

A NEW FOSSIL PINNIPED (MAMMALIA: OTARIIDAE) FROM THE MIDDLE MIOCENE SHARKTOOTH HILL BONEBED, CALIFORNIA

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ABSTRACT. A large, derived extinct otariid, *Pelagiartcos thomasi*, new genus and species, is the third fossil pinniped species to be named in the Middle Miocene age Sharktooth Hill Local Fauna from Kern County, California, U.S.A. The two previously named species in this fossil assemblage are the common, large, and highly derived allodesmine, *Allodesmus kernensis* Kellogg, 1922, and the less common, small, primitive imagotariine, *Neotherium mirum* Kellogg, 1931. Remains of these and other fossil vertebrates occur in a vertically restricted and laterally extensive stratum, the Sharktooth Hill Bonebed. *Pelagiartcos thomasi*, an extremely rare species in this bonebed, is apparently a member of the subfamily Imagotariinae, and has a primitive dentition but relatively derived mandibular morphology. Its ankylosed mandibular symphysis, a derived character, is convergent with the condition in living walruses. Its cheek tooth morphology is derivable from that of the earlier and more primitive species in the subfamily Enaliartinae. Its tooth and mandibular morphology, large body size, and extreme rarity in the fossil assemblage suggest that it may have been a predator of large marine vertebrates.

INTRODUCTION

The Middle Miocene age Sharktooth Hill Bonebed, a fantastically rich fossil deposit in the upper part of the Round Mountain Silt in Kern County, California, has yielded the most diverse and best studied Tertiary fossil marine vertebrate assemblage yet known from anywhere within the Pacific realm (Mitchell, 1966; Barnes, 1976; Barnes and Mitchell, 1984). This fossil assemblage, called the Sharktooth Hill Local Fauna (Wood et al., 1941), is comprised of more than one hundred species of sharks, bony fish, turtles, birds and mammals, including the rare fossils of some contemporaneous terrestrial mammals, reptiles, and birds that originated from the adjacent Miocene land mass. The Sharktooth Hill Bonebed is a single, relatively thin, but laterally widespread horizon. It has been correlated with the Barstovian North American Land Mammal Age, and with the "Temblor" provisional provincial mega-invertebrate stage of Addicott (1972), and is, therefore, between approximately 13 and 15 million years old (Wood et al., 1941; Mitchell, 1966; Barnes,

1976; Barnes and Mitchell, 1984:4). Two extinct otariid pinnipeds have previously been recognized from this bonebed: a numerically abundant, large, and highly derived allodesmine—*Allodesmus kernensis* Kellogg, 1922; and a less common, small, and primitive imagotariine—*Neotherium mirum* Kellogg, 1931.

Allodesmus kernensis was originally described on the basis of a partial mandible (the holotype) and some referred postcranial bones (Kellogg, 1922); Kellogg later (1931) assigned some additional bones to the species. After collecting a nearly complete skeleton from the same bonebed, Mitchell (1966) provided a definitive analysis of the osteology of *Allodesmus* Kellogg, 1922, and named a new species, *Allodesmus kelloggi*. I subsequently (Barnes, 1972) synonymized *A. kelloggi* Mitchell, 1966, with *A. kernensis*, and analyzed variation in what, by then, had become a significantly large sample of the species from the bonebed.

The basis for Kellogg's (1931) recognition of another pinniped, *Neotherium mirum*, in the same deposit was some isolated foot bones (the "type material") and other referred postcranial elements. A few other isolated postcranial bones have been subsequently assigned to this species by Mitchell (1961), Mitchell and Tedford (1973), and Repenning and Tedford (1977), and *N. mirum* has become regarded as a primitive relative of *Imagotaria downsi* Mitchell, 1968 (see Repenning and Tedford, 1977). In fact, *Neotherium mirum* is the smallest and possibly the most primitive imagotariine yet known. I have now identified many more bones of this species in museum collections. The available sample now includes jaws and cranial parts, showing sexual dimorphism, and these conform with the above conclusions about the relationships of the species (Barnes, unpublished data).

In addition to the two previously named species (including the synonymized *Allodesmus kelloggi*), Mitchell (1966:29)

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recognized two additional, unnamed pinnipeds from the Sharktooth Hill Bonebed. Represented only by postcranial bones, Mitchell listed them in the faunal assemblage as "Otariidae, n. genus" and "Odobenidae, undet." I have also (Barnes, 1972:57-60, figs. 23, 24) described and illustrated two partial mandibles representing two possibly unnamed species in the same assemblage, referring to them as "Desmatophocine B" and "Desmatophocine C." The first of these is the larger and is approximately the same size as *Allodesmus kernensis*. The second is smaller and more primitive. In light of his re-definition (Mitchell, 1968) of the subfamilies Desmatophocinae and Allodesminae, Mitchell (1975:15-17) subsequently suggested that both of the species that I called desmatophocines may actually belong in the subfamily Allodesminae. It is impossible at this time to correlate the two unnamed taxa that were recognized by Mitchell (1966) on the basis of limb bones with those that I later (1972) recognized on the basis of mandibles, and more fossil material must be obtained and studied to clarify the identities of these enigmatic taxa.

The purpose of the present paper is to describe and name another species of otariid pinniped from the Sharktooth Hill Bonebed. It is the fifth one now known from this deposit on the basis of separate mandibular morphotypes, and it is the third to be named. The species is based on a partial mandible and several teeth and, therefore, can be compared directly with, and readily differentiated from, available material of its contemporaries: *Allodesmus kernensis*, *Neotherium mirum*, "Desmatophocine B," and "Desmatophocine C."

METHODS AND MATERIALS

All of the specimens described here are from the Sharktooth Hill Bonebed, and are housed in the Natural History Museum of Los Angeles County, Los Angeles, California (LACM), or the University of California Museum of Paleontology, Berkeley, California (UCMP). Precise locality data for these specimens may be obtained from these institutions upon request by qualified investigators.

Anatomical terminology used in this study follows that of Miller, Christensen, and Evans (1964) and Barnes (1972). Homologies and nomenclature of the cheek tooth structures are those commonly employed for mammals (e.g., Hershkovitz, 1971) and as applied to otariids (Mitchell and Tedford, 1973; Barnes, 1979). The measurements of the mandible were made following the methods explained by Barnes (1972:4-5, fig. 2). Measurements of the cheek tooth crowns are the overall maximum length (anteroposteriorly) and the overall crown height, from the enamel margin to the apex of the main cusp. Specimens in Figures 2 and 4 were coated for photography with a sublimate of ammonium chloride. All artwork is by the author. My restoration of the mandible (Fig. 3) is a composite, and is based on both sides of the holotype. Images of some of the referred premolars were reversed in order to yield the restored partial dentition.

