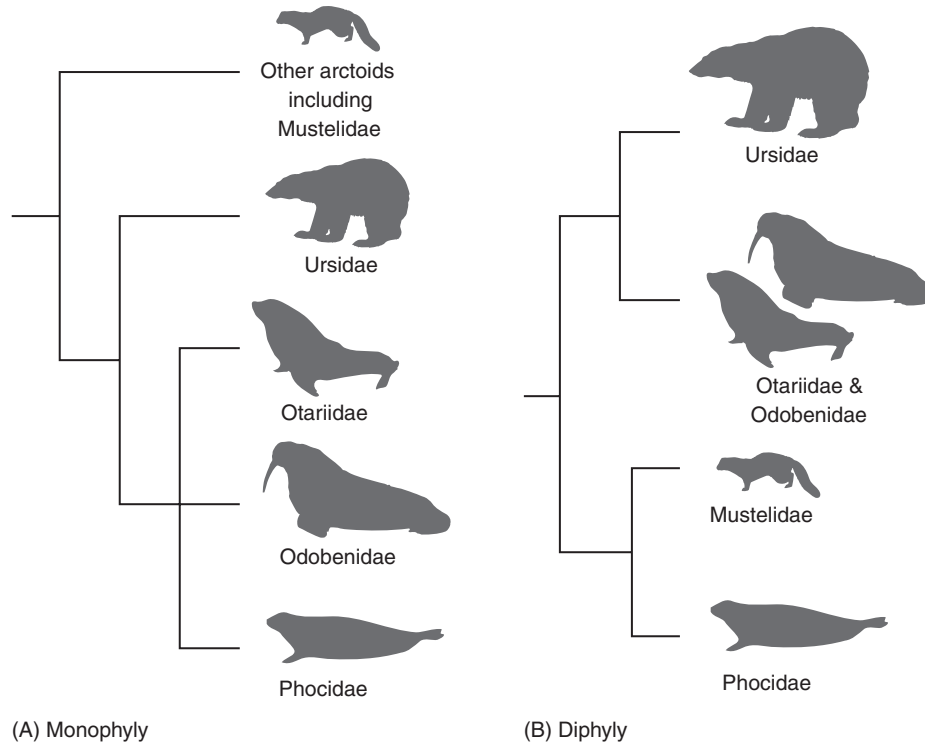
The earliest pinnipeds were aquatic carnivores with well-developed paddle shaped limbs and feet. A North Pacific origin for pinnipeds has been hypothesized; the group subsequently diversified throughout the world's oceans.

## I. Pinniped Ancestry: Origin and Affinities

There has long been a debate about the relationship of pinnipeds to one another and to other mammals. The traditional view, also referred to as diphyly, proposes that pinnipeds originated from two carnivore lineages, an odobenid (walrus) plus otariids (fur seals and sea lions) grouping affiliated with ursids (bears) and phocids (seals) being related to mustelids (weasels, skunks, otters, and kin) (Fig. 1a). The current view overwhelmingly supported by both morphologic and molecular data confirms pinnipeds as monophyletic (having a single origin). Although the hypothesis presented here positions ursids as the closest relatives of pinnipeds, it is acknowledged that there is difficulty separating the various lineages of arctoid carnivores (mustelids, procyonids, and ursids) at their point of divergence (Fig. 1b). An alternative hypothesis supports pinnipeds as having an ursid-mustelid ancestry (see PINNIPEDIA). With regard to relationships among pinnipeds most current data robustly supports a link between odobenids and otariids.

## II. Divergence of Major Lineages

The broad pattern of evolution within pinnipeds shows divergence of five major lineages. These include the three extant lineages: Otariidae, Phocidae, and Odobenidae and two extinct groups, the Desmatophocidae and a basal lineage *Enaliarctos* (Fig. 2). At times the Odobenidae have been included in the Otariidae, although current studies consistently support these as distinct monophyletic groups that share a sister group relationship.

Within Pinnipedimorpha (living pinnipeds plus their fossil allies) are included archaic pinnipeds *Enaliarctos* and *Pteronarctos* + pinnipeds (Fig. 2). Unequivocal synapomorphies include: large infraorbital foramen, anterior palatine foramina anterior of maxillary-palatine suture, upper molars reduced in size, lower first molar metaconid reduced or absent, humerus short and robust, deltopectoral crest on the humerus strongly developed, digit I on the manus and digit I and V on the pes emphasized. The basal taxon *Enaliarctos* from the late Oligocene and early Miocene (27–18 Ma; Fig. 3) of California is known by five species, one represented by a nearly complete skeleton (Fig. 4). *Enaliarctos* was a small, fully aquatic pinnipedimorph with shearing teeth (as is typical of most terrestrial carnivorans), flexible spine, and fore and hindlimbs modified as flippers. Several features of the hindlimb suggest that *Enaliarctos* was capable of maneuvering on land although probably spent more time near the shore than extant pinnipeds. *Enaliarctos* shows features that are consistent with both fore- and hindlimb swimming, but seems slightly more specialized for forelimb swimming (Berta and Adam, 2001). A later diverging lineage more closely allied with pinnipeds than with *Enaliarctos* is *Pteronarctos* from the late Miocene (19–15 Ma) of coastal Oregon. *Pteronarctos* is recognized as the earliest pinniped to have evolved the unique maxilla diagnostic of modern pinnipeds. The maxilla of pinnipeds makes a significant contribution to the orbital wall. This differs from the condition in terrestrial carnivores in which the maxilla is limited in its posterior extent by contact of several facial bones (jugal, palatine, and/or lacrimal). Ecologically, the earliest pinnipedimorphs were coastal dwellers that evolved a pierce feeding strategy and likely fed on fish and other aquatic prey (Adam and Berta, 2002).

