Callorhinus gilmorei n. sp., (Carnivora: Otariidae) from the San Diego Formation (Blancan) and its implications for otariid phylogeny

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Abstract. A new species of fur seal, Callorhinus gilmorei, described from the San Diego Formation of southern California and Mexico, fills a critical stratigraphic and evolutionary gap in our knowledge of otariids. This Late Pliocene (Late Blancan) occurrence of Callorhinus represents the earliest record of modern otariid genera. Mandibular and dental characters distinguish Callorhinus gilmorei from the living northern fur seal, C. ursinus.

Cladistic analysis supports a sister group relationship between Callorhinus and the Hemphillian fur seal “Thalassoleon” macnallyae. Relationships among Arctocephalus species are unresolved. Re-evaluation of Hydrarctos lomasiensis from the Pliocene of Peru suggests that it is the primitive sister taxon of all modern otariids. Modern fur seals and sea lions form separate monophyletic groups.

INTRODUCTION

The poor representation and isolated occurrences of the Otariidae (fur seals and sea lions, following the classification of Repenning and Tedford 1977) in the fossil record inhibits our understanding of phylogenetic relationships within this group. The earliest known otariid is Pithanotaria starri Kellogg 1925 from the Clarendonian (late Middle and early Late Miocene; 11–12 MYA) of California. Better preserved and more complete material of a younger otariid, Thalassoleon mexicanus Repenning and Tedford, 1977 is known from the Hemphillian (late Late Miocene; 5–8 MYA) of Mexico. A second species of Thalassoleon, T. macnallyae Repenning and Tedford 1977, from the late Hemphillian (late Late Miocene and Early Pliocene; 5–6 MYA) of California, is less well known. At this point the record of otariids becomes scant, and as noted by Repenning and Tedford a major gap exists between Thalassoleon at about 5 MYA and the more diverse otariid faunas of the Pleistocene and Recent. These authors suggested that within this gap, which involves most of the Blancan (Pliocene; 2–5 MYA), lies the history of fur seal diversification and the origin of sea lions.

The modern fur seals include the monotypic northern fur seal, Callorhinus ursinus (Linnaeus), and the polytypic southern fur seal, Arctocephalus (F. Cuvier), with eight species currently recognized (Repenning et al. 1971). Until now, the earliest record of a fur seal referred to a modern genus was based on a partial skeleton from the Pliocene of Peru, “Arctocephalus” (Hydrarctos) lomasiensis de Muizon, 1978. However, we question this generic assignment and suggest that the subgenus Hydrarctos be elevated to generic rank to include this primitive taxon.

We provide evidence of a new fur seal from the Blancan of California and Mexico which represents the oldest known fossil otariid referable to a modern genus. This new species is described from a partial skeleton lacking the skull, collected from the Upper
Pliocene San Diego Formation. In addition, a number of isolated dentaries, maxilla and postcranial elements from the San Diego Formation are referred to this new species. Included in this referred material is a fragmentary lower jaw, previously described by Burleson (1948) and Repenning and Tedford (1977).

In the initial stages of this study we were primarily concerned with the identity and relationship of this new fur seal. However, as our study progressed, we soon realized that in order to determine systematic affinities of the fossil taxon we needed to understand the broader phylogenetic relationships among all otariids. From this we expanded our study to include a cladistic analysis of all living and some fossil otariids.

Recent otariids examined in this study are listed in Table 1. Additional osteological data for extant and fossil otariids were obtained from the literature (de Muizon 1978, Repenning et al. 1971, King 1960, Repenning and Tedford 1977, Scheffer 1958, Sivertsen 1954).

The following institutional abbreviations are used in the text. SDSNH, San Diego Natural History Museum, San Diego, California. LACM, Natural History Museum of Los Angeles County, Los Angeles, California. USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

### Systematic Paleontology

**Family Otariidae Gill, 1866**

**Subfamily Arctocephalinae von Boetticher, 1934**

**Genus Callorhinus Gray, 1859**

*Callorhinus gilmorei*, new species

Figures 1, 2

**Pithanotaria** sp., Burleson, 1948:248.


**Holotype.** —SDSNH 25176, partial young adult female skeleton including: left I¹ and P¹, right upper C, I¹ or ², and P¹, right I¹, right dentary with P₂, P₃ and M₁; left I₂ and P₂, P₃; right and left innominates each lacking posterior one-third of pubis and ischium; ribs and rib fragments; lumbar, thoracic, and caudal vertebrae and fragments; all associated and from the same individual.

**Type locality.** —SDSNH locality 3174-D, San Diego, San Diego County, California; San Diego Formation, lower member (of Deméré 1983); collected by B. O. Riney and R. A. Cerutti, 9 August 1982.

