The Origin and Evolutionary Biology of Pinnipeds: Seals, Sea Lions, and Walruses

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Abstract

The oldest definitive pinniped fossils date from approximately 30.6–23 million years ago (Ma) in the North Pacific. Pinniped monophyly is consistently supported; the group shares a common ancestry with arctoid carnivorans, either ursids or musteloids. Crown pinnipeds comprise the Otariidae (fur seals and sea lions), Odobenidae (walruses), and Phocidae (seals), with paraphyletic "enaliarctines" falling outside the crown group. The position of extinct Desmatophocidae is debated; they are considered to be closely related to both otariids and odobenids or, alternatively, to phocids. Both otariids and odobenids are known from the North Pacific, diverging approximately 19 Ma, with phocids originating in the North Atlantic or Paratethys region 19–14 Ma. Our understanding of pinniped paleobiology has been enriched by studies that incorporate anatomical and behavioral data into a phylogenetic framework. There is now evidence for sexual dimorphism in the earliest pinnipeds, heralding polygynous breeding systems, followed by increased body sizes, diving capabilities, and diverse feeding strategies in later-diverging phocid and otarioid lineages.

INTRODUCTION

Pinnipeds are aquatic members of the mammalian order Carnivora and comprise three mono-phyletic families: the Otariidae (fur seals and sea lions), the Odobenidae (walruses), and the Phocidae (true or earless seals). Pinnipeds make up slightly more than one-fourth (28%) of marine mammal diversity, with thirty-three living species distributed worldwide. Of these, seven species are endangered or threatened, while two species have become extinct in the last century (Caribbean monk seal and Japanese sea lion; IUCN 2017). The name pinniped comes from the Latin *pinna* and *pedis*, meaning "feather footed," referring to the paddle-like fore- and hind limbs of seals, sea lions, and walruses. Pinnipeds lead dual lives, spending considerable amounts of time in the water but also routinely spending time on land or ice—unlike cetaceans (whales, dolphins, and their kin) and sirenians (sea cows and manatees), which spend their entire lives in water.

All pinnipeds, including both fossil and recent taxa, are diagnosed by a suite of derived mor-phological characters, although some of these traits have been modified or lost secondarily in later-diverging taxa. Well-known pinniped synapomorphies include a large infraorbital foramen, a maxilla that makes a significant contribution to the orbital wall, a lacrimal that is absent or that fuses early in ontogeny, a short and robust humerus with enlargement of the deltopectoral crest and greater and lesser humeral tubercles, an emphasized digit I on the hand, and emphasized digits I and V on the foot (**Supplemental Figures 1** and **2**; for a complete list of characters, see Wyss 1987, 1988; Berta & Wyss 1994).

The crown group Pinnipedia includes the three living families of pinnipeds, with the pa-raphyletic "enaliarctines" falling outside the crown group. The Pinnipedimorpha clade includes crown pinnipeds as well as stem taxa such as *Enaliarctos*, *Pteronarctos*, *Pacificotaria*, and *Pinnarctidion* (**Figure 1**). The diversification of crown pinnipeds was driven by a combination of environmental factors such as increased sea surface temperatures, primary productivity, and habitat availability and biological processes (e.g., competition) that promoted new ecological opportunities (Valenzuela-Toro et al. 2013, Churchill et al. 2014a).

OCCURRENCE AND PRESERVATION

Pinniped fossils are typically preserved in shallow marine rocks deposited on the continental shelf and may occur as articulated skeletons, incomplete semi- or disarticulated skeletons, and isolated bones and teeth. Censuses of fossil marine mammal assemblages demonstrate that pin-nipeds are numerically rare (9%, Boessenecker et al. 2014; ~2–3%, Pyenson et al. 2009). Marine death assemblages of pinnipeds are unknown, but Holocene nonmarine mass death assemblages of mummified seals from Antarctica (Dort 1978) and *Otaria* from Patagonia (Serran et al. 2008) have been reported. Specimens preserved in bonebeds consist of isolated bones and teeth that have been abraded, fragmented, and on occasion phosphatized and polished (Boessenecker et al. 2014).

The earliest well-documented record of pinnipeds is from the late Oligocene [30–23 million years ago (Ma)]. Pinniped fossils have been reported worldwide (Miyazaki et al. 1995, Deméré et al. 2003, Avery & Klein 2011), including from Japan (early Miocene–Holocene), western North America (late Oligocene–Holocene), eastern North America (middle Miocene–Holocene), South America (middle Miocene–Holocene), and Europe (middle Miocene–Holocene); more limited records exist from Libya, Morocco, and South Africa (Miocene–Holocene), from Australia and New Zealand (late Miocene–Holocene), and from Antarctica (Holocene) (**Figure 2**). Associated and articulated fossil skeletons are common only in North Pacific deposits and the Pisco Formation of Peru; North Atlantic assemblages are dominated by isolated skeletal elements, likely reflecting taphonomic biases caused by the differing sedimentation rates of active (Japan,
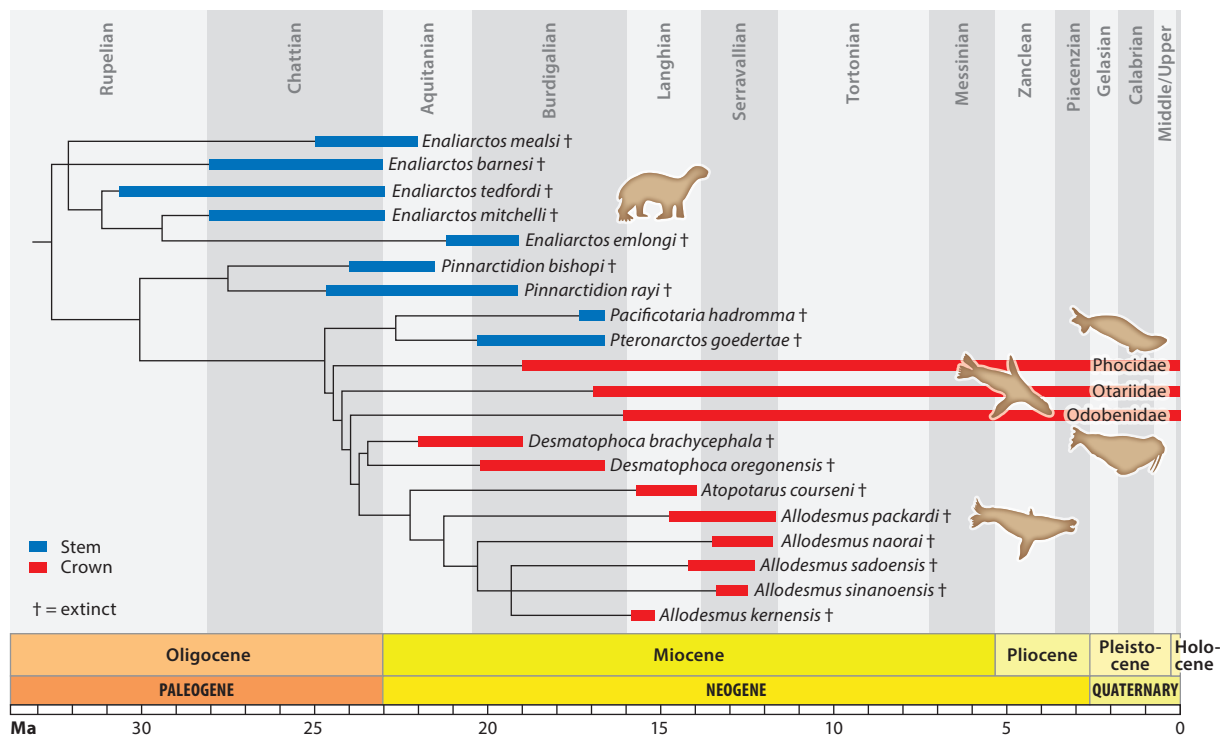
Supplemental Material

Figure 1

Time-calibrated phylogeny of pinnipeds, showing relationships among major clades.

California, Peru) versus passive (Atlantic Coastal Plain, North Sea Basin) continental margins (Boessenecker et al. 2014).

Biogenic bone modifications have been reported for pinniped remains, including bite marks attributable to sharks and bony fish (Bigelow 1994, Boessenecker et al. 2014, Collareta et al. 2017), mammalian (likely pinniped) tooth punctures (Boessenecker & Perry 2011), ring-shaped barnacle etchings (Boessenecker 2013b), possible *Osedax* (bone-eating worm) borings in teeth (Boessenecker et al. 2014), and acid etching resulting from partial digestion by a shark (Boessenecker et al. 2014). These examples demonstrate trophic and scavenging interactions between pinnipeds and sharks, possible intraspecific fighting/cannibalism, and postmortem colonization of skeletons by boring and encrusting invertebrates. Occasionally, pinniped skeletons may be preserved with gut contents (e.g., fish bones; Cozzuol 2001); although modern pinnipeds swallow gastroliths (Wings 2007), they have not been reported from fossil pinnipeds.