The authority I selected for Recent species is the book by Ridgway and Harrison (eds., 1981), and that reference may be consulted for distributions and nomenclature of living

taxa. In cases where a family-group name is not used at the same rank and/or in the same context as originally described, the original author is listed in parentheses.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Infraorder Arctoidea Flower, 1869

Parvorder Ursida Tedford, 1976

Family Otariidae Gill, 1866

INCLUDED SUBFAMILIES. Enaliarctinae Mitchell and Tedford, 1973; Otariinae (Gill, 1866); Desmatophocinae (Hay, 1930); Allodesminae (Kellogg, 1931); Imagotariinae Mitchell, 1968; Dusignathinae Mitchell, 1968; Odobeninae (Allen, 1880).

?Subfamily Imagotariinae Mitchell, 1968

INCLUDED GENERA. *Neotherium* Kellogg, 1931; *Imagotaria* Mitchell, 1968; *Pontolis* True, 1906; and apparently *Pelagiartcos*, new genus.

Pelagiartcos, new genus

DIAGNOSIS OF GENUS. A genus of Otariidae apparently belonging to the subfamily Imagotariinae; having relatively large body size (estimated to be ca. 2.5 to 3 m long for males); with body of dentary thick, but deep dorsoventrally (as in *Allodesmus* Kellogg, 1922); anterior end of mandible extremely vascularized; prominent genial tuberosity on each dentary lateral to ventral extremity of mandibular symphysis, and continuous with anteroposterior crest on ventrolateral margin of dentary; mandibular symphysis ankylosed, elongate and sloping posteroventrally, with trapezium-shaped articular surface; I₁ slightly posteromedial to I₂; lower canine large and procumbent, with longitudinal sulcus on both lateral and medial sides of root, resulting in bilobed cross section; cheek teeth with prominent, conical cusps, arranged anteroposteriorly, and with cuspidate lingual cingulae; two roots each on P₂₋₃; tooth enamel thick and slightly crenulated; taxon differing from both *Neotherium* Kellogg, 1931, and *Imagotaria* Mitchell, 1968, by having ankylosed mandibular symphysis; differing further from *Neotherium* by being much larger and by having cheek tooth crowns bearing more prominent lingual cingulae with numerous small cusps, roots of two-rooted cheek teeth closer together; and differing further from *Imagotaria* by having cheek teeth with larger and more irregularly sized and spaced cusps on the lingual cingulae, a more prominent labial cingulum, one secondary cusp (metacone on uppers, metaconid on lowers) on the posterior cristae of the crowns, and more widely spread roots on lower cheek teeth posterior to P₁.

TYPE SPECIES. *Pelagiartcos thomasi*, new species.

ETYMOLOGY. The generic name, *Pelagiartcos*, is derived from Greek (*pelagios*, of the sea; plus *arktos*, bear), in reference to the relatively primitive, somewhat arctoid form of the cheek tooth crowns of this marine carnivore. The root, "arctos," also appears commonly in otariid nomenclature and reflects the bear-like appearance of some otariids and/or the reputed phyletic relationships between them and the terrestrial arctoid carnivores, especially the bears, family Ursidae.

Pelagiartcos thomasi, new species

Figures 1-3

DIAGNOSIS OF SPECIES. The same as for the genus.

HOLOTYPE. LACM 121501, anterior ends of right and left dentaries, joined at the mandibular symphysis, with roots of right I_1 , both canines, and right P_3 ; collected by Howell W. Thomas ca. March 1980.

TYPE LOCALITY. LACM locality 3162, Sharktooth Hill Bonebed, Round Mountain Silt, Sharktooth Hill area, Kern River district, Kern County, California.

REFERRED SPECIMENS. LACM 123415, right P^3 or P^4 from LACM locality 3162, collected by Howell W. Thomas in 1979; LACM 38812, right P_1 from LACM locality 1557, collected by Wilma Maughan in 1973; UCMP 93058, left P_2 from UCMP locality V-71013, collected by Robert Machris; LACM 72856, cast of right P_3 or P_4 , original specimen from LACM locality 4116, collected by Gregory Art in February 1972 and still owned by the collector; LACM 122310, left P_3 or P_4 from LACM locality 4874, collected by Stephen F. Black in 1980; all from the Sharktooth Hill Bonebed in the Kern River district, Kern County, California.

ETYMOLOGY. The species name, *thomasi*, is in honor of the discoverer of the holotype and of one of the referred specimens, Howell W. Thomas, Senior Museum Technician, LACM. Mr. Thomas has collected extensively in the Sharktooth Hill Bonebed, and has placed many valuable and unique specimens in museums.

DESCRIPTION. Mandible. The holotype, LACM 121501, consists of the anterior extremities of the right and left dentaries, ankylosed at the symphysis (Fig. 1). The right dentary is broken vertically between the alveoli for P_3 and P_4 and the left is broken obliquely just posterior to the canine. This breakage occurred after death, but prior to final deposition. The body of the dentary is deep dorsoventrally, as in the contemporaneous allodesmine otariid, *Allodesmus kernensis*, but it is much thicker transversely, and is thickest just ventral to its mid-portion. The bone surface of the mandible is very rugose and pitted by numerous foramina and sulci, especially near the symphysis and between the canines (Fig. 1d). Lateral to the most ventral part of the symphysis is a prominent, rugose genial tuberosity. This tuberosity is continuous with a rounded crest that extends posteriorly along the ventrolateral margin of the dentary.

There are three large mental foramina on the lateral side of the right dentary, but only one large one in the same location on the left. This contrasts with the condition in *Allodesmus kernensis*, in which several smaller mental fo-

ramina are scattered on the lateral surface of each dentary. One large anterior mental foramen is located ventral to the incisor alveoli, on the anterior surface of each dentary (Fig. 1a). This contrasts with the usual presence of two smaller anterior mental foramina in the same location in *Allodesmus kernensis*. Ventral to this foramen in *Pelagiartcos thomasi*, the bone at the symphysis projects anteriorly, and from that point, the anterior margin of the symphysis then slopes uniformly posteroventrally. A sagittal section through the articular surface of the symphysis itself is trapezium-shaped in cross section and the perimeter of the symphysis is variably marked by irregular pits and raised crests in the bone. There are two large, deep, median pits in its posterior side dorsal to the genial tuberosity (Fig. 1b).