**Known distribution.** —Late Pliocene (late Blancan), of California and Mexico.

**Referred material and localities.** —SDSNH 26239, partial right dentary with P₂, P₃ and M₁ from La Joya, Baja California Norte, Mexico (SDSNH locality 3125), San Diego Formation (lower member), collected by A. B. Brockmeir; LACM 115253, left

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of specimens</th>
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<tr>
<td>Callorhinus ursinus</td>
<td>20</td>
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<tr>
<td>Arctocephalus australis</td>
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<tr>
<td>Arctocephalus forsteri</td>
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</tr>
<tr>
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<td>Arctocephalus townsendi</td>
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<tr>
<td>Arctocephalus tropicalis*</td>
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<tr>
<td>Eumetopias jubata</td>
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</tr>
<tr>
<td>Neophoca cinerea</td>
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</tr>
<tr>
<td>Otaria byronia</td>
<td>7</td>
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<tr>
<td>Phocarctos hookeri</td>
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<td>Zalophus californicus</td>
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Figure 1. *Callorhinus gilmorei*, n. sp., Holotype: A–D, SDSNH 25176, (A) medial, (B) occlusal, and (C) lateral views of right dentary with P3–4, M1, (D) lingual view of right P3. Referred material: E–H, LACM 115253, (E) medial, (F) occlusal, and (G) lateral views of left dentary with P3, SDSNH 25531, (H) occlusal view of right maxilla with P1–4. Scales = 1 cm.
diagnosis.—A species of Callorhinus with a long, shallow pterygoid process on the mandible that does not form a medial shelf; with double-rooted lower third and fourth premolars and closely spaced upper first and second molars; small third upper incisor with oval cross section; and dorsally directed anterior margin of the mandibular foramen.

etymology.—The name honors the late Dr. Raymond M. Gilmore for his lasting contributions to the field of marine mammalogy.

description.—Except where noted, the following description refers to the holotype. The dentary has a gently sloping symphysal area (Fig. 1). Two large mental foramina are below P₂ and P₃, just above the midline of the ramus; smaller foramina mark the anterior one-half of the jaw. The mandibular foramen has a dorsally directed anterior margin (Fig. 3). The coronoid process is broad at the base but tapers to a relatively high, narrow dorsal margin. The pterygoid process of the mandible is long and shallow with a reduced medial surface that slopes ventromedially and is not produced into a shelf as in living Callorhinus. The articular condyle is at the same level as the base of the ascending ramus. The cheektooth row is short relative to the distance from P₁ to the ascending ramus as shown on Figure 4. The horizontal ramus is elongate...
Table 2. Mandible and lower tooth measurements for Callorhinus gilmorei (a, alveolus only; c, estimated; *, holotype).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>USNM 184065</th>
<th>SDSNH* 25176</th>
<th>SDSNH 26239</th>
<th>SDSNH 25554</th>
<th>SDSNH 25535</th>
<th>LACM 115253</th>
<th>LACM 4323</th>
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<tr>
<td>Depth of mandible behind M₁</td>
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<td>16.5</td>
<td>17.0</td>
<td>15.5</td>
<td>18.9</td>
<td>15.5</td>
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<tr>
<td>Length of toothrow P₁–M₁</td>
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<td>—</td>
<td>42.5</td>
<td>35.6c</td>
<td>41.1c</td>
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<tr>
<td>Height of mandible</td>
<td>36.4</td>
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<td>—</td>
<td>—</td>
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<td>C, anteroposterior length</td>
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<td>8.6a</td>
<td>—</td>
<td>13.5</td>
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<td>5.7a</td>
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<td>6.5a</td>
<td>10.7a</td>
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<tr>
<td>P₂, transverse width</td>
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<td>4.7</td>
<td>3.5a</td>
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<td>P₄, anteroposterior length</td>
<td>6.7a</td>
<td>6.5a</td>
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<td>P₄, transverse width</td>
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<td>M₁, transverse width</td>
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<td>3.8</td>
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</tr>
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</table>

and slender in the type, and in SDSNH 26239, SDSNH 25554 and LACM 4323, which, presumably represent females. The robust jaw and larger canines in SDSNH 25535 and LACM 11523 suggest that these specimens represent males.

Isolated lower incisors are associated with the type jaw. The top one-half of the crown of I₁ is worn flat. The tooth is single-cusped, triangular in cross section, and has a strongly compressed root. I₂ is larger, with a high medial cusp and a low basal cusp that slopes posteromedially. The small size of the canine alveolus in the type and SDSNH 25554 suggests that the canine was relatively small and slender in contrast to the large, robust canine in SDSNH 25535 and LACM 11523. Again these differences are attributed to sexual dimorphism.

Relative to the size of the jaw, the check teeth are proportionately small and high crowned with prominent lingual cingula (Table 2, Fig. 1). P₁ has a large central cusp preceded by a small accessory cusp. The tooth crown slopes posteriorly. P₂ is single-rooted with a vertical sulcus on the labial surface of the root. There is a small anterior accessory cusp on P₂. The left P₃ is double-rooted with strongly divergent roots, whereas the right P₃ is single-rooted with a vertical sulcus on the lateral and medial surfaces of the root. This tooth is double-rooted in LACM 4323, LACM 11523, SDSNH 25554, SDSNH 25535 and single-rooted in SDSNH 26239. P₄ is double-rooted in all specimens except SDSNH 26239. Apart from its larger size, P₄ is very similar to P₃. M₁ is double-rooted in all specimens except SDSNH 25535 in which the alveolus indicates a single root. The tooth consists of a central cusp that is strongly inclined posteriorly and followed by a small accessory cusp on the tooth heel. The anterior accessory cusp is indistinct in the holotype but prominent in SDSNH 26239.