ORIGINS OF PINNIPEDS

Debate over the last century on pinniped evolution has focused on whether pinnipeds are mono-phyletic and what group of terrestrial mammals they are most closely related to. Although all studies agree that pinnipeds are members of the carnivoran clade Arctoidea, what group they are most closely related to within this clade is still debated. Two major hypotheses have been proposed. A monophyletic hypothesis proposes that the three pinniped families share a single common evolutionary origin and are most closely related either to Ursidae (bears), based mostly
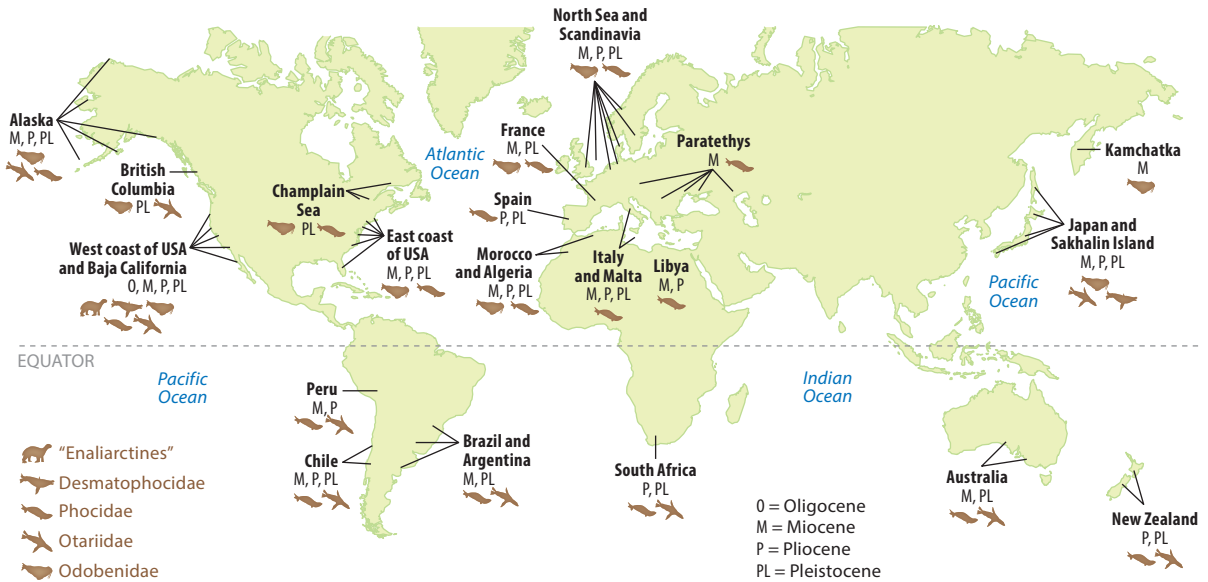
Figure 2

Major localities for fossil pinnipeds.

on morphology (e.g., Wyss & Flynn 1993, Berta & Wyss 1994, Luan et al. 2013), or to Musteloidea (weasels, skunks, and raccoons), based mostly on molecular data (e.g., Bininda-Emonds et al. 1999, Fulton & Strobeck 2006, Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012). The diphyletic view claims that pinnipeds actually evolved from two separate carnivore lineages, with the clade containing odobenids and otariids being most closely related to Ursidae and the phocids originating separately from the mustelids (weasels, skunks, otters, and their kin). Early studies of morphological evidence supported pinniped diphyly (e.g., Tedford 1976, Repenning et al. 1979, de Muizon 1982, Barnes 1989), while pinniped monophyly has received support from both recent morphological (Wyss 1987, Wyss & Flynn 1993, Berta & Wyss 1994) and molecular studies (e.g., Higdon et al. 2007, Fulton & Strobeck 2010, Nyakatura & Bininda-Emonds 2012).

Problematic Pinnipedimorphs or Close Arctoid Relatives

Unlike for cetaceans, the early stages of pinniped evolution are not clear. Possible close pinniped relatives include the otter-like semantorids (e.g., *Potamotherium*, *Puijila*) and the bear-like amphicynodont *Kolponomos*. *Potamotherium valletoni*, known from numerous postcranial elements but no complete skeletons, from the lower Miocene freshwater deposits of central France, has been described as a lutrine mustelid (Savage 1957), a mustelid/musteloid (Wang et al. 2005), or a pinniped (Tedford 1976, de Muizon 1982, Wolsan 1993). Another possible pinniped relative is *Semantor*, recovered from upper Miocene deposits in Kazakhstan (Orlov 1933). *Puijila darwini*, found in 24–20 Ma lacustrine deposits on Devon Island, Canada, was described (Rybczynski et al. 2009) as a morphological intermediate in the land-to-sea transition of pinnipeds (**Figure 3**). The large opening below the eye socket, the infraorbital foramen, suggests enhanced sensitivity of the snout, useful in both seals and terrestrial (particularly fossorial) carnivorans. *Puijila*, unlike pinnipeds, did not have flippers and more closely resembles otters in its limb proportions and its possession of a long tail and large, probably webbed feet.
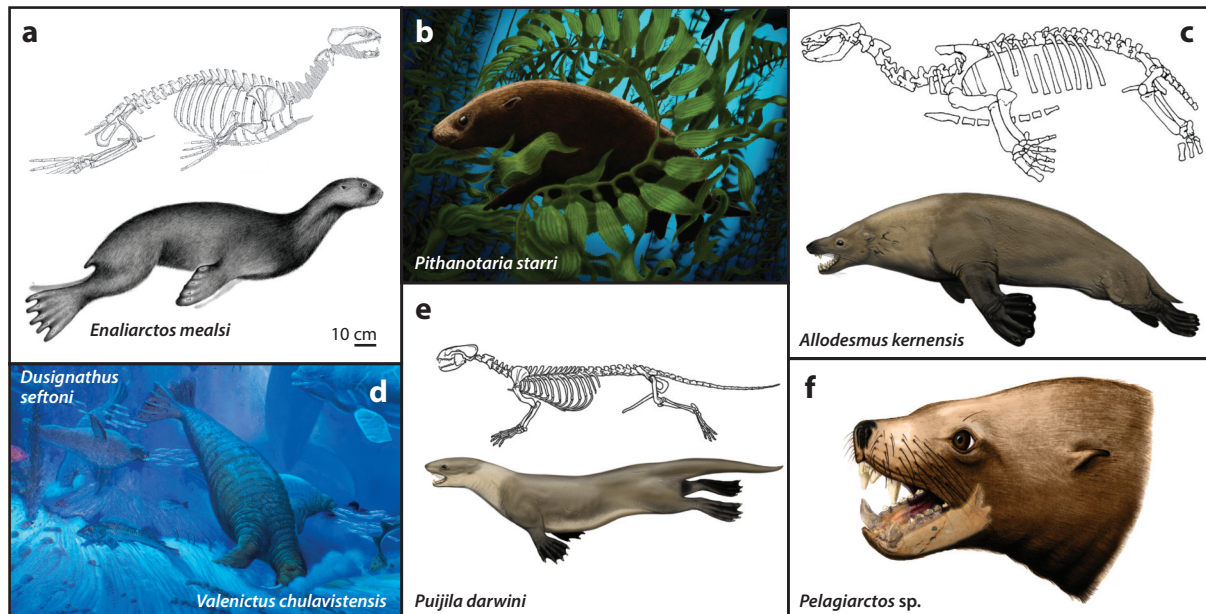
Figure 3

Life restorations of fossil pinnipeds and a close relative. (*a*) *Enaliarctos mealsi* (total length 1.4–1.5 m); illustrated by M. Parrish. (*b*) *Pithanotaria starri* (total length 1.26 m); illustrated by R. Boessenecker. (*c*) *Allodesmus kernensis* (total length 2.2 m); illustrated by C. Buell. (*d*) *Dusignathus seftoni* (skull length up to 40 cm) and *Valenictus chulavistensis* (skull length 40 cm); illustrated by W. Stout. (*e*) *Puijila darwini* (total length just over 1 m); illustrated by C. Buell. (*f*) *Pelagiarctos* sp. (ca. 2.7 m); illustrated by R. Boessenecker.

Kolponomos, originally thought to be a marine raccoon relative, has been posited as belonging to the Amphicynodontinae, hypothesized as the stem group from which the Pinnipedimorpha arose (Tedford et al. 1994). *Kolponomos* is known by two species from the Miocene of Washington and Oregon (Tedford et al. 1994) and skull fragments from Alaska (Jacobs et al. 2009). *Kolponomos* had a massive skull with a markedly downturned snout, binocular vision, and broad, crushing teeth suited to a diet of hard-shelled marine invertebrates such as crabs or clams; invertebrates were pried or twisted off rocks using enlarged caniniform teeth and powerful neck muscles (Tedford et al. 1994, Tseng et al. 2016). Further research is needed to determine what fossil arctoids are the closest relatives to pinnipeds and how the above taxa fit into the story of pinniped evolution since most have not yet been included in comprehensive phylogenetic data sets.

"ENALIARCTINES": STEM PINNIPEDS

The "enaliarctines" represent the earliest-diverging lineages of unambiguous stem pinnipeds belonging to the Pinnipedimorpha clade, which originated in the eastern North Pacific during the mid–late Oligocene (30.6–28 Ma). Formerly considered monophyletic, they are best treated as a paraphyletic grade outside of the crown group (see the sidebar titled Phylogenetic Terms). The earliest well-represented pinnipedimorph, *Enaliarctos*, is known by five species (Barnes 1979, Mitchell & Tedford 1973, Berta 1991). The ancestral pinnipedimorph dentition, exemplified by *Enaliarctos barnesi*, is heterodont, with large blade-like cusps on the upper fourth premolar and lower first molar (carnassials) that were well adapted for shearing. These dental features together with features from the skull (when compared with those of terrestrial carnivores) indicate close

similarities in terms of derived characters with archaic bears. Other species of *Enaliarctos* show a trend toward a decreasing shearing function of the cheek teeth, heralding the development of the simple homodont cheek teeth of extant pinnipeds (Berta 1991, Churchill & Clementz 2016). The latest record of *Enaliarctos* (*Enaliarctos* sp.) is from 17.3–16.6 Ma rocks along the Oregon coast (Poust & Boessenecker 2018).

