

Evolution and adaptation of marine mammals in the pacific rim

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The Cetacea

The Cetacea are taxonomically and morphologically the most diverse and highly aquatically evolved of all mammals. Their fossil record goes back to the Middle Eocene (*circa* 50 Ma), and undoubtedly earlier, judged by the relatively high state of adaptation of the earliest known whales. The most likely terrestrial ancestors of whales are mesonychids, primitive, omnivorous, hoofed mammals. Recent discoveries by P. Gingerich, J. Thewissen and others of primitive archaeocetes with large, mesonychid-like heads and dentitions, and functional hind limbs reconfirm earlier ideas about a mesonychid origin of cetaceans and the amphibious adaptations of the transitional forms. Fossil cetaceans are relatively abundant and diverse throughout the world, and are now known from every continent, including Antarctica. Because so many cetaceans are cosmopolitan, cetacean research tends to foster international collaborative research.

The odontocetes evolved echolocation to find their food; mysticetes evolved filtering, "bulk feeding" methods. Both groups apparently evolved from archaeocetes, and the monophyly of Cetacea is the most likely hypothesis. Chromosomal and molecular evidence has had an increasingly important role in understanding cetacean relationships, and fossils and classical comparative morphological studies are an important source of information about cetacean phylogeny.

Many recent publications have reported new taxa and range extensions of fossil Cetacea in the Pacific realm. The oldest Pacific fossil cetaceans are Late Eocene archaeocetes from New Zealand (work by R. Fordyce) and archaic whales from Washington, U. S. A. (work by J. Goedert). Early Oligocene deposits contain archaic mysticetes (Llanocetidae) and odontocetes (aff. Agorophiidae). Late Oligocene time was one of increasing cetacean diversity, with the appearance of several families of archaic toothed and baleen-bearing Mysticeti (Mammalodontidae, Aetiocetidae,

Cetotheriidae) and Odontoceti (Agorophiidae, Squalodontidae, Waipatiidae, Kentriodontidae, etc.), and the oldest records of the living sperm whale family Physeteridae. Early and Middle Miocene assemblages are characterized by archaic dolphin-like odontocetes of the families (Squalodontidae, Acrodelphidae, Kentriodontidae, etc.), the early Ziphiidae (beaked whales), and mysticetes of the family Cetotheriidae. By Late Miocene time, most of the living families had appeared; Pontoporiidae, Kogiidae (pygmy sperm whales), Monodontidae (belugas and narwhals), Phocoenidae (porpoises), Delphinidae (oceanic dolphins), Balaenopteridae (rorquals). Latest Miocene and Pliocene time saw the appearance of several rather bizarre cetaceans, most of which belong to living families. These surprises in the fossil record demonstrate morphologic and taxonomic diversity that was previously unsuspected. These are some large gaps in the fossil record; for example, no Miocene record of balaenids, no predecessors of the Pleistocene and Recent gray whales, no record of the origin of the living sperm whale (*Physeter*), and no ancestor of the narwhal.

Fossil Cetacea of Japan are abundant and diverse, and the record extends from Middle or Late Oligocene to Pleistocene, and includes representatives of both the suborders Odontoceti and Mysticeti. No Eocene Cetacea and no Archaeoceti are recorded from Japan. As is typical of the eastern North Pacific and the South Pacific, the Oligocene and Early Miocene assemblages are comprised of archaic and usually extinct families, and the younger assemblages are represented by modern groups comprised of extant genera and families.

The oldest known odontocete has been found by Goedert in Washington State, in rocks just stratigraphically above the Eocene/Oligocene boundary in the lower part of the Lincoln Creek Formation in southwestern Washington. This cetacean has 11 teeth on each side of the palate and mandible, as do protocetid archaeocetes and generalized

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eutherian mammals, and this number corresponds to the dental formula I3, C, P4, M3. As is typical of odontocetes, each premaxilla has a flattened spiracular plate on either side of the narila opening, and a foramen accompanied by three emanating sulci. It has such primitive cranial characters as elongate nasal bones overhanging the posterior part of the narial opening, a flat-topped intertemporal region with a wide exposure of parietal bones, large temporal fossae, and ascending processes of the maxillae spreading posteriorly over the supraorbital processes of the frontals. For its early age, this odontocete has relatively derived cranial morphology, even more derived than many "typical" Late Oligocene odontocetes, including *Agorophius pygmaeus*, and this indicates that the Suborder Odontoceti must have originated at least in Late Eocene time. This is much earlier than previously expected.