Isolated upper teeth were found in association with the type jaw and are presumed to be from the same individual. A tooth broken near the base of the crown is identified as either I₁ or I₂ based on lateral compression of the root. I₃ is small and caniniform with a strongly curved root and an oval cross section. The slender upper canine displays less curvature than the corresponding lower tooth. The anterior premolars, P₁–3, are single-rooted and lack accessory cusps. P₂ differs from P₁ in its slightly larger size and vertical sulcus on the lateral and medial surfaces of the root.

A right maxillary with P₃–4, SDSNH 25531, and a left P₃ in a maxillary fragment, SDSNH 25616, probably from the same individual, are provisionally referred to this species. In occlusal view, the cheek tooth row converges at P₂–₃ and diverges at M₁, creating a sinuous toothrow (Figs. 1, 5). P₂–₃ and M₁–₂ are double-rooted. The teeth are proportionally small and high crowned with strong lingual cingula. No accessory cusps are developed. Judging from the alveoli, M₁–₂ were positioned close together. Mea-
measurements are as follows: P\textsuperscript{3}, anteroposterior length 5.8 mm, transverse width 4.3 mm; P\textsuperscript{4}, anteroposterior length 6.3 mm, transverse width 4.3 mm.

That the type specimen was a young adult is indicated by the only slightly worn dentition and the lack of epiphyses on the innominate and vertebrae. Although most of the pubis and ischium is missing, the pubis appears to be relatively broad dorsoventrally, characteristic of a female. This specimen has a broad, low pectineopoasoal process projecting ventrally from the ilium at the acetabulum (Fig. 2). The holotype includes the shafts and heads of two ribs, the shafts of two ribs, the heads of three ribs, the centra of three thoracic, two lumbar (L2 and 3\textsuperscript{3}) (Fig. 2), and four caudal vertebrae.

Discussion.—Callorhinus gilmorei appears to be more primitive than the living northern fur seal, C. ursinus on the basis of dental and mandibular characters. In C. gilmorei, P\textsubscript{3-4} are usually double-rooted by contrast to their single-rooted condition in C. ursinus. In addition, the pterygoid process of the mandible in C. gilmorei has a ventromedially sloped medial surface rather than the strongly produced medial shelf characteristic of C. ursinus. Also, in C. gilmorei M\textsubscript{1-2} are positioned close to one another, whereas in C. ursinus M\textsubscript{1-2} are separated by a persistent diastema.

Repnenning and Tedford (1977) commented on the similarity between Thalassoleon macnallyae and Callorhinus and suggested that a large sample of the former species might provide evidence for the origin of the genus Callorhinus from T. macnallyae. As noted by Repnenning and Tedford similarities between these taxa include smaller cheekteeth, greater ornamentation of the medial lip of the ectotympanic bone, postcruciate sulcus separating postcruciatus and lateral gyrus, unconvoluted and relatively narrow gyrus ectosylvius posterior, and posterior position of the frontal-parietal suture. Unfortunately, neither a cranium nor endocranial cast are available for the fossil species Callorhinus gilmorei. The following characters distinguish C. gilmorei from T. macnallyae: considerably smaller size, small I\textsuperscript{3} with oval cross section and M\textsubscript{1-2} positioned close together.

Our study offers additional support for a closer relationship between Callorhinus and Thalassoleon macnallyae than between Callorhinus and Thalassoleon mexicanus, or between Callorhinus and Arctocephalus. Thalassoleon mexicanus is more primitive than T. macnallyae in its possession of smaller vertebral foramina, less ornamentation of the medial edge of the ectotympanic and lack of fusion of the tibia and fibula. Arctocephalus, together with all sea lions, is more derived than either Thalassoleon or Callorhinus in having a mandibular foramen with a ventrally directed anterior margin.

Although relationships among Arctocephalus species are largely unresolved, and will be discussed below, Callorhinus gilmorei can be readily distinguished from A. townsendi, the only modern fur seal in addition to C. ursinus with a known distribution along the Pacific coast of North America. In C. gilmorei the length of the cheek tooththrow relative to the distance from P\textsubscript{1} to the ascending ramus is short, rather than long as in A. townsendi (Fig. 4). Additionally, in the fossil species the pectineopoasoal process on the ilium is broad and low rather than narrow and projecting as in A. townsendi. Finally, in C. gilmorei the pterygoid process of the mandible is long and shallow rather than
short and deep as in *A. townsendi*. Earlier, Burleson (1948) noted that a mandibular ramus (LACM 4323) from the San Diego Formation, here referred to *C. gilmorei*, could be distinguished from *A. townsendi* in having P4 and M1 on the dorsal crest of the ramus rather than on the medial side of the crest as in *A. townsendi*. Our study of other dentaries referred to *C. gilmorei* confirms Burleson’s observation.