Enaliarctos mealsi is represented by a nearly complete skeleton from central California (**Figure 3**) (Berta et al. 1989, Berta & Ray 1990). The entire animal is estimated to have been 1.4–1.5 m in length and between 73 and 88 kg in weight, roughly the size and weight of a small male harbor seal. *E. mealsi* was capable of considerable lateral and vertical movement of the vertebral column. In addition, both its forelimbs and hind limbs were modified as flippers and used in aquatic locomotion. Several features of the hind limb suggest that *E. mealsi* was also capable of maneuvering well on land and probably spent more time near or on shore than extant pinnipeds. The deeply grooved articulations between the finger and toe bones on *E. mealsi* provide some evidence of the use of the limbs to grasp prey (Hocking et al. 2017).

Skull size differences between male and female skulls of *Enaliarctos* and *Pteronarctos* suggest that early pinnipedimorphs were sexually dimorphic, and it has been further suggested that these ancestral pinnipeds had a harem-based polygynous mating system that may that evolved in response to climate change and increased food availability during the late Oligocene and early Miocene (27 Ma) (Berta 1994b, Cullen et al. 2014). In this way, harem-based colonies would have developed at upwelling sites along coastal margins, as seen in some extant pinnipeds.

A later-diverging lineage of fossil pinnipeds, more closely allied with pinnipeds than with *Enaliarctos*, includes *Pteronarctos* and *Pacificotaria* from the early–middle Miocene (20.7–16.6 Ma) of coastal Oregon (Barnes 1989, 1992; Berta 1994b) (**Figure 1**). A striking osteological feature in all pinnipeds is the geometry of bones that compose the orbital region (Wyss 1987). In *Pteronarctos*, the first evidence of the uniquely developed maxilla is seen. In addition, in *Pteronarctos* the lacrimal is greatly reduced or absent, as in Pinnipedia. A shallow embrasure pit on the palate between the last premolar and the first molar, seen in *Pteronarctos* and pinnipeds, is indicative of reduced carnassials and shearing capability of the teeth and marks the beginning of a trend toward homodonty. Another "enaliarctine," *Pacificotaria*, is closely related to *Pteronarctos* (or perhaps a junior synonym; Berta 1994b) and is from the same stratigraphic unit. *Pacificotaria* is distinguished from *Pteronarctos* and *Enaliarctos* in possessing protruding orbits positioned farther anteriorly on the cranium, larger bony nares, a robust rostrum, a vaulted palate, and straighter upper cheek tooth rows (Barnes 1992). *Pinnarctidion* represents another lineage with two species described from the early Miocene of California and Oregon. Although *Pinnarctidion* has previously been allied with Phocoidea (Berta 1994a, Berta & Wyss 1994), it is more likely a stem pinniped (Boessenecker & Churchill 2018).

Polygynous mating system: social system where a single male protects and breeds with a large harem of females; associated with sexual dimorphism in body size and skull shape

Ecologically, the earliest pinnipedimorphs were coastal dwellers that evolved a pierce feeding strategy and likely fed on fish and other aquatic prey (Adam & Berta 2002, Churchill & Clementz 2016).

PHOCIDAE: SEALS

The Phocidae are the most morphologically diverse group of pinnipeds, known by 19 extant species. Most morphologic and molecular data consistently support phocid monophyly and recognition of two monophyletic subfamilies, Monachinae (Southern Hemisphere seals) and Phocinae (Northern Hemisphere seals) (Davis et al. 2004, Higdon et al. 2007, Amson & de Muizon 2014). Molecular data have provided strong support for three clades of crown monachines [Monachini (monk seals, *Neomonachus* and *Monachus*), Miroungini (elephant seals, *Mirounga*), and Lobodontini (i.e., *Hydrurga*, *Lobodon*, *Ommatophoca*, and *Leptonychotes*)] and three clades of phocines [Erignathini (bearded seals, *Erignathus*), Cystophorini (hooded seals, *Cystophora*), and Phocini (all remaining genera)] (Davis et al. 2004, Higdon et al. 2007, Fulton & Strobeck 2010).

Phocid seals can be distinguished from otariid seals and odobenids on the basis of several characters of the ear region, including a pachyostotic mastoid region and greatly inflated entotympanic (Wyss 1987). Among postcranial characters is a lack of the ability to draw the hind limbs forward under the body, due to an ankle joint with a massively developed astragalar process over which passes the tendon of the flexor hallucis longus muscle. Tension on this tendon prevents the foot from being dorsiflexed (de Muizon 1982, King 1983a). Compared to otariids, phocids inhabit higher latitudes, spend more time in water, exhibit different locomotor patterns, and have more diverse skull morphologies as well as dietary and reproductive strategies (Ferguson & Higdon 2006, Bebej 2009, Jones & Goswami 2010, Berta et al. 2015b).

The oldest definitive fossil phocid is the stem monachine *Afrophoca* (see discussion below) from 19–14 Ma rocks in Africa (Koretsky & Domning 2014). One of the best represented stem phocids is *Devinophoca*, belonging to the extinct clade Devinophocinae from the early–middle Miocene (16.26–14.89 Ma) of Slovakia with two described species (Koretsky & Holec 2002, Koretsky & Rahmat 2015). Older records of phocids (Koretsky & Sanders 2002) are problematic given questionable stratigraphic provenances (Dewaele et al. 2017b).

Members of both Monachinae and Phocinae are known in the middle Miocene, ~15 Ma, on both sides of the North Atlantic (Deméré et al. 2003) and congruent with molecular clock estimates for the divergence of these two clades (Higdon et al. 2007, Fulton & Strobeck 2010). In the absence of a robust phylogenetic analysis for phocids that includes extant and extinct taxa, we provide a composite tree (**Figure 4**) based on molecular data (Fulton & Strobeck 2010) with the addition of fossil taxa based largely on the work of Amson & de Muizon (2014). The occurrence of both monachine and phocine lineages during the middle Miocene in the North Atlantic suggests that they evolved either there or earlier in the North Pacific. A southern route of dispersal is more likely, as discussed by Costa (1993) and Bininda-Emonds & Russell (1996), given that the Bering land bridge blocked access to the Arctic through much of the late Oligocene and early Miocene. It may also be that the colder climate through the Arctic Basin hindered early phocid dispersal along the northern route. The Central American Seaway was open during this time and is in agreement with the warm-water affinities of North Atlantic phocids at this time.

Monachines had established a circum-Atlantic distribution by the late Miocene that included the Mediterranean and Paratethys Seas. Remains of an indeterminate monachine from the middle Miocene of Malta (Bianucci et al. 2011) and the even older purported monachine *Afrophoca libyca* (Koretsky & Domning 2014), based on a partial lower jaw from lower–middle Miocene, 19–14 Ma rocks of Libya, implies a long history of monachines in the Mediterranean. Other stem monachines include *Pontophoca* from the late Miocene of Eastern Europe (Koretsky & Grigorescu 2002) and
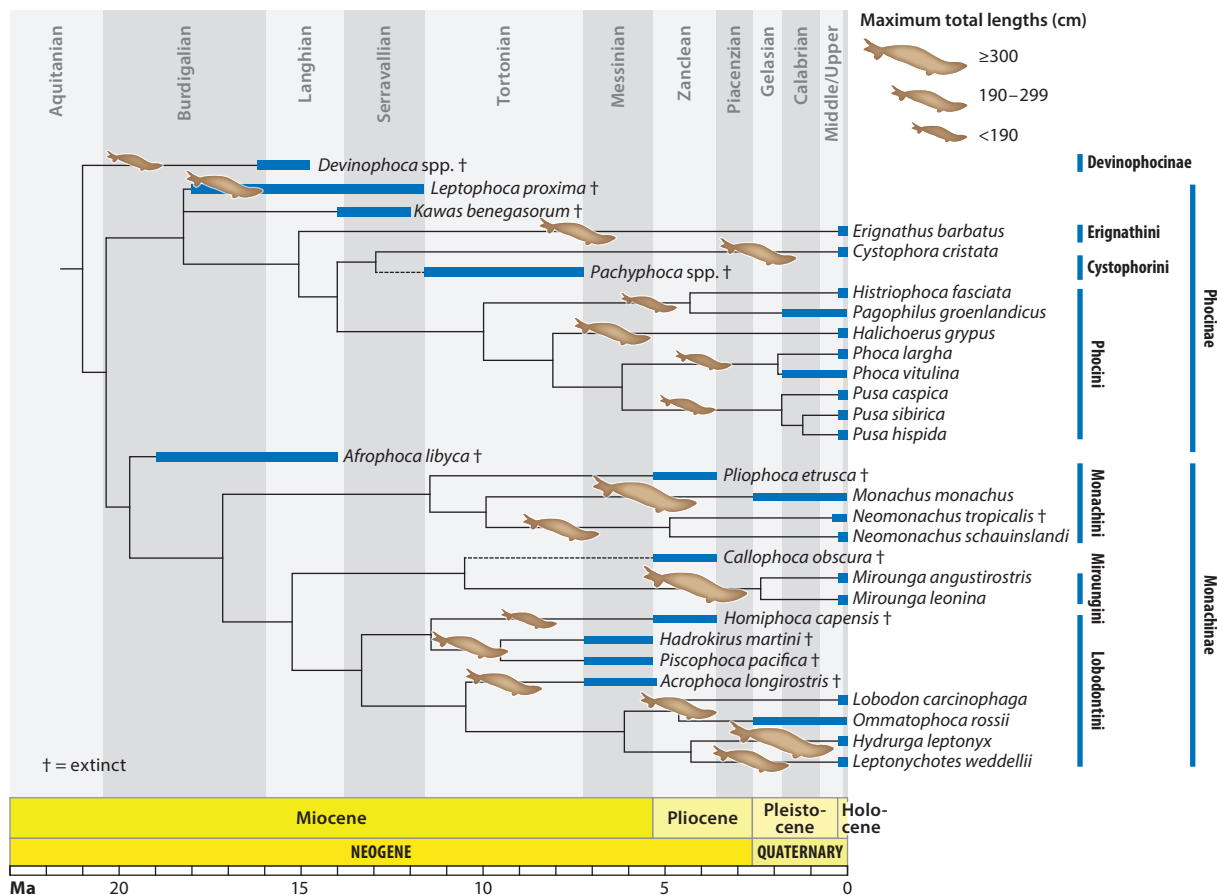
Figure 4

Time-calibrated composite phylogeny of phocids. Figure modified from Fulton & Strobeck (2010) and Amson & de Muizon (2014).

the North Sea (Koretsky et al. 2014). The status of several other middle Miocene monachines is problematic [e.g., *Monotherium* (see Ray 1976) and *Miophoca vetusa*, the latter of which is considered a nomen dubium (Dewaele et al. 2017b)].

