NEW SKELETAL MATERIAL OF *THALASSOLEON* (OTARIIDAE: PINNIPEDIA) FROM THE LATE MIOCENE-EARLY PLIOCENE (HEMPHILLIAN) OF CALIFORNIA

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New crania, dentitions, and postcrania of the fossil otariid *Thalassoleon mexicanus* are described from the latest Miocene–early Pliocene Capistrano Formation of southern California. Previous morphological evidence for age variation and sexual dimorphism in this taxon is confirmed. Analysis of the dentition and postcrania of *Thalassoleon mexicanus* provides evidence of adaptations for pierce feeding, ambulatory terrestrial locomotion, and forelimb swimming in this basal otariid pinniped. Cladistic analysis supports recognition of *Thalassoleon* as monophyletic and distinct from other basal otariids (i.e., *Pithanotaria*, *Hydrarctos*, and *Callorhinus*). Re-evaluation of the status of *Thalassoleon* supports recognition of two species, *Thalassoleon mexicanus* and *Thalassoleon macnallyae*, distributed in the eastern North Pacific. Recognition of a third species, *Thalassoleon inouei* from the western North Pacific, is questioned.

Key Words: Otariidae; pinniped; systematics; anatomy; Miocene; California

INTRODUCTION

Otariid pinnipeds are a conspicuous element of the extant marine mammal assemblage of the world's oceans. Members of this group inhabit the North and South Pacific Ocean, as well as portions of the southern Indian and Atlantic oceans and nearly the entire Southern Ocean. Interestingly, there are no otariids in the North Atlantic Ocean. Although most species occur in coastal waters of mid- to high latitudes, a few species range into low latitudes where eastern boundary currents and upwelling combine to bring cool water to equatorial regions (e.g., Galapagos Islands). Given this wide geographic distribution it is somewhat surprising that the evolutionary history of otariids is so poorly understood.

Previous studies using morphology (Repenning & Tedford 1977; Berta & Deméré 1986; Brunner 1998) and molecular sequence data (Wynen et al. 2001) have attempted to determine phylogenetic relationships among taxa and to understand the history of otariid diversification. Unfortunately, the otariid fossil record is depau-

perate, with a very limited number of recovered specimens available for study. The earliest otariid, *Pithanotaria starri* Kellogg 1925, is known from the early late Miocene (Tortonian Stage equivalent) and is based on a few poorly preserved fossils from California. The holotype is an impression in diatomite of a partial skeleton of an immature individual and preserves only limited anatomical information. The same is generally true for referred material of this taxon described by Repenning and Tedford (1977). In contrast, fossil remains of *Thalassoleon mexicanus* Repenning and Tedford 1977 from the late late Miocene (Messinian Stage equivalent) of Baja California are more complete and provide a better understanding of basal otariids. Currently, the Messinian otariid record has virtually no diversity and is confined to the eastern North Pacific region. The Pliocene (Zanclian and Piacenzian stage equivalents) otariid record includes specimens from the western and eastern North Pacific region and consists of early Pliocene species from central California (*Thalassoleon macnallyae* Repenning & Tedford 1977) and Japan (*Thalassoleon inouei* Kohno 1992) and a later Pliocene species, *Callorhinus gilmorei* Berta and Deméré 1986 from California and Japan (Kohno & Yanagisawa 1997). The earliest southern hemisphere

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otariid is *Hydractos lomasiensis* (Muizon & de Vries 1985) from the early Pleistocene of Peru with a later Pleistocene record of the extant species *Neophoca cinerea*, reported from New Zealand (King 1983), and *Otaria byronia* from Brazil (Drehmer & Ribeiro 1998). A series of poorly documented fossil occurrences has been reported from the Pleistocene of Japan (*Callorhinus ursinus*, *Zalophus californianus*, and *Eumetopias jubata*; Miyazaki et al. 1995), with a few additional fragmentary fossil remains reported from the late Pleistocene of southern California (*Zalophus californianus*; Miller 1971). Although the later Pleistocene record includes several reports of extant taxa, these reports are not based on good cranial and/or dental remains. Even accepting the reported fossil occurrences, the majority of extant species have no fossil record. This implies a dramatic and rapid adaptive radiation of otariids during the Pleistocene (see also Deméré et al. 2003) that has yet to be documented by adequate fossil material.

In addition to the problems of a depauperate fossil record, there currently is uncertainty regarding otariid phylogenetic relationships (e.g., Berta & Deméré 1986; Lento et al. 1995; Wynen et al. 2001), with major questions concerning the monophyly of fur seals (Arctocephalinae) and sea lions (Otariinae), and even the monophyly of the genus *Arctocephalus* (Robinette & Stains 1970; Repenning et al. 1971; Lento et al. 1995). Proposed avenues for resolving some of these phylogenetic difficulties include expansion of the meager otariid fossil record and careful examination of extant and fossil taxa for phylogenetically useful characters. In this light, the present paper describes new fossil remains of *Thalassoleon mexicanus* from the late late Miocene and early Pliocene of southern California and considers the taxonomic status and phylogenetic position of this fossil species among otariids.

METHODS

Measurements, to the nearest 0.1 mm, of crania, dentitions, dentaries, and postcrania were taken using mechanical calipers and are listed in Tables 1-5. The functional limb lengths, defined as the distance between centers of rotation of the limb, were measured as described by English (1977:338) and Hildebrand (1952) (Table 6). Comparisons of limb proportions (i.e., limb indices) among pinnipeds and other carnivores are provided in Table 7. To facilitate anatomical comparisons among pinnipeds the following cranial indices (see also Deméré & Berta

2001) were employed: **facial index**, length of face (approximate level of cribriform plate to prosthion) divided by condylobasal length (CBL) X 100; **orbital index**, length of orbit (shortest distance from antorbital rim of maxilla to apex of postorbital process of jugal) divided by CBL X 100; and **palatal width index**, palatal width at lingual margin of canine alveoli divided by palate width at lingual margin of posterior root of M1 X 100.

Acronyms for institutions housing specimens used in this study are as follows: **CBMPV**, Natural History Museum and Institute, Chiba, Department of Earth Sciences, Vertebrate Paleontology Collections; **IGCU**, Instituto de Geologia, Ciudad Universitaria, Universidad Nacional Autonoma de Mexico; **OCPC-MV** , Orange County Paleontological Collection – Mission Viejo subcollection; **SDSNH**, San Diego Natural History Museum; **UCMP**, Museum of Paleontology, University of California, Berkeley; **UCR**, University of California, Riverside; and **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Within the text the following abbreviations are used: **AP**, anteroposterior measurement; **CBL** condylobasal length; **DV** dorsoventral measurement; **M**, mean; **Ma**, mega annum (10^6 years); **MC**, metacarpal; **MT**, metatarsal; **N**, sample size; **NALMA**, North American Land Mammal Age; **T**, transverse measurement.

Specimens illustrated in Figures 1, 5, and 6 were treated with an air-brushed coating of neutral gray poster paint followed by a light spray of water-soluble hair spray.

MATERIALS

The following fossil specimens were studied and compared with the new fossil material: (1) *Thalassoleon mexicanus*- cast of IGCU 902, holotype skull and jaws (Repenning & Tedford 1977); (2) *Thalassoleon inouei* – cast of CBMPV 087, holotype skull and jaws (Kohno 1992); (3) *Thalassoleon macnallyae* – UCMP 112809, holotype partial skeleton (Repenning & Tedford 1977); (4) *Pithanotaria starri* – rubber peel of impression of USNM 11050, holotype skeleton (Kellogg 1925); rubber peel of impression of USNM 11055, left forelimb (Kellogg 1925); rubber peel of impression of USNM 11056, right hindlimb (Kellogg 1925); referred palate UCMP 74813 (Repenning & Tedford 1977); (5) *Pacificotaria hadromma* – cast of LACM 127973, holotype skull (Barnes 1992); (6) *Enaliarctos emlongi*, USNM 250345, holotype skull and dentary with probable associated postcrania (Berta 1991); (7) *Enaliarctos mealsi* –cast of USNM skeleton (Berta & Ray 1990); (8)

Desmatophoca oregonensis, USNM 335541, referred skull (Deméré & Berta 2002); (9) *Proneotherium repenningi*, USNM 215068, referred skull (Deméré & Berta 2001).

LOCATION, STRATIGRAPHY AND CORRELATION

Marine sedimentary rocks of late Miocene to early Pliocene age exposed in Orange County, California, are generally assigned to the Capistrano Formation of Woodford (1925). Near the city of San Clemente in southern Orange County, the Capistrano Formation is at least 850 meters thick and divisible into a basal deepwater turbidite unit of breccia, sandstone, and siltstone overlain by 240 meters of massive diatomaceous siltstone and concretionary mudstone, and capped by 180 meters of massive micaceous siltstone (Ingle 1979). To the north, near El Toro, the formation is dominated by a lenticular sandstone unit, the Oso Member, which has a maximum thickness of about 450 meters (Vedder 1972). The Oso Member of the Capistrano Formation is probably a temporal and lithofacies equivalent to the San Mateo Formation near Oceanside (Domning & Deméré 1984). The lower portion of the Capistrano Formation was deposited at bathyal depths of up to 2,000 meters and contains displaced neritic microfossils (White 1956; Ingle 1979), as well as remains of marine mammals (Barnes & Raschke 1991). The Oso Member was probably deposited at shallower, continental shelf depths (Vedder 1972).

The age of the Capistrano Formation is established on benthonic and planktonic foraminifers and siliceous microfossils. Ingle (1979) reported on late Miocene foraminifers (Mohnian Benthic Foraminiferal "Stage") in the lower half of the Capistrano Formation and early Pliocene foraminifers (Repettian Benthic Foraminiferal "Stage") in the upper half of the formation as exposed near San Clemente. Barron (1986) reported that the Capistrano Formation as exposed to the north at Newport Beach contains diatoms correlative with the upper portion of his subzone "b" of the *Nitzschia reinholdii* Partial Range Zone, latest Miocene (ca. 5.6-6.4 Ma). At San Juan Capistrano in Orange County diatomaceous layers from the middle of the Capistrano Formation, above the primary marine mammal producing horizons, contain diatoms of the lower *Thalassiosira oestruppi* Partial Range Zone (S.A. Kling pers. comm.), earliest Pliocene (4.9-5.6 Ma). This indicates that the Miocene/Pliocene boundary occurs within the Capistrano Formation and sug-

gests a correlation with the Messinian and lower Zanclian stages of international usage (Harland et al. 1990). In northern San Diego County, shallow sublittoral marine sandstones of the San Mateo Formation have been correlated with the Capistrano Formation (Elliott 1975). Domning and Deméré (1984) showed that two superposed lithostratigraphic units (a lower sandstone unit and an upper gravel unit) in the San Mateo Formation at Oceanside are correlative with the late late Miocene and early Pliocene, respectively. A sparse land mammal assemblage from the lower sandstone unit of the San Mateo Formation contains taxa correlative with the Hemphillian NALMA (Domning & Deméré 1984).

The otariid fossil remains reported here were collected from the siltstone lithofacies of the Capistrano Formation as exposed at San Clemente (SDSNH locality 4160) and San Juan Capistrano (SDSNH localities 3841, 3843, and 3845). The stratigraphic section exposed at the San Juan Capistrano site consists of approximately 100 m of massive siltstone with occasional interbeds of diatomaceous shale and fine-grained sandstone. Siliceous microfossils analyzed from this section suggest that localities 3843 and 3845 are late late Miocene (*Nitzschia reinholdii* Partial Range Zone), while locality 3841 is early Pliocene (*Thalassiosira oestruppi* Partial Range Zone).

The fossil pinniped genus *Thalassoleon* was founded on the basis of an adult male skull, dentary, and associated postcranial elements collected from the base of the Almejas Formation, Cedros Island, Baja California Norte, Mexico. The holotype was collected by R.H. Tedford and D.P. Whistler and described by Repenning and Tedford (1977) as *Thalassoleon mexicanus*. A second species known by fragments of an adult male skeleton (i.e., basicranium, maxillary fragment, mandibular fragment, vertebral and costal fragments, and anterior and posterior limb elements) collected from the early Pliocene portion of the Purisima Formation (originally published as the Drakes Bay Formation) of northern California was described by Repenning and Tedford (1977) as a new species, *Thalassoleon macnallyae*. A third species, *Thalassoleon inouei*, was described by Kohno (1992) based on the basicranial portion of a skull and both dentaries from the lower Pliocene Senhata Formation on the Boso Peninsula, Honshu, central Japan. Barnes (1998) suggested that new otariid fossil remains from beds stratigraphically higher in the Almejas Formation than the holotype of *T. mexicanus* may represent a new species of this genus.

PREVIOUS WORK

Thalassoleon is traditionally classified in the family Otariidae (equals subfamily Otariinae of Mitchell 1968 and Barnes 1989), which is included within the suborder Otarioidea of Repenning and Tedford (1977) along with the Odobenidae, Desmatophocidae, and Enaliarctidae. Barnes (1989) suggested that the Otariinae (Otariidae of this report) are most closely linked with *Pteronarctos* in a clade that also included the Enaliarctinae (i.e., *Enaliarctos*, *Pteronarctos* and *Pinnarctidion*). The Otariidae s.l. of Barnes (1989) (i.e., Enaliarctinae +Desmatophocinae+ Allodesminae+ Imagotariinae+ Dusignathinae+Odobeninae+Otariinae) was rejected by Wyss (1987), Berta (1991), and Berta and Wyss (1994) as a paraphyletic grouping that is based largely on shared primitive characters. For the same reasons, these authors also questioned the monophyly of the Otarioidea. Berta and Wyss (1994) recognized *Thalassoleon* as a basal otariid pinniped, with the Otariidae forming a sister group relationship to the Phocomorpha (Odobenidae+Desmatophocidae+ Phocidae).

SYSTEMATIC PALEONTOLOGY
Order CARNIVORA Bowdich 1821
Family OTARIIDAE Gill 1866
THALASSOLEON Repenning and Tedford 1977

Type Species.—*Thalassoleon mexicanus* Repenning and Tedford 1977

Distribution.—Late late Miocene-early Pliocene (Hemphillian NALMA) of California, Baja California, Mexico, and Japan.

Included Species.—*Thalassoleon mexicanus*, *T. macnallyae*, and *T. inouei*.
Emended Diagnosis.—Otariid pinniped with crown of I3 lacking a posterior accessory cusp, simple triangular postcanine teeth that lack anterior accessory cusps but possess variably developed posterior accessory cusps, postcanine teeth without labial cingula, double-rooted P2-M1 and p2-m1, supraspinous fossa lacking a sharply keeled scapular ridge, distal position of the pronator teres muscle attachment on the radius, weakly developed spine on the distal epiphysis of the radius, calcaneum lacking a secondary shelf of the sustentaculum, broad supraorbital processes of the frontals that lack triangular terminations, multiple palatine foramina with deep grooves, and unfused proximal tibia/fibula articulation.

THALASSOLEON MEXICANUS
Repenning and Tedford 1977
Emended Diagnosis of Species.—A species of

Thalassoleon distinguished from *T. inouei* and *T. macnallyae* by smaller size; crescentric mastoid process; broader ectotympanic crest lacking lateral projections; postcanine teeth of the mandible with sinuous crown bases; and broad, shallow masseteric fossa

Holotype.—IGCU 902 adult male skull, right and left dentaries, and associated postcranial elements. Collected by R.H. Tedford and D.P. Whistler on August 4, 1965.