### Implications For Otariid Phylogeny

Traditionally, modern otariids have been grouped into two subfamilies: Otariinae (sea lions) and Arctocephalinae (fur seals) (see Scheffer 1958). Repenning et al. (1971) suggested that subfamilial distinction is unwarranted since they were unable to find osteological characters that consistently separated these two groups. Repenning and Tedford (1977) retained the “Otariinae” and “Arctocephalinae” only as nomenclatural conveniences and did not use them in their formal classification. Our analysis provides support for the traditional view that fur seals and sea lions belong to different groups. Sea lions, which include five living, monotypic genera, *Zalophus, Neophoca, Phocarctos, Otaria*, and *Eumetopias*, are recognized by most workers as a monophyletic group. The monophyly of fur seals, which include the living genera *Arctocephalus* and *Callorhinus*, has been questioned, most recently by Repenning and Tedford (1977) and de Muizon (1978).
Interpretations of otariid relationship are summarized in Figure 6. Both previous studies and this one view sea lions as monophyletic. Traditionally, fur seals have been recognized as polyphyletic, although this study distinguishes modern fur seals as monophyletic. While Repenning and Tedford (1977) recognized Pithanotaria as the earliest known otariid, they suggested that the better known, more derived fossil taxon Thalassoleon might be ancestral to both lineages of living fur seals and the living sea lions. De Muizon (1978) used the distinctive morphology of the baculum to argue that Thalassoleon and Callorhinus are more closely related and should be recognized as a separate subfamily, the Callorhininae.

Cladistic analysis was used to evaluate relationships among all living and some fossil otariids, using the characters discussed in the Appendix. Fossil otariids studied include Pithanotaria starri (Clarendonian, California), Thalassoleon mexicanus (Hemphillian, Mexico), Thalassoleon macnallyae (latest Hemphillian, California [? Blancon, Repenning, personal communication]) and “Arctocephalus” (Hydractos) lomasiensis (Pliocene, Peru [Montehermosan or Chapadmalalan?]). The polarity of characters was determined by outgroup comparison using the most primitive known otarioid (includes fur seals, sea lions, walruses and their extinct relatives), Enaliarctos melasi Mitchell and Tedford (1973) from the Late Oligocene/Early Miocene of California. Published descriptions of this species (Mitchell and Tedford 1973, Barnes 1979) were supplemented by an evaluation of unpublished enaliarctic material housed in the Emlong collection at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. and the U.S. Geological Survey (Denver). An attempt was made to use only material that could be definitely assigned to Enaliarctos; although those characters that were present among all enaliarctids (including Enaliarctos and Pinnarctidion) were noted.

In our analysis we attempted to account for variation by examining, when possible, more than just a single specimen of a taxon (Table 1). Only those characters that withstood careful scrutiny were used in the analysis. A total of 41 osteological, soft anatomical and behavioral characters were selected. We acknowledge the fact that while some of these characters are undoubtedly related, both functionally and phyletically (e.g., characters 5, 6, 7 tooth and root simplification), our recognition of these as separate characters has not biased their weighting in the analysis. We independently examined those special cases where double-weighting of characters may have applied, and found no difference in the branching pattern than that obtained by considering these characters separately.

Characters were analyzed and minimum-step cladograms generated by computer using the PHYSYS program written by J. S. Farris. Cladograms were constructed by
Figure 6. Cladistic representation of previous and present interpretations of otariid relationships.
Figure 7. Cladogram of proposed relationship of Recent and some fossil otariids. Numbers at each node refer to shared derived characters discussed in text and Appendix. (*, reversals and ( ), convergences.)
the Wagner procedure (Farris 1970) and its global branch swapping option (Micklewich 1978). One Wagner and a single Pimentel tree were obtained, with the Wagner tree being shorter. Several modifications of the computer generated trees necessitated construction of a consensus cladogram based in large part on the Wagner tree (Fig. 7). These modifications involve two characters (14, 15) that the computer analysis showed to be derived for both fur seals and sea lions, prior to divergence of these two groups. Although the analysis indicated that sea lions must have lost these characters, we feel that it is more parsimonious to consider that they were derived only once in the modern fur seals.

Monophyly of the Otariidae and its distinction from Enaliarctos is supported by four shared derived characters: absence of lacrimal foramen, nasolabialis fossa, fissipedia-like dentition, and presence of large, well-developed supraorbital processes (characters 1–4). Pithanotaria starri, the most primitive otariid analyzed is distinguished from all other otariids in lacking M2 (character 8). The fossil otariid, Thalassoleon mexicanus and all other otariids share a single derived character, a simple lateral upper incisor (character 5). “Arctocephalus” (Hydrarctos) lomasiensis, fur seals and sea lions can be distinguished from Thalassoleon mexicanus by five synapomorphies (characters 6, 7, 9, 12, 13). Our analysis of “Arctocephalus” (H.) lomasiensis suggests that it should not be recognized as a species of Arctocephalus. This taxon is recognized here as a primitive otariid distinct from the Arctocephalus-Calorhinus clade. Based on this we recommend elevation of the subgenus Hydrarctos to generic status.

In this analysis advanced otariids share a single derived character—calcaneum with well-developed secondary shelf of the sustentaculum (character 11). Although relationships among fur seals are here represented as an unresolved polychotomy, three separate groups can be identified which share the following two derived characters: narrow basioccipital, and I1 with oval cross section (characters 14, 15). The fossil otariid Thalassoleon macnallyae and the northern fur seal, Callorhinus ursinus share a sister group relationship that is supported by four shared derived characters (characters 23, 32, 33, 34). The identity of the fossil fur seal described in this paper as a species of Callorhinus is supported by mandibular and dental characters as previously discussed. Callorhinus gilmorei is more primitive than C. ursinus in having a long, shallow pterygoid process that does not form a medial shelf, P3–4 that are usually double-rooted, and M1–2 positioned close together.