The two lower incisors are not aligned transversely as in the generalized mammalian condition, but they are compressed between the large canines so that the I_2 is slightly anterolateral to I_1 . This condition is not as derived as in *Allodesmus kernensis*, however, in which more extreme constriction has caused these two teeth to be aligned almost anteroposteriorly. *Pelagiartcos thomasi* also differs further from *A. kernensis* in that the I_1 is relatively larger in diameter and closer to the anterior margin of the dentary. The incisors are sufficiently crowded, however, to cause their shared alveolar walls to be incomplete. The medial wall of the I_1 alveolus thus thins to less than 1 mm, but the anterior wall is thicker. The anterolateral wall of the alveolus did not form, and the two incisor alveoli are therefore almost entirely confluent. The I_1 alveolus is approximately 25 mm deep and oval in cross section. The proximal end of the root of the broken right I_1 is still firmly lodged in its alveolus. The alveolus for I_2 is larger in diameter than that for I_1 , more than 30 mm deep and more nearly circular in cross section than that of I_1 . Its posterolateral wall is incomplete and this alveolus is confluent with the canine alveolus. The canine root is extremely procumbent and the symphysis, correspondingly, forms an angle of approximately 45 degrees relative to the top of the cheek tooth row (see method of measurement in Barnes, 1972:fig. 2c). The alveolus of the canine is bilobed anteroposteriorly and has a very thin lateral wall.

The preserved anterior part of the cheek tooth row is straight and extends posterolaterally directly in line behind the canine alveolus (Fig. 1d). The lingual walls of the cheek tooth alveoli are higher than the labial walls, the opposite of the condition in *Allodesmus kernensis*, and the alveolar rims are thick and bear numerous small foramina and shallow grooves that mark the previous courses of many small blood vessels. A bony interalveolar septum separates the alveolus of P_1 from that of the canine. The P_1 alveolus is procumbent, approximately 17 mm deep, and is separated from the anterior alveolus of P_2 by a well-formed interalveolar septum. The presence of a small, vertical crest on the labial side of the P_1 indicates that the root of the tooth was bilobed in cross section near the gum line. The P_2 has two alveoli that are separated by an incompletely formed transverse septum (Fig. 1d). The alveolus for the anterior root of P_2 is 14 mm deep and 9.5 mm in transverse diameter. It is slightly compressed anteroposteriorly and, at its widest dimension, is oriented obliquely

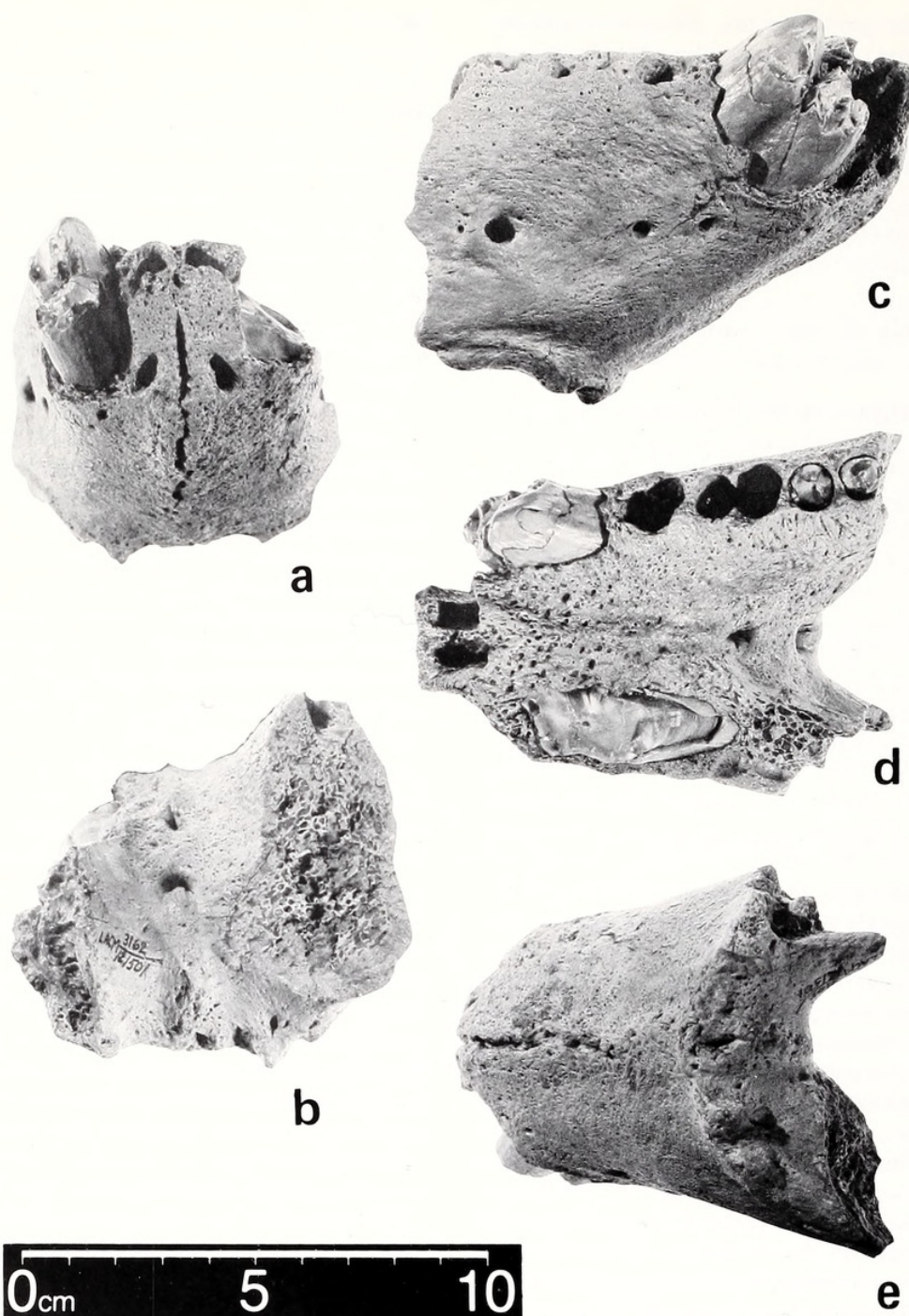


Figure 1. *Pelagiartcos thomasi*, new genus and species, holotype, partial mandible, LACM 121501, LACM locality 3162; **a**, anterior view; **b**, posterior view; **c**, right lateral view; **d**, dorsal or occlusal view; **e**, ventral view.

to the long axis of the dentary. The alveolus for the posterior root of P_2 is deeper (17 mm) and wider (12 mm) than that for the anterior root, and its widest dimension is canted at yet a more oblique angle to the axis of the dentary than the anterior root.