In contrast to otariid seals, phocids reached the Southern Hemisphere very early in their evolutionary history. The oldest record consists of the poorly known monachine *Properiptychus argentinus* from the upper Miocene Parana Formation, Argentina (de Muizon & Bond 1982, Perez et al. 2010). South American monachine seals include four closely related genera: *Acrophoca*, *Piscophoca*, *Hadrokirus*, and *Australophoca*. Recent phylogenetic analyses (e.g., Amson & de Muizon 2014) place the South American fossil seals (*Hadrokirus*, *Acrophoca*, and *Piscophoca*) and the South African seal *Homiphoca* in a clade with lobodontine seals (**Figure 4**).

Extant lobodontine seals, also known as Antarctic seals, include four monotypic genera: the crabeater seal, *Lobodon carcinophaga*; the leopard seal, *Hydrurga leptonyx*; the Weddell seal, *Leptonychotes weddellii*; and the Ross seal, *Ommatophoca rossii* (**Figure 4**). This clade diverged approximately 6.9 Ma from elephant seals and may have dispersed along the western South American coastline and spread eastward around Antarctica via the Antarctic Circumpolar Current beginning at least

3.4 Ma based on the occurrence of *Homiphoca* in South Africa. Extant genera are not documented in the pre-Holocene fossil record with the exception of *Ommatophoca*, reported from the Plio-Pleistocene of New Zealand (King 1983a).

One of the most unusual phocids is *Acrophoca longirostris*, from the late Miocene–early Pliocene of Peru and Chile (de Muizon 1981; Walsh & Naish 2002; Valenzuela-Toro et al. 2013, 2015); it is unique among phocids in its long skull, its slender, flexible neck, and its elongated body [approximately 2 m, according to the Churchill et al. (2014c) body size estimation]. The tooth morphology of *Acrophoca* is consistent with generalized pierce feeding and a diet that likely consisted of fish. The everted pelvis and modified hind flippers suggest that is was a hind limb–dominated swimmer.

Hadrokirus, from the upper Miocene–lower Pliocene, 5.75 Ma Pisco Formation, Peru, displays sexual dimorphism, similar to extant lobodontine seals such as *Hydrurga* (Amson & de Muizon 2014). The skull is long and heavily built, and the jaws are robust and stout. The strong masticatory and neck muscles and robust teeth, some showing breakage and extensive wear, suggest that the diet of *Hadrokirus* was durophagous and included hard prey items such as molluscs and/or echinoderms.

Australophoca changorum was described by Valenzuela-Toro et al. (2015) based on postcrania from the upper Miocene Bahia Inglesa Formation of northern Chile and the Pisco Formation of southern Peru. This new seal is smaller than all known fossil and extant monachines and is in the size range of the smallest phocines (e.g., the extant genus *Pusa* and the even smaller fossil seal *Praepusa boeska*; Valenzuela-Toro et al. 2015). Together with the long-snouted *Acrophoca* and the durophagous *Hadrokirus*, this suggests an exceptional degree of ecological diversity in South American phocid seals. The South American fossil record is dominated by phocids, whereas today, the extant pinniped fauna in this region is dominated by otariids. Changing sea levels during the Pleistocene may have reduced the number of haul out sites suitable for phocids and increased the number of rocky islands surrounded by a deeper-water environment that favored otariid seals (Valenzuela-Toro et al. 2013). In some ways this parallels replacement of the Neogene desmatophocid and odobenid fauna by a Quaternary otariid/phocid fauna in the North Pacific. However, there are some differences. The transition in South America appears to have been quite rapid, whereas that in the North Pacific seems to have yielded more overlap between desmatophocids and odobenids, and both groups evolved in the same regions. This is in contrast to the situation with phocids and otariids. Phocids first evolved in the North Atlantic, while otariids evolved in the North Pacific, with little overlap in range for most of the duration of the evolution of these clades.

Phocids from Langebaanweg, South Africa, include *Homiphoca capensis* and as many as six additional seal taxa (Govender 2015). Evidence for *Homiphoca* breeding in this area is indicated by the remains of a number of pups and immature animals. The presence of long nasal bones, voluminous maxilloturbinates, and the posterolateral expansion of the maxilla (suggesting the presence of countercurrent exchangers enabling the reduction of heat loss) imply that *Homiphoca* was adapted to cold climates. In addition to the well-documented presence of lobodontines in South Africa and South America, undescribed monachines have been reported from the Pliocene of Australia and New Zealand (Fitzgerald et al. 2013), which supports a broader distribution of this lineage in the Southern Hemisphere.

The best-known Mediterranean monachine seal is *Pliophoca etrusca*, known by a partial skeleton from the late Pliocene (3.19–2.82 Ma) of Italy. Phylogenetic analysis (Berta et al. 2015a) found that *Pliophoca* is closely related to the Mediterranean monk seal *Monachus monachus*. Study of morphologic and molecular data (Scheel et al. 2014) supported a New World genus of monk seals, *Neomonachus*, distinct from *Monachus*. According to the biogeographic scenario proposed by Scheel et al. (2014), the common ancestor of *Neomonachus* may have been distributed throughout the Central American Seaway during the late Pliocene. Final closure of the Central American Seaway 2.5–2.0 Ma created allopatric populations in two oceans, giving rise to the Caribbean

species, *Neomonachus tropicalis*, and the Hawaiian species, *Neomonachus schauinslandi*. The earliest fossil record for *Neomonachus tropicalis* is from the middle Pleistocene (1.7–1.05 Ma) of Florida (Berta 1995).

Callophoca, at nearly 3 m, is an exception to the relatively moderate body size of stem monachines. The sexually dimorphic *Callophoca* has been hypothesized to be involved in the ancestry of elephant seals (Amson & de Muizon 2014); however, this relationship is not strongly supported (Berta et al. 2015a, Boessenecker & Churchill 2016). A fragmentary *Mirounga*-like rostrum from the early Pleistocene (2.6–2.4 Ma) of New Zealand suggests a Southern Hemisphere origin for Miroungini (Boessenecker & Churchill 2016). Middle–late Pleistocene fossils of *Mirounga* sp. are reported from Chile (Valenzuela-Toro et al. 2015); undescribed specimens of *Mirounga* sp. cf. *M. angustirostris* are also recorded from the upper Pleistocene of southern California (Miller 1971).

Phocine seals are a largely Northern Hemisphere radiation. The earliest stem phocines are two taxa from the middle Miocene of Antwerp, Belgium: *Leptophoca proxima* (formerly known as *Prophoca proxima* and *Leptophoca lenis*) and *Prophoca rousseaui* (Dewaele et al. 2017b). *Leptophoca proxima* is also found in the eastern Atlantic (Virginia and Maryland); reexamination of the occurrence of the holotype of *L. lenis* (Plum Point Member, Calvert Formation, Maryland) suggests that it may be the oldest record of this taxon at approximately 18 Ma (Dewaele et al. 2017b). *Leptophoca amphiatlantica* from the early–late Miocene in the eastern (Maryland) and the western (Netherlands) Atlantic (Koretsky 2001, Koretsky et al. 2012) has been considered a junior synonym of *L. proxima* with specimens reassigned to *Leptophoca* cf. *L. proxima* (Dewaele et al. 2017b). A new genus and species, *Nanophoca vitulinoides* (formerly "*Phoca*" *vitulinoides*), described on the basis of a partial skeleton, among the smallest of pinnipeds, from the early–late Miocene of the North Sea, is positioned as sister to crown Phocinae (Dewaele et al. 2017a). Other extinct phocines, including *Cryptophoca*, *Gryphoca*, *Monachopsis*, *Pachyphoca*, *Phocanella*, *Platyphoca*, and *Praepusa*, are largely represented by disarticulated, nonassociated postcranial material from various Miocene and Pliocene European localities in the Paratethys region (Koretsky 2001, Koretsky & Grigorescu 2002, Koretsky & Holec 2002, Koretsky & Rahmat 2013), and their exact phylogenetic affinities remain uncertain.

Stem phocines are only poorly known from the Southern Hemisphere. *Kawas benegasorum* was described by Cozzuol (2001) on the basis of an articulated partial skeleton from the middle Miocene (12–14 Ma) of Patagonia, Argentina, although its relationship to other phocines remains unclear. Notable among fossil pinnipeds, the preserved gut contents of *Kawas* indicate a diet predominantly of bony fish.