Relationships among Arctocephalus species are less well resolved, owing to a high degree of convergence among several of the characters (e.g., characters 18, 26, both of which appear to be independently derived among the various fur seal and sea lion clades). In an earlier discussion of arctocephaline relationships, Repenning et al. (1971) recognized A. pusillus and A. gazella as distinct from all other Arctocephalus species. Our analysis provides further support for this interpretation. Although A. pusillus is distinguished from all other species of the genus by three characters, two of these are convergences (characters 18, 20) that occur in other Arctocephalus species. Arctocephalus townsendi, A. australis, A. philippii, A. galapagoensis, and A. forsteri are separated from A. gazella and A. tropicalis in having a short, deep pterygoid process on the mandible (character 25).

Recognition of sea lions as a natural group is supported by osteological (19, 27, 28, 29), soft anatomical (31, 35, 36) and behavioral (37) characters. Eumetopias, Neophoca, Phocarctos and Otaria are more derived than Zalophus in their possession of a single derived character, apex of baculum further expanded laterally (character 30). The southern sea lions, Otaria, Neophoca, and Phocarctos share well-developed accessory cusps on cheek teeth and a deep palate (characters 20, 39). The most derived sea lions, Otaria and Phocarctos share two derived characters, both of which represent convergences elsewhere on the cladogram.

A classification of modern genera in the Family Otariidae developed in this paper is presented in Table 3. Fossil otariids, Pithanotaria starri, Thalassoleon mexicanus, and Hydrarctos lomasiensis are recognized as primitive members of the Otariidae. Modern fur seals and sea lions are defined here as belonging to separate monophyletic
groups and designated as subfamilies. The Arctocephalinae, which includes the modern fur seals, *Arctocephalus* and *Callorhinus*, as well as the fossil fur seal “*Thalassoleon* macnallyae” is defined by two derived characters—rectangular basioccipital, and I\(^1\) with oval cross section. Although we do not recognize the Callorhininae at the subfamilial level, our analysis does support the close relationship between *Thalassoleon macnallyae* and *Callorhinus* originally suggested by de Muizon (1978). Pending further analysis of the *Callorhinus-Arctocephalus* clade, we have chosen not to formally designate this monophyletic group. More derived otariids, the sea lions are grouped in the Otariinae, which includes *Eumetopias*, *Neophoca*, *Phocarctos*, *Otaria*, and *Zalophus*. The following derived characters distinguish this group: M\(^1\) single-rooted, cheektooth row straight, humerus stout, pectoral crest directed toward midpoint of distal articulation, apex of baculum broad with keels, more convoluted neopallium, sparse underfur, sucking louse host specificity, and strongly thigmotactic behavior.

**CONCLUSIONS**

A new fur seal, *Callorhinus gilmorei* n. sp., from the Late Pliocene of California and Mexico represents the oldest fossil otariid referable to a modern genus. As the only nominal Blancan-aged otariid from North America, this taxon helps to fill a gap in the fossil record of the group.

The new fur seal shares numerous dental and mandibular characters with the living Northern fur seal *Callorhinus ursinus* while retaining several primitive characters such as double-rooted cheekteeth.

Cladistic analysis utilizing 41 osteological, soft anatomical and behavioral characters supports monophyly of the family Otariidae. The Late Oligocene/Early Miocene genus *Enaliarctos* represents the primitive sister taxon of all otariids. The sea lions and modern fur seals represent separate monophyletic groups. The Peruvian fossil fur seal “*Arctocephalus*” (*Hydrarctos*) *lomasiensis* is sufficiently primitive to warrant placing it in the newly elevated genus *Hydrarctos*. The suggested sister group relationship between *Callorhinus ursinus* and “*Thalassoleon* macnallyae” indicates the need of a new generic concept for the latter species. This relationship also points to the antiquity of this group of fur seals, and serves to highlight the lack of a recognized *Arctocephalus* ancestor. Unfortunately, the analysis failed to resolve the confusing relationships between taxa presently grouped in the genus *Arctocephalus*.

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**Table 3. Classification of Recent Otariidae.**

<table>
<thead>
<tr>
<th>Order Carnivora Bowdich, 1821</th>
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</thead>
<tbody>
<tr>
<td>Family Otariidae Gill, 1866</td>
</tr>
<tr>
<td>Subfamily Arctocephalinae von Boetticher, 1934</td>
</tr>
<tr>
<td><em>Arctocephalus</em> Geoffrey and Cuvier, 1826</td>
</tr>
<tr>
<td><em>Callorhinus</em> Gray, 1859</td>
</tr>
<tr>
<td>Subfamily Otarinae von Boetticher, 1934</td>
</tr>
<tr>
<td><em>Eumetopias</em> Gill, 1866</td>
</tr>
<tr>
<td><em>Otaria</em> Peron, 1816</td>
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<tr>
<td><em>Neophoca</em> Gray, 1866</td>
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<tr>
<td><em>Phocarctos</em> Peters, 1866</td>
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<tr>
<td><em>Zalophus</em> Gray, 1859</td>
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</tbody>
</table>
The Gersten Companies of Chula Vista, California, are acknowledged for permitting and supporting the collection of fossils (including the holotype specimen) on their property. In addition the Planning Department, City of Chula Vista, and especially Doug Reid of that office are to be commended for realizing the significance of paleontological resources within their jurisdiction.