Only a very thin interalveolar septum separates the posterior alveolus of the P_2 from the anterior one for P_3 . Like the P_2 , the P_3 also had two roots, but it has two distinct alveoli, separated, in this case, by a complete transverse septum (Fig. 1d). The two roots of P_3 are more divergent at their

extremities than those of P_2 . The alveoli of P_3 are more nearly cylindrical, smaller, and more nearly equal in size than are those of P_2 . The two roots of the broken right P_3 remain lodged in their alveoli. Neither root has an open pulp cavity, further confirming that this specimen is from an adult individual.

Measurements of the mandible are: maximum length of symphysis—96.8 mm; maximum breadth of symphysis—48.6 mm; depth of ramus at P_3 —64.9 mm; anteroposterior diameters of alveoli, I_1 —13.6 mm, I_2 —13 mm, C—35 mm

(estimated), P_1 —14 mm, P_2 —18.5 mm, P_3 —21 mm (estimated) (the latter two are measured across both alveoli); C— P_1 septum—3.5 mm; P_1 — P_2 septum—2.3 mm; P_2 — P_3 septum—1 mm.

Canine. Parts of both canines are in place in the mandible. Breakage reveals that the pulp cavities of both teeth are nearly closed, with only a tiny vacuity remaining, again indicative of the advanced age of the individual. The right canine was apparently broken off near the gum line in life, and became worn down during subsequent use. This is suggested by the condition of the apex of this broken tooth, which is rounded and polished. The surface of the mandible is otherwise unabraded, so the canine undoubtedly was not affected by significant postmortem geologic abrasion, but was worn during life. The left canine shows fresh, angular breakage far down in the alveolus (Fig. 1d). This apparently occurred postmortem, but prior to fossilization. The left canine root has a thin (ca. 1 to 2 mm-thick) outer layer of cementum over the inner, sequential cones of cementum (for tooth structure see, e.g., Scheffer and Kraus, 1964:308, pl. 17). The canine of *P. thomasi* differs from that of *Allodesmus kernensis* by being relatively larger and by having a root that is bilobed in cross section, with a groove on both the lingual and labial sides. Of these, the labial groove is the deeper and wider (Fig. 3c).

P_1 . I identify an isolated cheek tooth, LACM 38812 (Figs. 2d–f), as a right P_1 of *Pelagiarctos thomasi* because it has a single root that is slightly bilobed in cross section and which corresponds to the shape and size of the alveolus for the right P_1 in the holotype mandible. The crown of this tooth is 15.8 mm long with a conical central cusp (the protoconid) and a cuspidate lingual cingulid bearing a small posterior cusp (the hypoconid). The gum line, paralleled by the lower margin of the enamel, was oblique to the long axis of the root, but when the tooth is correctly inserted into the procumbent P_1 alveolus of the holotype mandible, the gum line is parallel to the dorsal margin of the dentary. (The P_1 alveoli of carnivores with large, procumbent canine roots are likewise necessarily procumbent if they are crowded close to the canine.) The root of the P_1 is mostly broken away, revealing the absence of a pulp cavity. The anterolabial quarter of the crown is also missing. The complete crown was oval-shaped in occlusal view, with a slightly flattened labial side. The undamaged enamel surface is faintly crenulated over all the crown. I estimate that when the central cusp was complete, the crown was at least 15 mm high. It has a posterior cristid (the epicristid) with a tiny cusp (the reduced metaconid) near the base, and must have had an anterior paracristid as well. The cingulid, bearing minute cusps, encircles the crown and is not prominent labially. On the lingual side of the crown the cingulid is prominent, irregular, and almost entirely comprised of small cusps measuring approximately 1.5 mm across.

P_2 . Another isolated cheek tooth, UCMP 93058 (Figs. 2g–i), I identify as a left P_2 of *Pelagiarctos thomasi* because it has two roots whose size, depth, cross-sectional shape, and degree of divergence (except for being morphologically reversed) are appropriate to fit into the right P_2 alveoli of the

holotype mandible. In its basic morphology, this tooth resembles the P_2 , P_3 , or P_4 of many generalized fissiped carnivores. It has two long, nearly straight roots, a triangular, slightly recumbent central cusp (the protoconid) with a smooth anterior paracristid and a posterior epicristid with a minute metaconid and an encircling cingulid that is most prominent lingually and bears a posterior hypoconid. In these same characters it also resembles the P_2 in a mandible (UCMP 114474) which I identified (Barnes, 1979:11) as belonging to a primitive, Early Miocene species of the enaliarctine otariid genus, *Enaliarctos* Mitchell and Tedford, 1973. This P_2 of *P. thomasi* differs from that of the enaliarctine by having a more bulbous central cusp (protoconid), a less prominent posterior cingular cusp (hypoconid), and an additional small cusp on the posterior cristid in addition to the metaconid, and by lacking an anterior cingular cusp (paraconid). The crown is 18 mm long, 14 mm high, and has the same types of derived characters as the P_1 described above: rugose enamel surface, prominent and cuspidate lingual cingulid, and less prominent labial cingulid.

P_3 or P_4 . Two isolated cheek teeth (Figs. 2j–o), a right (LACM 72856) and a left (LACM 122310), have root morphologies that conform with the alveoli of the P_3 in the holotype mandible. These two teeth have an arrangement of the cusps and cingulids similar to P_3 's and/or P_4 's of Early Miocene age that have been identified as belonging to *Enaliarctos mealsi* Mitchell and Tedford, 1973 (see Barnes, 1979:figs. 2d, e, g, h; LACM 17035, 72733). In *E. mealsi*, however, the central cusps (protoconids) are labio-lingually compressed (somewhat blade-like), whereas in *Pelagiarctos thomasi* they are more inflated and conical. The left premolar, LACM 122310, that I refer to *P. thomasi* is slightly more constricted medially at the lingual cingulid, and has a less prominent labial cingulid and less divergent roots than the other one, LACM 72856. Its roots are not complete.

As with the first two premolars, these have rugose enamel, prominent, cuspidate lingual cingulids, and less prominent labial cingulids. They differ from the P_2 by having larger anterior and posterior cingular cusps and a single, larger cusp (metaconid) on the posterior cristid rather than two small ones. There is apical wear on both the main cusp (protoconid) and the smaller cusp posterior to it (metaconid) of each of these teeth. The crowns of LACM 72856 and 122310, respectively, measure 18.4 mm and 18.9 mm long and 11.6 mm and 12.2 mm high. In some generalized fissiped carnivores, the P_4 differs from the P_3 by having a large metaconid and, therefore, by having a crown with four rather than three cusps in a row. The presence of four cusps in a row on these teeth of *Pelagiarctos thomasi* may indicate a greater likelihood that they are P_4 's rather than P_3 's.