Among extant phocines, consistent strong support is found for recognition of the bearded seal, *Erignathus barbatus* (Erignathini), and the hooded seal, *Cystophora cristata* (Cystophorini), as successive sister taxa to remaining phocines (**Figure 4**). This deepest phocine split was dated to 11 Ma, followed by a divergence time of 5.5 Ma for the hooded seal lineage based on molecular data (Fulton & Strobeck 2010). The earliest record of bearded seal remains is middle–late Pleistocene (800–100 thousand years ago) from Norfolk, England (Harington 2008). The hooded seal is unknown in the fossil record, although the mid-Miocene *Pachyphoca* from the Paratethyan Basin of Ukraine (Koretsky & Rahmat 2013) has been suggested to be a close relative. Most recent studies (e.g., Fulton & Strobeck 2010) have found support for the next branch of the tree being the ribbon seal, *Histriophoca*, and the harp seal, *Pagophilus*, as a sister group to remaining taxa. The ribbon and harp seals diverged approximately 3.4 Ma, and their split has been hypothesized as the result of glacial and interglacial fluctuations that drove allopatric speciation. Disagreements about phylogenetic relationships exist for remaining species (the harbor seal, *Phoca*; the ringed seal, *Pusa*; and the gray seal, *Halichoerus*; e.g., Árnason et al. 2006). The gray seal (*Halichoerus grypus*),

found on both sides of the Atlantic, is positioned as the sister species of the land-locked Caspian seal (*Pusa caspica*) in several studies (e.g., Fulton & Strobeck 2010, Nyakatura & Bininda-Emonds 2012), but in other studies *Halichoerus* clusters within the more broadly distributed *Phoca* species found in both the North Pacific and the Atlantic (e.g., Fulton & Strobeck 2010). Evolutionary trends in later-diverging phocines (e.g., the *Histriophoca-Pagophilus* clade and the *Phoca-Pusa* clade) in comparison to monachines include a reduction in body size (Churchill et al. 2014b).

DESMATOPHOCIDS: PHOCID RELATIVES OR OTARIOIDS?

An extinct family of relatively large archaic pinnipeds, the Desmatophocidae, are known from the early and middle Miocene (23–10 Ma) of the western United States and Japan (Mitchell 1966, Repenning & Tedford 1977, Barnes & Hirota 1995, Deméré & Berta 2002). Desmatophocids are characterized by elongate skulls, relatively large eyes, interlocking contact between two cheek-bones, and bulbous cheek teeth. The phylogenetic position of desmatophocids is controversial, and they have been allied either with otariids plus odobenids in the Otarioidea (Barnes 1989) or, alternatively, with phocids in the Phocoidea (Deméré & Berta 2002, Dewaele et al. 2017b, Velez-Juarbe 2017, Boessenecker & Churchill 2018).

Desmatophocids were the first large pinnipeds to evolve, ranging from the "enaliarctine"-sized *Desmatophoca brachycephala* (approximately 1.30 m in length) to species of *Allodesmus* that reached up to 3 m in length (**Figure 3**), and cranial material from Japan suggests that some individuals attained even larger body sizes (Churchill et al. 2014b). *Desmatophoca* is known by two species from the lower Miocene Astoria Formation of Oregon and Washington (Barnes 1987, Deméré & Berta 2002). *Desmatophoca* is sexually dimorphic (Deméré & Berta 2002), although to a lesser degree than allodesmines, and may have had a harem-style polygynous reproductive strategy similar to otariids and extant elephant seals with dominant males controlling females on the breeding beaches (Mitchell 1966).

Allodesmines replaced desmatophocines in the middle Miocene. They are considered to have been large pelagic predators, ecologically similar to elephant seals (*Mirounga* spp.; Mitchell 1966). Four genera (*Allodesmus*, *Atopotarus*, *Brachyallodesmus*, and *Megagomphos*) and at least nine species of allodesmines are recognized from the North Pacific (California, Oregon, Washington, and Baja California) and Japan (Barnes & Hirota 1995), although a review of the evidence suggests that they may be oversplit (Kohno 1996, Boessenecker & Churchill 2018). This is especially true for species of *Allodesmus* from California, three of which alone are reported from a very limited stratigraphic interval within the middle Miocene Round Mountain Silt (Deméré & Berta 2002). The large eyes of *Allodesmus*, as deduced from large bony orbits, provide evidence that they may have been specialized for deep diving, similar to living elephant seals (Debey & Pyenson 2012). Functional analysis of postcrania suggests *Allodesmus* was a forelimb rower, like modern otariids (Bebej 2009).

OTARIIDAE: FUR SEALS AND SEA LIONS

Otariidae (fur seals and sea lions) are the second most diverse clade of extant pinnipeds and are today represented by 14 to 15 species distributed in cold temperate waters of the North Pacific and the Southern Hemisphere (Berta & Churchill 2012). Otariidae can generally be distinguished from other pinniped clades by possession of a shelf-like supraorbital process of the frontal, loss of the M_2, and simplified dentition (King 1983a, Boessenecker & Churchill 2015). In contrast to phocids or odobenids, otariid seals are morphologically conservative (Churchill et al. 2014a) and mostly lack the ecological specializations seen in other pinniped clades (Adam & Berta 2002, Jones & Goswami

2010). They are the most variable in size, with extant taxa ranging from the ~27-kg female Galapagos fur seal (*Arctocephalus galapagoensis*) to the 1,000-kg male Steller's sea lion (*Eumetopias jubatus*; Lindenfors et al. 2002). All species are polygynous (King 1983a, Lindenfors et al. 2002), with significant sexual dimorphism, a trait also observed in fossil taxa such as *Thalassoleon mexicanus* (Deméré & Berta 2005).

Monophyly of Otariidae has been consistently recovered in all phylogenetic analyses (Árnason et al. 2006, Higdon et al. 2007, Yonezawa et al. 2009, Churchill et al. 2014a, Boessenecker & Churchill 2015), and molecular divergence dating suggests that they split from Odobenidae ~19 Ma (Yonezawa et al. 2009). Relationships within the family have been more disputed. Studies based on morphology have largely supported the presence of two subfamilies, the fur seals (Arctocephalinae), characterized by a small body size and thick furry pelage, and the sea lions (Otariinae), characterized by large body size and reliance on blubber, rather than fur, for insulation (Berta & Deméré 1986, Barnes et al. 2006). Some morphologic studies, however, have suggested arctocephaline paraphyly, recovering the northern fur seal (*Callorhinus ursinus*) as the earliest-diverging lineage of extant otariid seal (Berta & Wyss 1994, Boessenecker & Churchill 2015). This finding is consistent with combined evidence and molecular analyses, which also find Otariinae to be paraphyletic, with northern sea lions (*Zalophus* and *Eumetopias*) as the sister clade to a southern otariid group comprising southern fur seals (*Arctocephalus*) as well as the South American (*Otaria*), New Zealand (*Phocarctos*), and Australian (*Neophoca*) sea lions (**Figure 5**) (Árnason et al. 2006, Higdon et al. 2007, Yonezawa et al. 2009, Churchill et al. 2014a). These studies suggest fur was lost multiple times, probably as a consequence of increased body size and increased reliance on blubber for insulation (Churchill et al. 2014a). No consensus exists currently on phylogenetic relationships within the southern clade.

A North Pacific origin for Otariidae is strongly supported based on the fossil record as well as biogeographic analysis of modern taxa (Repenning et al. 1979, Deméré et al. 2003, Yonezawa et al. 2009, Churchill et al. 2014a). Early Odobenidae were sympatric with early Otariidae and have a rich fossil record, unlike the relatively poor pre–late Miocene otariid record, which consists of isolated, incomplete specimens. Otariids thus appear to have been rare and local elements of Miocene marine mammal faunas. This may be indicative of a pelagic habitat preference in early otariids, with fossil taxa rarely entering coastal waters with higher fossil preservation potential (Boessenecker & Churchill 2015).

The oldest known otariid taxa are *Eotaria crypta* and *Eotaria citrica*, from the 17–15 Ma middle Miocene Topanga Formation in southern California (Boessenecker & Churchill 2015, Velez-Juarbe 2017). These taxa are known only from partial jaws with teeth, but they exhibit a relatively simplified dentition, as seen in later-diverging taxa. However, in contrast to later-diverging otariids, both species of *Eotaria* still retain an M_2, a feature absent in all other described otariids. The next-oldest otariid is *Pithanotaria starri*, from the 10–7 Ma Monterey Formation and Santa Margarita Sandstone of California (**Figure 3**) (Repenning & Tedford 1977). In common with *Eotaria*, this taxon was small in body size, similar in size to the extant *A. galapagoensis* (Churchill et al. 2014b). This suggests that small body size may be the ancestral condition for Otariidae (Churchill et al. 2014b), retained from "enaliarctines." *Pithanotaria* is known from more complete material than *Eotaria*, but much of it still remains undescribed (e.g., Velez-Juarbe 2017). *Pithanotaria* has generally been considered a stem otariid (Berta & Deméré 1986, Churchill et al. 2014a), although one recent analysis suggests that it may be part of the lineage that eventually gave rise to the extant *C. ursinus* (Boessenecker & Churchill 2015).