The fur seals and sea lions (eared seals), the Otariidae, are diagnosed by frontals that extend anteriorly between the nasals, large and

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**Figure 1** *Alternative hypotheses for relationships among pinnipeds (A) Monophyly with ursids as the closest pinniped relatives. (B) Diphyly in which phocids and mustelids are united as sister taxa as are otariids, odobenids, and ursids. (From Berta* et al.*, 2006.)*
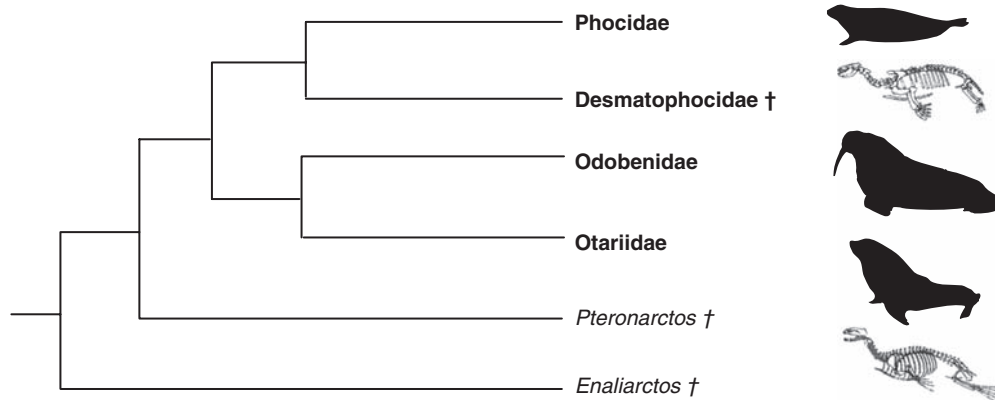


**Figure 2** *A cladogram depicting the relationships of the major clades of pinnipeds. (Modified from Berta* et al.*, 2006.)*

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shelf-like supraorbital process of the frontal, secondary spine dividing the supraspinous fossa of the scapula, uniformly spaced pelage units, and by the presence of a trachea with an anterior bifurcation of the bronchi (Fig. 5). Although otariids are often divided into two subfamilies, the Otariinae (sea lions) and the Arctocephaline (fur seals), both groups have been shown to be paraphyletic on the basis of molecular data. The otariids are the earliest diverging pinniped lineage originating approximately 11–12 Ma (Fig. 3) and including the poorly known *Pithanotaria* from the late Miocene of California and three species of *Thalassoleon* described from the late Miocene and early Pliocene of California, Mexico and Japan (Deméré and

Berta, 2005; Fig. 6). An extinct species of the Northern fur seal, *Callorhinus* has been described from the late Pliocene of southern California, Mexico, and Japan. *Hydrarctos* is an extinct fur seal from the Pleistocene of Peru. Several extant species of *Arctocephalus* have a fossil record extending to the Pleistocene in South Africa and North America (California). The fossil record of modern sea lions is poorly known. The following taxa are reported from the Pleistocene: *Neophoca* (New Zealand), *Eumetopias* and *Zalophus* (Japan), and *Otaria* (Brazil).

