Otarioid Seals of the Neogene

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March 3, 1849

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By CHARLES A. REPENNING *and* RICHARD H. TEDFORD

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Classification, historical zoogeography, and
temporal correlation of the sea lions and
walruses from the North Pacific region

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OTARIOID SEALS OF THE NEOGENE

By CHARLES A. REPENNING and RICHARD H. TEDFORD[1]

ABSTRACT

The otarioid seals originated in the North Pacific region and most of their history is centered in this area. They include four families: the extant Odobenidae (walruses) and Otariidae (fur seals and sea lions) and the extinct Desmatophocidae and Enaliarctidae.

Early in their development, the odobenids dispersed through the Central American Seaway to the North Atlantic, where the living walrus evolved. By late Pliocene time, the odobenids had become extinct in the North Pacific but the modern walrus spread from the Atlantic to the Pacific by way of the Arctic Ocean in late Pleistocene time. The history of the odobenids is known back to the early middle Miocene, at which time they seem to have evolved out of the ancestral otarioid family, the Enaliarctidae. The odobenids were most diverse in the North Pacific during the late Miocene when six genera belonging to two subfamilies are known. A new genus and species, *Aivukus cedrosensis,* from the Almejas Formation of Baja California, is a privitive odobenid of the Subfamily Odobeninae. Three Pliocene and younger genera, including the living genus, are recognized in the Atlantic, but evolution in this area was essentially unidirectional toward modern walrus.

The history of the otariid seals began in the late middle or early late Miocene when this family evolved out of the last of the Enaliarctidae. The otariids remained a family with little variety, and, relative to the odobenids, slight evolutionary change until the late Pliocene or early Pleistocene, more or less the time of extinction of the odobenids in the Pacific. During this period of little diversification, one new otariid genus, *Thallassoleon,* is recognized. This genus contains two new species: *T. mexicanus,* from the Almejas Formation of Baja California, and *T. macnallyae,* from the Drakes Bay Formation of Point Reyes, California. The otariids are today in their period of greatest diversification—there are seven living genera. By early Pliocene time, the otariids had dispersed to the South Pacific Ocean, whence during the Pleistocene, they spread to their present circumantarctic distribution. They have never reached the North Atlantic.

The extinct desmatophocids evolved out of the enaliarctid group in the early Miocene and became most diverse in the middle Miocene. They are last known from rocks of late Miocene age, at about the time that the odobenids began to diversify. The desmatophocids seem never to have left the North Pacific, but they are known from southern California to Alaska and from Japan.

The Enaliarctidae were ancestral to the other three families and are largely unstudied. They were derived from primitive ursid land carnivores, presumably during the Oligocene, and may be described as flippered marine carnivores with heterodont dentition in which the premolar, carnassial, and molar teeth are differentiated in form, reflecting their land-carnivore ancestry. The evolutionary stage at which all cheek teeth become homodont is herein arbitrarily taken as that point where the descendant families are to be taxonomically recognized. The Enaliarctidae were most diverse in the early Miocene.

From the beginning of the Miocene to the late Pleistocene, eight otarioid faunal units based on generic composition are recognizable in the eastern North Pacific. Otarioid species, as now recognized, seem to have existed for about 2 m.y. on the average, although some genera have persisted for 5 or more m.y.

INTRODUCTION

The seals of the world were divided into two major groups by Allen (1880): the "walkers" and the "wrigglers." Smirnov (1908) subsequently applied the name Otarioidea to those seals which could flex their hind legs beneath them and walk on land, the name Phocoidea to those seals which could not, but rather wriggled on their bellies in terrestrial locomotion, their hind limbs permanently extended behind them. The two groups have been placed in the mammalian Order Pinnipedia (sensu Scheffer, 1958) or Suborder Pinnipedia (sensu Simpson, 1945) since Illiger (1811) first defined the group in its present context.

The pinnipeds have always been considered to be related to the fissiped carnivores, and, the widespread belief, since about 1960, that the group is not monophyletic (McLaren, 1960) has led to the rejection of ordinal or subordinal distinction from the fissiped carnivores by some workers (McKenna, 1969, p. 235; Mitchell and Tedford, 1973, p. 278).

The question of polyphyly is largely a matter of definition. According to some definitions (Simpson, 1961, for example), the Order Pinnipedia would be monophyletic in that it is derived from a group of equivalent or lower taxonomic rank, in this case the Superfamily Arctoidea (or Canoidea). The debate really centers over whether there was one or two protopinnipeds from which all pinnipeds derive: whether the pinnipeds derive from one, two, or three, invasions of the marine environment by fissiped carnivores. The obviously different centers of origin, the phocoids in the Atlantic area and the otarioids in the North Pacific, certainly suggest two protopin-

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[1] The American Museum of Natural History, New York City.

nipeds which, nevertheless, may have been closely related. In addition, Mitchell and Tedford (1973) have described a protopinniped from the North Pacific which may have been ancestral to all otarioid seals and which, in their analysis, bears only limited resemblance to what might be expected of a protophocoid.

This report describes several of new otarioid fossils which, along with other evidence, indicate that the sea lions (Family Otariidae) and the walruses (Family Odobenidae) have had long, different, and separate evolutionary histories. The retrospection permitted by these new records supports the opinion that they must have evolved at different times out of one group of primitive otarioids rather than from different terrestrial carnivores.