Type Locality and Horizon.—UCR locality RV-7301, about 4.5 m above the base of the upper Miocene Almejas Formation, Cedros Island, Baja California Norte, Mexico.

Referred Specimens.—The following referred specimens from the Almejas Formation catalogued into the UCR collections were originally described by Repenning and Tedford (1977), but are now missing and presumed lost (C. H. Repenning pers. comm.):

- UCR 15249 astragalus; about 18 to 21 m above base of formation.
- UCR 15250, radius; about 12 m above base of formation.
- UCR 15251 partial adult male skull; 6-9 m above base of formation.
- UCR 15252, crushed juvenile male skull; 6-9 m above base of formation.
- UCR 15253, rostrum and temporal bone of adult female skull; approx. 7.5 m above base of formation..
- UCR 15254 most of two anterior limbs, vertebrae, and ribs; about 31 m above base of formation.
- UCR 15255 fragments of skull, dentary, two anterior limbs, and vertebrae; about 21 m above base of formation.
- UCR 15256 female humerus; between 12 and 18 m above base of formation.
- UCR 15257 male humerus, ulna, and distal termination of radius; between 12 and 18 m above base of formation.
- UCR 15258 hindquarters including os penis of adult male skeleton; about 21 m above base of formation.

The following referred specimens (SDSNH specimens collected by B. O. Riney) from the Capis-trano Formation have not been previously described:
- SDSNH 65155 - articulated left forelimb (partial scapula, humerus, radius, and ulna), sterne-

Table 1. Cranial and upper dentition measurements (mm) for SDSNH *Thalassoleon mexicanus* and *T. macnallyae*. a= measurement for alveolus; d= distorted; e=estimated measurement; *=measurement doubled for missing half; += broken specimen; da=damaged; D=dorsal; V=ventral; AP= anteroposterior; T= transverse; r=right; l= left.

Measurements	Thalassoleon mexicanus				T. macnallyae
	SDSNH 65172	SDSNH 68313	SDSNH 65164	OCPC-MV 3172	UCMP 112809
Condylobasal length	276.7+	245d	——	98.5	——
Palatal length	128.2+	——	——	——	——
Postpalatal length	149.5+	——	——	——	——
Facial length	158.5+	135d	——	——	——
Braincase length	120.6+	116d	——	68.5	——
C-M2 length	95.0	76d	72	56.4	——
Postcanine length	79e	63.5	58	——	——
Orbit length	——	58.7d	——	——	——
Rostral width at C1	64.3	——	——	38.2d	——
Palate width at P4 (anterior root)	38*	34e*	——	27.4d	——
Width at suprorbital processes	56.8*	44e*	——	——	——
Least interorbital width	36*	32e*	——	——	——
Width of braincase	112*	——	——	——	——
Zygomatic width	156*	——	——	——	138
Auditory width	112*e	——	——	——	96.4
Mastoid width	——	——	——	——	135.2
Basioccipital width	48e	——	——	——	40.5
Greatest width, occipital condyles	——	58	——	——	——
Greatest width, foramen magnum	——	28	——	——	——
I1, AP/T	——	3.8/2.9 (l)	4.0/2.5(l)	4.6/2.3(l)	——
I2, AP/T	——	4.6/3.6(l)	4.3/3.0(l)	4.1/2.8(l)	——
I3, AP/T	8.8/5.7(l)	—/4.5(r)	5.0/4.5(l)	7.3a/5.1a(l)	——
C1, AP/T	17.4e/13.4+ (l)	8.6/7.5e (l)	7.8/6.5(l)	8.9/7.9(l)	——
P1, AP/T	——	8.0/5.2(r)	6.5/4.8(l)	8.7a/4.8a(l)	——
P2, AP/T	7.3/5.2+(r)	8.6/5.9	7.3/4.6(l)	7.9/4.3(l)	——
P3, AP/T	7.2/4.1+	8.1/—(r), 7.2a/—(l)	7.3/4.6(r)	7.4/4.5 (l)	——
P4, AP/T	——	10e/—(r), 7.8a/—(l)	——	7.4/4.6(l)	——
M1, AP/T	13.4/—a (r)	——/— , 8.2a/—(l)-	8.1/4.3(l)	9.1/5.0(l)	——
M2, AP/T	12.2/—a	——/— , 7.4a/—(l)	7.1/4.4(r)	6.4/3.6(l)	——

brae, ribs, articulated hindlimb (femur, tibia, and fibula), right astragalus, left calcaneum, and right MT I or III. Collected from SDSNH Locality 3841.

- SDSNH 65158 – partial right scapula, ulna, and radius. Collected from SDSNH Locality 3842.
- SDSNH 65159 - partial right hindlimb (femur, tibia, and fibula). Collected from SDSNH Locality 3842.
- SDSNH 65163 - right and left dentaries, articulated right forelimb (partial humerus, complete radius and ulna, and carpals) in siltstone matrix slab; isolated left p3. Probable adult female based on size of C1. Collected from SDSNH Locality 3843
- SDSNH 65164 - crushed skull with partial dentition (left I1-3, C1, P1-2 and right I1, P1-3, M2). Collected from SDSNH Locality 3843.
- SDSNH 65165 - partial left hindlimb (femur, tibia, and fibula). Collected from SDSNH Locality 3843.
- SDSNH 65172 - poorly preserved skull with left I2, portions of right P2-4 and lower jaws (right dentary with tooth crown, probably p4, and left dentary with c1 and p4). Collected from SDSNH Locality 3845
- SDSNH 68313 - crushed skull with lower jaws and partial skeleton in well-cemented siltstone matrix slab; cervical and thoracic vertebrae, sternebrae, ribs, articulated right forelimb (scapula, humerus, radius, and ulna), articulated left forelimb (humerus, radius, and ulna), right MC I, and isolated phalanges. Probable subadult female based on size of C1, supraorbital processes, and presence of unfused metacarpal epiphysis. Collected from SDSNH Locality 4160.
- SDSNH 68315 – distal end of left tibia, right astragalus, left calcaneum, and metatarsal III. Collected from SDSNH Locality 4161.
- OCPC-MV 3172 - nearly complete skull with partial dentition (left I1-I2, C, P2-P4, M2 and right I1, C, P2-P4). Collected by Hugh M. Wagner from OCF-MV locality 35.

DESCRIPTION AND COMPARISON OF CRANIAL MORPHOLOGY

Skull.—The state of preservation of the Capistrano Formation skulls is such that it is not possible to determine complete suture ages using the methods of Doutt (1942) and Sivertsen (1954). The degree of closure of the sutures that are visible, however, does provide some indication of relative developmental age of individual specimens. These age estimates when combined with sex determinations based primarily on canine size indicate that one skull (SDSNH 65172) is probably an adult male individual, while the other skulls (SDSNH 68313, 65164, and OCPC-MV 3172) are probably subadult females.

None of the Capistrano Formation skulls are as complete or as well preserved as the holotype from the Almejas Formation. However, because the holotype skull represents a mature male individual, it possesses a number of secondary sexual characters that would not be present on skulls of females or immature males. In addition, the holotype skull has a very worn dentition and does not preserve any details of crown morphology. Several of the Capistrano Formation skulls, on the other hand, have well-preserved, unworn teeth. By combining the type and referred material from the Almejas Formation with specimens from the Capistrano Formation it is possible to assess morphological and sexual variation in this fossil otariid (Table1).

The Capistrano Formation adult male skull SDSNH 65172 is just a few mm longer (CBL = 277 mm) than the holotype (IGCU 902) suggesting similar sized individuals. The most complete female skull (SDSNH 68313) has a CBL (245 mm) that is 88.4% of that of the largest male skull (Fig. 1). This degree of sexual dimorphism in CBL is similar to that of the least dimorphic extant otariids (*Arctocephalus townsendi* - 88.3%, *Zalophus californianus wollebaeki* - 87.6 %, *Arctocephalus galapagoensis* - 86.5%, and *Arctocephalus foresteri* - 85.9%; data in Brunner 2000:tables 6, 11, 14, 15) and is distinctly less than that of the more highly CBL dimorphic otariid species (*Arctocephalus australis* - 74.3%, *Otaria byronia* - 76.8%, *Callorhinus ursinus* - 77.3%, and *Z. c. japonicus* - 77.6%; data in Brunner 2000:tables 2, 7, 8, 16). Sexual dimorphism in AP diameter of the lower canine is also similar to that observed in extant otariids. Comparing the lower canines in SDSNH 65172 (18.6 mm) with those in SDSNH 68313 (9.1 mm) and 65163 (8.9 mm) indicates that female canines are only 48 to 49% of the size of male teeth. This degree of lower canine dimorphism is similar to the median values for extant otariids (data in Brunner 2000:tables 1-14).

It was not possible to measure the facial angle as defined by Repenning et al. (1971) for the new skulls, but we were able to measure the angle formed by the
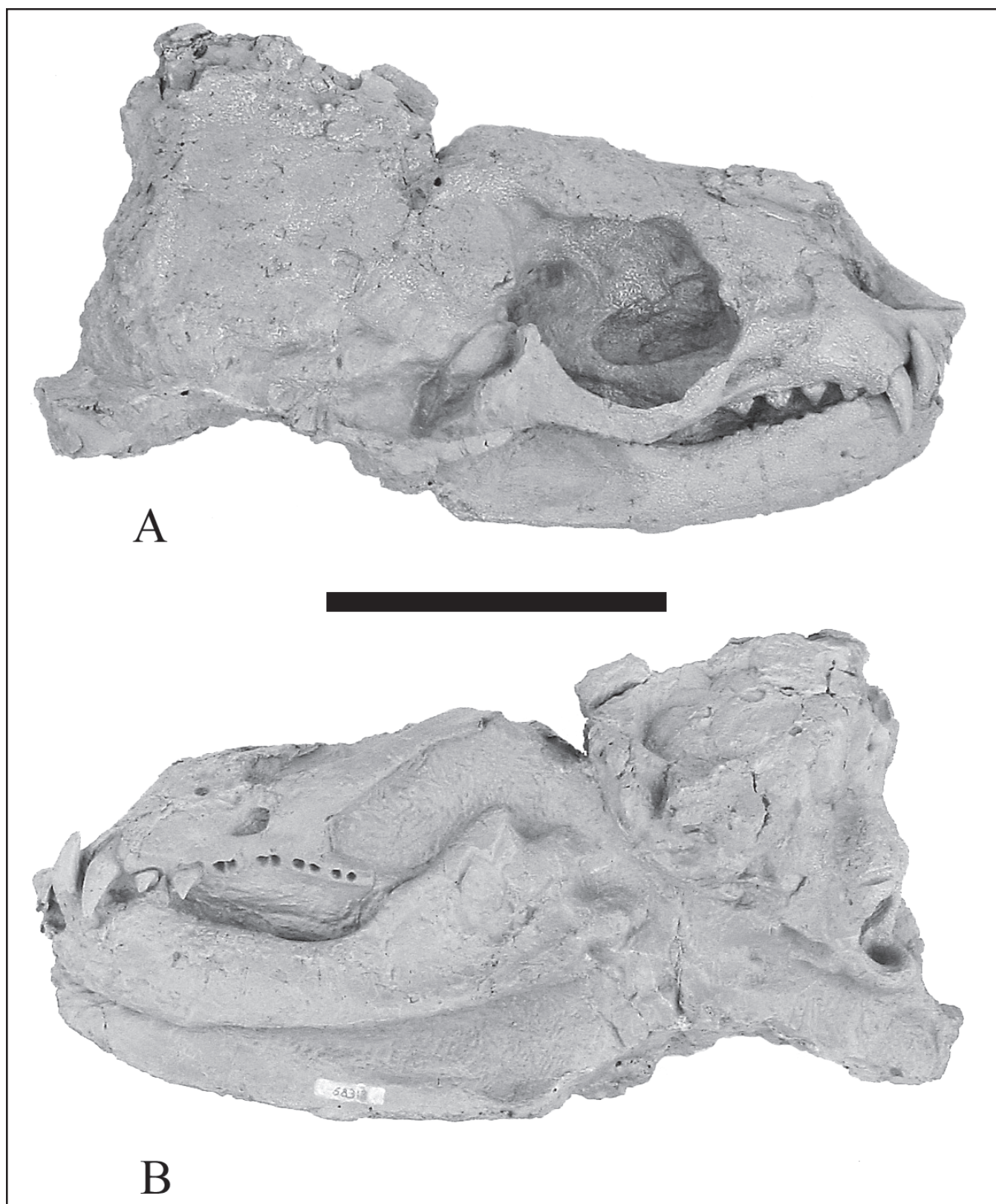
Figure 1. *Thalassoleon mexicanus* SDSNH 68313, skull and mandible. A, right dorsolateral aspect; B, left ventrolateral aspect. Scale bar equals 10 cm.

Table 2. Cranial indices in *Thalassoleon mexicanus* and selected extant otariids (see text).

Specimen	Facial Index	Orbital Index	Temporal Fossa/ Orbital Index	Palatal Width Index
Thalassoleon mexicanus				
holotype cast	56.4	24.2	64.2	89.0
SDSNH 65172	57.3	15.2	——	84.8
SDSNH 68313	55.0	24.0	77.6	——
Callorhinus ursinus (n=4)	50.1	27.4	66.6	64.8
Arctocephalus townsendi (n=2)	53.1	25.1	65.1	56.2
Zalophus californianus (n=4)	58.8	22.0	73.1	57.4
Eumetopias jubata (n=4)	57.3	19.6	89.7	78.2

intersection of the plane of the nasals and the plane of the premaxillary margins of the external nares. This prenasal angle in SDSNH 68313 is estimated at 161°. The prenasal angle measured on the cast of the holotype is 148°, 144° in *Callorhinus ursinus*, and 160° in *Zalophus californianus*.

Using the standardized cranial indices of Deméré and Berta (2001) we calculated facial indices in *Thalassoleon mexicanus* and a small sample of extant otariids (Table 2). The facial index of the cast of the holotype of *T. mexicanus* is 56, compared to 57 in SDSNH 65172 and 55 in SDSNH 68313. This indicates that *T. mexicanus* had a relatively short face in comparison to other extinct pinnipeds such as *Neotherium mirum* and *Allodesmus kernensis*, which have relatively longer faces and facial indices of 59 and 65, respectively. A small sample of extant adult otariids (N= 14) including both males and females of two fur seal species (*Callorhinus ursinus* and *Arctocephalus townsendi*) and two sea lion species (*Zalophus californianus* and *Eumetopias jubata*) suggests that the facial index of *T. mexicanus* is most similar to that for sea lions. It is interesting to note that a growth se-

ries of skulls (SDSNH) of extant *Z. californianus* displays variation in facial indices from 56 (short) in the youngest skull to 61 (long) in the oldest. This pattern of developmental lengthening of the face has also been documented in phocids (King 1972) and needs to be considered when evaluating facial indices in fossil pinnipeds.

The orbital index is 24 in the cast of the holotype and 24 in SDSNH 68313. These measurements suggest relatively large orbits in *Thalassoleon* in comparison to *Enaliarctos* and basal odobenids, which have indices in the range of 18-21 (Deméré & Berta 2001). Among the extant otariid sample discussed above the orbital index for *Thalassoleon mexicanus* is more similar to values for fur seals than sea lions and indicates that the orbits in *T. mexicanus* are proportionally smaller than in *Arctocephalus townsendi* and *Callorhinus ursinus*. Orbital indices for the *Zalophus* sample were 23 for the youngest skull and 22 for the oldest.