The basal split between otariids and odobenids based on molecular data is close to the age of the oldest enaliarctid fossils and much
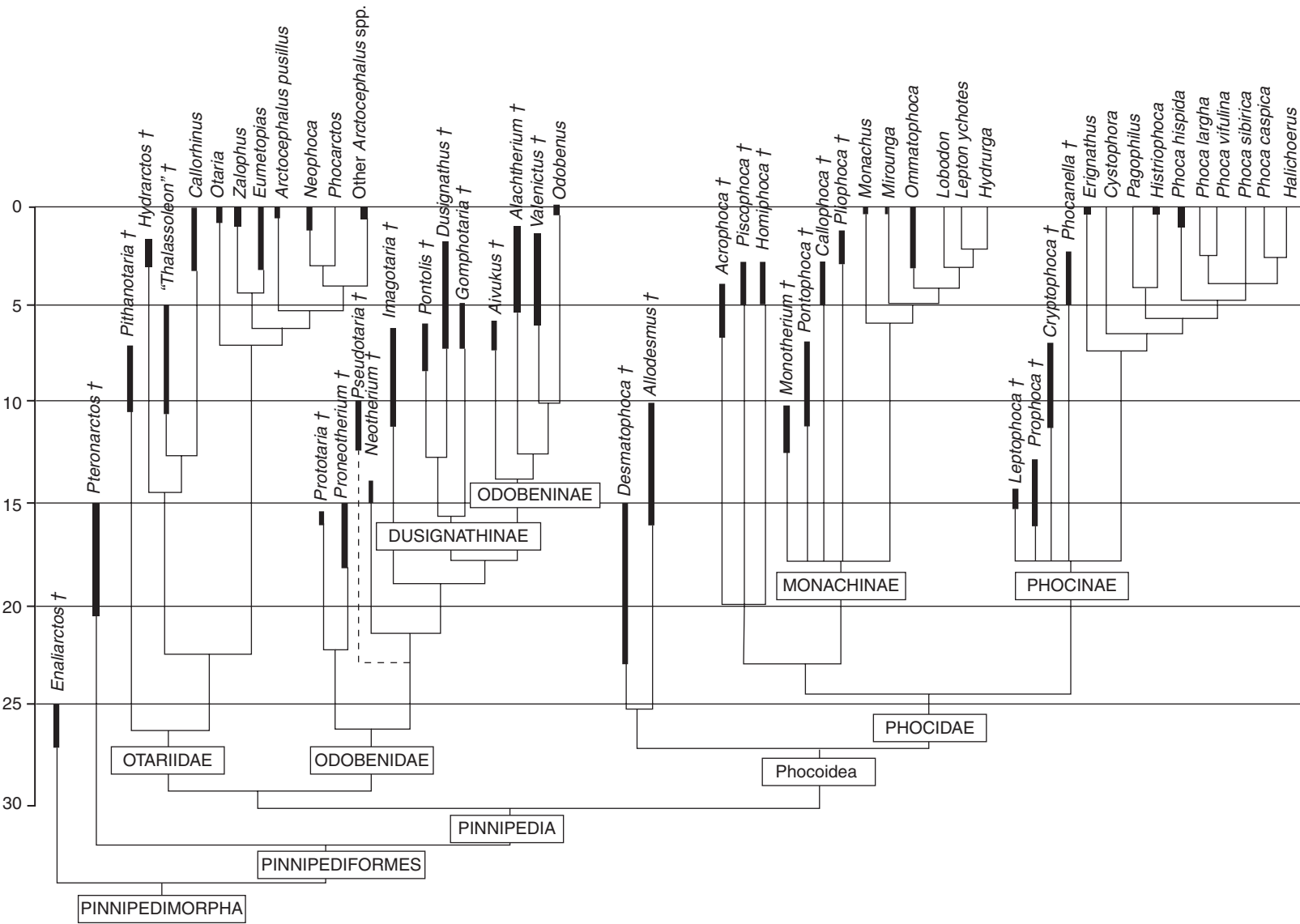
**Figure 3** *Chronologic ranges of major lineages and genera of extinct and living pinnipeds. Time scale in millions of years. Thick lines show stratigraphic ranges of taxa and thin lines indicate their phylogenetic relationships (otariid and phocid phylogeny based on Arnason* et al.*, 2006). Position of fossil walrus* Pseudotaria *indicated by dashed line is based on Kohno (2006). Branching points are not necessarily correlated with the time scale. (Modified from Deméré* et al.*, 2003.).*
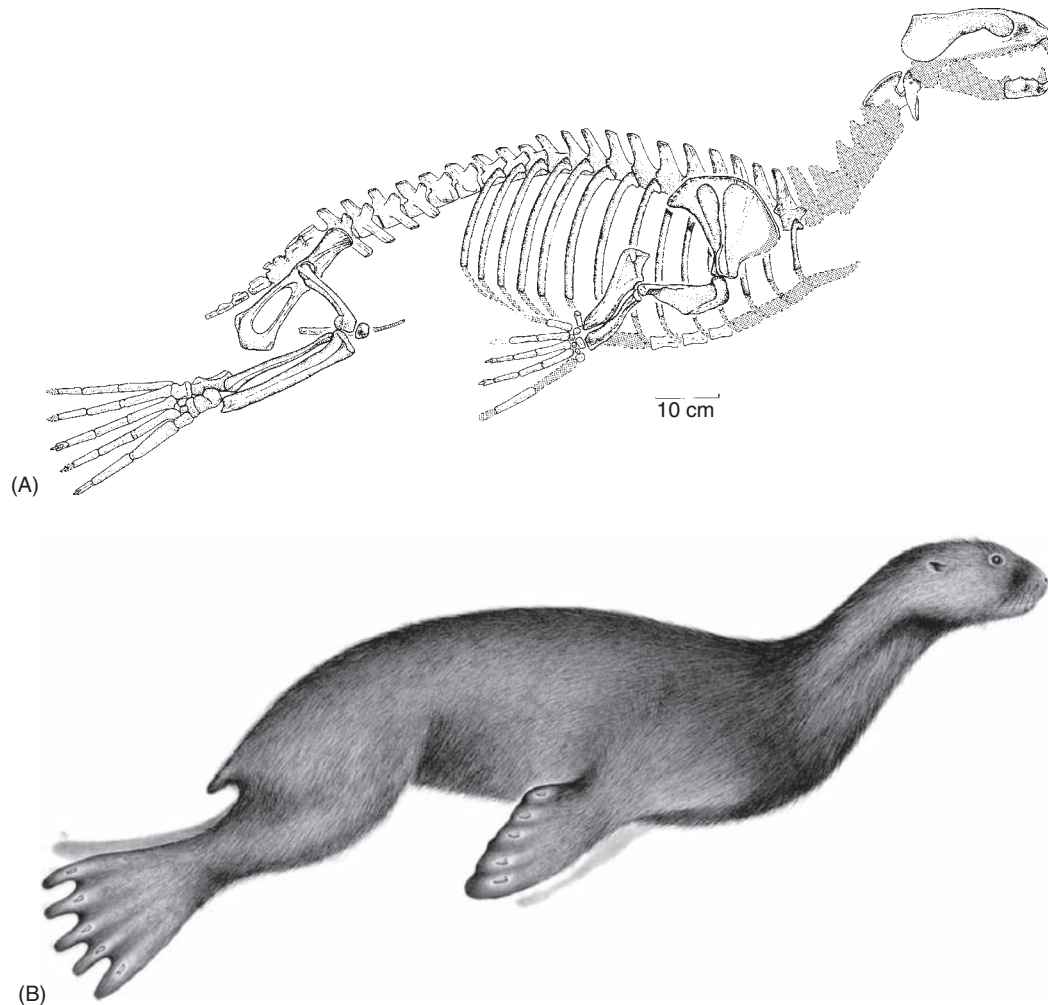
(A)