P_3 or P_4 . Another isolated cheek tooth, LACM 123415 (Figs. 2a–c), is probably a right P_3 or P_4 of *Pelagiarctos thomasi*. Its root is relatively short and curves medially, appropriate for one of the upper, or maxillary, teeth which, in most otariids, have relatively shallow alveoli that curve medially. Such a condition exists in species of *Allodesmus*, for example, as well as in most other fossil and living otariids. Instead of having two separate roots, this tooth has them fused into a

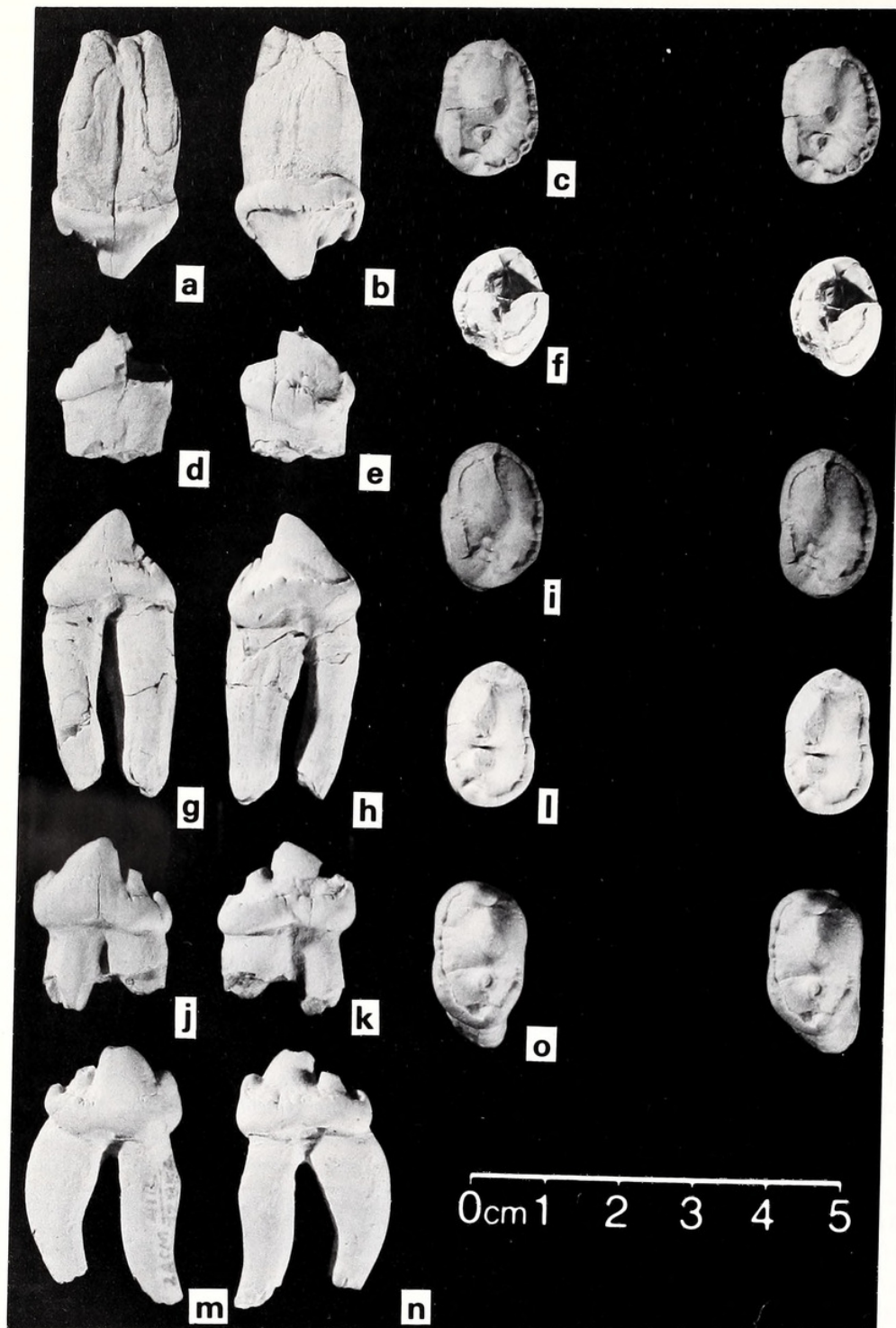


Figure 2. *Pelagiartcos thomasi*, new genus and species, referred cheek teeth; right upper premolar, LACM 123415; **a**, labial view; **b**, lingual view; **c**, occlusal view; right P₁, LACM 38812; **d**, labial view; **e**, lingual view; **f**, occlusal view; left P₂, UCMP 93058; **g**, labial view; **h**, lingual view; **i**, occlusal view; left P₃ or P₄, LACM 122310; **j**, labial view; **k**, lingual view; **l**, occlusal view; cast of right P₃ or P₄, LACM 72856; **m**, labial view; **n**, lingual view; **o**, occlusal view. All natural size, all occlusal views are stereophotographs in which the anterior edge of the tooth is toward the top of the page.

single, bilobed one. The crown is considerably wider labiolingually than those of the lower cheek teeth described previously. The crown is 17.4 mm long and 10.3 mm high, and like the lower premolars, has rugose enamel, a very promi-

nent, cuspidate lingual cingulum and a less prominent labial cingulum. It has only a minute anterior cingular cusp (the parastyle), but like the P₃ or P₄ referred to the species, it has a slightly larger posterior cingular cusp (in this case, the meta-

style) and, a single, small round cusp, the metacone, posterior to the paracone.

DISCUSSION

Pelagiartcos thomasi might have evolved from some species within the Enaliarctinae. Its cheek tooth crowns resemble those of species of the primitive Early Miocene enaliarctine genus, *Enaliarctos*, by having similar proportions and shapes, a similar anteroposterior arrangement of the main cusps on the tritubercular crowns, and well-developed labial and lingual cingulae.

Pelagiartcos thomasi and the Late Miocene imagotariine otariid, *Imagotaria downsi*, both have a dentary with a horizontal ramus that is thick in cross section and bears an elongate eminence on the ventrolateral side extending posteriorly from the genial tuberosity, a thick and robust symphyseal region with a trapezium-shaped sagittal section through the symphysis, bone around the symphysis that is rugose and perforated by numerous small foramina, a prominent genial tuberosity, a few mental foramina of large diameter on the labial side of the dentary rather than several small ones, and a lower canine root that is bilobed in cross section, cheek tooth crowns with similar height to length proportions, a large central cusp and cuspsules on an undulating lingual cingulum, and a tendency toward coalescence of the cheek tooth roots (see Mitchell, 1968; Barnes, 1971; Repenning and Tedford, 1977). These similarities indicate a likelihood that *P. thomasi* belongs in the subfamily Imagotariinae, but this affinity cannot now be proven for certain in the absence of cranial material. In contrast with those of *Imagotaria downsi*, the cheek tooth crowns of *Pelagiartcos thomasi* have larger and more variably sized cuspsules on the lingual cingulae, a smaller (or absent) anterior cingular cusp (both derived characters), a more prominent labial cingulum, one or more small cusps posterior to the largest central cusp, and more widely divergent mandibular roots (all three primitive characters).