The palatal width index is 85 in SDSNH 65172 and 89 in the cast of the holotype, indicating a narrow, nearly parallel palate in *Thalassoleon mexicanus*. These values are slightly lower (i.e., slightly wider pal-

ate) in *Eumetopias jubata* (78) and *Pithanotaria starri* (75) and even lower (i.e., even wider palate) in *Callorhinus ursinus* (65), *Arctocephalus townsendi* (56), and *Zalophus* (57). The other cranial indices of Deméré and Berta (2001) could not be determined due to poor preservation.

External Nares, Premaxilla, and Nasal.—The external narial region as preserved in SDSNH 68313 has been deformed by crushing of the left side (Fig. 1). A prominent premaxillary eminence lies at the anterior border of the nares. This structure is more gracile than the one preserved in the holotype male skull and probably represents a sexually dimorphic feature. Well-developed premaxillary eminences appear to be features related to developmental age and are variably seen in other fossil and recent pinnipeds (pers. obs.). The premaxillae along the margins of the external nares are smooth and do not preserve any obvious processes for attachment of the nasal cartilage. The premaxilla-maxilla suture adjacent to the nasals is partially preserved in OCPC-MV 3172. In this specimen the ascending process of the premaxilla has a relatively short overlap of the lateral side of the nasals (37%; 12.1 mm of 32.8 mm). This is similar to the condition in *Callorhinus ursinus* and contrasts with the longer overlap seen in species of *Arctocephalus* (55%-62%) and *Zalophus* (51%). The nasals in OCPC-MV 3172 are widely flared anteriorly as in many species of *Arctocephalus* and measure approximately 27 mm and 10 mm at their anterior and posterior borders, respectively. The anterior borders of the nasals form an anteriorly concave dorsal outline, with the lateral borders extending more anteriorly than the medial borders. The posterior borders of the nasals are not preserved well enough to determine whether the characteristic otariid W-shaped nasal-frontal-maxilla suture was present (Deméré 1994). A shallow fossa occurs on the right side of the rostrum below the floor of the nares and anterior to the canine root.

The posterolateral corner of the premaxillae in SDSNH 65164, SDSNH 68313, OCPC-MV 3172, and the cast of the holotype are retracted dorsally adjacent to the canines to form embrasure slots for the lower canines. These premaxillary embrasure slots appear to be characteristic otariid features and have not been reported for other groups of fossil and extant pinnipeds.

Maxilla.—The lateral maxillary surface of the rostrum of SDSNH 68313 is smooth and convex, although somewhat damaged by crushing on the right side. A distinct, narrowly keeled antorbital process occurs low on the anterior border of the orbit approximately in the position of similar shaped antorbital processes in extant otariids. Much larger processes occur in male skulls of *T. mexicanus*. Although the maxilla-frontal suture is not clearly visible in SDSNH 68313, it appears likely that the antorbital process is confined entirely to the maxilla as in extant otariids (Deméré 1994). Below the antorbital process is a small (relative to odobenids and certain phocids) infraorbital foramen that is transversely elongate and measures 15.2 mm by 7.5 mm on the left side of the holotype cast and 12.2 mm by 6.0 mm on the right side of SDSNH 68313. The maxillary shelf forming the floor of the foramen is relatively broad AP, measuring 20.6 mm in the cast of the holotype, 20.2 mm in SDSNH 65172, 13.7 mm in SDSNH 68313, 14.5 mm in SDSNH 65164, and 12.6 mm in OCPC-MV 3172. The maxilla-jugal suture is weakly preserved on the right side of OCPC-MV 3172 and is constructed as in extant otariids and fossil odobenids, desmatophocids, and basal pinnipediformes (i.e., the jugal has dorsal and ventral processes that interdigitate with a triangular maxillary process).

Frontal.—The supraorbital processes are present but incompletely preserved in SDSNH 65172 and 68313. They form broad based shelves similar to those seen in the holotype of *Thalassoleon mexicanus*, although not as large. The Capistrano Formation specimens and the holotype lack the sharply triangular terminations of the supraorbital processes seen in most extant otariids. In other described fossil otariids, only *Hydrarctos lomasiensis* preserves supraorbital processes that are sharply triangular. Unfortunately, the condition in *Pithanotaria starri* is currently unknown. In basal fossil pinnipeds (e.g., *Pacificotaria*, *Desmatophoca*, and *Proneotherium*) tiny rounded swellings mark the position of the supraorbital processes. Such processes are lacking in all known dusignathine and odobenine odobenids (Deméré 1994), as well as in fossil and most extant phocids.

The frontal posteriorly forms the square anterolateral corners of the braincase as seen in most basal and extant pinnipeds. This contrasts with the condition seen in later diverging odobenine walruses where there is no distinct cranial corner and instead the anterolateral border of the braincase merges gradually with the orbital wall. At the midline of the frontal in the interorbital region of the male Capistrano Formation skull (SDSNH 65172) are distinct temporal crests that diverge anteriorly toward the supraorbital processes. These are also present in the holotype male skull and are probably sexual dimorphic features.

Orbital Wall.—Although the orbital wall appears

to be preserved in the holotype skull, its morphology was not described by Repenning and Tedford (1977). The orbital wall is partially preserved in OCPC-MV 3172 and has a relatively large, rectangular vacuity that extends from the level of the pterygoid notch to the orbital rim. Similar anteriorly placed vacuities occur on the orbital walls of extant otariids. Due to poor preservation the configuration of the optic foramen and the orbital fissure cannot be determined on any of the Capistrano Formation specimens.

Parietal.—A sagittal crest is well developed on the holotype male skull and extends anteriorly onto the frontal. A sagittal crest is not preserved on the Capistrano Formation skulls except for a short remnant segment at the coronal suture in the male skull (SDSNH 65712). The female skulls show no indication of having possessed a sagittal crest; another probable sexually dimorphic feature. The pseudosylvian sulcus is distinct in SDSNH 68313 and the holotype of *Thalassoleon mexicanus* and equivocal in other specimens.

Pterygoid and Alisphenoid.—In the holotype of *Thalassoleon mexicanus* the foramen ovalis and the anterior lacerate foramen occupy a deep common fossa at the base of the alisphenoid. The pterygoid strut adjacent to the internal nares is transversely narrow as in *Pithanotaria* (UCMP 74813), *Hydrarctos* (Muizon 1978), and extant otariids, and not broad as in odobenids like *Imagotaria*, *Pontolis*, and *Dusignathus* (Deméré 1994). The narrow pterygoid strut in *Thalassoleon inouei* is longer and nearly straight and is associated with a relatively robust hamular process. A similar hamular process is preserved in the type of *T. mexicanus*.

Squamosal and Zygomatic Arch.—The squamosal fossa in the cast of the holotype is broad and continuous from the level of the preglenoid process to the lambdoidal crest. The broad anterior portion of the fossa (above the glenoid fossa) is weakly divided from the broad posterior portion of the fossa (above the external auditory meatus) by a slightly raised transverse region, as is the condition in desmatophocids (Deméré & Berta 2002). The weakly developed squamosal fossa in OCPC-MV 3172 is probably a result of sexual dimorphism. A continuous squamosal fossa without a raised medial region is the primitive condition and occurs in species of *Enaliarctos*, *Pteronarctos*, *Proneotherium*, *Neotherium*, *Imagotaria*, and fossil otariids (e.g., *Hydrarctos*). In many extant otariids the posterior portion of the squamosal fossa is reduced to absent (especially in juvenile specimens).

The zygomatic process of the squamosal is long and slender and broadly overlaps the posterior process of the jugal. The posterior process of the jugal is itself slender and extends posteriorly beneath the zygomatic process of the squamosal to the anterior margin of the glenoid fossa forming an elongate scarf joint. The postorbital process of the jugal is broad based and has a bluntly rounded termination.

Palate.—There are multiple palatine foramina with deep grooves opening anteriorly in the holotype of *Thalassoleon mexicanus*. This contrasts with the distinct right and left elongate anterior palatine foramina seen in early diverging pinnipeds (i.e., *Enaliarctos*, *Pacificotaria*, *Proneotherium*, and *Neotherium*). The palate of *Pithanotaria* (UCMP 74813) does not preserve adequate detail to evaluate the condition of palatine foramina in this basal otariid. The same appears to be true for the palate of *Hydrarctos* (de Muizon 1978).

The palate of *Thalassoleon* is narrow posteriorly (see previous discussion of cranial indices) and not arched transversely or longitudinally (Fig. 2). The toothrows are slightly sinuous in palatal aspect and curve inward at P2, outward at P4-M1, and inward again at M2. This is the primitive condition as noted by Berta and Deméré (1986) and occurs in basal pinnipedimorphs, fossil otariids (e.g., *Pithanotaria* and *Callorhinus gilmorei*), and extant fur seals (e.g., *Callorhinus ursinus* and *Arctocephalus* spp.). The toothrows are nearly straight in extant sea lions. A weak pterygoid process occurs in the holotype and OCPC-MV 3172 and extends well behind M2 as a narrow shelf. This shelf is more strongly developed than in extant otariids (i.e., *Zalophus*, *Arctocephalus*, and *Callorhinus*), but weaker than in basal pinnipedimorphs, which typically possess a notched lateral margin to accommodate passage of the minor palatine artery (Deméré & Berta 2001).

Mastoid and Basicranium.—In the cast of the holotype the mastoid process is distinctly crescentic in lateral aspect and the fossa posterior to it is distinctly embayed and elongated anteroposteriorly. In extant otariids the mastoid process is more cubic in shape in lateral aspect and the fossa is less embayed and tends to have a more vertical orientation. In *Thalassoleon inouei* the mastoid process is similar in size and structure to the holotype of *Thalassoleon mexicanus*. The mastoid process in *Thalassoleon macnallyae* differs in its relatively larger size and more vertically oriented posterior fossa. On the ventral surface of the mastoid in *T. mexicanus*, *T. inouei*, and *T. macnallyae* is a distinct embayment, the mastoid fossa. Extant otariids also possess distinct mastoid fossae. The mastoid-paroccipital crest preserved in the holotype skulls of *T. mexicanus*

Figure 2. Stereophotographs of *Thalassoleon mexicanus* OCPC-MV 3172, palate and upper dentition. Scale bar equals 2 cm.

and *T. inouei* forms a continuous horizontally oriented edge that is not dorsally arched as in species of *Enaliarctos* (Deméré & Berta 2002). The continuous mastoid-paroccipital crest in *T. mexicanus* is nearly straight with its ventralmost portion occurring at the mastoid process. In contrast, the continuous mastoid-paroccipital crest in *T. macnallyae* is more broadly convex ventrally as in extant otariids and has its ventralmost portion occurring midway between the mastoid process and the paroccipital process. The paroccipital processes in *T. mexicanus* and *T. macnallyae* are distinct but plate-like, and smaller than the processes in *T. inouei*. Paroccipital processes are not preserved in specimens of *Pithanotaria* and *Hydrarctos*.

The auditory bulla in the holotype of *Thalassoleon mexicanus* is mostly ectotympanic with a small, transversely narrow entotympanic. This is the general con-

dition in other fossil and extant otariids and contrasts with the phocid condition in which the entotympanic is transversely expanded at the expense of the ectotympanic. The medial portion of the ectotympanic in *T. mexicanus* projects ventrally as an anteroposteriorly elongate crest. The anterior portion of this crest is broad, while its posterior region is more sharply keeled (Repenning & Tedford 1977:pl.20). *Callorhinus* also shows complexity of the medial portion of the ectotympanic, however, it seems to be more sharply keeled anteriorly and more broadly rounded posteriorly. The ectotympanic crest of *T. mexicanus* is much broader than in the holotypes of *T. macnallyae* and *Thalassoleon inouei*. In these taxa the medial portion of the ectotympanic is produced into an extremely narrow, keel-like crest (Repenning & Tedford, 1977; Kohno 1992). In *T. macnallyae* the outline of this crest in lat-

eral aspect is marked with several distinct projections (Repenning & Tedford 1977:pl. 23, fig. 14). As noted by Kohno (1992), *T. inouei* lacks these projections and the degree of ornamentation observed in the holotype of *T. macnallyae*. The incomplete preservation of *T. inouei*, however, leaves open the possibility that the ornamentation has been altered by taphonomic processes. In *Zalophus* and species of *Arctocephalus* the ectotympanic is broad and lacks a medial crest. The medial ectotympanic crest in *Otaria* is only distinctly keeled posteriorly.

The stylomastoid foramen is visible in all specimens of *Thalassoleon* and separated from the hyoid fossa by a distinct strut.

The right petrosal has been prepared in the holotype of *Thalassoleon macnallyae* and preserves features not included in the type description by Repenning and Tedford (1977). The internal auditory meatus (IAM) is broadly oval with a common opening for the facial and vestibulocochlear nerves as in odobenids and desmatophocids (Deméré & Berta 2002). This contrasts with the smaller and nearly circular IAM reported in extant otariids (Wyss 1987). This distribution of character states indicates that in otariids the small, circular IAM represents the derived condition.

Upper Dentition.—The holotype male skull preserves a well-worn dentition consisting of three incisors, a canine, four premolars, and two molars per side. Repenning and Tedford (1977) reported that all postcanine teeth behind P1 are double-rooted and that there is a distinct diastema between M1 and M2 and a weaker diastema between P4 and M1. They noted that
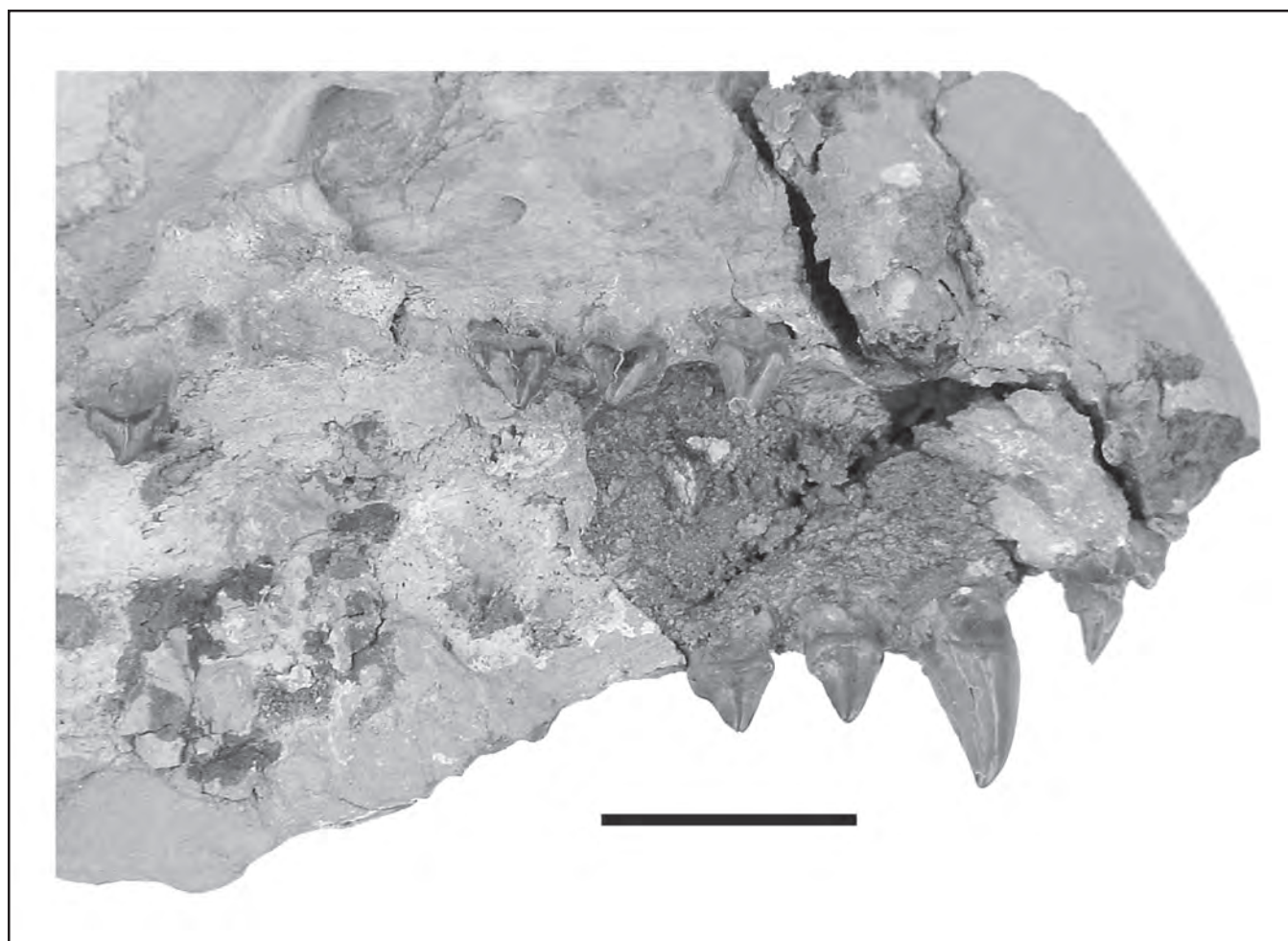

Figure 3. *Thalassoleon mexicanus* SDSNH 65164, right ventrolateral aspect of crushed skull and dentition. Scale bar equals 2 cm.

the postcanine tooth crowns "…form a single lanceolate cusp with moderate and rounded cingulum and no accessory cusps…." Because the holotype skull is an old adult male with its postcanine teeth well worn and lacking crown morphology, it is assumed that this limited description was based on referred cranial/dental material from the Almejas Formation. Unfortunately, this referred fossil material from the UCR collection is missing and presumed lost and it is not possible to examine this material for additional morphological features. The Capistrano Formation fossils, however, do preserve good crown morphology for most tooth positions. The following descriptions highlight features preserved in these fossils and provide an expanded view of the dental morphology of *Thalassoleon mexicanus* (Figs. 2-3).