(B)

**Figure 4**    *The pinnipedimorph* Enaliarctos mealsi *showing pinnipedimorph synapomorphies described in text. (From Berta and Ray, 1990.)*

older than the earliest recognized fossils of these lineages (Arnason *et al.*, 2006). Otariids appear to have originated in the North Pacific (Fig. 7). The basal split between *Callorhinus* and other otariids dated to 16 mya is older than the oldest otariid fossil *Pithanotaria* from 11 mya rocks in California. The subsequent divergence of *Otaria*, *Zalophus* + *Eumetopias* from other otariids likely took place in the North Pacific with *Otaria* dispersing along the west coast of South America and later along the Atlantic coast. The diversification of remaining otariids took place in the southern hemisphere with the exception of *Arctocephalus townsendi* which remained in the North Pacific.

The walruses or Odobenidae are diagnosed as a monophyletic group by the presence of a broad, thick pterygoid strut, fourth upper premolar with a strong posterolingually placed protocone shelf, lower first molar with the talonid heel absent, and a calcaneum with a prominent medial tuberosity (Deméré and Berta, 2001 but see also Kohno, 2006; Fig. 6). Morphologic study of the evolutionary relationships among walruses has identified the following taxa: *Prototaria*, *Pseudotaria*, *Proneotherium*, *Neotherium*, *Imagotaria*, dusignathines and odobenines, the latter includes the modern walrus (see PINNIPEDIA).