In most characters, therefore, the tooth morphology of *P. thomasi* is more primitive than that of *Imagotaria downsi*, but its mandibular morphology, especially the ankylosed symphysis, is more derived and this would exclude it from consideration as an ancestor of any of the known imagotariines. The subfamily Imagotariinae became relatively diverse and abundant in the Late Miocene (see Repenning and Tedford, 1977). Unfortunately, among the known species of Imagotariinae, *P. thomasi* cannot be directly compared with published materials of *Pontolis magnus* (True, 1905), a species that was described on the basis of the posterior part of a cranium. However, newly acquired (LACM) specimens referable to *Pontolis magnus* include mandibles, and these are distinctly different from that of *P. thomasi*. Furthermore, *Pontolis magnus* is considerably younger, geochronologically, than *Pelagiartcos thomasi*, being of latest Miocene age, ca. 5 to 6 million years old (Repenning and Tedford, 1977), and the two species are therefore separated in time by approximately 8 to 10 million years.

Ankylosis of the mandibular symphysis is an unusual and

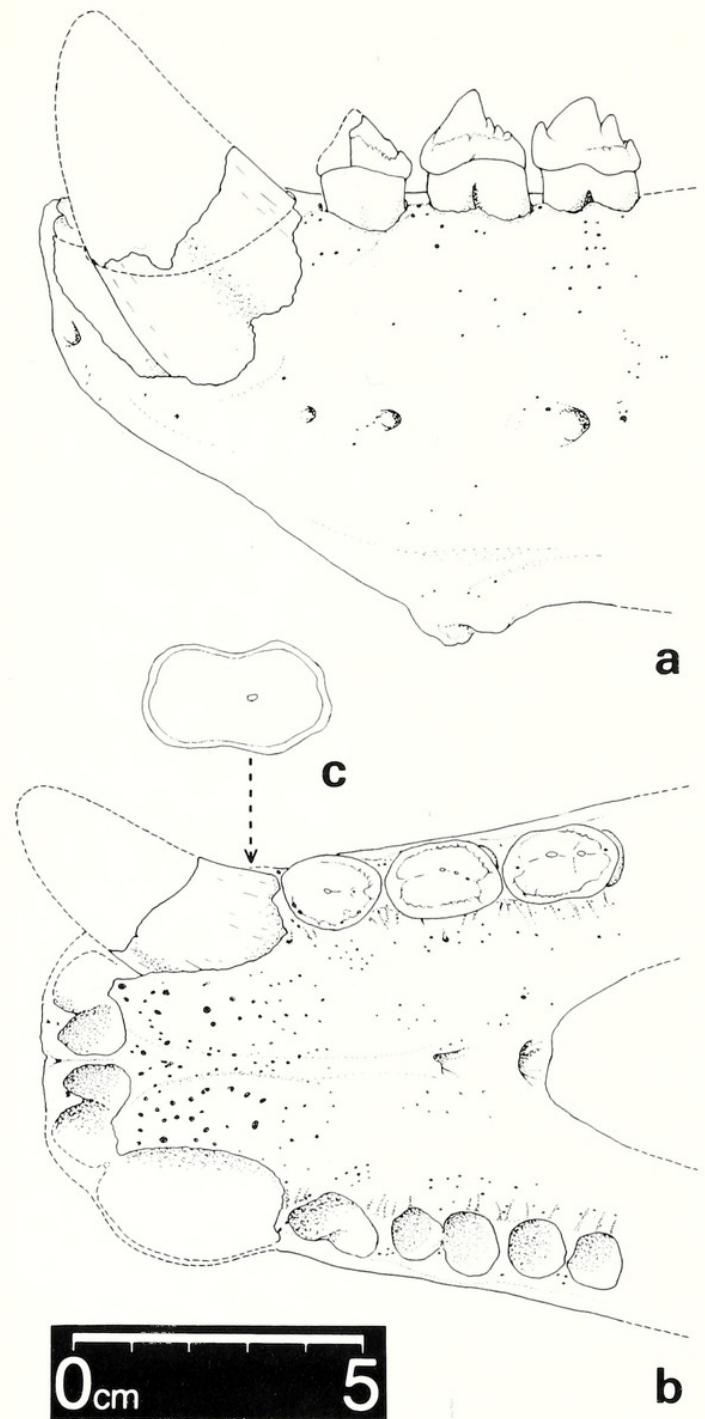


Figure 3. *Pelagiartcos thomasi*, new genus and species, reconstruction of the anterior end of the mandible based on holotype and referred specimens. The cheek teeth are shown in the right dentary only so that the shapes of the alveoli on the left side may be seen. **a**, left lateral view; **b**, dorsal or occlusal view; **c**, cross section of right canine below alveolar rim.

derived character that is present also in Recent walruses, *Odobenus rosmarus* (Linnaeus, 1758). Fossil walruses, such as *Prorosmarus alleni* Berry and Gregory, 1906, and *Aivukus cedrosensis* Repenning and Tedford, 1977, do not have ankylosed symphyses. Because *Pelagiartcos thomasi* is otherwise relatively primitive and not walrus-like in its anatomy,