The most diverse documented Late Oligocene fossil cetacean fauna from the western North Pacific margin is known from the Late Oligocene Morawan Formation, exposed near Ashoro-cho, Hokkaido, Japan. This assemblage is being studied by M. Kimura, H. Sawamura, H. Furusawa, and L. Barnes, and includes at least 11 species. The Suborder Mysticeti is represented by five primitive toothed mysticetes belonging to the family Aetiocetidae; *Ashorocetus eguchii* Barnes and Kimura, 1995; *Morawanocetus yabuki* Kimura and Barnes, 1995; *Morawanocetus*, new species; *Aetiocetus tomitai* Kimura and Barnes, 1995; and *Aetiocetus polydentatus* Sawamura, 1995. Six species of fossil toothed whales, Suborder Odontoceti, are; a possible new genus and species of large physeteroid; a new genus and species of large Agorophiidae; a new genus and species apparently having affinities with *Sachalinocetus*; a new genus and species of very aberrant Agorophiidae or early platanistoid; a small dolphin-like cetacean of uncertain familial assignment; and a new genus and species of large Kentriodontidae. This fossil cetacean assemblage is nearly comparable to other Oligocene cetacean assemblages from Washington (work by Goedert and Barnes), New Zealand (work by Fordyce) South Carolina (work by A. Sanders and Barnes), and the Caucasus (work by G. Mchedlidze). However, various baleen-bearing mysticetes have been reported from other deposits of the same age, but are notably absent in the Morawan Formation. The odontocetes are more diverse morphologically and taxonomically than are the mysticetes, and their stage of evolution is similar to those from elsewhere of the same age. Despite the fine-grained nature of the sediments in the Morawan Formation, the deposit was probably laid down in a near-shore environment. The

occurrences of desmostylians are consistent with this. This may explain the absence of baleen-bearing mysticetes. The absence of squalodontids is inexplicable, but is consistent with their absence elsewhere in North Pacific.

The Aetiocetidae is small, relict, toothed mysticetes that persisted into Late Oligocene time in the North Pacific after more highly derived baleen-bearing mysticetes had already evolved. No known aetiocetid could be ancestral to baleen-bearing mysticetes, but aetiocetid morphology is in many ways intermediate between archaeocetes and baleen-bearing mysticetes, demonstrating some of the transitional steps in the evolution of baleen-bearing mysticetes. Their discovery indicates that mysticetes evolved from Archaeoceti, and supports theories of the monophyly of cetaceans. The fossil record now indicates considerable diversity in the family, and aetiocetids have been found on both sides of the North Pacific Ocean; on Vancouver Island, British Columbia, Canada; in Oregon and Washington, USA; in Baja California Sur, Mexico; and the Islands of Kyushu and Hokkaido, Japan. Kimura, Sawamura, Furusawa, Goedert, Barnes and A. Cruz-Marin continues to investigate this group. Aetiocetids are unknown outside of the North Pacific, but because many Recent mysticetes are essentially cosmopolitan, aetiocetids might have also been relatively widely dispersed. We suspect that with time their remains might be found around other ocean basins also.