Fossil walruses first appear in the early Miocene (16–18 Ma; Fig. 3) fossil record with *Prototaria* in Japan and *Proneotherium* in North America (Oregon). These archaic walruses are characterized by unenlarged canines and narrow, multiple rooted premolars with a trend toward molarization (Fig. 8), adaptations suggesting retention of the fish diet hypothesized for archaic pinnipeds rather than evolution of the specialized mollusc diet for the modern walrus. Portions of the axial and hindlimb skeleton of *Proneotherium* preserve evidence of a number of aquatic adaptations including a laterally flexible spine, a broad, shortened femur, and a paddle-shaped foot (Deméré and Berta, 2001). In addition to *Proneotherium*, *Prototaria*, and the recently described *Pseudotaria* (Kohno, 2006) a monophyletic clade of walruses comprised of *Neotherium*, *Imagotaria*, and Dusignathinae and Odobeninae diversified in the middle and late Miocene Fig. 3). Dusignathine walruses which include *Dusignathus*, *Pontolis*, and *Gomphotaria* developed enlarged upper and lower canines. *Gomphotaria pugnax* the most completely known dusignathine is distinct cranially and dentally in its possession of large, procumbent upper lateral incisors and canines; the latter with deeply fluted roots and a small orbit. Odobenines which include *Aivukus*, *Ontocetus* (=*Alachtherium* fide Kohno, 2006), *Valenictus*
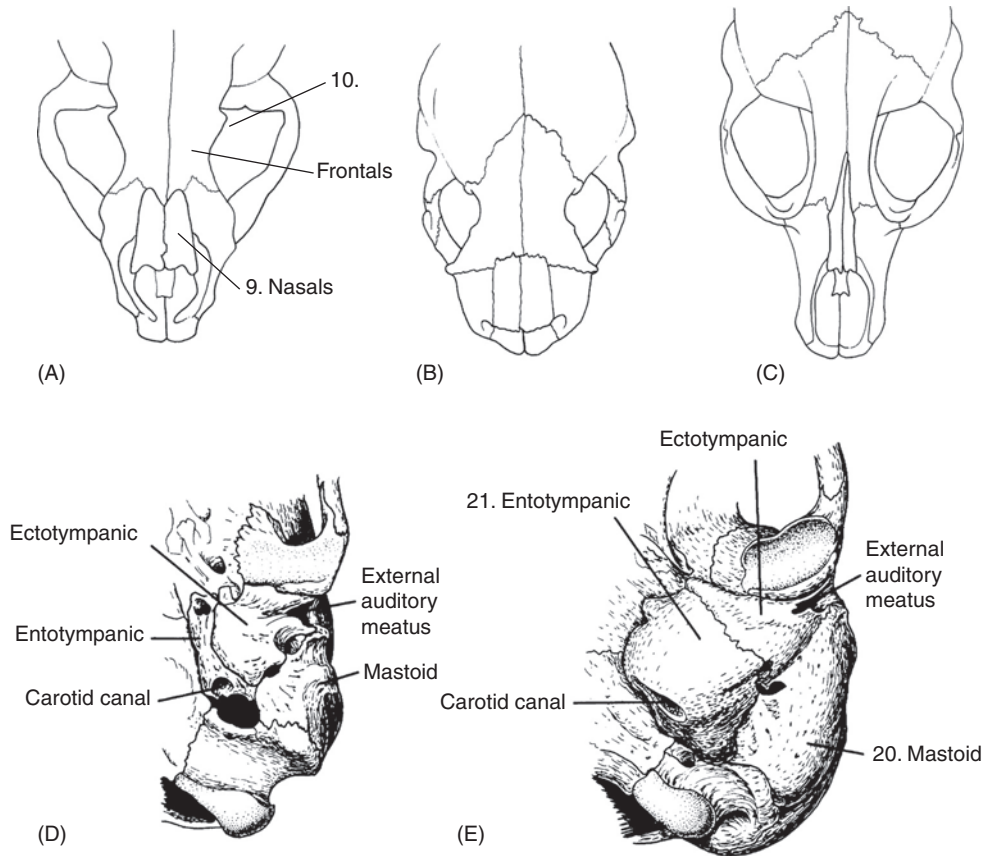
**Figure 5** *Skulls/ventral view of ear regions of (A, D) otariid, (B) walrus, (C, E) phocid illustrating otariid synapomorphies: frontals extend anteriorly between nasals (contact between these bones in transverse, walrus, or V-shaped, phocids and phocid synapomorphies: pachyostotic mastoid bone (not seen in other pinnipeds) and greatly inflated ectotympanic bone. (From Berta* et al.*, 2006.)*
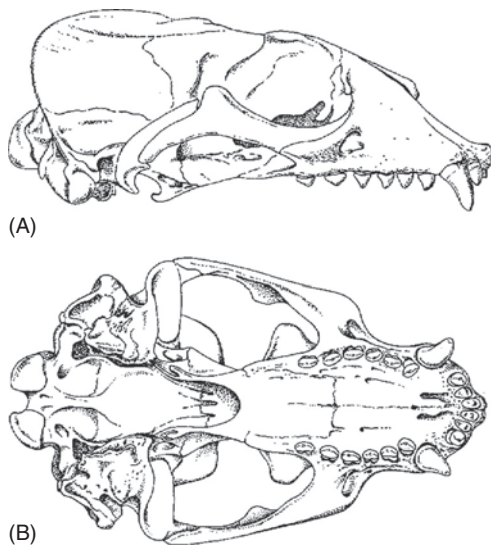


**Figure 6** *Skull of an early otariid,* Thalassoleon mexicanus *from the late Miocene of western North America in (A) lateral (B) ventral views. Original 25 cm long (From Repenning and Tedford, 1977.)*

and *Odobenus* evolved the enlarged upper tusks seen in the modern walrus. Unique among pinnipeds is the toothlessness of *Valenictus chulavistensis* from the late Pliocene of California, presumably an adaptation for suction feeding.

It has been proposed that the modern walrus lineage (odobenine walruses) entered the Caribbean from the Pacific via the Central American Seaway (between 5 and 8 Ma) and dispersed northward into the North Atlantic (Fig. 7). Less than 1 Ma the living genus *Odobenus* returned to the North Pacific through the Arctic Ocean. Alternatively, on the basis of a new, earlier record of the modern walrus lineage from Japan it has been suggested that this lineage may have evolved in the North Pacific and dispersed instead to the North Atlantic through the Arctic during the Pleistocene.