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**Literature Cited**


Lyon, G. M. 1937. Pinnipeds and a sea otter from the Point Mugu shell mound of California, University of California Los Angeles Publications in Biological Sciences 18(8):133–168.


Note Added in Proof

The framework under which this research was undertaken assumed a working hypothesis of pinniped diphyly. Repenning and Tedford’s (1977) definition of the Otarioida as including the Enaliarctidae, Otariidae, Odobenidae, and the Desmatophocidae was followed. Recent compelling evidence (Wyss, in prep.) casts doubt on pinniped diphyly and argues that the otarioids are not a natural group and are nested within the Pinnipedia which includes the above mentioned families and the Phocidae.

While we support relationships among members of the Otariidae proposed herein we acknowledge the fact that several basal characters used to separate the Otariidae from *Enaliarctos* are also found among other pinnipeds.

**APPENDIX**

Definitions and evaluations of the characters used in the cladistic analysis.

1. *Lacrimal foramen absent*  
   Presence of the lacrimal foramen in enaliarctids distinguishes them from all other otarioids (Mitchell and Tedford 1973) with the exception of some allodesmids (Repenning, personal communication).

2. *Supraorbital processes large and well-developed*  
   The presence of large supraorbital processes, especially strong in adult males, is diagnostic of the Otariidae and distinguishes them from the Enaliarctidae (Repenning and Tedford 1977).

3. *Nasolabialis fossa absent*  
   The nasolabialis fossa described by Mitchell and Tedford (1973:232, 234) as a triangular, shallow fossa on the side of the snout is found in enaliarctids. The absence of this fossa is a derived condition in otarioids.

4. *Carnassials absent*  
   The enaliarctids can be distinguished from all other otarioids in their possession of a fissipeded-like dentition in which P4 has a protocone or protocone shelf, and M1 has a talonid. A homodont dentition is derived and characteristic of later otarioids.

5. *P1 simple*  
   A simple lateral upper incisor characterizes most fossil and modern otariids. *Pithanotaria starri* shows the primitive urinary condition, in which P1 displays a posterior broadening of the crown near the base with a distinct posteromedial lingual cingulum preserved in a referred specimen (Repenning and Tedford 1977).

6. *P3 single-rooted*  
   The development of single-rooted cheekteeth, a trend that began with P3, is a derived condition among otarioids, also seen in more advanced desmatophocids and odobenids (Mitchell 1975).

7. *P3a4 single-rooted*  
   Further modification of the trend towards single-rooted cheekteeth occurs in the posterior premolars, P3a4; a feature long recognized as diagnostic of living fur seals and sea lions (Repenning and Tedford 1977).

8. *M2 absent*  
   Since, as noted by Repenning and Tedford (1977), the absence of M2 in the holotype and only known referred specimen of *Pithanotaria starri* may be the result of individual variation, its absence is tentatively regarded as a uniquely derived character for the monotypic genus.

9. *Mandibular foramen anteroventrally directed*  
   The anterior margin of the mandibular foramen is directed anterodorsally in *Enaliarctos* (this study), *Thalassoleon mexicanus* and *Callorhinus*. In the derived condition seen in *Arctocephalus* and sea lions this margin slopes anteroventrally (Fig. 3).

10. *Mandibular condyle elevated high above the base of the ascending ramus*  
    A high mandibular condyle is described and figured by Repenning, Peterson and Hubbs (1971:21; Fig. 7) as diagnostic of *Arctocephalus australis*. According to de Muizon (1978, Fig. 2) the derived condition is also seen in the fossil *Hydrarctos lomasiensis* and *Otaria*.

11. *Calcaneum with well-developed secondary shelf of sustentaculum*  
    All living otariids possess a well-developed secondary shelf of the sustentaculum (Robinette and Stains 1970). This shelf is lacking in *Enaliarctos* (this study). As reported by Repenning and Tedford (1977), this shelf is also lacking in *Thalassoleon mexicanus* and only slightly developed in *Hydrarctos lomasiensis* (de Muizon 1978).

12. *Vertebral foramen enlarged*  
    *Thalassoleon mexicanus* is diagnosed as having vertebral foramina of all vertebrae small relative to those of living otariids (Repenning and Tedford 1977), but they are larger than in terrestrial carnivores. The derived condition, enlarged vertebral foramen, characterizes all other living otariids.

13. *Tibia and fibula fused proximally*  
    The unfused tibia and fibula of *Callorhinus* noted by Lyon (1937) is tentatively interpreted as retention of the primitive condition, seen in *Enaliarctos* (this study) and reported by Kellogg (1925) for *Pithanotaria*. "Thalassoleon" macnallyae, in contrast to *T. mexicanus*, has a fibula fused proximally to the head of the tibia (Repenning and Tedford 1977). In all other living otariids the tibia and fibula are likewise fused at their proximal ends.