An important and relatively complete baleen-bearing mysticete was collected from the Late Oligocene age Ashiya Group in Kyushu, Japan. The specimen, under study by Y. Okazaki, provides important information about the early evolution of cetotheriids and the transitional steps from the Archaeoceti to Mysticeti. Several features of the specimen, such as the anterior position of the nasal opening and large mandibular foramen, are primitive, but others are derived, such as the wide maxilla, broad supraorbital process of the frontal, occipital shield overhanging the temporal fossae, and the flat articular surfaces on the distal end of the humerus. This animal, therefore, has a mixture of primitive and derived characters, and represents a stage of evolution in mysticetes that has been previously unrecognized. Also from the Ashiya Group, Okazaki has recovered some possible Aetiocetids and some archaic odontocetes. This fauna differs from that of Ashoro by including various types of baleen-bearing mysticetes.

The Late Oligocene fauna (circa 25-28 Ma) from the Olympic Peninsula in Washington, U.S.A., being studied principally by Goedert, Barnes, and B. Crowley, is also a

more balanced fauna like that of Kyushu. The National Geographic Society has supported some of this work. Included are diverse aetiocetids (work by Barnes, Kimura, Furusawa, and Sawamura), baleen-bearing mysticetes, and numerous archaic odontocetes.

A partial skeleton of a very primitive, relatively large, baleen-bearing mysticete whale from the area, being studied by Crowley and Barnes, is the first report of such a primitive mysticete from the eastern North Pacific Ocean margin. It has an elongate and narrow intertemporal region of the cranium with wide exposures of the parietals and frontal, and a low sagittal crest. The narial opening is located relatively far anteriorly on the rostrum. These primitive cranial characters are shared with the Archeoceti. The palate is smooth, except for nutrient grooves which indicate that baleen was present. This whale would traditionally be classified as a primitive member of the Family Cetotheriidae, and affiliated with the genus *Mauicetus* Benham, 1939. The holotype of the type species of *Mauicetus*, *M. parki* (Benham, 1937) (a very incomplete braincase), has a shorter intertemporal region, so the whale from Washington is more primitive than *Mauicetus*. The only other reported mysticete with similarly primitive characters is the undescribed taxon from the Late Oligocene Ashiya Group in Kyushu, Japan, that was reported by Okazaki (1995).

Earliest Miocene (circa 23-24 Ma) North Pacific cetaceans are best represented by the assemblage from the Pyramid Hill Sand near Bakersfield, California, where several species of Eurhinodelphidae and Platanistoidea are known. These were first published by A.R. Kellogg and L.E. Wilson, and are now undergoing re-study by Barnes. Wildon's identification of Cetotheriidae in the fauna is incorrect. No mysticetes are known in the assemblage, it is composed totally of long-snouted "dolphins".

Middle Miocene (circa 13-15 Ma) cetaceans from the younger Sharktooth Hill Bonebed in the same area, originally studied by Kellogg, are the standard of comparison for animals of this age in the Pacific realm. The cetacean assemblage is comprised of two sperm whales, a platanistoid, several kentriodontids, a delphinid, and perhaps eight species of baleen-bearing mysticetes. Under study by McLeod, Barnes, and Mitchell, this is the most taxonomically "balanced" Miocene assemblage in the Pacific realm, but it lacks ziphiids and squalodontids.

In Japan, there are quite a few Middle Miocene cetaceans, and an important assemblage has been recognized from Mizunami by Okazaki, it includes a

primitive sperm whale and several species of kentriodontid dolphins (the reference to *Eurhinodelphins* actually is another family).

The Middle Miocene sperm whale from Shiga-mura, *Scaldicetus shigensis* Hirota and Barnes, 1995, is the most complete fossil physeterid skeleton found in Japan. Its abruptly tapered rostrum, deep supracranial basin, and high occipital crest are typical of physeterids, but it is relatively primitive, having a relatively long, slender rostrum, large zygomatic arches, large tympanic bullae, prominent occipital condyles, few teeth, and a sloping occipital shield that is deeply emarginated laterally by large temporal fossae. The probable mandibular tooth count is 12, only one more than the primitive eutherian mammalian dentition. Despite its abundant primitive characters, *Scaldicetus shigensis* has very asymmetrical external nares, comparable to the living sperm whale, *Physeter catodon*, and is in this way more derived than most of the contemporaneous fossil physeterids. At a time when other sperm whales were more highly evolved, it was a relict from in Middle Miocene time, and provides an indication of a primitive stage of sperm whale evolution heretofore undocumented. Large teeth with crenulate enamel on conical crowns, present in both the palate and mandible, are consistent with the genus *Scaldicetus* du Bus, 1867, a genus originally based on fossils discovered in the Antwerp Basin, Belgium.