The earless seals, the Phocidae, are diagnosed as a monophyletic group by pachyostic mastoid region, greatly inflated entotympanic bone, complete absence of the supraorbital process of the frontal, strongly everted ilia and lack of an ability to draw the hindlimbs forward under the body due to a massively developed astragalar process, and greatly reduced calcaneal tuber (Fig. 5). Although phocids have traditionally been divided into two or four major subgroupings, recent molecular studies consistently support monophyly of Monachinae and Phocinae (see also PINNIPEDIA).
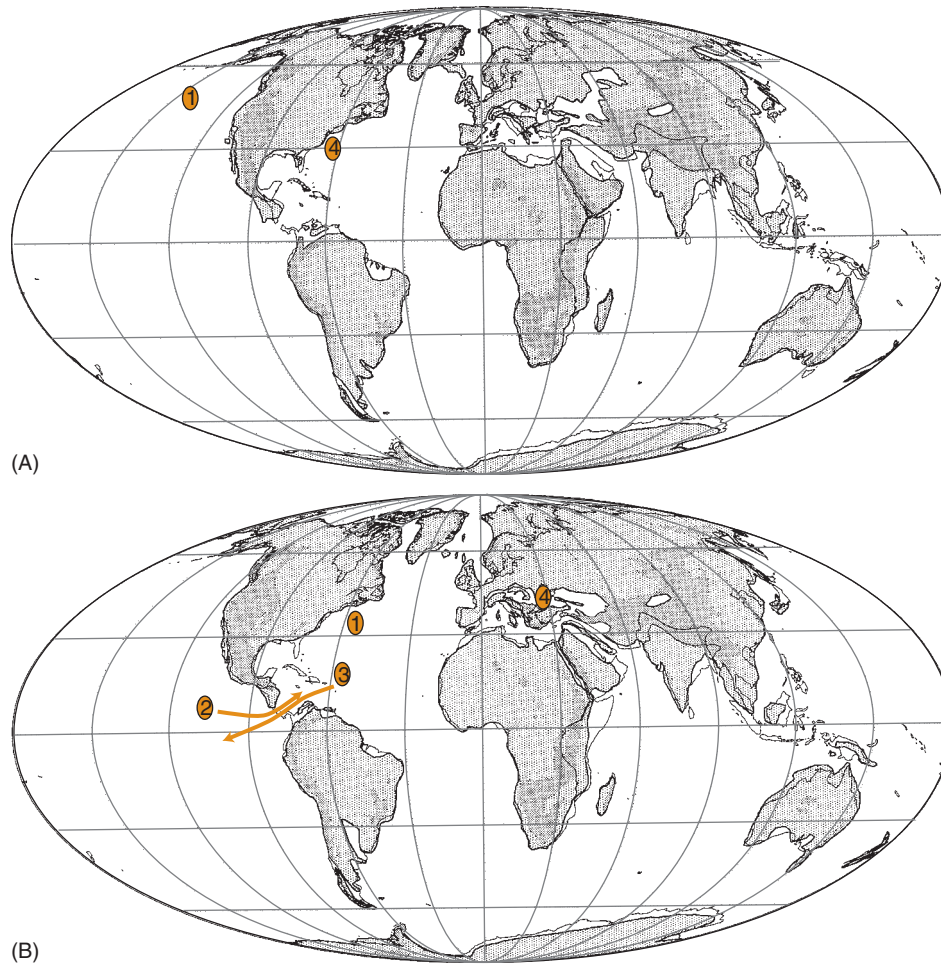
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**Figure 7** *Reconstruction of continents, ocean basins, and paleocoastlines in the (A) early Miocene (20Ma) (1: 5 early records of archaic pinnipeds, odobenids, and desmatophocids) and (B) middle Miocene (12Ma) (1: 5 early well documented phocids, 2: 5 dispersal of "monachines" and odobenids to Atlantic, 3: 5 dispersal of phocines to South Pacific, 4: 5 isolation of phocines in remnants of Paratethys Sea and in North Atlantic). (From Berta et al., 2006; base map from Smith et al., 1994.)*
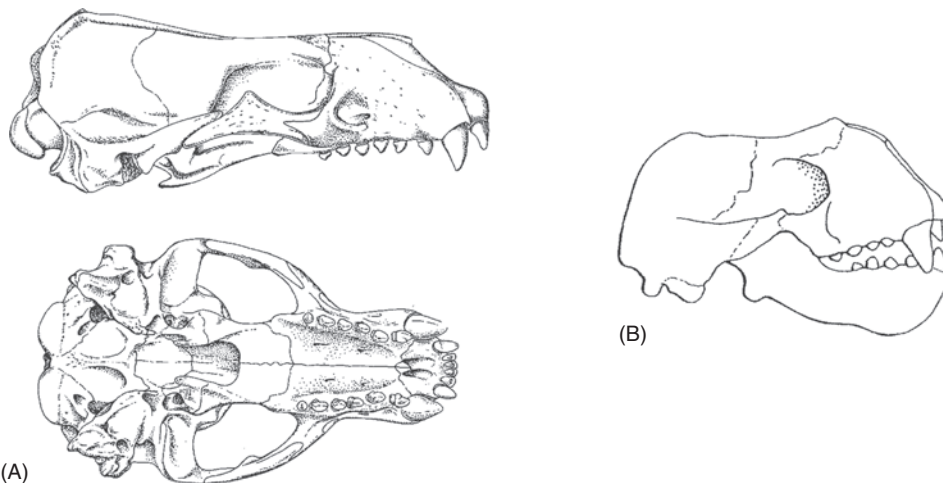
**Figure 8** *Lateral and ventral views of skulls of fossil odobenids (A)* Imagotaria downsii *from the Miocene of western North America. Original 30cm long. (From Repenning and Tedford, 1977.) (B) Lateral view of* Protodobenus japonicus *from the early Pliocene of Japan. Original 25cm. (From Horikawa, 1995.)*
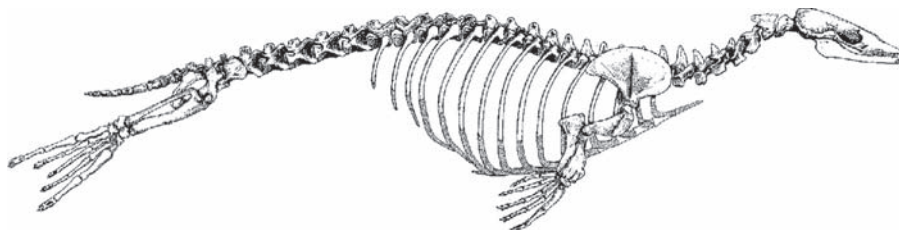
**Figure 9**  *Skeleton of an archaic phocid,* Acrophoca longisrostris *from the Miocene of Peru. (From Muizon, 1981.)*