The six incisors are arranged in a tightly packed arc well anterior to the canines. The crowns of I1-I2 on SDSNH 65164 and 68313 show apical wear, the former with greater wear than the latter. On the latter a transverse cleft bisects the crown, creating the bifid medial incisor crown morphology characteristic of extant otariids, but also preserved in *Pithanotaria*, and species of *Enaliarctos*, *Pteronarctos*, *Pacificotaria*, and *Proneotherium*. This transverse cleft extends onto the lateral margins of the crowns where it creates a slight indentation in the enamel surface. The crowns of the left I1 and I2 on SDSNH 65164, although worn nearly flat, preserve a flattened figure-8 shape where the remnants of the transverse cleft meet the lateral enamel surface. The I3 in SDSNH 65164 is approximately 50% larger than the I2 and has a nearly circular cross section as in extant sea lions and unlike the more oval cross sections of most extant fur seals (Repenning et al. 1971). A large wear facet on the posterolateral corner of the I3 crown was presumably produced by occlusion with the lower canine (Fig. 3). A much smaller longitudinal wear facet occurs on the medial side of the crown, presumably from occlusion with the lower lateral incisor. The crown of I3 consists of a strong conical principal cusp with a broad posterior cingulum most of which has been removed by the posterolateral wear facet. The posteromedial corner of the cingulum is slightly enlarged and has a small swelling or cuspule in the position occupied by a strong accessory cusp in *Pithanotaria starri* (UCMP 74813). A distinct diastema (approximately 5 to 8 mm wide) separates I3 from the canine in both skulls.

The canines in female skulls (SDSNH 65164 and 68313 and OCPC-MV 3172) are distinctly smaller (approximately 50%) and more gracile than in the male skull

SDSNH 65172 (Table 1). The medial border of the tooth is encircled by a narrow cingulum that merges posteriorly with a well-defined longitudinal crista and anteriorly with a less distinct longitudinal crista on the anteromedial border of the crown (Figs. 2-3). These cristae have smooth (non-serrated) edges and their position and orientation are similar to that in canines of many fossil and living pinnipeds including *Pacificotaria* (Barnes 1992), *Proneotherium* (Deméré & Berta 2001), *Callorhinus ursinus*, *Eumetopias jubata*, and *Zalophus californianus* (pers. obs.). The canine enamel is smooth.

The postcanine dentition is generally homodont, with all teeth characterized by a single principal cusp, triangular in lateral aspect. Several teeth preserve weakly to moderately developed accessory cusps (termed cuspids by Muizon 1978 and accessory cuspules by Kohno 1992). The lingual cingula of the postcanine teeth often have fine bead-like crenations.

The crown of the P1 in SDSNH 65164 consists of a single, sharply pointed principal cusp positioned slightly labial to the center of the crown (Fig. 3). A narrow cingulum encircles the lingual border, beginning and ending at the dorsal limit of the weak anterior and strong posterior cristae, respectively. Small crenations occur on the posterior 2/3 of the cingulum. There are no accessory cusps and no labial cingulum.

The crown of the P2 consists of a principal cusp less sharply pointed than in P1. There is no obvious anterior longitudinal crista, while the posterior crista is sharply developed with a slight flaring at the level of the cingulum. The cingulum encircles the lingual border forming a narrow shelf that extends from the anterior border of the crown to the apex of the posterior crista. Small crenations are irregularly spaced along the cingulum and are strongest on the anteromedial corner of the crown. The posteromedial corner of the cingulum is open. A small accessory cusp occurs just below the cingulum at the anterior corner of the crown in OCPC-MV 35-3172 (Fig. 2). A tiny circular wear facet in this position in SDSNH 65164 probably marks the worn base of an accessory cusp. Neither specimen preserves a labial cingulum. The root condition appears to be variable, consisting of two separate and diverging roots in the Capistrano Formation specimens and two coalesced roots in the Almejas Formation specimen.

The principal cusp of P3 is similar in size and shape to that of P2. There is a very weak anterior crista, while the posterior crista is sharply developed with a slight dorsal swelling on the dorsoposterolateral corner

Table 3. Measurements of the dentaries and lower dentition (mm) of SDSNH *Thalassoleon mexicanus* and *Thalassoleon macnallyae* (holotype*)*. Abbreviations as in Table 1.

Measurements	*Thalassoleon mexicanus*		*T. macnallyae*	
	SDSNH 65172	SDSNH 65163	SDSNH 68313	UCMP 112809
Total length	185.8	139.1 (l)	165.5 (l)	——
Length of toothrow c-m1	76.7	58.0	65e	——
Length of toothrow p1-m1	55e	45.0	——	——
Depth of mandible at m1	34.0	22.2	25.6e	35.5
Width of mandible at m1	16.0	9.2	9.8	16.2
Height of mandible at coronoid process	73	58	52	——
c, AP/T	18.0/11.0	9.6/6.0	8.5/7.4e (r), 9.0/6e (l)	——
p1, AP/T	——	4.6a/—(l)	——	——
p2, AP/T	——	7.4/4.0	——	——
p3, AP/T	——	8.0/4.5	——	——
p4, AP/T	9.0/5.7(l)	8.2/4.6(r)	——	8.5/5.0
m1, AP/T	——	9.1a/—(l)	——	11.3a/4.3a

of the crown (Fig. 2). This swelling is not produced as an accessory cusp, but occurs in the position of the posterior accessory cusp observed on some extant and fossil fur seals and sea lions. A cingulum encircles the lingual border forming a narrow shelf that extends from the anterolateral corner of the crown to at least the posteromedial corner where it is open posteriorly. The cingulum possesses small, irregularly spaced crenations, the largest of which occurs on the anteromedial corner of the crown and could be interpreted as a weak accessory cusp. There is no labial cingulum. Longitudinal wear facets occur on the anterior and posterior crown margins of some specimens. The root condition consists of two separate and diverging roots in all available specimens.

The principal cusp of P4 as preserved in OCPC-MV 35-3172 (Fig. 2) is similar in size and shape to those of P2 and P3. The anterior margin is rounded and there is no anterior crista. The posterior crista is sharply developed with a very slight flaring on the dorsal portion of the posterolateral corner of the crown (Fig. 2). A cingulum encircles the lingual border forming a narrow shelf that extends from the anterolateral corner of the crown around to at least the posteromedial corner where it is open posteriorly. As with P2-P3, the cingulum possesses irregularly spaced small crenations, the largest of which

on the anteromedial corner of the crown could be interpreted as a weak accessory cusp. There is no labial cingulum. The root condition consists of two separate and diverging roots in all available specimens.

A dislodged tooth found with SDSNH 65164 is almost certainly the left M1. The crown is characterized by a low, broadly triangular principal cusp, the apex of which is recurved slightly in the posteromedial direction. A weak longitudinal crista ascends the anterior border of the crown and terminates in a minute crenation on the anterior corner just below the enamel rim. A well-defined longitudinal crista ascends the posterior border of the crown and terminates in a conspicuous accessory cusp located at the posterolateral corner. A weak cingulum encircles the lingual border becoming better developed on the posteromedial corner of the crown. Several small crenations occur on the cingulum in this region and together with the posterior accessory cusp serve to define a weak "talon" basin. There is no anterior accessory cusp and no labial cingulum. The root condition consists of two separate and diverging roots in all available specimens. A distinct diastema occurs between M1 and M2 in the male skull (SDSNH 65172), but is lacking in the female skulls (SDSNH 65164 and OCPC-MV 35-3172).

The right M2 is preserved in its alveolus in SDSNH

65164 (Fig. 3) and the left M2 occurs as a dislodged tooth. The left M2 is also preserved in OCPC-MV 35-3172 (Fig. 2). Although slightly smaller, the M2 crown morphology is very similar to that observed for M1. The principal cusp is low and recurved posteromedially. A weakly developed posterior accessory cusp occurs at the apex of the short posterior crista. There is no anterior crista. Small crenations occur on the posteromedial corner of the very weak lingual cingulum, as well as on the anterior border of the crown. A small anterior accessory cusp occurs on the left M2 in SDSNH 65164 but not on the right. The posteromedial corner of the crown is produced as a weak 'talon' basin. Unlike the M1, the labial margin of the M2 crown is conspicuously swollen. As with all other teeth, there is no labial cingulum. The root condition consists of two separate and diverging roots in all available specimens.

The upper postcanine dentition of *Thalassoleon mexicanus* is similar to that of extant *Callorhinus ursinus* in certain aspects including: simple triangular principal cusps with smooth enamel; weakly developed anterior accessory cusps where present; weak anterior cristae and stronger posterior cristae sometimes flared posterodorsally; distinct lingual cingula with crenations; and no labial cingula. The extant species, however, has smaller, more sharply pointed principal cusps; stronger anterior cristae; wider lingual cingula; weaker crenations; weak posterior accessory cusps on P4-M2; and single-rooted P1-M2. The upper postcanine dentition of *Callorhinus gilmorei* (only P3-P4 and M2 reliably known) consists of smaller, more sharply pointed principal cusps; weak anterior cristae; narrow lingual cingula; small but distinct anterior accessory cusps (P3-P4); weaker crenations; and double-rooted P2-M1. The partial upper postcanine dentition of *Pithanotaria starri* as preserved in UCMP 74813 consists of sharply pointed principal cusps, weak lingual cingula without crenations, and no accessory cusps. The postcanine dentitions of extant species of *Arctocephalus* present a range of crown morphologies as discussed by Repenning et al. (1971). Well-developed anterior and posterior accessory cusps occur in *Arctocephalus pusillus* and *A. australis*. Weak to variably present anterior accessory cusps occur in *A. forsteri*, *A. tropicalis*, and *A. galapagoensis*. *Arctocephalus gazella*, *A. townsendi*, and *A. philippi* lack accessory cusps. The postcanine teeth of these taxa all apparently lack labial cingula and are typically single-rooted. The postcanine dentition of *Hydrarctos lomasiensis* as described by Muizon (1978) consists of simple triangular principal cusps with weak

lingual cingula. Weak anterior and posterior accessory cusps are reported on P4 and M1. A distinct diastema separates M1 and M2. The root condition includes single-rooted P1-3, bi-lobed single rooted P4 and M1, and distinctly double-rooted M2. Extant sea lions possess generally more complex postcanine crown morphologies with anterior and posterior accessory cusps (Brunner 2000). A limited survey of extant taxa by us revealed additional complexity as expressed in the variable development of labial cingula (totally absent from species of *Callorhinus* and *Arctocephalus*), distinct anterior and posterior cristae, cingular crenations, anterior and posterior cristae, and generally rough enamel. *Zalophus californianus* and *E. jubata*, for example, possess postcanine crowns with well developed labial cingula with weak crenations, narrow lingual cingula with strong crenations, and distinct anterior and posterior accessory cusps. This morphological series from simple crowns in basal otariids like *T. mexicanus* to more complex crowns in extant sea lions like *Z. californianus*, although perhaps counterintuitive, appears to reflect a true phylogenetic series.

Dentary.—The available sample of lower jaws of *Thalassoleon mexicanus* displays variation in size and shape, which is probably a reflection of sexual dimorphism. The jaws that are longer in total length with deeper and thicker horizontal rami and larger canines (IGCU 902 and SDSNH 65172) are assumed to be male, while the shorter and more slender lower jaws (SDSNH 65163 and 68313) are assumed to be female (Table 3). Using these morphological criteria it is also assumed that the holotypes of *Thalassoleon macnallyae* (UCMP 112809) and *Thalassoleon inouei* (CBMPV 87) are male.