From Hokkaido, F. Egashira is studying a typical Middle Miocene Cetotheriid mysticete from Hokkaido, and H. Ichishima has recently named the dolphin *Kentriodon hobetsu*. Discovery of more Middle Miocene cetaceans from Hokkaido would be very important. Fossil dolphins belonging to the extinct family Kentriodontidae are small to medium-sized toothed cetaceans, which probably include the ancestors of some living species. Kentriodontids of Late Oligocene to Late Miocene age are known in various parts of the world. Among kentriodontids, species in the subfamily Kentriodontinae are the most ubiquitous and generalized. These are now known from latest Oligocene to earliest Miocene strata in New Zealand and Patagonia, and Middle Miocene deposits in Maryland, Virginia, California, and Japan. The diversity, morphologies, and distributions of Miocene species of Kentriodontinae seem to parallel those of the living species of mostly pelagic delphinids in the Subfamily Delphininae, and the fossil group may have been an ecological counterpart of delphinids. Kentriodontines were probably wide-ranging neritic to pelagic animals that ate small fish and other nectonic organisms; they were probably active echolocators, and might have formed large

schools. They are relatively common as fossils and, therefore, are potentially useful for intercontinental correlations of marine deposits.

In coastal Peru is an important sequence of strata from late Middle Miocene through Pliocene age, including the Pisco Formation. de Muizon studied these as part of his doctoral work, and has recognized several phocoenids (*Piscolithax*, *Lomacetus*), kentriodontids (*Belonodelphis*, *Incacetus*, *Atocetus*), and the first short-snouted pontoporiids. Also in the strata are strange pygmy sperm whales and the bizarre, tusked dophin, *Odobenocetops peruvianus*, which might be a highly modified monodontid. Pilleri has reported on the mysticetes from here, recognizing cetotheriids and balaenopterids.

The latest Miocene age (circa 9 to 6 Ma) Lower Member of the Almejas Formation on Isla de Cedros, off the west coast of Baja California, México, has yielded an important assemblage of cetaceans. Three recent expeditions by Mexican and US geologists and paleontologists in 1992, 1993, and 1994 to Isla de Cedros added many important new taxa to the fauna, and this is now the most diverse fossil marine vertebrate assemblages of its age known from the North Pacific realm. It includes a mixture of nearshore and offshore animals. Some are related to species that still live in the same area; two or three species of Balaenopteridae, a large sperm whale (Physeteridae), a pygmy sperm whale (*Praekogia cedrosensis* Barnes, 1973), and three species of phocoenidae. The closest living relatives of others, such as a pontoporiid dolphin (*Parapontoporia pacifica* Barnes, 1984), and beluga-like monodontid (*Denebola brachycephala* Barnes, 1984), now live in different ocean basins and/or different latitudes. A third component of the assemblage includes animals with no living relatives; for example, the cetotheriid mysticetes *Herpetocetus* and *Nannocetus*, and an albireonid dolphin (*Albireo whistleri* Barnes, 1984).

The Almejas Formation was probably deposited in a relatively calm, nearshore environment on the protected side of the ancestral Isla de Cedros. The Almejas Formation and correlative parts of the Pisco Formation in Peru contain apparently antitropical (=bitemperate) taxon pairs of marine vertebrates, analogous to some living northern and southern hemisphere species.