Although an earlier less well documented record of phocids from the late Oligocene of South Carolina exists, there is undisputed evidence for both monachine and phocine seal lineages from the middle Miocene (approximately 15 Ma) on both sides of the North Atlantic. Molecular estimates place monachine and phocine divergence at approximately 22 mya (Arnason *et al.*, 2006). The earliest phocine *Leptophoca* and the earliest monachine *Monotherium* (Fig. 3) are known from the southeastern North America. Despite the fact that a number of fossil monachines have been described not all are known by comparable elements. In addition to *Monotherium* among the better known taxa from eastern Europe are *Pontophoca* from the middle Miocene and *Callophoca* from the early Pliocene (Koretsky, 2001). Several archaic seals (i.e., *Acrophoca* and *Piscophoca*) represented by complete skeletons are known from the late Miocene and/or early Pliocene of South America (Peru and Chile; Walsh and Naish, 2002) and *Homiphoca* from South Africa (Fig. 3). *Acrophoca* is unique among phocids with its long, slender skull, flexible neck, and elongated body (Fig. 9). Although these fossil monachines have been referred to the lobodontines (see also PINNIPEDIA), new discoveries as well as restudy of material previously referred to these taxa suggests that they may in fact be phocines. The fossil record of extant monachines is poorly known and includes only *Monachus* and *Mirounga* from the late Pleistocene and the lobodontine *Ommatophoca* from the late Pliocene (Fig. 3). With regard to fossil phocines among the best known taxa are *Prophoca* (middle Miocene) in the eastern North Atlantic, *Cryptophoca* (late Miocene) in the Black Sea region, and *Phocanella* (early Pliocene) in both the eastern the western North Atlantic (Fig. 3). Extant phocine genera with a fossil record include *Phoca* from the late Pliocene and *Erignathus* and *Histriophoca* from the late Pleistocene (Fig. 3).

The purported first appearance of phocids in the North Atlantic suggests that the common ancestor of phocids had migrated to the North Atlantic, either northward through the Arctic Basin or southward through the Central American Seaway (Fig. 7). Support for a southern route is based on the hypothesized close relationship of phocids and the extinct desmatophocids, the latter occurring as far south as Mexico, and the fact that the Bering land bridge blocked access to the Arctic through much of the late Oligocene and early Miocene. Fyler *et al.* (2005) confirmed an earlier proposal by Muizon (1982) that monk seals originated in the Mediterranean (*Monachus monachus*) with dispersal first to the Caribbean (*M. tropicalis*) and later to the central North Pacific (Hawaiian monk seal, *M. schauinslandi*). The 4 mya molecular divergence of northern and southern elephant seals (*Mirounga*) may be the result of vicariance following emergence of the Panamanian isthmus (Arnason *et al.*, 2006).