Perhaps the best known fossil otariid genus is *Thalassoleon* from the latest Miocene and early Pliocene. This genus comprises three taxa: the sea lion–sized *Thalassoleon mexicanus*, of southern California and Mexico (Repenning & Tedford 1977, Deméré & Berta 2005); *Thalassoleon*
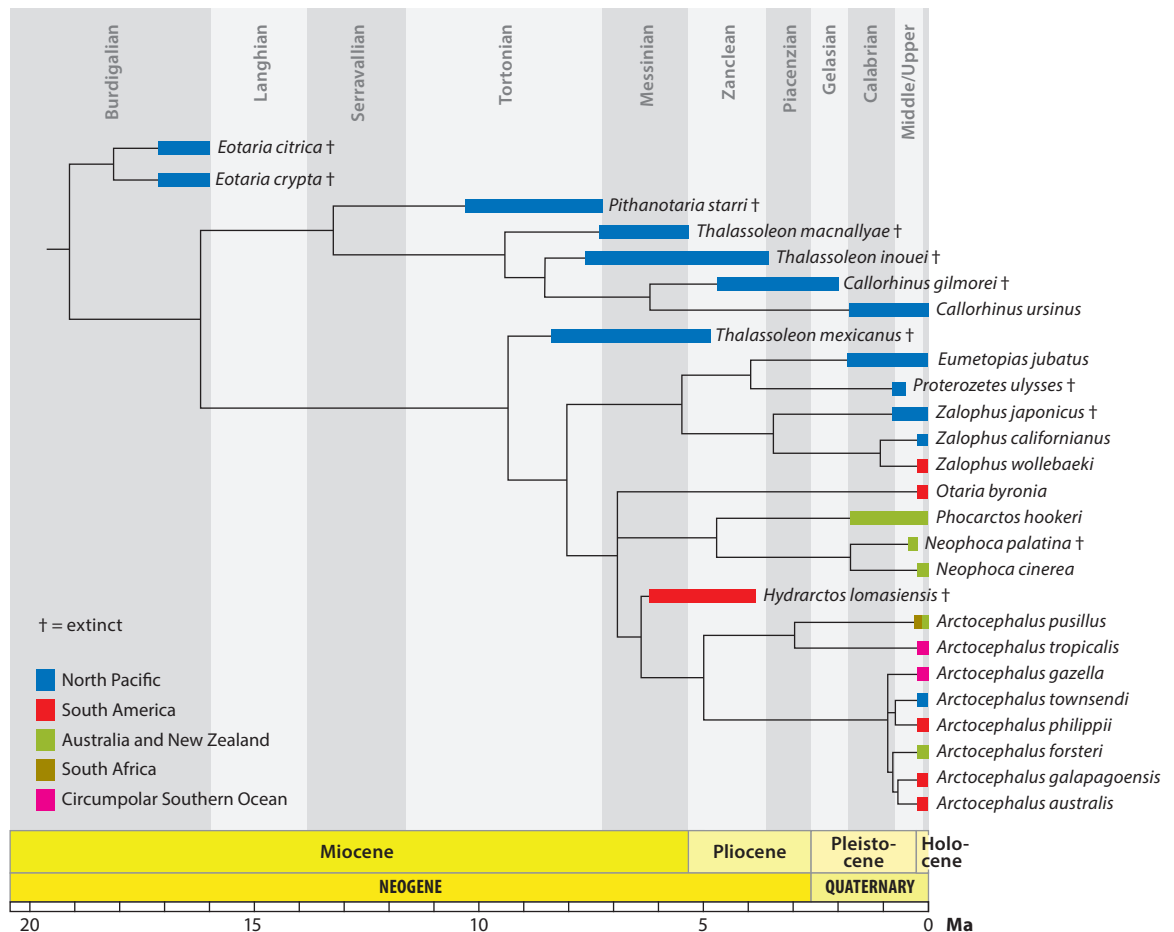
Figure 5

Time-calibrated phylogeny and biogeography of otariids. Figure modified from Churchill et al. (2014a).

inouei, a poorly known Japanese taxon (Kohno 1992); and *Thalassoleon macnallyae*, from northern California (Repenning & Tedford 1977). These taxa are represented by numerous skeletal elements and skulls, allowing determination of extensive sexual dimorphism within *T. mexicanus* (Deméré & Berta 2005), suggesting that the modern polygynous system of breeding was established for Otariidae by the end of the Miocene. Phylogenetic analyses, however, suggest possible paraphyly of the genus, with *T. mexicanus* as the sister taxon to a clade comprising *T. macnallyae* and all later-diverging taxa (Churchill et al. 2014a), or *T. mexicanus* diverging after a clade comprising *T. macnallyae* and *Callorhinus* (Boessenecker & Churchill 2015).

Fossils of crown group otariids (sensu Churchill et al. 2014a) are unknown until the Pliocene in the North Pacific. Among the earliest of these taxa are *Callorhinus gilmorei* from the late Pliocene of California and Japan (Berta & Deméré 1986, Kohno & Yanagisawa 1997, Boessenecker 2011), as well as early Pleistocene *Callorhinus* sp. from the Rio Dell Formation, California (Boessenecker 2011), both taxa of which may represent members of a lineage arising from anagenesis evolving into the extant *Callorhinus ursinus* (Boessenecker 2011). The sea lion *Proterozetes ulysses*, known

from the middle Pleistocene of Oregon (Barnes et al. 2006, Poust & Boessenecker 2017), is a sister taxon to extant *Eumetopias*; it represents the oldest known definitive occurrence of a northern sea lion. Sea lions are unknown from well-sampled Pliocene rocks in California, though *Zalophus* and *Eumetopias* have been reported from fragmentary material from the Pliocene and Pleistocene of Japan (Miyazaki et al. 1995), suggesting delayed dispersal to the eastern North Pacific, perhaps following extirpation of temperate walruses at the end of the Pliocene (Boessenecker 2013a).

Otariids are important components of North Pacific marine mammal faunas, but they achieve their greatest diversity in the Southern Hemisphere. However, in contrast to phocids, otariids appear to have been very late immigrants to this region, with the oldest records being only early Pliocene in age (de Muizon 1978). Differences in the timing of each group's entry into the Southern Hemisphere likely point to differences in environmental tolerances; phocids are adapted to a wide variety of marine environments, from polar ice shelves to tropical beaches. In contrast, otariids are limited to largely cool, highly productive upwelling regions (Churchill et al. 2014a). To reach the Southern Hemisphere, otariids needed to wait for a period of unusually cold equatorial sea surface temperature and high productivity to cross the otherwise inclement equatorial regions. Data from climatic proxies place this period as being around 6 Ma, and only after that do we see evidence of Southern Hemisphere fossil otariids (Churchill et al. 2014a) (**Figure 5**).

After this initial dispersal, otariids underwent an explosive radiation aided by fluctuating climate during the Pliocene (Yonezawa et al. 2009, Churchill et al. 2014a). The oldest known Southern Hemisphere otariid is *Hydrarctos lomasiensis*, from the Pliocene Pisco Formation of Peru (de Muizon 1978) (**Figure 5**), which may be close to the ancestry of *Arctocephalus* (de Muizon 1978, Churchill et al. 2014a). By the end of the Pliocene otariids reached South Africa (*Arctocephalus* sp.; Avery & Klein 2011), and by the middle Pleistocene they reached Australia (*Neophoca palatina*; King 1983b, Churchill & Boessenecker 2016) (**Figure 5**). Although we have a better understanding of how otariids reached the Southern Hemisphere, it's still unclear what role they played in extinction of temperate Southern Hemisphere phocids. Did the first otariid colonizers compete with phocids? Or did changes in sea level and haul out space drive phocids to extinction, allowing otariids to fill their niches (Valenzuela-Toro et al. 2013)? Hopefully, future work and discoveries in the Southern Hemisphere can answer these questions and provide more insight as to how otariids become the dominant pinnipeds in the Southern Hemisphere.