Except where noted, the following description is based on the Capistrano Formation specimens and the holotype (IGCU 902). The masseteric fossa is broad and shallow relative to the deeper fossa in the holotype of *Thalassoleon macnallyae* (UCMP 112809). The coronoid process is broad at its base and apex and does not have an overhanging posterior margin. The anterior margin of the coronoid process meets the horizontal ramus at an angle of 111 to 120º. The mandibular condyle is positioned low on the dentary (at the level of the toothrow) relative to the condition in some species of *Arctocephalus* (i.e., *A. australis* as discussed by Repenning et al., 1971). The left dentary of the holotype preserves a distinct marginal process for insertion of the digastric muscle. This process is placed rather forward on the ventral margin and at the level of the
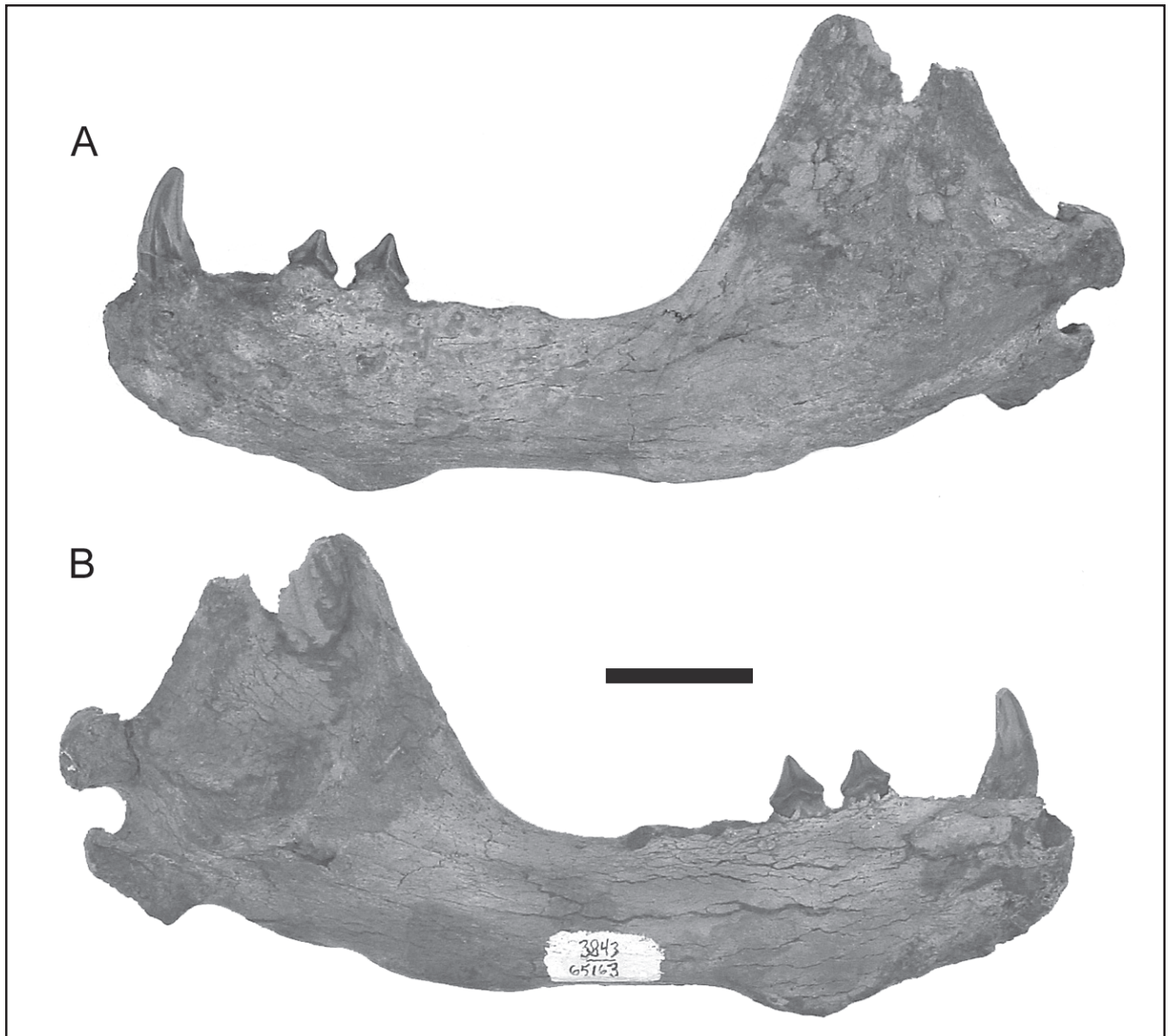
Figure 4. *Thalassoleon mexicanus* SDSNH 65163, left dentary. A, lateral aspect; B, medial aspect. Scale bar equals 2 cm.

anterior border of the masseteric fossa. The marginal process on the left dentary of SDSNH 65163 is more weakly developed, but occurs in the same location on the ventral margin. It is noteworthy that the dentaries of *Thalassoleon inouei* (CBMPV 087T) lack a well-defined marginal process, even though their robustness suggests that they represent an adult male individual. As discussed by Repenning and Tedford (1977) the pterygoid process on the holotype dentary of *Thalassoleon mexicanus* is shallow with little development of a mediad directed shelf. On the left dentary of SDSNH 65163 the pterygoid process is deeper than in

the holotype, but is also not directed as a shelf (Fig. 4). There are large mental foramina on the midline of the horizontal ramus. The anterior foramen is below the contact between p2 and p3. It is large and open anteriorly. The other large foramina occur together in a common shallow fossa below p3. A genial tuberosity is generally weakly developed and on the female dentaries SDSNH 65183 and 65164 is represented by a sharply edged keel (Fig. 4). In the Senhata Formation specimen of *T. inouei* the genial tuberosity is more strongly developed.

Lower Dentition.—Repenning and Tedford (1977)

reported that the holotype dentary of *Thalassoleon mexicanus* has two lower incisors per side. Although probably also true for the Capistrano Formation specimens, this feature cannot be confirmed because of poor preservation. The postcanine toothrow in all specimens begins on the lateral side of the ramus but moves to the medial side at the position of m1, giving the toothrow a straight (not concave or convex) occlusal alignment as in extant otariids. The teeth are closely positioned in the toothrow such that no diastemata are present. The m1 is positioned well anterior to the midpoint of the dentary length yielding MM$_1$/DL ratios (Adam & Berta 2002:92) between 59 and 62. These ratio values are consistent with those reported in extant otariids and are correlated with a pierce feeding prey capture strategy. Articulation of the dentaries with the skull reveals that the posterior upper postcanines (M1-M2) lie well lingual to the lower postcanine teeth and do not occlude with them. This is another unique otariid feature noted by Adam and Berta (2002:91).

No incisor crowns are preserved in any available specimens. The canines are 50% larger in the male dentary (SDSNH 65172) than in the female dentaries (SDSNH 65163 and 68313). A medial longitudinal crista is preserved on the broken crown of the right canine in SDSNH 65172. The crista is located on the anteromedial corner of the crown and curves posteriorly as it descends toward the alveolar margin. A similar medial crista is seen in the canine of SDSNH 65163 (Fig. 4). The large, well developed wear facets on the posterior margin of all available specimens of c1 extend the full height of the crown and obliterate any trace of a posterior crista, were one present. The enamel is smooth and approximately 0.1 mm thick.

With the exception of p1 the postcanine teeth are all double rooted. In all of the postcanine teeth in the Capistrano Formation sample the base of the enamel crown in lateral aspect is sinuous and dorsally arched in contrast to the straight crown base seen in the holotype of *Thalassoleon macnallyae*.

The lateral side of the left p1 is preserved in SDSNH 68313. The crown consists of a single central cusp that broadens posteromedially at the base. The cusp is triangular in lateral aspect and does not appear to have any accessory cusps.

The p2 is well preserved in both jaws of SDSNH 65163 (Fig. 4). The crown is broadly triangular and lacks obvious accessory cusps. There are, however, several small crenations on the anterior half of the lingual cingulum. Kohno (1992) referred to such crenations as accessory cuspules in *Thalassoleon inouei*.

There is no labial cingulum. Distinct longitudinal wear facets occur on the anterior and posterior margins of the left p2 suggesting an interlocking occlusion of the upper and lower postcanine teeth. The anterior margin of the right p2 lacks a distinct crista and is unworn.

The p3 is similar in shape to the p2, although the lingual cingulum is less well developed with even weaker crenations. There are anterior and posterior longitudinal wear facets on the left p3 of SDSNH 65163 (Fig. 4). The anterior margin of the right p3 of this specimen is unworn and preserves a weak crista that is slightly expanded at the base of the crown. The enamel on the labial surface of the crown is locally roughened and there is no cingulum.

The right p4 on SDSNH 65163 is very similar to p3 but has a slightly better developed rudimentary anterior accessory cusp. Although worn the margin of the lingual cingulum does preserve small crenations. Wear facets on the anterior and posterior slopes of the crown have removed traces of all but the base of the anterior crista. The enamel on the labial surface of the crown is locally roughened and there is no cingulum. The p4 in the holotype of *Thalassoleon macnallyae* possesses a lingual cingulum marked by well-developed crenations along its entire length. A distinct crista is also preserved on the posterior margin of the crown and a broad wear facet on the anterior margin of the crown has obliterated any trace of a crista or accessory cusp. The p4 of *T. macnallyae* is nearly the same size as in the female Capistrano Formation specimen (Table 3), yet the latter specimen is a male with a more robust jaw. Kohno (1992) reported the presence of a posterior accessory cusp on the p4 of *Thalassoleon inouei*, but no such structure occurs in either *Thalassoleon mexicanus* or *T. macnallyae*.

An isolated left postcanine tooth preserved with SDSNH 65163 is most likely an m1. This tooth is broadly triangular with broad anterior and posterior wear facets that have obliterated all but the base of the posterior crista. There is no posterior accessory cusp. The lingual cingulum is narrow and marked by a series of worn crenations. The enamel on the labial surface of the crown is locally roughened and there is no cingulum. This tooth in the holotype of *T. mexicanus* is completely worn leaving no crown preserved.

The lower postcanine dentition of *Thalassoleon mexicanus* differs from that of other fossil and extant otariids in its general crown simplicity and lack of distinct anterior and posterior accessory cusps. The postcanine dentition of *Callorhinus ursinus* consists of

tooth crowns with relatively smaller and more sharply pointed triangular principal cusps; small but distinct anterior accessory cusps, and no posterior accessory cusps. All teeth are single-rooted. *Callorhinus gilmorei* has a lower postcanine dentition similar to that of *C. ursinus* with sharply pointed principal cusps and small anterior accessory cusps. The crowns of *C. gilmorei*, however, are relatively larger and m1 possesses a posterior accessory cusp. The root condition in this taxon consists of single-rooted p1-p2 and double-rooted p3-m1. The lower postcanine dentitions of extant species of *Arctocephalus* reveal a great deal of variation for the upper dentition and include well-developed anterior and posterior accessory cusps in *A. pusillus* and *A. australis*; weak to variably present anterior accessory cusps

in *A. forsteri*, *A. tropicalis*, and *A. galapagoensis*, and simple crowns without any accessory cusps in *A. gazella*, *A. townsendi*, and *A. philippi*. These taxa also lack labial cingula and are typically single-rooted. The lower postcanine dentition of *Hydrarctos lomasiensis* has weak anterior accessory cusps on at least p1, p4, and m1 and a weak posterior accessory cusp on m1 (Muizon 1978). A partial survey of extant sea lions by us found a pattern of generally more complex lower postcanine crown morphologies similar to that observed for the upper dentition. This crown complexity is expressed in the rather distinct anterior and posterior accessory cusps and the variable development of labial cingula, anterior and posterior cristae, cingular crenations, anterior and posterior cristae, and generally roughened enamel.

Figure 5. *Thalassoleon mexicanus* SDSNH 68313, partial skeleton in siltstone slab. Scale bar equals 10 cm.

DESCRIPTION AND COMPARISON OF POSTCRANIA

Vertebrae.—All seven cervical vertebrae and at least three anterior thoracic vertebrae of SDSNH 68313 are preserved in well-cemented siltstone matrix (Fig. 5). Only the right lateral portions of two of the thoracic vertebrae, however, have been prepared. These specimens possess a narrow vertical neural spine and large, knoblike transverse processes. Unfortunately, the diameter of the neural canal cannot be determined. A broken lumbar or thoracic vertebra is preserved in SDSNH 65155, but is too poorly preserved to warrant description.

Sternebrae.—Four sternebrae are preserved in matrix in SDSNH 68313 (Fig. 5). They range in length from approximately 43 to 48 mm and are approximately 30 mm in transverse thickness. Two sternebrae are preserved in SDSNH 65155. One of these is the xiphoid, which has been distorted by torsion. It measures 69 mm in length and has a sharp ventral keel. The anterodorsal half is compressed transversely in contrast to the distal half, which is broad and laterally flared.

Ribs.—Portions of eight ribs are partially prepared in relief on the matrix block of SDSNH 68313 (Fig. 5). These include a probable first rib and several middle ribs. The former measures 85 mm in length and has a cubic tubercle and small head at the end of a very elongate neck. The shaft of this rib is oval in cross section.

Scapula.—The following description is based primarily on new specimens from the Capistrano Formation including SDSNH 68313 (complete right scapula with only lateral surface prepared), SDSNH 65159 (partial right scapula), and SDSNH 65155 (glenoid portion of left scapula). SDSNH 68313 has the elongated fan-shape that is typical of otariid scapulae (English 1977) and possesses a height (dorsal-ventral dimension) to length (cranial-caudal dimension) scapular index of 72 (Fig. 5). In contrast, Repenning and Tedford (1977) report that topotypic scapulae of *T. mexicanus* from the Almejas Formation have a scapular index of nearly 100. This proportional difference is primarily due to the shape of the cranial scapular angle, which in the Almejas Formation scapulae consists of vertebral and cranial borders that form one continuous arc extending to the caudal angle (Repenning & Tedford 1977:pl. 22, fig. 9). This is similar to the condition reported for *Pteronarctos* (Berta 1994) and contrasts with the condition in SDSNH 68313 (Fig. 5) and extant otariids where the cranial border is expanded and makes a more angular contact with the vertebral border. Repenning and Tedford (1977:64) suggest that this morphological difference may reflect

the lack of, or rudimentary development of, the episubscapularis muscle (cranial portion of subscapularis muscle) in *T. mexicanus*. However, this seems unlikely given the importance of this muscle in controlling otariid forelimb retraction (English 1977).

Except for the differences in cranial border outline, the Almejas and Capistrano formation scapulae are distinctly otariid. The supraspinous fossa in scapulae from both samples is more than twice the size of the infraspinous fossa and the caudal scapular angle is distinctly expanded for attachment of the deltoid and serratus ventralis muscles. The cranial and caudal portions of serratus ventralis are considered to be important scapular rotators involved in forelimb retraction and protraction. The deltoid is especially well-developed in extant otariids and is implicated in forelimb abduction and lateral rotation at the glenohumeral joint. The supraspinous fossa in the fossil scapulae is divided longitudinally by a broad fold that corresponds medially with a distinct flexure marking the division between the origins of the medial and cranial portions of the subscapularis muscle. Similar broad longitudinal folds have been noted on scapulae of *Enaliarctos* (Berta & Ray 1990), *Pteronarctos* (Berta 1994), *Desmatophoca* (Deméré & Berta 2002), and fossil (*Pithanotaria*) and extant otariids. However, in extant otariids (English 1977:fig 1) a sharply keeled scapular ridge (= secondary spine of Berta & Wyss 1994) is superimposed on this broad fold but diverges from it dorsally. King (1983) suggested that a well-developed scapular ridge (especially large in *Otaria*) is a feature unique to otariid pinnipeds. The Capistrano Formation fossils, however, clearly demonstrate that evolution of a well-developed scapular ridge in the supraspinous fossa of otariids occurred later than *Thalassoleon*.

The infraspinous fossa in SDSNH 68313 has a distinct caudal scapular ridge separating the origin of the infraspinatus and deltoid muscles as seen in extant otariids (English 1977). An additional ridge occurs at the caudal border of the deltoid fossa and serves to define the region for attachment of the teres major muscle. In contrast, the infraspinous fossa in *Enaliarctos*, *Pteronarctos*, and *Desmatophoca* is undivided.

The prominent scapular spine in SDSNH 68313 does not reach the vertebral border of the scapula and is tall, thin, and strongly recurved caudally to overhang the cranial border of the infraspinous fossa. The scapular spine in *Zalophus* and *Callorhinus* also does not reach the vertebral border, but is shorter and thicker and has a broad flattened distal crest. The acromion process is

distinct in SDSNH 68313 and projects caudally and ventrally to overhang the neck of the scapula. In *Pteronarctos* (Berta 1994) the acromion is larger and projects cranially, while in *Desmatophoca* (Deméré & Berta 2002) the large acromion projects caudally and ventrally. The glenoid cavity in SDSNH 65158 is deep and hemispherically shaped with delicate margins (probable adult features). The coracoid process is small and not enlarged as in *Pteronarctos* and *Desmatophoca*. The ventral caudal corner of the scapula adjacent to the infraglenoid tuberosity is deeply excavated for attachment of the teres minor and triceps longus muscles (Howell 1929; English 1977). The ventral margin of the cranial border dorsal to the coracoid process is slightly concave in *Thalassoleon mexicanus*, nearly straight in *Zalophus* and *Callorhinus*, and broadly concave in *Pteronarctos*, *Desmatophoca*, and *Pithanotaria*.