The Family Phocoenidae, whose living members include the harbor porpoises and other related species, has a primarily Pacific fossil record, and probably originated in the North Pacific. *Piscolithax tedfordi* Barnes, 1984, from Isla de Cedros, is the most primitive known phocoenid. Originally the species was known only by the cranium,

periotic, tympanic bulla, and mandible, collected in 1964, but in 1992 much of the remainder of the holotype skeleton was found and collected. The additional data supplied by this new material indicates that the porpoise was approximately 2.5m long in life, and had a relatively large skull for its body size. This is different from the small, paedomorphic skulls of all modern phocoenids and some fossil species. *Piscolithax tedfordi* had a long rostrum of moderate width, numerous large teeth elongate vertebral centra, and a long flipper. Its body shape in life might have resembled the living bottlenose dolphin, *Tursiops truncatus*.

The family Pontoporiidae includes long-snouted, relatively primitive dolphins, represented by Recent *Pontoporia blainvillei* Gervais and d'Orbigny, of the coastal southwest Atlantic, various Late Miocene and Pliocene fossil genera and species, and possibly by Recent freshwater *Lipotes vexillifer* Miller, of China. Pontoporiids in the extinct genus *Parapontoporia* Barnes, 1984, are known from Isca de Cedros, California, and Japan (M. Oishi) in Late Miocene and Pliocene (8 - 2 Ma) deposits. They are the most abundant fossil cetacean in some deposits on the west coast of North America. Like the living *P. blainvillei*, these dolphins apparently lived in near shore shallow water over sandy substrates. The genus *Parapontoporia* was first proposed for a fossil from Baja California, and three species are now recognized. Other related fossils should be expected in Late Miocene and Pliocene deposits around the Pacific margin. For some reason pontoporiids became extinct in the North Pacific only about 2 million years ago, although suitable habitat appears to continue to exist for them.

Assemblages of Early Pliocene *Mysticeti* (Cetacea) from the Sendai-Iwate area and Choshi area in eastern Japan were studied by Y. Hasegawa and Oishi. The early Early Pliocene Tatsunokuchi and Yushima Formations of the Sendai-Iwate area contain Cetotheriids assigned to *Herpetocetus* and some extinct rorquals (Family Balaenopteridae) assigned to *Burtinopsis* and other genera. The late Early Pliocene Na-arai Formation of the Choshi area has yielded more than three hundred mysticete ear bones which fall into seven morphotypes. Assemblages from the two areas differ greatly in taxonomic composition. Archaic mysticetes are dominant in the Sendai-Iwate area, while modern mysticetes are dominant and diverse in the Choshi area. Oishi and Hasegawa concluded that the diversity of the Early Pliocene mysticetes in the western North Pacific is comparable to that of the Recent time.

Important latest Miocene to early Pliocene age odontocetes

have recently been found in Hokkaido, Japan. Under study by Kimura and students, with collaboration from Barnes, a preliminary assessment of these fossils indicates that there are two and possibly three species of phocoenids and a very modern-appearing depphinapterine monodontid (beluga). The beluga appears to be truly related to the living beluga, (*Delphinapterus leucas*) and not to be related to unusual, broad-headed monodontids of the genus *Denebola* that have been reported from similar age rocks in North America. The discovery of this early true beluga in Hokkaido attests to the antiquity of the Subfamily Delphinapterinae and to a previously southerly distribution of this now exclusively arctic group of dolphins. The phocoenids have a symmetrical cranial vertices, like Delphinidae, and they will provide important information about the question of relationships with Delphinidae and the origin of Phocoenidae.

Two species of primitive Cetotheriidae, both represented by mandibles, have been found in the Early Pliocene part of the Horokaosirarika Formation near Numata-cho in Hokkaido, Japan. Of these, the smaller one is a species of *Nannocetus* Kellogg, 1929, the larger one is a species of *Herpetocetus* Van Beneden, 1872. Both species share with previously reported specimens of *Herpetocetus* a modified posterior part of the dentary with a narrow, anteroposteriorly aligned condyle, and posteriorly prolonged angular process. This unusual mandibular morphology is related to the modifications of the glenoid fossa in *Herpetocetus* and *Nannocetus*. Among the last members of the Family Cetotheriidae, they are under study by Furusawa, Egashira, and Barnes.