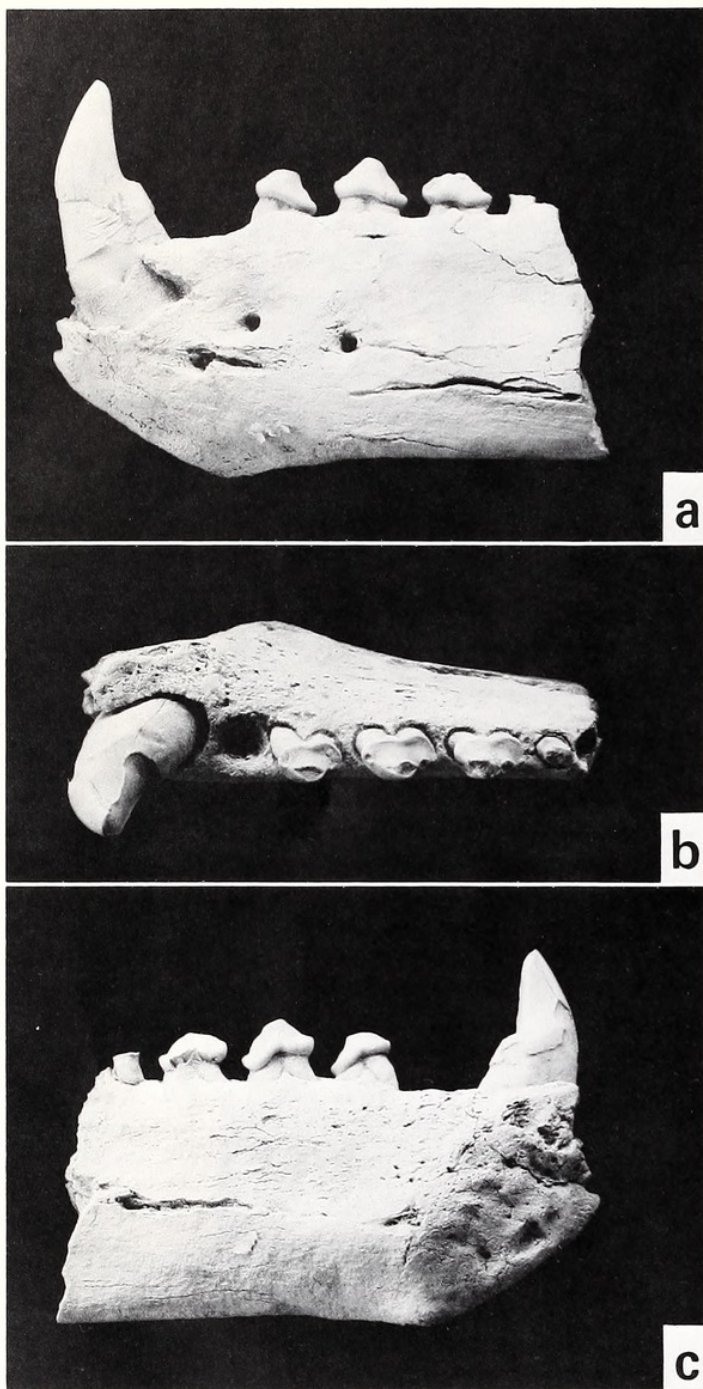


Figure 4. *Neotherium mirum* Kellogg, 1931, referred partial left dentary with P₂₋₄, LACM 123000, LACM locality 3808, Sharktooth Hill Bonebed; **a**, labial view; **b**, occlusal view; **c**, lingual view; natural size.

its ankylosed symphysis is certainly an independently acquired, derived character (autapomorphy), and indicates only convergence with the Recent walrus, not phylogenetic relationship. The mandibles and teeth of these two species are in other respects very different.

Although *Pelagiarctos thomasi* has a mandible approximately the size of that of the contemporaneous (and possibly sympatric) *Allodesmus kernensis*, it differs by having a wider and ankylosed symphysis, mandibular cheek teeth that are two-rooted instead of single or bilobed, much more complex

cheek tooth crowns with multiple cusps and cuspules instead of being smooth and bulbous, a canine root that is bilobed rather than nearly round in cross section, a much thicker dentary, and it differs from most individuals of *Allodesmus kernensis* by having a symphysis that is larger and more procumbent. In those comparisons that are possible with the available specimens, many of these same differences serve also to separate *P. thomasi* from approximately contemporaneous *Allodesmus courseni* (Downs, 1956), and the teeth of *P. thomasi* are different from those of *A. packardii* Barnes, 1972.

Pelagiarctos thomasi is also distinguishable from *Neotherium mirum*, the other named species of otariid in the Sharktooth Hill Bonebed. Several mandibles referable to *N. mirum* have now been collected, and one of these, LACM 123000, is illustrated here (Fig. 4) to demonstrate the differences between that species and *P. thomasi*. My referral of this mandible to *N. mirum* is based on the relative and numerical abundances of isolated elements in the available sample of specimens from the Sharktooth Hill Bonebed, on persistent similarities among homologous bones of *N. mirum* and *Imagotaria downsi* (a relationship noted by Repenning and Tedford, 1977), and on consistencies in stage of evolution and of size (= sex) bimodality in the sample.

Both *Neotherium mirum* and *Pelagiarctos thomasi* have two roots on each of the lower cheek teeth following the first premolar, and transversely compressed cheek tooth crowns on which the major cusps are aligned anteroposteriorly. The mandible of *Neotherium mirum* differs from that of *Pelagiarctos thomasi* by being much smaller and by having a smaller, non-ankylosed symphysis, a less prominently bilobed canine root, shallower cheek tooth alveoli, and less vascularization of the bone surface. All of these characters are exhibited by the specimen shown in Figure 4, and they are consistent in the relatively large, unpublished sample of *N. mirum* now available (Barnes, manuscript in preparation). Mandibles representing both sexual morphs of *N. mirum* are represented, and this demonstrates that *P. thomasi* was not the male of *N. mirum*.

The mandibles of "Desmatophocine B" and "Desmatophocine C" (see Barnes, 1972) differ from that of *P. thomasi* by having, among other features, a narrow and non-ankylosed mandibular symphysis, less vascularization of the bone surface, a horizontal ramus that is thinner transversely, and by having single-rooted rather than double-rooted lower premolars.

Thus, *Pelagiarctos thomasi* is demonstrably distinct from all known contemporaneous otariids, including those found with it in the same deposit as well as those from other localities. It is furthermore separable from all other fossil and Recent otariids based on morphological, size, or chronological differences. It is clearly a rare animal in the Sharktooth Hill Bonebed, and is demonstrably a previously unrecognized taxon. It is directly comparable with the majority of other described fossil otariid genera, because most of them were either originally based upon mandibles, or have had mandibles subsequently referred to them. Only *Pinnarctidion*, *Pliopedia*, and *Valenictus* are not known by mandibles, but they are separable from *Pelagiarctos* on the basis of their

different sizes and geologic ages, and/or have been assigned to different subfamilies. It is useful to name *Pelagiarctos thomasi* at this point in time so that it may be discussed in the context of the composition of the Sharktooth Hill Local Fauna and of the evolution and systematics of otariid pinnipeds.

Pelagiarctos thomasi is an extremely rare species in the Sharktooth Hill Local Fauna. It is represented by only six specimens, compared with the literally hundreds that are now known of *Allodesmus kernensis* and the dozens that are referable to *Neotherium mirum*. By the standard method of minimum number analysis (see Shotwell, 1955), these six specimens would represent only one individual, because there are no duplicated elements in the sample. Because of their differing stages of tooth wear and because the specimens were obtained over tens of square miles of bonebed outcrop, they probably represent six different individuals.