The medial surface of the scapula is only partially visible in SDSNH 65158, but consists of a flattened cranial scapular area for attachment of the cranial portion of the subscapularis muscle, a broad subdivided central fossa for attachment of the middle portion of the subscapularis muscle, and the ventral portion of a distinct caudal subscapular ridge presumably marking the anterior limit of the caudal subscapularis muscle (English 1977).

The taxonomic distribution of the scapular characters discussed above suggests a mosaic pattern for otariids with most taxa possessing a fan-shaped scapula (expanded cranial and caudal angles) with scapular indices less than 100, a longitudinally divided supraspinous fossa roughly twice the size of the longitudinally divided infraspinous fossa, an incomplete scapular spine, and a reduced coracoid process. The distinct scapular ridge in the supraspinous fossa as discussed by English (1977) and King (1983) seems to only occur in later diverging otariids.

Humerus.—The Capistrano Formation sample includes two humeri (SDSNH 65155 and 68313), which measure 173.5 and 178.2 mm in total length, respectively, compared to 215 mm in the holotype of *Thalassoleon mexicanus*. This size difference (81-83%) is here attributed to sexual dimorphism. The overall slenderness of the referred humeri, however, is also seen in the holotype humerus and may represent a distinct morphological aspect of the fossil taxon relative to the more robust humeri of extant otariids (e.g., *Zalophus*).

The lesser tuberosity is below the level of, and distinctly separated from, the capitulum. The lesser tuberosity in non-otariid pinnipeds is more closely appressed to the capitulum (e.g., *Desmatophoca*; Deméré & Berta 2002). The greater tuberosity extends well above the capitulum as in extant otariids and in contrast to the opposite condition in phocids (Howell 1929). The deltopectoral crest is long, extending nearly two-thirds the length of the humerus, and is distinctly elevated from the shaft (Figs. 5-6). Distally, the crest is directed toward the medial ulnar lip of the trochlea as described by Repenning and Tedford (1977) and unlike the condition in odobenids where the crest is directed towards the midpoint of the distal trochlea. The area for attachment of the deltoid muscle on the crest is flattened distad in the anteroposterior direction. The deltoid attachment site in the partial right humerus of *T. macnallyae* is more posterolaterally directed and forms a raised shelf that overhangs the brachialis fossa. The area for attachment of the pectoralis musculature in both taxa is not expanded medially as in extant otariids. The bicipital groove in *Thalassoleon mexicanus* is broad and open and not overhung proximally by the greater tuberosity as in *Zalophus* and *Callorhinus*. The entepicondyle is well developed and projects medially such that the proximal portion of the process distinctly overhangs the distal portion. The ectepicondyle is broad anteroposteriorly, but not expanded laterally. The supinator ridge is narrow and forms a sharply keeled ridge without any enlarged boss for attachment of the lateral collateral ligament. The proximal portion of the supinator ridge merges with the diaphysis near midshaft, in contrast to the more distal placement of the ridge in extant otariids. The insertion for the teres major is developed as a broad swelling on the anteromedial portion of the diaphysis near midshaft. The medial ulnar trochlea is slightly smaller than the radial capitulum as in extant otariids and unlike the condition in odobenids where the medial trochlea is distinctly flared and larger than the radial capitulum.

The humerus of *Thalassoleon mexicanus*, although relatively slender, is decidedly otariid in general form. English (1977) noted that the anteriorly extended and proximodistad elongated deltopectoral crest of otariids is correlated with a well-developed humeral rotator musculature for both forelimb abduction (i.e., deltoid muscle) and adduction (i.e., pectoralis and latissimus dorsi). In addition, the large greater tuberosity is correlated with a large supraspinatus muscle, implicated in extension of the humerus and increased control of humeral rotation (Howell 1929; English 1977). Such movements are fundamental to strong forelimb swimmers like otariids and it is likely that *T. mexicanus* swam in this fashion. This hypothesis is also supported by the
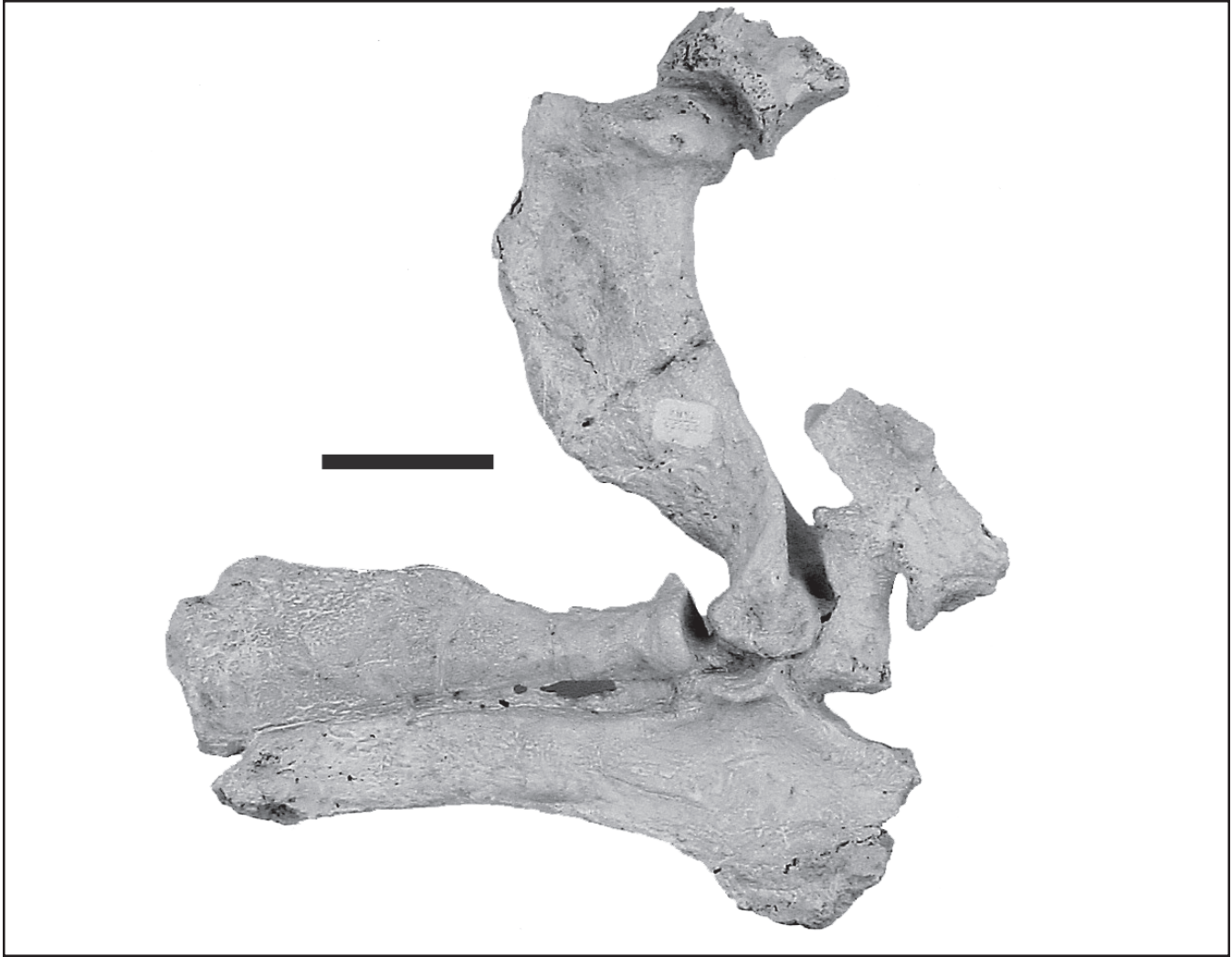
Figure 6. *Thalassoleon mexicanus* SDSNH 65155, articulated left forelimb, lateral aspect. Scale bar equals 10 cm.

presence of a well developed entepicondyle, which English (1977) suggested is a feature correlated with enlargement of the medial collateral ligament of the elbow joint, thought to be involved in resisting the strong tensional forces at the elbow joint created during adduction of the forelimb.

Radius.—Portions of four radii are represented in the Capistrano Formation sample (SDSNH 65155, 65158, 65163, and 68313) and are similar to extant otariids in general form (i.e., narrow proximad, expanded distad, and thin dorsoventrally). The neck of the radius is nearly circular in cross-section in contrast to the transversely oval neck of the radius of *Thalassoleon macnallyae* and *Callorhinus ursinus*. Repenning and Tedford (1977) noted that the origin for the pronator teres muscle

in Almejas Formation specimens of *Thalassoleon mexicanus* is located slightly more distad on the shaft in comparison to its more proximal position in extant otariids. This condition is confirmed in the Capistrano Formation specimens and suggests a longer moment arm for the pronator teres. Repenning and Tedford (1977) also noted the occurrence of prominent grooves for the tendons of the extensor muscles on the distal half of the lateral surface, but this is a variable feature in the Capistrano Formation fossil material. The distal half of the radius, especially the radial crest, is more expanded anteroposteriorly when compared to the more slender radii of *Callorhinus*. The distal radial styloid process, which is distinctly expanded in odobenids, is not expanded in *Thalassoleon mexicanus* nor extant otariids. The

otariid radius is capable of only a limited degree of pronation and with its distal broadening and flattening serves as a platform for flexors and extensors of the manus (English 1977).

Ulna.—Three ulnae are preserved (SDSNH 65155, 65163, and 68313) and are similar to extant otariids (Figs. 5-6) in general form (i.e., expanded proximad and narrow distad). A weakly developed spine occurs on the proximal epiphysis of the olecranon process in *Thalassoleon mexicanus* (Repennning & Tedford 1977:pl 22, fig 6). This spine is well developed in extant otariids and extends distad on the lateral surface of the shaft and separates attachment areas for the flexor carpi ulnaris from the flexor digitorum communis muscles (En-

glish 1977). The spine is absent in odobenids and phocids. As noted by Repenning and Tedford (1977), the insertion area for the triceps muscles on the anterior border of the olecranon in *T. mexicanus* is markedly narrow and the shaft anteroposteriorly broader in comparison to extant otariids. The olecranon process in *T. mexicanus* is not extended as a hook as in extant otariids suggesting a more limited area of attachment for extensor and flexor muscles (Figs. 5-6). The ulnar articular region is modified as in extant otariids and has a well-developed medial coronoid process, a medially expanded humeral articulation, and a weak lateral half of the semi-lunar notch. English (1977) proposed that these modifications (especially the coronoid process) represent an adaptation for

Table 4. Measurements (mm) of humeri, radiae, and ulnae of SDSNH *Thalassoleon mexicanus* and the holotype of *Thalassoleon macnallyae*. Abbreviations as in Table 1.

| | *T. mexicanus* | | *T . macnallyae* |
	SDSNH 65155(l)	SDSNH 68313(r)	UCMP 112809
Humerus			
Total length, greater tuberosity to radial capitulum	173.5	178.2e	——
T width, head	45	——	——
Greatest width across epicondyles	58.5	——	73.6
T width at narrowest part of shaft	30	——	——
T width across tuberosities	49	——	——
AP width, midshaft	54.6	56.5	——
Greatest AP diameter, medial edge of trochlea	30.9	——	——
Greatest width of distal articulation	41	——	——
Greatest AP diameter, radial capitulum	32e	34e	31.8
Radius			
Total length	152.8	151.4	——
Greatest width, proximal end	36.1	27.3e	——
Greatest width, distal end	45.6	38	——
Least width, proximal articulation	28.4e	——	——
Depth of shaft at pronator teres origin	38e	32.6	——
Ulna			
Total length	199.8	175.3e	——
Depth, humeral sigmoid notch to posterior end of olecranon	60	54.6	——
Depth, narrowest part of shaft	27.6	22	——
Width, narrowest part of shaft	8d	——	——

bracing the elbow joint against the strong tensional loading created during adduction of the forelimb.

Together, the otariid radius and ulna form a broad and thin antebrachium that serves as a platform for origination of the flexors and extensors of the manus. Although other groups of pinnipeds also possess these flipper adaptations, it seems that the otariid condition is for an especially thin antebrachium.

Metacarpals.—A right MC I is preserved with SDSNH 68313, but is missing the proximal epiphysis. This specimen is 74.4 mm long (as preserved) and 22.2 mm wide at the proximal end, 18 mm at the distal end, and 12. 5 mm at the shaft midpoint. The shaft is longitudinally concave in the ulnar direction.

Femur.—Two left (SDSNH 65155, 65165) and one right (SDSNH 65159) femora are represented in the Capistrano Formation sample. One specimen (SDSNH 65165) represents a juvenile individual. Repenning and Tedford (1977) illustrated a referred hindlimb (UCR 15258) of *T. mexicanus*, but provided no measurements except the total length of an undesignated femur. These authors also did not provide measurements of the hindlimb elements of *Thalassoleon macnallyae* (UCMP 112809) so we include them in Table 5. In comparison to the holotype of *T. macnallyae*, the Capistrano Formation and Almejas Formation femora (Fig. 7) are markedly more robust with proportionally broader proximal and distal ends (Table 5). The lesser trochanter in the Capistrano Formation specimens is a small distinct process not as large as in the holotype of *T. macnallyae*, but larger than in extant otariids. The femoral head in the Capistrano Formation specimens is hemispherical and like all extant pinnipeds lacks a distinct fovea capitis. The head is not positioned on a distinct neck as seen in *Zalophus*. The head and greater trochanter are closely positioned in the Capistrano Formation femora, the Almejas Formation femur (UCR 15258), and *T. macnallyae*. The greater trochanter does not extend above the head in *T. mexicanus*. A shallow trochanteric fossa is present in *T. macnallyae*, but there is no indication of a fossa in the Capistrano Formation specimens. The condition of the trochanteric fossa in UCR 15258 is equivocal. The distal end of the femur of *T. mexicanus* is grossly similar to the condition in all pinnipeds with the articular surfaces of both condyles oriented entirely posteriorly and separated by a deep and wide intercondyloid fossa.

The femur of *Thalassoleon mexicanus* is clearly otariid in general form and closely resembles femora of many extant species except *Callorhinus ursinus*. Both *C. ursinus* and *Thalassoleon macnallyae* have more slender and gracile femora with proportionally narrower proximal and distal ends. Although, intuitively, this would appear to represent the primitive condition, the taxonomic distribution of mediolaterally slender/gracile femora within pinnipedimorphs suggests that it is a derived condition at the level of Otariidae.

Tibia.—There are two complete tibiae from the Capistrano Formation, SDSNH 65155 and 65159. The tibia of *Thalassoleon mexicanus* illustrated by Repenning and Tedford (1977) from the Almejas Formation (UCR 15258) is not fused proximally with the fibula. This also appears to be the condition in the Capistrano Formation specimens. These elements, however, are fused proximally in the holotype of *Thalassoleon macnallyae* as noted by Repenning and Tedford (1977). The tibiae of the Capistrano Formation specimens are concavely bowed laterad and nearly straight mediad. This is also the condition in *T. macnallyae*. The Capistrano Formation tibiae are apparently shorter than the Almejas Formation *T. mexicanus* sample, although this may be a function of sexual dimorphism. The proximal ends of the Capistrano Formation tibiae are not preserved well enough to describe. The distal ends, however, are better preserved and possess an anterior crest of the shaft that is sharp and distinct and extends further distad than in *T. macnallyae*. The posterior tibial fossa is deeply excavated in SDSNH 65159 and the holotype of *T. macnallyae*. The tibioastraglar articular surface of SDSNH 65159 is more quadrate than seen in the holotype of *T. macnallyae* and the malleolus has two distinct grooves on the medial side for tendons of flexors and abductors of the pes.