From the same formation, a very important primitive phocoenid, whose collection was supervised by M. Kimura, is under study by H. Ichishima. The species is more derived than *Piscolithax tedfordi*, and indicates considerable diversity in the Phocoenidae and the early presence of the family in the western North Pacific.

Various discoveries of Pleistocene cetaceans in California, Oregon, and Japan include balaenids, eschrichtiids, balaenopterids, and delphinids. The record is not as diverse as some of the earlier fossil assemblages, nor as the living fauna. More diversity should be expected in the fossil record, and some undescribed species are probably present. A review of the Pleistocene Pacific cetaceans is needed.

The Pinnipeds

The pinnipeds are marine arctoid carnivorans, the phocoids and the otarioids. These two groups appear to have had a long-separate evolutionary history, the phocoids primarily in the Atlantic and the otarioids primarily in the

Pacific. Both groups undoubtedly evolved from different groups of terrestrial arctoid carnivorans, although the origin of neither is known for certain. Hunt and Barnes have recently indicated a possible relationship between amphicyonodontines and otarioids based on the presence of an enlarged basioccipital venous sinus in both groups.

The fossil pinniped record of the North Pacific Ocean includes both Phocidae and Otariidae (*sensu lato*), extends from the Late Pleistocene, is taxonomically diverse, and is constantly becoming more complete owing to additional important discoveries. The earliest and most diverse fossil pinnipeds in the North Pacific are otariids, the first phocids not appearing until the latest Pliocene (Phocidae reported by Kellogg and Bertin in Western North American Miocene deposits are Otariidae).

The theoretical center of otariid pinniped evolutionary history is apparently in the North Pacific. Fossils from the subfamilies Enaliarctinae, Imagotariinae, Odobeninae, and Otariinae on both sides of the North Pacific indicate that pinniped evolutionary patterns were basin-wide phenomena, and that a more complete record undoubtedly will reveal numerous trans-Pacific distributions. These would be expected considering the distributions of living species. The absence of Phocidae from pre-Pliocene deposits are consistent with theories that the family primarily evolved outside the North Pacific.

The earliest otarioids are the North Pacific Enaliarctinae known by the genera *Enaliarctos*, *Pteronarctos*, *Pinnarctidion*, and *Pacificotaria*, and they range from latest Oligocene to early Middle Miocene. They were small, generalized, probably piscivorous, and retained remnants of the fissiped carnassial dentition. They appear to be the ancestral otarioid stock from which other groups evolved.

The sea lions and fur seals, Otariinae, are the least changed of all later otarioids. They range from Latest Miocene *Pithanotaria starri* and are relatively diverse now. Fossils are species of *Thalassoleon* from Baja California, California and Japan. Like the enaliarctines, they retained a generalized diet, but evolved homodont dentition.

Imagotariines probably arose from some species of Early Miocene enaliarctines, became diverse in Middle and Late Miocene time, and are only known from the North Pacific realm. Although they might include the ancestors of true walruses of the subfamily Odobeninae, no known imagotariines appear to have been adapted for mollusk feeding as are the highly evolved modern walruses. Instead, imagotariines appear to have retained a primitive piscivorous diet, as did the fur seals and sea lion of the

Otariinae (sea lions and fur seals).

Prototaria Takeyama and Ozawa, 1984, and *Neotherium* Kellogg, 1931, known from Middle Miocene deposits bordering the North Pacific Ocean, are small, primitive pinnipeds in the subfamily Imagotariinae and probably evolved from enaliartines. They have a small supraorbital process of the frontal or have lost it entirely, a three-rooted first molar, small paroccipital process, and imagotariine ear morphology. Their unique derived characters include extreme intertemporal constriction and highly modified cheek teeth, the premolars having become molarized by the addition of protocones and lingual cingula.