All of the specimens apparently represent the same size, sex, and age group: adult male. All of the teeth have roots of the appropriate size to occupy the alveoli of the holotype mandible, and all have closed, or nearly closed, pulp cavities indicating maturity (see Scheffer and Kraus, 1964:307). At least three lines of evidence suggest that the holotype mandible is from a male individual. (1) The bone surface is extremely rugose and pitted. This is a common osteological secondary sex character of adult male otariids (and other Carnivora). (2) The canine is relatively large in size compared with the cheek teeth. Canine proportional disparity among the two sexes is one of many dimorphic characteristics of all modern and of all adequately represented fossil otariids, and it is the males that have the largest canines. (3) The right canine of the holotype mandible was broken during life. Such breakage is known to result from fights between extant male pinnipeds. Therefore, all the specimens are judged to be from adult male individuals.

If the evidence cited above is accurate, it indicates an absence of female specimens and the area in which the Sharktooth Hill Bonebed was deposited might not have been within the geographic range of the females of the species. The phenomenon of partial allopatry among the sexes of Recent otariids is well known. For example, along the Pacific Coast of North America the males of the California sea lion, *Zalophus californianus* (Lesson, 1828), range much farther northward than do the females during the non-breeding season. During the breeding season both sexes are together in the southern part of the range of the species.

The extreme development of foramina and sulci on the surface of the bone of the holotype mandible of *P. thomasi* suggests that the lip and gum regions of the animal were very vascular. This evidence of vascularization is especially pronounced in the areas between the canines and on the lingual sides of the premolar alveoli (Fig. 3b). The mental foramina on the lateral and anterior surfaces of the dentary are also unusually large in diameter, further indication of enhanced blood circulation in this area. The lips of *P. thomasi* may, therefore, have been very fleshy, as are those of some living phocid seals. The absence of cranial material, however, precludes speculation at this time as to whether or not *P. thomasi* also had a proboscis as do elephant seals (*Mirounga* spp.).

The cheek teeth (Fig. 3) of *Pelagiarctos thomasi* are somewhat similar in their shape, mass, and position to those of large predatory and scavenging terrestrial carnivorous mammals, especially hyaenids and fossil borophagine dogs. This, coupled with the cuspidate crowns and large roots of the cheek teeth and the ankylosed mandibular symphysis, suggests that *Pelagiarctos thomasi* was possibly an active marine predator with strong crushing and biting abilities. It might have fed on small- to medium-sized warm-blooded marine vertebrates (birds and mammals), in addition to (or instead of) the expected diet of fishes. Such an idea is given credibility by the fact that some species of living pinnipeds, even those with dentitions that are modified for specialized feeding modes, are known to kill and eat other large marine vertebrates. For example, the South American sea lion, *Otaria flavescens* (Shaw, 1800), and the leopard seal of the Antarctic, *Hydrurga leptonyx* (Blainville, 1820), prey upon penguins (Boswall, 1972; Penny and Lowry, 1967); and the Steller sea lion, *Eumetopias jubata* (Schreber, 1776), has been known to kill and eat other pinnipeds (Tikhomirov, 1959; Gentry and Johnson, 1980; Pitcher and Fay, 1982), as does even the walrus (Lowry and Fay, 1984). A postulated trophic position of *Pelagiarctos thomasi*, as a predator relatively high in the food chain, is therefore plausible in the context both of its known anatomy and of information about the feeding behavior of living pinnipeds. Being a predaceous carnivore may also help explain its relative rarity within the Sharktooth Hill Local Fauna.

At least five species of otariid pinnipeds have now been recognized in the Sharktooth Hill Bonebed on the basis of different types of mandibles. These five otariids might have fed on different food items, or they might have occupied the central California coastal region at different times of the year due to different migration and/or reproductive cycles. Either situation could have served to reduce competition among them for food or space through resultant niche partitioning and/or seasonal allopatry of the species or the sexes. Several other fossil marine vertebrate assemblages from the west coast of North America are also known to include two or more species of pinnipeds (see Repenning and Tedford, 1977: 77-82). Such diversity is not unexpected, considering that up to six extant pinniped species, otariids as well as phocids, are regularly present at one time or another of the year along the California coast. At times as many as three pinniped species may even simultaneously occupy the same beach (Orr, 1965; Bartholomew, 1967; Odell, 1971). Furthermore, up to five species of pinnipeds occupy similar ice habitats in the Bering Sea (Burns, Shapiro, and Fay, 1981).

CONCLUSIONS

Four contemporaneous species of fossil otariid pinnipeds have been previously reported from the Middle Miocene Sharktooth Hill Local Fauna in California, and are now known by directly comparable mandibles. These include the large, derived allodesmine, *Allodesmus kernensis* Kellogg, 1922, the small, primitive imagotariine, *Neotherium mirum* Kellogg, 1931, and the possible allodesmines that were called "Desmatophocine B" and "Desmatophocine C" by Barnes

(1972). Of these, *Allodesmus kernensis* is the most abundant, *Neotherium mirum* is the next most abundant, and the other two species are extremely rare. A fifth species, even rarer than any of these, is *Pelagiartcos thomasi*, new genus and species. It is now known by material sufficient to name, diagnose, and differentiate it from other otariid pinnipeds.

Pelagiartcos thomasi has a mixture of derived and primitive characters. It has large, cuspidate premolars and those in the mandible following the first premolar each have two roots. The known cheek teeth are of a tritubercular form, and have a relict, enaliarctine-like cusp pattern, but the cusps are more conical in their shapes in contrast to the relatively more blade-like, transversely compressed cusps of *Enaliartcos mealsi*. This basic similarity in cheek tooth cusp patterns suggests that *Pelagiartcos thomasi* might have evolved from some species related to or within the subfamily Enaliarctinae.

Pelagiartcos thomasi possesses a very specialized and interesting combination of otariid mandibular and dental characters. The cheek teeth have labial and lingual cingulae, the latter being particularly enhanced by multiple, conical cusps (derived characters). *Pelagiartcos thomasi* has an ankylosed mandibular symphysis such as is also present in Recent walruses (*Odobenus rosmarus*). This character does not indicate relationship between *P. thomasi* and walruses, however, because of the many other dental and mandibular differences between them, and because extinct true walruses of the subfamily Odobeninae (e.g., *Aivukus cedrosensis* Reppening and Tedford, 1977; *Prorosmarus alleni* Berry and Gregory, 1906) that lived between about 9 and 5 million years ago have non-ankylosed mandibular symphyses. *Pelagiartcos thomasi* is a highly derived, large, early type of otariid, perhaps an imagotariine, perhaps predaceous on large, warm-blooded, marine vertebrates, and probably belongs to no living lineage.

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