Fibula.—A complete fibula is preserved in articulation with the tibia in SDSNH 65155. Overall, it appears to be more slender than UCR 15258 from the Almejas Formation (Repenning & Tedford 1977:pl. 23), but again this may be the result of sexual dimorphism. Although the distal end of SDSNH 65155 is poorly preserved, it is marked by distinct grooves on the posterior border for tendons of extensors of the pes.

Astragalus.—Two right astragali (SDSNH 65155 and 68315) were collected from the Capistrano Formation. The lateral border of the dorsal surface lacks deep grooves present in some species of *Arctocephalus* (i.e., *A. forsteri* and *A. australis*, Berta & Adam in prep.). The holotype astragalus of *Thalassoleon macnallyae* also lacks deep grooves in this region. Although Repenning and Tedford (1977) noted a well-developed

Table 5. Measurements (mm) of femora, tibiae, fibulae, and tarsals of SDSNH *Thalassoleon mexicanus* and the holotype of *T. macnallyae*. Abbreviations as in Table 1.

| | *T. mexicanus* | | | *T. macnallyae* |
	SDSNH 65155	SDSNH 65159	SDSNH 68315	UCMP 112809
Femur				
Total length	102.8	108.6	——	136
Head, T diameter	26.0	24.0	——	26.0
Greater trochanter, length	34.3	25.5	——	36.3
Greater trochanter, width	16.4		——	17.8
T width, proximal end	55.2	56.4	——	60.7
Minimum midshaft T width	26.4	27e	——	27.7
Minimum midshaft AP width	17.5	13.0	——	16.4
T width, distal end	53.2	57.0	——	56.2
AP width, distal shaft above condyles	13.6	13e	——	12.8
Lateral condyle, T width	20.0	——	——	22.0
Medial condyle, T width	22.4	——	——	20.4
Tibia				
Total length	206.2	200.5	——	238.3
T width, proximal end	59e	——	——	51
Minimum midshaft transverse width	17.4	——	——	18.9
Minimum midshaft AP width	18.7	——	——	18.8
Transverse width, distal end	40.5e	37.5	27.3	42.6
Astragalus				
Total length	37	——	44.5	45.2
Greatest T width at navicular art.	24.3	——	28	22.5
D/V thickness at navicular articulation	12.6	——	15	15da
Greatest trochlear T width	23.5	——	26.4	26
Angle between neck & trochlear surface	45°	——	45°	——
Calcaneum				
Total length	46.7	——	60.3 d	——
T width of tuber	22.0	——	24.5+	——
Greatest T width, proximal end	28.8	——	29.9	——
D/V thickness of tuber	17.3	——	16.2	——
D/V thickness at cuboid articulation	13.9	——	16.8+	——

astragalar foramen on all Almejas Formation specimens of *Thalassoleon mexicanus*, no foramen is preserved on the Capistrano Formation astragali. A deep astragalar foramen is preserved on the holotype of *T. macnallyae*. As in all fossil and extant otariids, the lateral process is large and forms the lateral margin of a deep notch in the anterior border of the trochlea dorsal to the sulcus tali

(Fig. 8C). Repenning and Tedford (1977) noted that the lateral process extends further onto the lateral malleolar process in extant sea lions than it does in the Almejas Formation sample, an observation that we could not confirm in our specimens because of poor preservation. The dorsal articular surface has a weak median trochlear groove dividing the trochlea into medial and lateral sur-

Table 6. Functional limb lengths (mm) of SDSNH *Thalassoleon mexicanus,* holotype of *Thalassoleon macnallyae,* and *Pithanotaria starri.* Abbreviations as in Table 1.

	T. mexicanus		*T. macnallyae*		*Pithanotaria starri*
	SDSNH 68313	SDSNH 65155	UCMP 112809	USNM 11050	USNM 11055
Scapula					
length	168.0	——	——	81.58e	——
width	233.6	——	——	120.19e	——
Humerus					
length	153e	143	——	104.10e	118.31e
deltoid crest	107e	100	——	64. 94e	——
teres major		80	——	——	——
Radius/Ulna					
length	151	143	150*	82.96e	104.29e
bicipital tub.	26.6	24	——	——	——
olecranon	54	55e	——	23.70e	30.59e
	SDSNH 65159	SDSNH 65155			
Femur					
length	90	86	121	——	——
Tibia					
length	199	205	237	——	——

faces. The medial and lateral malleolar surfaces are sharply defined and meet the dorsal trochlear surfaces at nearly 90°. A very reduced calcaneal process is preserved in SDSNH 65155 and the holotype of *T. macnallyae*. The condition of the calcaneal process is difficult to evaluate in the Almejas Formation specimens. In ventral (plantar) aspect, the ectal facet extends anteriorly to the terminus of the lateral process. In *Zalophus* this facet does not reach the anterior border of the lateral process. This is also the condition in *T. macnallyae*. The sustentacular facet extends across the neck of the astragalus where it joins the navicular facet at the anterior border (Fig. 8D). The sustentacular facet is separated from the ectal facet by a continuous sulcus tali. The long axis of the neck of the astragalus forms an angle of approximately 32° with the long axis of the trochlea.

The broad nature of the trochlea together with the presence of a distinct trochlear saddle, parallel and sharply angled medial and lateral malleolar surfaces, and

an extended lateral process suggest that the upper ankle joint in *T. mexicanus* was a relatively tight hinge joint as in extant otariids. Among pinnipeds this represents the primitive condition and is characteristic of a hind foot that is capable of being rotated forward during terrestrial locomotion. The derived condition is seen in phocid pinnipeds in which the upper ankle joint is more of a ball-and-socket joint that allows a wider range of rotational movement for hindlimb propulsion, but which cannot accommodate rotation of the hind foot into a posture suitable for terrestrial locomotion.

Calcaneum.—Two left calcanea, SDSNH 65155 and 68315 (Figs. 8A-B), were collected from the Capistrano Formation (Table 5). Both are rather slender relative to the more robust calcanea of fossil and extant odobenids and lack the well-developed medial tuberosity of the calcaneal tuber so characteristic of the latter taxa. The ectal facet is long and extends for nearly 70% of the calcaneal tuber. The broad convexity of the ectal facet suggests a considerable degree of oblique
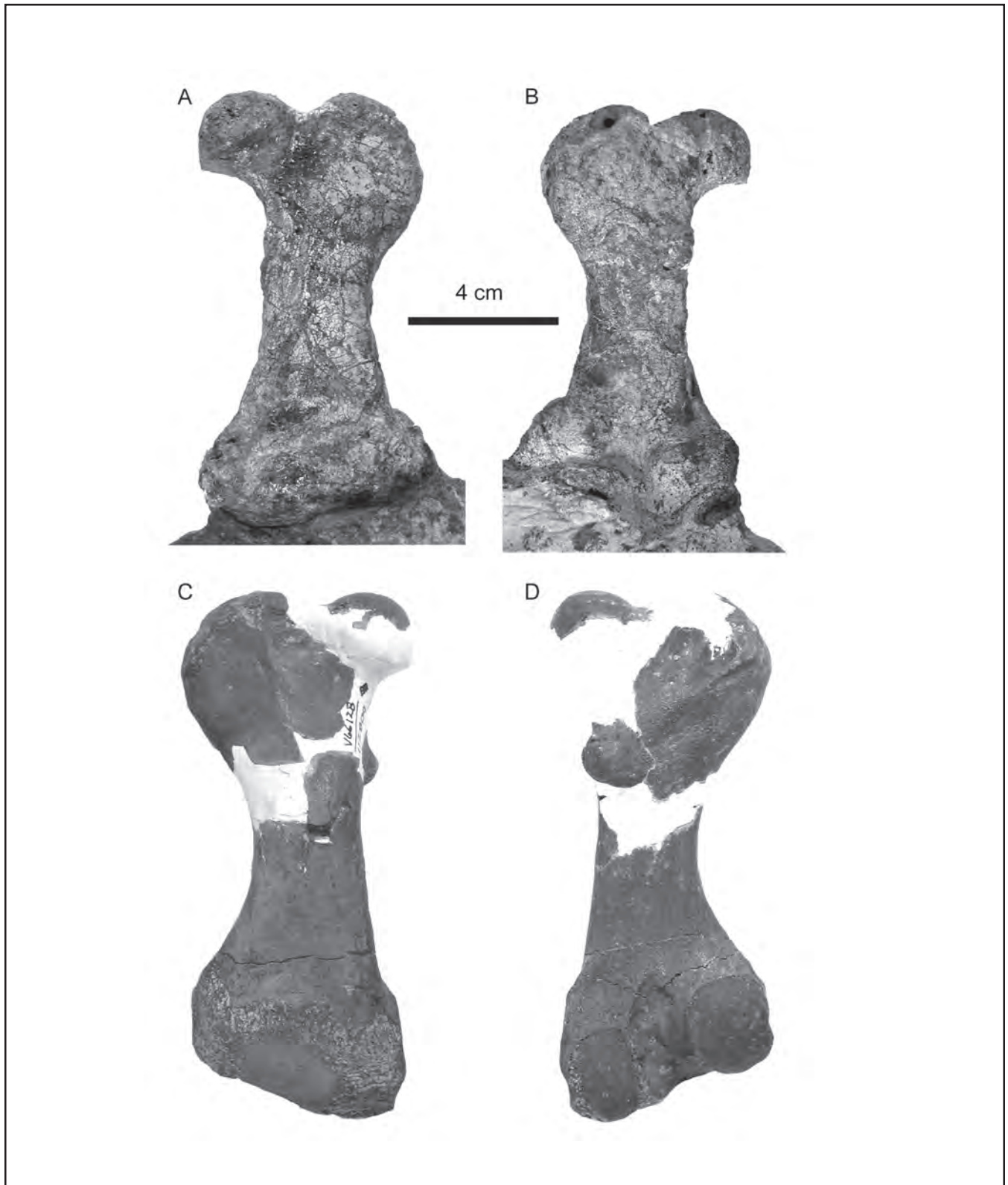
Figure 7. Left femur of *Thalassoleon mexicanus* SDSNH 65155, distal end obscured by matrix. A, anterior aspect; B, posterior aspect. Right femur of *Thalassoleon macnallyae* UCMP 112809. C, anterior aspect; D, posterior aspect. Scale bar equals 4 cm.

rotation of the lower ankle joint. The sustentacular facet is broadly lobate posteriorly and extends as a continuous articular surface to the anterior border of the calcaneum (Fig. 8A). Importantly, the secondary shelf of the sustentaculum, considered to be a unique feature in extant otariids (Robinette & Stains, 1970), is absent in both specimens, as well as in the Almejas Formation specimens of *Thalassoleon mexicanus*. The long axis of the sustentaculum tali does not align with the anterior border of the calcaneum, but is instead deflected from the latter at an angle of approximately 40°. The ectal and sustentacular facets are separated by a continuous sulcus calcanei. Anterior to the ectal facet is a pitted shelf, presumably the area of origin of the extensor digitorum brevis muscle laterally and the lateral talocalcaneal ligament medially. Lateral to this shelf is a broad sulcus for passage of the peroneus longus and brevis tendons. The lateral margin of this sulcus forms the peroneal tubercle, the ventral side of which serves as the area of origin of the quadratus plantae muscle and the dorsolateral corner of which serves as the attachment site of the dorsal calcaneocuboid ligament. On the lateral border of the calcaneal tuber, approximately one-third the distance between the heel and the peroneal process, is a distinct circular scar for attachment of the calcaneofibulare ligament. In anterior aspect, the cuboid articular facet is roughly rectangular in outline.

The calcaneum of *Thalassoleon mexicanus* possesses a mosaic of primitive and derived features. The slender calcaneal tuber and unexpanded heel are characters seen in extant otariids, while the absence of a secondary shelf of the sustentaculum represents a retention of the primitive pinniped condition. This taxonomic distribution of character states suggests that the secondary shelf of the sustentaculum developed late in otariid evolution.

DENTAL FEATURES AND FEEDING

Adam and Berta (2002) developed a classification of prey capture strategies for fossil and extant pinnipeds recognizing the following categories: pierce feeding, suction feeding, filter feeding, and grip-and-tear feeding. Combining the use of discrete morphological characters with a phylogenetic-based analysis of taxonomic distributions of those characters and a reliance on inference evaluation techniques (Witmer 1995), Adam and Berta (2002) concluded that pierce feeding was the primitive prey capture strategy for pinnipeds, that suction feeding evolved independently as many as three times in otariids (*O. byronia*), phocine phocids (*Erignathus barbatus*),

and odobenine odobenids (*Odobenus rosmasus*), that filter feeding evolved only once (*Lobodon carcinophagus*), and that grip-and-tear feeding also evolved only once (*Hydrurga leptonyx*). Pierce feeding remains the most common pinniped feeding strategy, being found in most extant otariids, monachine phocids, and phocine phocids. Adam and Berta (2002) further postulated that *Thalassoleon* was a pierce feeder based on the occurrence of a homodont dentition, an m1 positioned anterior to the midline of the dentary, and an enlarged infraorbital foramen located on the zygomatic arch. This hypothesis is confirmed in our study of new fossils of *Thalassoleon mexicanus* from the Capistrano formation, which found a generally homodont dentition (premolars and molars with simple triangular principal cusps, smooth enamel, weakly developed anterior accessory cusps where present, lack of posterior accessory cusps, weak anterior cristae and stronger posterior cristae, and distinct lingual cingula with crenations and no labial cingula), an m1 positioned slightly anterior to the midline of the dentary, and an enlarged infraorbital foramen.
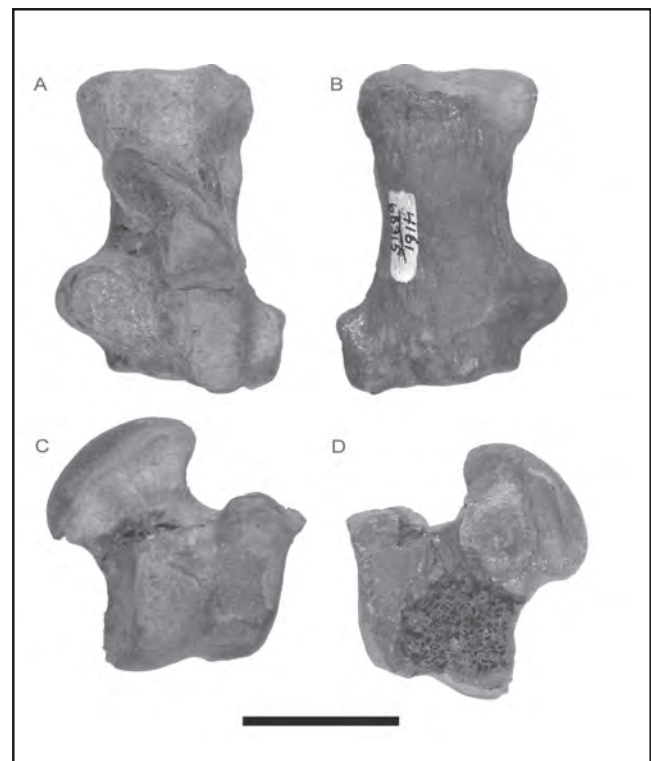

Figure 8. *Thalassoleon mexicanus* SDSNH 68315. Left calcaneum. A, dorsal aspect; B, plantar aspect. Right astragalus. C, dorsal aspect; D, plantar aspect. Scale bar equals 2 cm.