Prototaria contains two species, *P. primigena* Takeyama and Ozawa, 1984, and *P. planicephala* Kohno, 1994, both of early Middle Miocene age from Japan. *Prototaria* has a few derived characters, including a large antorbital process, narrow intertemporal region, and large orbit, but its primitive characters apparently were inherited from enaliartine ancestors, *Proneotherium repenningi* Barnes, 1995, related to *N. mirum*, is from the early Middle Miocene Astoria Formation in coastal Oregon. It shares some derived characters with *Prototaria* and shares many other important derived characters with *N. mirum*. *Neotherium mirum* Kellogg, 1931, of Middle Miocene age from California, is related to *Prototaria*, but differs by having an elongate skull, very slender zygomatic arch, ventrally exposed median lacerate foramen, and smaller but more molarized premolars.

The Dusignathinae are large "pseudo-walruses" that had large canines, and in some taxa, tusks, in both the upper and lower jaws. The genera included are *Dusignathus* and *Gomphotaria*, and these have only been found in California. Dusignathines appear to have evolved from the Imagotariinae.

The Odobeninae, or true walruses, are benthic suction feeders. They appear to have evolved either from the Imagotariinae or the Dusignathinae. The earliest true odobenine is *Protodobenus japonicus* Horikawa, 1995, of Early Pliocene age from Japan. The strange walrus-like *Aivukus cedrosensis* (circa 8 Ma) from Mexico appears to be more closely related to Dusignathinae than to Odobeninae. The focus of walrus evolution now appears to be in the North Pacific, not the Atlantic. Pleistocene members of the genus *Odobenus* are known in temperate latitudes in both the North Atlantic and the North Pacific, and the Recent Arctic distribution is a relict.

The extinct Allodesminae are large, relatively highly evolved pinnipeds that became abundant and diverse in

Middle Miocene time and were restricted to the North Pacific Ocean. Their record extends from early Middle Miocene through Late Miocene, with records from California, Oregon, Washington, Baja California, and Japan. Allodesminae are characterized by extreme sexual dimorphism, a large orbit, retracted orbital margin of the zygomatic arch, a deeply mortised jugal-squamosal junction, wide palate, bulbous cheek tooth crowns, nearly flat tympanic bulla with wrinkled ventral surface, a large tympanohyal fossa, large ear ossicles, and deep mandible.

Eleven allodesmine species are known (eight of which are named), in at least four genera, and most belong to the typical genus *Allodesmus* Kellogg, 1922. The earliest and most generalized allodesmine known is an unnamed animal from the early Middle Miocene (circa 16 Ma) Astoria Formation in coastal Oregon. *Atopotarus courseni* Downs, 1956, is the most primitive named allodesmine and has slender limbs and two-rooted cheek teeth. *Brachyallodesmus packardi* (Barnes, 1972) is primitive basicranially but has a wide skull and flat palate. *Megagomphos sinanoensis* (Nagao, 1941) is a large Middle Miocene species from Japan. Species in the genus *Allodesmus* have elongate heads, large eyes, and a pre-narial shelf. Middle Miocene Japanese species include *A. sadoensis* Hirota, 1995, and the giant *A. megallos* Hirota, 1955. The North American Middle Miocene species are *A. kernesis* Kellogg, 1922, *A. gracilis* Barnes, 1995, and *A. kelloggi* Mitchell, 1966. The last known records are from Late Miocene rocks (circa 10 Ma) in California and Washington.

Allodesminae were apparently a rapidly evolving group, and most appear to have been adapted to roles later filled by otariine, dusignathine, and imagotariine otariids, and the Phocidae (true seals). They become extinct in Late Miocene time and left no living descendants. Although some of their characters evolved convergently with various living species of the pinniped family Phocidae, Allodesminae are an otariid group and not part of the evolutionary history of Phocidae.

The true seals of the family Phocidae appear in the North Pacific as Late Pliocene Phocinae, related to *Phoca*, the harbor seal. Fossils of the elephant seal, *Mirounga* sp., have been found in Late Pleistocene deposits of California. These fossil phocids seem to be antecedents of the living North Pacific Phocidae, and added diversity to the North Pacific pinniped fauna, which had become restricted in diversity after the Pliocene decline of the Imagotariinae and Dusignathinae.

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