The biogeographic pattern for phocine seals is no less complicated given the different phylogenetic hypotheses proposed. Although it was suggested earlier that phocines were a northern hemisphere radiation, a considerable diversity of phocine seals is known from the southern hemisphere during the late Miocene and/or early Pliocene (assuming that *Acrophoca*, *Homiphoca*, and *Piscophoca* are phocines rather than lobodontines). In addition other phocine lineages appear to have been isolated in the Paratethys Sea (northern arm of the Tethys Sea stretching across the area now occupied by the Black, Caspian, and Aral Seas of Asia) and the North Atlantic during the late Miocene and Pliocene. Several dispersal routes for phocines seem likely. The deepest phocine split, that between the bearded (*Erignathus*) and hooded seals (*Cystophora*) was dated to 17 mya based on molecular data (Arnason *et al.*, 2006). This suggests an eastward and northward migration of phocines in the North Atlantic. The hooded seal occurs at high latitudes of the Atlantic basin and apparently never successfully dispersed to the Pacific. The bearded seal is presently confined to the Arctic and subarctic around the North Atlantic but Pleistocene records extend as far south as Portugal. A subsequent dispersal route for phocines involved initial migration from Paratethys Sea into the Arctic Basin, followed by an eastward migration to give rise to modern *Phoca/Pusa*. In this scenario the landlocked Baikal seal (*Pusa sibirica*) gained access to Lake Baikal from the Arctic via large lakes at the southern margin of the Siberian ice sheet. A second landlocked species, the Caspian seal (*Pusa caspica*) remained in the Caspian Sea an isolated remnant of Paratethys as judged by the presence of fossils similar to living Caspian seals in this location. Another hypothesis argues for a North Atlantic origin for all phocines with glacial events causing speciation. For example, cyclical fluctuations in glacial maxima (with concomittant variations in sea level) through the Pleistocene mediated range expansions of *Phoca* spp. ultimately leading to isolation of populations in refugial centers (i.e., Arctic, Okhotsk, Aleutian) and divergence of populations (e.g., ribbon seal, *Histriophoca fasciata*, ringed seal, *Pusa hispida*, largha seal, *Phoca largha*, harbor seal, *Phoca vitulina*, harp seal, *Pagophilus groenlandica*).

An extinct family of archaic pinnipeds, the desmatophocids are characterized by elongate skulls, relatively large eyes, mortised contact between two cheekbones, and bulbous cheek teeth (Fig. 10). Cladistic analysis has identified the Desmatophocidae which includes two genera, *Desmatophoca* and *Allodesmus* as the common ancestors of phocid pinnipeds. This clade, phocids + *Allodesmus* and *Desmatophoca*, termed the Phocoidea, is supported by four synapomorphies including: premaxilla–nasal contact reduced, squamosal–jugal contact mortised, marginal process below ascending ramus well-developed (Deméré and Berta, 2002; Fig. 2). This interpretation differs from previous work that recognized desmatophocids as otarioid pinnipeds (a paraphyletic group than includes walruses but excludes phocids). Desmatophocids are known from the early and middle Miocene (23–10 Ma) of western US and Japan (Fig. 3). Newly reported occurrences of *Desmatophoca* confirm the presence of sexual dimorphism and large body size in these pinnipeds (Deméré and Berta, 2002). *Allodesmus* is a diverse taxon (as many
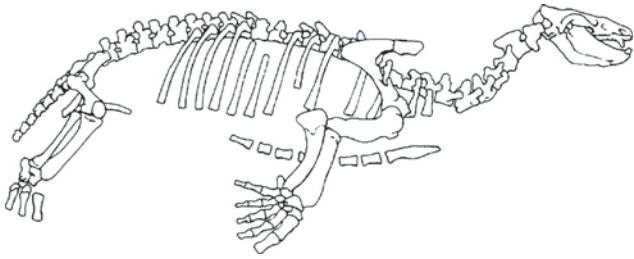
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**Figure 10** *Skeleton of the desmatophocid, Allodesmus kernenesis from the Miocene of western North America. Original 2.2 m long. (From Mitchell, 1975.)*

as six species have named) with taxa informally divided into "broad headed" and "long headed"subgroups. The previous suggestion that *Allodesmus* retained a mobile proboscis, much like the modern elephant seal seems unlikely on anatomical grounds. *Allodesmus*, known by several complete skeletons, retains several features consistent with forelimb propulsion but also displays adaptations for hindlimb swimming (Berta and Adam, 2001).

### See Also the Following Articles

Pinnipeds, Overview ∎ Fossil Record

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# Pinniped Life History

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The life history of an individual is the pattern of allocation of resources to maintenance, growth, and reproduction throughout its lifetime. Life history analysis attempts to explain the scheduling of the allocation process throughout an organism's life. It assumes implicitly that it is appropriate to classify individuals by age because this is a major component of the independent variable representing time that is used to examine variation in resource allocation. However, we know that other properties of an individual, such as its body condition or foraging skill, are also important variables that affect reproduction and ultimately fitness.

Most life history studies involving pinnipeds have assumed that age is the main force in pinniped life histories when, in fact, age *per se* may have relatively little to do with influencing fitness. It is a paradox of life history studies that they are, by definition, time-based approaches to examining variation in the fitness between individuals when time itself probably has less biological importance than other factors. One such factor in pinnipeds is body size, long recognized as a determinant of sexual maturity in pinnipeds. Age at sexual maturity in pinnipeds can be expressed as a decreasing function of growth rate. Expressed at the level of populations, this is interpreted to mean that individuals within pinniped populations that are at a level well below the environmental carrying capacity would experience higher growth rates and would, therefore, become sexually mature at an earlier age (Bengston and Laws, 1985). This was an implicit acknowledgment that age was not the operant factor in pinniped life histories and was at best secondary to the size of the energy reserves of an individual. Nevertheless, despite the considerably greater difficulties that exist with measuring age in pinnipeds than there are with measuring body size (e.g., mass or some other suite of morphometrics), age has continued to be used as the primary independent variable in life history studies.