14. *Basioccipital rectangular*  
    According to Repenning and Tedford (1977) the basioccipital is trapezoidal in *Thalassoleon*, *Neoaphoca*, and *Zalophus*. Our analysis indicates that *Enaliarctos*, *Eumetopias* and *Otaria* also share...
the primitive condition. The shape of the basioccipital in *Pithanotaria* is equivocal, owing to incompleteness of this region of the skull in published specimens. In the derived condition, observed in all living fur seals and *Phocarctos*, this bone is rectangular with parallel lateral margins.

15. *P* oval in cross section

The size and shape of *P* has been recognized as distinguishing fur seals from sea lions (Repenning et al. 1971). A large *P* with a circular cross section typifies sea lions. Fossil otariids including *Enaliarctos*, *Thalassoleon* and *Pithanotaria* share the primitive condition of an oval *P* although they generally lack the large size of this tooth.

16. Coronoid process narrow

The coronoid process is very broad and overhanging along its posterior margin in *Enaliarctos* (this study) and *Thalassoleon mexicanus* (Repenning and Tedford, 1977). *Arctocephalus* has been distinguished by Repenning, Peterson, and Hubbs (1971, Fig. 7) on the shape of the coronoid process. The presumably derived condition, a narrow process with posterior margin undercut and overhanging at the base is found in *A. gazella*, *A. forsteri*, *A. galapagoensis*, *A. philippii*, *A. australis* and *A. townsendi* and *Callorhinus*.

17. Reduced premaxillary

The derived condition, defined as transverse width of premaxilla less than 40% of nasal length, especially apparent in lateral view, is an uniquely derived character for *Callorhinus ursinus* (Repenning et al. 1971, this study).

18. Lower cheek toothrow short

This character is defined as the length of the cheek toothrow relative to the distance from *P*, to the ascending ramus. The derived condition, a short toothrow, is here defined as a toothrow less than 75% of distance from *P*, to the ascending ramus (Fig. 4).

19. *M*¹ single-rooted

Among sea lions, *M*¹ is consistently single-rooted. Some variation was observed in fur seals, although in most species this tooth is double-rooted. The most variation recognized by Repenning et al. (1971) was in *Arctocephalus gazella*, where approximately 50% of this sample exhibited the double-rooted condition.

20. Accessory cusps on cheek teeth

The presence of prominent, anterior and posterior accessory cusps on the cheek teeth is a derived character observed in several species of fur seal, *Arctocephalus pusillus* and *A. australis* (variable) and sea lions *Neophoca*, *Otaria*, and *Phocarctos* (Repenning and Tedford 1977, this study).

21. *M*²⁻¹ positioned close together

Since a "persistent diastema between *M*¹⁻²" is diagnostic of *Thalassoleon* (Repenning and Tedford 1977), and was observed in *Enaliarctos* (Mitchell and Tedford 1973: fig. 5, Barnes 1979: fig. 20), the lack of a diastema is recognized as the derived condition.

22. Facial angle less than 125°

The facial angle is one of two characters identified by Repenning, Peterson, and Hubbs (1971 Fig. 1) that consistently distinguishes *Callorhinus* from *Arctocephalus* and all other otariids. In the derived condition, seen in *Callorhinus*, the facial angle is less than 125°.

23. Ectotympanic bone ornamented

In the derived state, the medial border of the ectotympanic bone is ornamented, producing a flat, knobby bulla especially characteristic of male *Callorhinus ursinus* and "*Thalassoleon" macnallyae*, unlike that of other species of *Arctocephalus* (Repenning et al. 1971, Repenning and Tedford 1977). Among sea lions, *Neophoca* has an ornamented ectotympanic bone although the degree and position of the ornamentation differs from that of *C. ursinus*.

24. Pterygoid process of mandible with medial shelf

Projection of the pterygoid process as a prominent medial shelf is recognized here as an autapomorphy in *Callorhinus ursinus*. *Zalophus* shows a tendency to develop a shelf of smaller size and different proportion.

25. Pterygoid process of mandible short and deep

The shape of the pterygoid process was used by Repenning, Peterson, and Hubbs (1971 fig. 7) to distinguish *Arctocephalus*. In *Thalassoleon mexicanus*, the pterygoid process was described as similar to that of *Arctocephalus pusillus* in being long and shallow (Repenning and Tedford 1977) and the same is true for *Enaliarctos* (this study). The derived condition, a short, deep pterygoid process, is observed in *Otaria* in addition to *A. galapagoensis*, *A. australis*, *A. forsteri*, *A. philippii*, and *A. townsendi*.

26. Nasals narrow

The derived condition defined as nasal width 70% of nasal length was recognized in *Arctocephalus philippii*, *A. tropicalis*, *Zalophus*, *Phocarctos* and *Otaria* (Repenning et al. 1971: fig. 7, Sivertsen 1954).

27. Cheek toothrow straight

In the primitive condition observed in fur seals, the cheek toothrow curves inward at *P*²⁻¹ and diverges at *M*¹ creating a sinuous toothrow. In the derived condition, diagnostic of sea lions, the cheek toothrow is nearly straight (Fig. 5). In *Otaria*, *Eumetopias* and *Phocarctos* the derived state is slightly modified and the teeth converge at *M*¹.