LIMB PROPORTIONS AND LOCOMOTION

The appendicular anatomy of *Thalassoleon mexicanus* preserves a number of morphological features that can be correlated with an ambulatory style of terrestrial locomotion and forelimb swimming. Ambulatory locomotion on land is the primitive condition in pinnipeds and is indicated by a mortise type tibioastragalar joint and lack of modification of the tarsal elements (Berta & Ray 1990). These features are preserved in the basal pinnipedimorph *Enaliarctos mealsi* and the extinct desmatophocids and are retained in extant otariids and odobenids. Forelimb swimming, the ancestral pattern of aquatic locomotion in pinnipeds, is indicated by a relatively low scapular index, an elongate deltopectoral crest of the humerus, a well-developed entepicondyle of the humerus, a large humeroradial index, a broad and thin antebrachium, and a prominent coracoid process of the ulna.

In comparisons with other pinniped taxa, the scapular index in *Thalassoleon mexicanus* is most similar to that found in extant otariids. English (1977) noted that much of the widening of the otariid scapula is related to muscle attachment sites for teres major and serratus ventralis. The action of these muscles is primarily involved in retraction and protraction of the forelimb during the forelimb propulsive and recovery phases, respectively.

The humeroradial index in *Thalassoleon mexicanus* is greater than in terrestrial carnivorans, which is the condition in most pinnipeds except walruses (Table 7). This index indicates shortening of proximal forelimb elements and is correlated with a shortening of the resistance arm of the forelimb relative to the moment arm of the humeral rotator musculature (English 1977). This overall shortening of the forelimb translates into an increased ability to produce forward thrust during swimming. A high humeroradial index (i.e., radius equal to or longer than humerus) can also be correlated with general streamlining, as relates to incorporation of the humerus within the body contour.

The broad and thin antebrachium of *Thalassoleon mexicanus* is similar to that of extant otariids and can be correlated with both increasing forelimb surface area during the propulsive phase and decreasing water resistance during the recovery phase of locomotion. A well-developed humeral entepicondyle and a prominent ulnar coracoid process are both associated with reducing range of motion at the ulnar/radial joint and with bracing the elbow joint against the strong tensional loading created during forelimb adduction and medial rotation.

General limb indices of *Thalassoleon mexicanus* provide interesting insights into the body proportions and locomotor adaptations of this extinct pinniped (Table 7). As already discussed, the low scapular index is characteristic of otariids and is associated with forelimb protraction and retraction. The humeroradial index falls within the range for extant otariids and is correlated with shortening of the proximal portion of the forelimb. The femorohumeral index in *T. mexicanus* is lower than in other otariids, reflecting the relatively longer femur in the former taxon. This approaches the primitive condition seen in *Enaliarctos mealsi*. The low femorohumeral indices in phocid pinnipeds may reflect adaptations related to hindlimb swimming. The femorotibial index of *T. mexicanus* is similar to that of extant otariids, especially sea lions, and is markedly higher than in terrestrial carnivorans. This high index value is related to proximal shortening of the hindlimb and retraction of the limb within the body contour. The tibioradial index in *T. mexicanus* is lower than in extant otariids, suggesting a relatively longer tibia in the fossil. *Thalassoleon macnallyae* also has a low index, which approaches the primitive condition seen in *Enaliarctos*. The elongate tibia of *T. mexicanus* is also evidenced by the femorotibial index in which the tibia is roughly twice the length of the femur. The intermembral index in *T. mexicanus* is slightly lower than that of extant otariids and walruses and indicates that the forelimb and hindlimb were nearly equally proportioned. This is in contrast to phocids and terrestrial carnivorans in which the intermembral values are low suggesting that the phocid hindlimbs are better developed than their forelimbs.

This analysis of limb proportions suggests that *Thalassoleon mexicanus* was a strong forelimb swimmer like modern otariids, but was more ambulatory on land.

PHYLOGENETIC RELATIONSHIPS

Recent hypotheses for the position of *Thalassoleon mexicanus* and related taxa are summarized in Figure 9. The relationship of *Thalassoleon* to other pinnipeds has been discussed by Repenning and Tedford (1977), Muizon (1978) and Berta and Deméré (1986) who recognize *Thalassoleon* as a basal otariid pinniped more derived than *Pithanotaria*. Berta and Deméré (1986) proposed a paraphyletic "*Thalassoleon*" and followed Muizon (1978) in suggesting that *Thalassoleon macnallyae* was near the base of the lineage leading to the extant northern fur seal *Callorhinus ursinus*. An-

Table 7. Limb indices in pinnipeds and other carnivores based on functional limb measurements from [1]English, 1975; averages of values of *Martes americana*, *Bassariscus astutus* and *Bassaricyon alleni*, [2]Mitchell, 1966, [3]Davis, 1964, and this study.

	Scapular (length/ width)	Humero-radial (radius/ humerus)	Femoro-humeral (humerus/ femur)	Femoro-tibial (tibia/ femur)	Tibio-radial (radius/ tibia)	Intermem-bral Index
Thalassoleon mexicanus (n=3)	72	99-100	100	221-238	70	98
Thalassoleon macnallyae (n=1)	——	——-	——	196	63e	——
Otariidae[1] (n=21)	82.18	102.58	159.44	——	77.03	105.49
Odobenus rosmarus[1] (n=7)	133.89	77.64	155.73	——	71.83	100.20
Phocinae[1] (n= 21)	94.04	100.87	122.15	——	50.56	72.79
Lobodontinae[1] (n= 10)	87.26	110.47	135.89	——	67.92	88.21
Allodesmus kernensis[2] (n=1)	——	92.31	152.51	——	96.5	——
Enaliarctos mealsi (n=1)	85.77	89	113	195	52	71.97
Terrestrial carnivorans[1]	133.23	78.95	94.09	——	67.15	80.68
Ursus americanus[3] (n =2)	——	81.1	86.4	72.2	96.9	90.8
Lutra canadensis[3] (n= 3)	——	71.5	98.9	111.4	63.5	80.2
Enhydra	——	75.7	95.9	112.4	64.6	79.7

other fossil otariid described as *Arctocephalus* (*Hydrarctos*) *lomasiensis* from the early Pleistocene of Peru (Muizon 1978; Muizon & De Vries 1985) was recognized by Berta and Deméré (1986) in an intermediate position between the earlier diverging *T. mexicanus* and the later diverging "*T.*" *macnallyae*. Based on these results, Berta and Deméré (1986) removed the Peruvian fossil fur seal from *Arctocephalus*, placing it in the newly elevated genus *Hydrarctos* (i.e., *H. lomasiensis*).

As a framework for this report we used the preliminary results of a more inclusive, species-level phylogenetic analysis of otariids (Berta & Adam in prep.) based on morphological and molecular datasets and including both fossil and extant taxa. This analysis includes 60 morphological characters (47 binary and 13 multistate). Employed as outgroups were representatives of the following taxa: Canidae (*Canis latrans*), Ursidae (*Ursus arctos*), Mustelidae (*Mustela vison*), Procyonidae (*Procyon lotor*), *Enaliarctos* (combined codings for *E. mealsi* and *E. emlongi*), *Pteronarctos goedertae,* Odobenidae (*Odobenus rosmarus*), *Proneotherium repenningi*, Phocidae (combined codings for *Monachus schauinslandi* and *Phoca vitulina*) and fossil Phocidae (combined codings for *Acrophoca longirostris*, *Homiphoca capensis*, and *Piscophoca pacifica*). The data were analyzed by PAUP* 4.0 (Swofford 1999) using the heuristic search option. Initial analysis considering all fossil otariids and 10 outgroup taxa resulted in over 100 most parsimonious trees. Principal differences were in the relationships among outgroup taxa and in the position of poorly known fossil otariids listed with % completeness: *Pithanotaria starri* (23%), *Thalassoleon inouei* (5%), *Thalassoleon macnallyae* (10%) and *Callorhinus gilmorei* (23%). Later analyses excluded these taxa and obtained better resolution among taxa. A strict consensus tree with a length of 95 steps and a rescaled C.I. of 0.438 is shown in Figure 9 with bootstrap percentages based on 100 replicates indicated.

This phylogenetic analysis (Fig. 9) confirmed otariid monophyly and identified the following otariid synapomorphies: strongly developed supraorbital process of frontals; antorbital process formed of maxilla and ethmoid; 'W-shaped' naso-frontal suture; and proximal olecranon process of ulna with median spine. *Thalassoleon mexicanus* is positioned as the most basal otariid (because of the incompleteness of the more basal *Pithanotaria starri*, this taxon had to be "hung" on the tree *a posteriori*). Among features that *Thalassoleon mexicanus* shares with later diverging otariids is visibil-

ity of the infraorbital canal in dorsal view. *Hydrarctos* is the next diverging lineage, although in an equally parsimonious arrangement this taxon is positioned as sister to the Otariinae. *Callorhinus* is sister taxon to a clade consisting of a monophyletic *Arctocephalus* species complex and a monophyletic Otariinae. The basal position of *Callorhinus* is also supported by molecular data (Wynen et al. 2001; Lento pers. comm.).

We discuss in more detail here only those characters that bear on the relationships of *Thalassoleon* and other basal otariids (i.e., *Pithanotaria*, *Hydrarctos*, and *Callorhinus*). *Thalassoleon mexicanus* can be distinguished from all other fossil and extant otariids by lack of a posterior accessory cusp on I3. Further detailed examination reveals that *Thalassoleon mexicanus* possesses a posterior cingulum (*contra* Berta & Deméré 1986) similar to that seen in *Pithanotaria*, although most of the cingulum in SDSNH 65164 has been obliterated by wear. *Thalassoleon mexicanus* is distinct from *Pithanotaria* in lacking development of a posterior accessory cusp. We discovered a few additional dental features, such as simple postcanine teeth that lack anterior or posterior accessory cusps, that appear to distin-
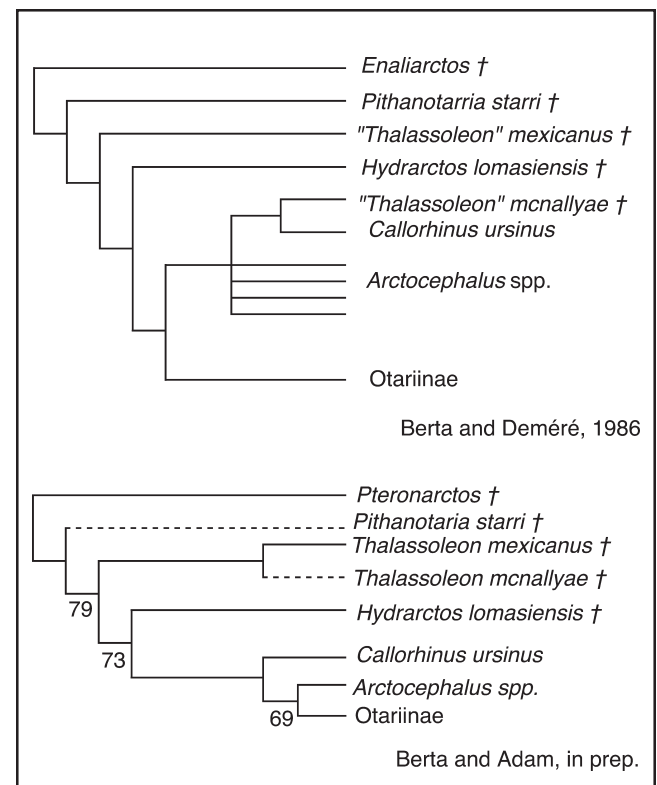

Figure 9. Alternate phylogenies for otariid pinnipeds.

guish *T. mexicanus* from other otariids. Comparison with a larger taxonomic sample of otariids is needed for confirmation of these findings since several of these characters were not part of a more inclusive phylogenetic analysis of otariids (Berta & Adam in prep.). Two other derived characters are equivocal autapomorphies for *T. mexicanus* since they cannot be evaluated in *Pithanotaria* because of incomplete preservation: broad supraorbital shelves that lack triangular terminations and multiple palatine foramina with deep grooves. Several possible autapomorphies of the postcrania of *T. mexicanus* include the following: division of the supraspinous fossa by a broad fold but lack of a distinct scapular ridge seen in extant otariids; distal position of the pronator teres muscle on the radius in comparison to a more proximal position seen in extant otariids; and a weakly developed spine on the proximal epiphysis of the radius versus a well developed spine in extant otariids. Preliminary results of the inclusive otariid analysis (Berta & Adam in prep) distinguish *Callorhinus* from all other otariids based on the following characters: fur on manus that terminates at wrist; nasal processes that are anterodorsally flared; facial angle less than 125°; cranial border of scapula rotated slightly toward vertebral border; and innominate significantly shorter relative to tibia-fibula.

Relationships among the three described species of *Thalassoleon* support the distinction of *Thalassoleon mexicanus* from *Thalassoleon macnallyae*. We cannot substantiate our earlier view (Berta & Deméré 1986) that *Thalassoleon* is paraphyletic and that *T. macnallyae* is more closely related to *Callorhinus*. Three of the four characters that were used to support that relationship are now viewed as juvenile features not observable in adults and hence not useful in phylogenetic analysis. The fourth character—ornamented ectotympanic—is developed differently and probably is not homologous in *T. macnallyae* and *Callorhinus*. *Thalassoleon macnallyae* can be distinguished from *T. mexicanus* in having the following character states: larger size; posteroventral orientation of mastoid process; and ectotympanic crest marked with distinct projections (possibly present in *Thalassoleon inouei* but that area is incompletely preserved). We question, however, whether the very poorly preserved *T. inouei* is a valid species. Several characters lend support to consideration of *T. inouei* as a junior synonym of *T. macnallyae* (i.e., similarities in the size and structure of the mastoid and medial portion of the ectotympanic that is produced into an extremely narrow, keeled crest). Confirmation of the taxonomic status of *T. inouei* will require more diagnostic material.

CONCLUSIONS

New material of *Thalassoleon mexicanus* from the Capistrano Formations of southern California provides evidence for morphological variation, especially sexual dimorphism in this taxon. The degree of sexual dimorphism is similar to that documented for some of the least dimorphic extant otariids. Compared to female skulls, male skulls of *T. mexicanus* have relatively larger CBL measurements, larger canines, robust premaxillary eminences, robust antorbital processes, robust supraorbital processes of the frontals, distinct sagittal crests, and broad squamosal fossae.

Features of the skull and teeth indicate that *Thalassoleon mexicanus* was a pierce feeder. The postcrania of *T. mexicanus* preserves evidence of adaptations indicative of an ambulatory style of terrestrial locomotion and forelimb swimming. The phylogenetic position of *T. mexicanus* as a basal otariid is confirmed as is its sister group relationship with *Thalassoleon macnallyae*. This taxon is distinguished from all other otariid pinnipeds by: lack of a posterior accessory cusp on I3; simple postcanine teeth that lack anterior or posterior accessory cusps; division of the supraspinous fossa by a broad fold; distal position of the pronator teres muscle on the radius; and a weakly developed spine on the proximal epiphysis of the radius. Cladistic analysis supports monophyly of the Otariidae, defined here as the clade containing the most recent common ancestor of *Pithanotaria* and the Otariinae, and all of its descendants including *Thalassoleon*, *Hydractos*, *Callorhinus*, and *Arctocephalus*.

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