ODOBENIDAE: WALRUSES

The walrus *Odobenus rosmarus* is the most bizarre and distinctive extant pinniped; it is large (800–1,200 kg; Fay 1982), with thick blubber, and possesses a pair of enormous canines enlarged into tusks. *Odobenus* is a shallow-water molluskivore largely confined to the Arctic Circle; the species is sexually dimorphic and polygynous. In contrast to the low diversity, ecological specialization, and Arctic distribution of Odobenidae today, extinct walruses were quite diverse, inhabited temperate and subtropical latitudes, displayed a wide range of body sizes, and included many piscivores that lacked tusks (Repenning & Tedford 1977, Deméré 1994a). Given that many pinnipeds were found to be more closely related to *Odobenus* than to otariids or desmatophocids, early workers (Repenning & Tedford 1977) redefined the family; synapomorphies for Odobenidae include an antorbital process constructed by the frontal and maxilla, an elliptical narial opening, a dorsoventrally thickened pterygoid strut, tentorium appressed to petrosal, premolars with cuspate lingual cingulum, and several derived features of the forelimb (**Supplemental Figure 1**). Odobenids include the paraphyletic sea lion–like "Imagotariinae," the double-tusked Dusignathinae, and the Odobeninae—including the long-tusked walruses (**Figure 6**).
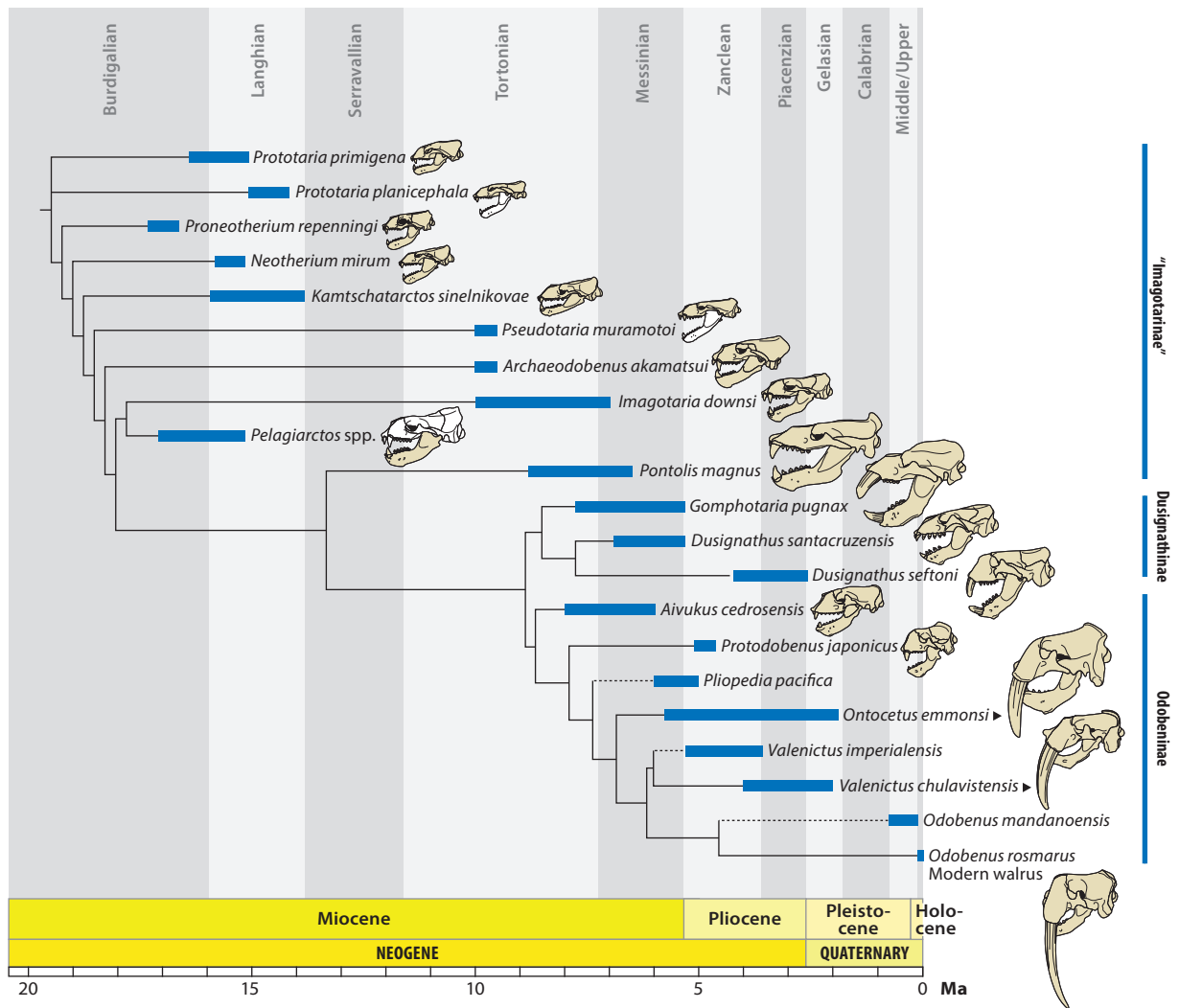
Supplemental Material

Figure 6

Time-calibrated phylogeny of walruses, with changes in skull morphology. Figure modified from Boessenecker & Churchill (2013).

The earliest odobenids are the small-bodied early Miocene (Burdigalian) "imagotariines" *Prototaria* (Japan) and *Proneotherium* (Oregon); aside from a cuspate lingual cingulum and a thickened pterygoid strut, these walruses are superficially "enaliarctine"-like and no doubt occupied a similar if not identical niche to theirs; *Proneotherium* co-occurs with the "enaliarctines" "*Pacificotaria*" and *Pteronarctos goedertae* (Berta 1994a, Kohno 1994, Kohno et al. 1995a, Deméré & Berta 2001). Middle Miocene odobenids were more diverse in body size and include *Neotherium mirum* (similar to but slightly larger than *Proneotherium*) and the sea lion–sized walrus *Pelagiarctos thomasi*, known only from mandibles and teeth (Barnes 1988, Kohno et al. 1995a). Older and more complete Burdigalian remains of *Pelagiarctos* are found alongside early *Allodesmus* and the early otariid *Eotaria* (Boessenecker & Churchill 2013, 2015), and contemporary with *Proneotherium*,

Pteronarctos, and *Desmatophoca*. *Pelagiarctos* (**Figure 3**) shares several dental features with the late Miocene large-bodied *Imagotaria downsi*, which may unite them in a clade within "Imagotariinae" (Boessenecker & Churchill 2013). A poorly known *Neotherium*-like walrus, *Kamtschatarctos sinelnikovae*, is known from Serravallian-correlative strata in Kamchatka, Russia (Dubrovo 1981). *Imagotaria* is well known by skulls and skeletons from Tortonian-Messinian strata in California; it has a large, elongate skull with a massive mandible; wide (but short) canines; and enlarged, bulbous cheek teeth. Contemporary but smaller taxa similar to *Imagotaria* include *Pseudotaria muramotoi* and *Archaeodobenus akamatsui* from the Tortonian of Japan (Kohno 2006, Tanaka & Kohno 2015). The youngest "imagotariines" include skulls and teeth of *Imagotaria* from the upper Miocene (8.7–6.5 Ma) Empire Formation of Oregon (Deméré 1994a) and the Purisima Formation (Messinian) of California (Boessenecker 2013a).

The Dusignathinae are superficially "imagotariine"-like large-bodied walruses known only from the eastern North Pacific, with enlarged, procumbent tusk-like upper and lower canines; these include the late Miocene *Gomphotaria pugnax* and *Dusignathus santacruzensis* and the Pliocene *Dusignathus seftoni* (Barnes & Raschke 1991; Deméré 1994a,b) (**Figures 3** and **6**). These walruses have unusually stocky forelimb bones, possibly reflecting otariid-like forelimb-dominated swimming (Barnes & Raschke 1991). *Dusignathus* and *Gomphotaria* have elongate, somewhat vaulted palates; enlarged and procumbent upper third incisors; and single-rooted cheek teeth with thickened roots and bulbous crowns (Barnes & Raschke 1991, Deméré 1994b). *Gomphotaria* has extensive tooth wear, which Barnes & Raschke (1991) interpreted as evidence of sediment ingestion and a durophagous mollusk diet. *Dusignathus seftoni* exhibits similar tooth wear, suggestive of a similar feeding behavior, whereas *Dusignathus santacruzensis* has sharp wear facets and lacks attritional damage, perhaps suggesting that it fed on fish within the water column rather than practicing durophagy or benthic feeding. The giant long-headed walrus *Pontolis magnus* from the upper Miocene of Oregon is the largest odobenid (6 m body length, 60 cm skull length) and may be a plesiomorphic dusignathine or a late "imagotariine" (Deméré 1994a, Kohno 2006, Boessenecker & Churchill 2013).

Odobenine fossils are known from the North Pacific and North Atlantic (Miyazaki et al. 1995) (**Figure 6**). The earliest known odobenine is *Aivukus cedrosensis*, a late Miocene tuskless odobenine from subtropical Baja California (Repenning & Tedford 1977). Long-tusked walruses from the tribe Odobenini, in addition to inflated maxillae and enlarged tusks, tend to have highly vaulted palates, reduced sagittal and nuchal crests, and a trend toward postcanine tooth reduction. The earliest clear Odobenini date to the early Pliocene (Kohno et al. 1995b). The early Pliocene *Protodobenus* (Japan) is small and exhibits a thickened rostrum but lacks tusks and abrasive dental wear (Horikawa 1995); other taxa, such as *Pliopedia*, are less completely known (Kellogg 1922, Repenning & Tedford 1977). The Pliocene walrus *Ontocetus emmonsi* has a complicated taxonomic history recently clarified by Kohno & Ray (2008) and is now known to have inhabited the shores of the North Atlantic from Florida north to New Jersey and in Europe from the North Sea south to Morocco. *Ontocetus* was 15% larger than extant *Odobenus* and was characterized by more procumbent tusks that were shorter and more curved, a rectangular occipital shield, retention of the I^2 and M^1, and an unfused mandibular symphysis (Deméré 1994a, Kohno & Ray 2008). Specimens of *Ontocetus* from Japan demonstrate dispersal through the Arctic during the Pliocene (Kohno et al. 1995b, 1998). The Pliocene tusked walrus *Valenictus* is the sister taxon to *Odobenus* and shares with it a fused mandibular symphysis and extensive osteosclerosis of the postcranial skeleton; the well-known species *Valenictus chulavistensis* notably differs from all other odobenines in lacking all teeth aside from the upper canines (**Figure 3**) and possessing a highly derived, pachyostotic humerus with inflated muscle attachment crests (Mitchell 1961, Deméré 1994b). Tooth loss is interpreted as a result of hyperspecialization toward mollusk suction feeding, as

modern *Odobenus* does not use its cheek teeth for chewing (Fay 1982, Deméré 1994b). *Valenictus* is known from a number of embayments in southern and northern California and Baja California, some of which were hypersaline (proto–Gulf of California); it is thought that pachyosteosclerosis of the postcranial skeleton served as ballast to overcome added buoyancy inflicted by hypersalinity (Deméré 1994b).