28. Humerus stout, pectoral crest directed toward midpoint of distal articulation

The derived condition of a robust humerus has been recognized as distinctive of sea lions. It has been suggested that the position of the pectoral crest resulted in a strengthening of the humerus, possibly related to their larger body size (Repenning and Tedford 1977).
29. Apex of baculum broad with keels  
The derived condition has been recognized as distinguishing sea lions from fur seals, which have a transversely narrow apex (Morejohn 1975). *Thalassoleon* and *Callorhinus* share a unique bacular morphology in which the bulbous ventral knob of the apex in anterior view resembles a "figure of eight" (Repenning and Tedford 1977).

30. Apex of baculum further expanded laterally  
A further modification of the derived state discussed above, in which the lateral edges of the apex are expanded, is observed in *Otaria, Neophoca, Eumetopias*, and *Phocarctos* (see references cited above).

31. Neopallium more convoluted  
The cerebrum of sea lions is characterized by more convolutions of the neopallium than that of fur seals (Repenning and Tedford 1977). More numerous neopallial convolutions are here interpreted as the derived condition based on the phylogeny established for fur seals and sea lions (see text).

32. Postcruciate sulcus  
The postcruciate sulcus which connects the longitudinal fissure to the lateral sulcus appears to be a unique feature of *Callorhinus*. Presence of this sulcus in a juvenile endocranial cast of a skull referred to "*Thalassoleon*" macnallyae is here considered a shared derived feature linking these taxa (Repenning and Tedford 1977).

33. Posterior ectosylvian gyrus, narrow and unconvoluted  
Among fur seals, *Callorhinus* appears unique in having a noticeably narrow and unconvoluted posterior ectosylvian gyrus relative to the width of the adjacent posterior suprasylvian gyrus (Repenning and Tedford 1977). Presence of this derived feature in "*Thalassoleon*" macnallyae is considered evidence of their close relationship.

34. Frontal-Parietal suture in posterior position  
A posterior position of the frontal-parietal suture relative to the distance between the front of the braincase and the lambdoidal crest was observed in immature *Callorhinus* and "*Thalassoleon*" macnallyae as a feature distinguishing them from *Thalassoleon mexicanus* and *Arctocephalus* (Repenning and Tedford 1977).

35. Underfur sparse  
The sparse underfur of sea lions has long been used to distinguish them from fur seals (Scheffer 1958). The presence of abundant underfur in fur seals has been considered retention of the primitive condition (Repenning and Tedford 1977).

36. Underfur terminates at wrist  
Among fur seals, *Callorhinus* can be distinguished from *Arctocephalus* in having the fur of the forelimb terminate in an abrupt line at the wrist, whereas in *Arctocephalus*, the fur extends distally past the wrist (Repenning et al. 1971). Since the loss of abundant underfur is recognized as the derived condition (see character 35) its more restricted occurrence in *Callorhinus* is judged derived.

37. Sucking louse host specificity  
The restricted occurrence of a more advanced sucking louse species, *Antarctophilus microchir*, on sea lions is interpreted as the derived condition. The presence of a more generalized taxon *Proechinophthirus* as a unique parasite on *Callorhinus ursinus* and *Arctocephalus pusillus* (and presumed, but not yet established on other species of *Arctocephalus*), judged to be the primitive condition, has been interpreted as evidence for the greater antiquity of fur seals. The fact that different species of *Proechinophthirus* inhabit the two genera of fur seals indicates that they have evolved separately for some time (Kim et al. 1975).

38. Strongly thigmotactic  
The tendency for sea lions and *Arctocephalus pusillus* to be strongly thigmotactic (limbs of different individuals in direct contact) while *Callorhinus ursinus* and other *Arctocephalus* species are not has been previously noted (Stirling and Warneke 1971 and references cited therein). Thigmotactic behavior is here interpreted as the derived condition based on the phylogeny established for fur seals and sea lions (see text).

39. Palate deep and concave  
The sea lions *Otaria, Neophoca* and *Phocarctos* share the derived condition of having deep, concave palates (Scheffer 1958, King 1960). The palate is more highly arched in *Phocarctos* and *Otaria* than in *Neophoca*. In *Phocarctos*, the palate is deep anteriorly like that in *Otaria* however it is flattened posteriorly like that in *Eumetopias* and *Neophoca* (Mitchell 1968).

40. Tympanic bulla with elongate posterior or posteroventral projection  
*Phocarctos* is characterized by having a "cylindrical projection of the bulla" (King 1960). As noted by Mitchell (1968) this projection is directed far posteroventrally in *Otaria* (where it is subequal in cross section) and posteriorly in *Eumetopias* (where it is more ovate in cross section). An elongate posterior or posteroventral projection of the tympanic bulla represents the derived condition.

41. Cheekteeth 5/5  
Reduction in number of cheekteeth from 6/5 to 5/5 is a derived feature in *Eumetopias* and *Neophoca*. According to King (1983) the number is variable in *Zalophus*; Californian animals more frequently having 5/5, Galápagos animals 6/5, while all variations are found in the Japanese animals.