The earliest fossils of *Odobenus* include tusks and crania from Japan of latest Pliocene and early Pleistocene age (Miyazaki et al. 1992, Kohno et al. 1995b), indicating that, like other odobenines, *Odobenus* had a wider environmental tolerance than it does today. Middle and late Pleistocene fossils (and trace fossils) of *Odobenus* are recorded from as far south as San Francisco in the eastern North Pacific (Harington 1984, Gingras et al. 2007), South Carolina in the western North Atlantic (Sanders 2002), and France in the eastern North Atlantic (Kardas 1965). Late Pleistocene specimens are commonly identified as the extant species, but taxa based on incomplete material, such as the middle Pleistocene *Odobenus mandanoensis*, from Japan (Tomida 1989), suggest as-yet-unknown species. The historical distribution of odobenines and early *Odobenus* indicates widespread temperate and even subtropical inhabitance and capability to disperse through colder polar regions (Kohno et al. 1995b), suggesting that Arctic adaptation is a very recent phenomenon in *Odobenus rosmarus* (Deméré 1994b). Pliocene *Odobenus* fossils from Japan predate those from the North Atlantic, indicating a Pacific origin followed by dispersal through the Arctic (Kohno et al. 1995b).

PALEOBIOLOGY AND FUNCTIONAL ANATOMY

As the fossil record of pinnipeds has steadily improved over recent decades, there has been increased interest in bringing new analytical methods to bear on deciphering the life history of fossil pinnipeds. Perhaps no aspect of their ecology has captured more interest than reconstructing the foraging behavior and diet of fossil taxa. These studies have made use of a variety of techniques, including consideration of qualitative characters of the skull and mandible (Adam & Berta 2002) as well as morphometric analyses of skull shape (Jones & Goswami 2010, Jones et al. 2013, Kienle & Berta 2016) and dentition (Churchill & Clementz 2015, 2016).

Analyses of skull shape and dentition have attempted to diagnose specific foraging behaviors based on morphology and interpret their evolution. Various studies have highlighted the unique dentition associated with filter feeding in *Lobodon* and grip-and-tear feeding in *Hydrurga* (Adam & Berta 2002, Churchill & Clementz 2015), although similar morphologies are unknown in the fossil record. Specializations for durophagy have also been identified within *Monachus* and *Neomonachus* (Churchill & Clementz 2015) as well as the fossil phocid *Hadrokirus* (Amson & de Muizon 2014). Two other styles of feeding often identified include suction and raptorial feeding (Adam & Berta 2002). In suction feeding, food is inhaled into the oral cavity via suction, with little use of teeth. Extreme adaptations for suction feeding can be most readily identified within Odobenidae (Deméré 1994b, Boessenecker & Churchill 2013), with this style of feeding probably evolving before the divergence between dusignathine and odobenine walruses (Adam & Berta 2002). Raptorial feeding consists of biting prey and is considered the ancestral condition in pinnipeds (Adam & Berta 2002). Although morphological features linked to suction feeding have been identified in only a relatively small number of taxa (*Odobenus*, *Erignathus*, *Cystophora*, *Mirounga*, and *Otaria*; Adam & Berta 2002), feeding experiments with live seals show the behavior to be widespread among living taxa that otherwise show no specific anatomical adaptations for this behavior (Klages & Cockcroft 1990, Hocking et al. 2013, Marshall et al. 2014, Marshall et al. 2015). This suggests that the identification of suction versus raptorial feeding in fossil seals may not be possible in many fossil taxa.

Morphometric approaches have been used to interpret foraging ecology, but studies using other approaches have been relatively few. Enamel ultrastructure has been recently used to refute the presence of hypercarnivory in the fossil walrus *Pelagiarctos* (Loch et al. 2016), and if expanded to other fossil pinnipeds, it might provide more clarity on the diet and evolution of dentition in pinnipeds. Detailed analyses of stable isotopes, microwear, and enamel ultrastructure have greatly expanded our knowledge of mammal paleoecology (Newsome et al. 2010, Fahlke et al. 2013, Loch et al. 2016), but use of these methods on fossil pinnipeds has been limited (Burton et al. 2001; Clementz et al. 2003a,b; Fahlke et al. 2013). Future work on the paleoecology of pinnipeds should focus on incorporation of these data into analyses of pinniped paleobiology.

Another frequent topic of interest is the evolution of locomotion. All three extant families of pinnipeds have very different styles of locomotion associated with differences in the anatomy of their limbs and axial skeleton (King 1983a, Giffin 1992, Berta et al. 2015b). While swimming, otariids rely upon pectoral oscillation, using their forelimbs to provide thrust while hind limbs assist with direction and maneuverability. On land, they rely upon all four limbs in movement, similar in mode to the style of locomotion exhibited by terrestrial mammals. In contrast, phocids rely upon pelvic oscillation, with hind limbs providing the majority of the propulsion while forelimbs provide direction. Locomotion on land is accomplished by vertical undulation of the entire body, with limbs contributing little to movement. Odobenids exhibit a hybrid pattern of locomotion, relying upon pelvic oscillation while swimming but possessing a pattern of terrestrial movement more similar to that exhibited by otariids.

The evolution of these distinctive locomotor patterns and their occurrence in different extinct pinniped clades have been frequently debated. For instance, Desmatophocidae have been considered to exhibit pelvic oscillation (Berta & Adam 2001), pectoral oscillation (Bebej 2009), and a style of swimming intermediate between these two modes, similar to walruses (Pierce et al. 2011). The style of swimming exhibited by *Enaliarctos* is similarly debated, with both pectoral-dominated (Berta & Adam 2001, Berta & Ray 1990) and pelvic-dominated (Bebej 2009) swimming suggested by different studies. Further studies of limb and vertebral morphology (e.g., Dewaele et al. 2017a), and extension of these studies to fossil arctoids potentially close to the common ancestor of pinnipeds, can resolve the question of how pinnipeds developed aquatic locomotion.

The evolution of diving abilities is also a topic ripe for future exploration. A novel study that combined body mass data with inferred concentrations of myoglobin (an oxygen-binding molecule in muscle cells) provided insight into the diving capabilities of living and extinct pinnipeds (Mirceta et al. 2013). Reconstruction of the diving capabilities of the stem pinniped *Enaliarctos* suggested that it occupied shallow-water habitats. There was also evidence to support independent increases in diving capacity in phocid and otarioid lineages after their divergence.

Although the above research areas have dominated discussion of fossil pinniped biology, there are many other potentially fruitful areas of inquiry for research. For instance, evolution of sensory systems still remains understudied, although some attention has been paid to changes in olfaction ability (Van Valkenburgh et al. 2011) and the relationship between eye size and deep diving ability (Debey & Pyenson 2012). In addition, although many studies have examined the evolution of breeding systems in extant pinnipeds, few of these studies have incorporated data from the fossil record, with the exception of Cullen et al. (2014), who found evidence for sexual dimorphism in *Enaliarctos*, suggesting a possible early evolution of polygyny in pinnipedimorphs. Studies of body size evolution in pinnipeds (Wyss 1994; Churchill et al. 2014b,c) and Wyss's (1994) suggestion that phocines exhibit juvenilization—reduced body sizes attributed to heterochrony—bear further investigation.

SUMMARY AND CONCLUSIONS

With progress in our understanding of the pinniped fossil record based on new discoveries and analytical methods, our knowledge of pinniped evolution will only increase. Thirty years after pinniped monophyly was first proposed (Wyss 1987), this hypothesis remains the most widely accepted (e.g., Berta & Wyss 1994, Higdon et al. 2007, Nyakatura & Bininda-Emonds 2012). The origin of pinnipeds from arctoid carnivorans is well supported, and the current consensus points toward an ancestry involving either mustelids or ursids (e.g., Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012, Luan et al. 2013). The description of new fossils reveals considerable morphological and ecological diversity among crown pinnipeds driven by environmental (i.e., climate and food supply) as well as biological factors (Valenzuela-Toro et al. 2013, Churchill et al. 2014a). Future work should be directed toward integrative study of pinniped feeding, locomotion, and life history patterns investigated within the context of a rigorous phylogenetic framework.

SUMMARY POINTS

1. Pinnipeds first appear in the fossil record approximately 30.6–23 Ma in the North Pacific.

2. Pinnipeds are derived from arctoid carnivorans and are most closely related to bears (Ursidae) or weasels and raccoons (Musteloidea).

3. The earliest "enaliarctine" pinnipeds were relatively small, shallow-water coastal inhabitants. They show evidence for sexual dimorphism, indicating a harem-based polygynous breeding system.

4. Crown pinnipeds include three living families—Otariidae (fur seals and sea lions), Odobenidae (walruses), and Phocidae (earless seals)—as well as the extinct family Desmatophocidae.

5. Otariids and odobenids are first known from the North Pacific 19 Ma, and phocids appear to have originated in the North Atlantic or Paratethys region 19–14 Ma. Environmental (i.e., climate and food supply) as well as biological (i.e., competition) factors drove the diversification of crown pinnipeds.

6. Crown pinniped lineages evolved diverse cranial morphologies and increased body sizes associated with ecological diversification (e.g., feeding, locomotion, sensory evolution).

FUTURE ISSUES

1. Pinniped phylogeny is in need of comprehensive revision to incorporate new fossil discoveries and both morphologic and molecular data.

2. Additional work is needed to identify the terrestrial carnivoran sister taxon of pinnipeds.

3. Few high-latitude fossil localities exist for pinnipeds, and thus little is known about the recent biogeography of polar pinnipeds.

4. Understanding of the evolution of locomotor patterns among pinnipeds would benefit from further studies of limb and vertebral morphology as well as biomechanical studies.

5. The evolution of body size in pinnipeds has not been well studied and could inform our understanding of the relationship between sexual dimorphism and life history (e.g., sexual selection).

6. There has been limited study of foraging paleoecology in pinnipeds, including quantitative approaches to tooth wear, diet, and stable isotopes.

DISCLOSURE STATEMENT

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