The fossil record of the pinnipeds is very poor. As much as anything, this seems to be the result of mammalian paleontology stopping at the water's edge. In the marine environment, with abundant invertebrate fossils available, there has been no stratigraphic need for vertebrate paleontology so pinniped remains frequently have been ignored or described as more or less isolated curiosities. Only in recent years has intensive collecting of fossil pinnipeds taken place.

The stratigraphic usefulness of fossil pinnipeds is potentially great, however. Despite their rarity relative to the abundant invertebrate fossil remains, the pinnipeds have rates of evolution comparable to those of other mammals; thus they are much more significant in temporal correlation than many marine invertebrates. In addition, the geographic range of many pinnipeds is far greater than that of many invertebrates. All that is needed is more specimens and more comprehensive study to fulfill this potential.

In the past decade, this need has been greatly lessened by the work of Edward D. Mitchell, Jr., both in description of new material and in repeated reevaluation of previously described fossil otarioids. Through Mitchell's work, it has become evident that in the Neogene of the North Pacific Ocean there existed a great assortment of different types of otarioid seals. Many of these seals belong to extinct groups and have been difficult to recognize as being clearly related to either of the two living otarioid families, the sea lions and the walruses.

In some of his publications (1966, 1968) Mitchell has provided a revised classification of the "walking seals." In his most recent publication (Mitchell, 1968; reaffirmed without explicit discussion in Mitchell and Tedford, 1973) he names, in the essence of established classification, four extinct families, each represented by only one genus, in addition to the two living families. Complexity of the recognition of so many pinniped lineages is made less conspicuous by lowering all categories one rank from that in the conventional classification system, but this does not eliminate the lack of pattern. For example, although Mitchell (1968, p. 1887) concurs with assumptions that the odobenids originated in the North Pacific region, he lists only the living genus and three extinct genera of walrus from the Atlantic in his Subfamily Odobeninae (equivalent in composition to the Family Odobenidae of other authors). Equally uninformative, only one extinct genus of the sea lions, *Pithanotaria,* is listed under his Subfamily Otariinae (which includes all species listed under the Otariidae by other authors).

It will be shown in this report that several of Mitchell's fossil "sea lions," two of his subfamilies, and both of his subfamilial incertae sedis are walruses in a familial sense, Family Odobenidae. In addition, the lineage of fossil sea lions, Family Otariidae, will be shown as an extremely conservative lineage as far as the present fossil record reveals not as diverse a group as the Odobenidae.

Reduced ad absurdum, the theme of this report is that it does not take tusks to make a walrus. It seems appropriate, therefore, to begin by defining what does make a walrus and, by diagnoses, to indicate how other otarioids differ. This is followed by the description of a fossil walrus without tusks. This, then, enables the recognition and description of other fossil odobenids and description of their known stratigraphic and geographic range to complete Part I of this report.

Part II of this report includes a description of fossil otariids new to the published record, a summary of published records, and a description of their known stratigraphic and geographic range. Part III contains no description of new material but summarizes the diversification of a third and extinct otarioid family, the Desmatophocidae (Hay, 1930); it also discusses the presumed ancestral family, the Enaliarctidae of Mitchell and Tedford described by these authors as a subfamily of the otariidae (=Otarioidea of this report) .

THE TERMINOLOGY OF GEOLOGIC TIME

Most of the fossil seals discussed in this report lived during the Miocene and (or) Pliocene Epochs. Confusion has existed for many years in the application of these terms to rocks in the same or different parts of the world by different paleontologists and stratigraphers. No report now dealing with these terms without definition can make geochronologic sense if it deals with interdisciplinary topics or with more than localized geography.

MIOCENE-PLIOCENE BOUNDARY

In recognition that typology is the only logical defense of usage, this report follows the 1959 recommendations of the Mediterranean Neogene Committee of the International Geological Congress regarding the typification of the Miocene-Pliocene boundary. Subsequent refinements have been summarized recently by Van Couvering (1972), Van Couvering and Miller (1971), and Berggren (1971, 1972). For the most part, our usage in this report (table 1) follows their most recent evaluation of the correlations involved (Berggren and Van Couvering, 1974). In this usage, the boundary between rocks of Miocene age and those of Pliocene age is placed at the top of the evaporitic deposits in southern Italy assigned to the Messinian Stage. This usage places most of the rocks that have been called Pliocene along the Pacific Coast of North America in the Miocene Series. The Pliocene Epoch now seems to have lasted only about 3.2 m.y., whereas as it has been used on the Pacific Coast of North America it was considered to have lasted as long as 10 m.y.[2] It is emphasized here that this difference is an insistence on a typological meaning of the epochs and not a change in estimation of the age of the rocks.

As closely as available radiometric dates can be correlated to fossil localities and to the stratotypes of the Miocene and the Pliocene Series, fossils from about 1.8 to about 5.0 m.y. old are herein called Pliocene. Although the fossil record of otarioid seals is poor during this time, there appears to have been significant evolution of the fauna, and the Pliocene is here subdivided into early and late parts at the Blancan-Hemphillian North American land mammal age boundary, which we approximate as being between 3.5 and 4 m.y., following Evernden, Savage, Curtis, and James (1964). This boundary between early and late Pliocene is somewhat older than the approximately 3.3 m.y. boundary used by Berggren and Van Couvering (intending to date the Zanclian-Piacenzian contact). At the present time, however, the faunal differences between the Hemphillian and Blancan Ages are recognizable and no such faunal difference is detectable in the West Coast marine invertebrate section (that is, in the San Joaquin Formation or equivalent).

The Miocene Epoch, which in past customary usage in the Pacific Coast area was about 10 m.y. in duration, is now considered to be of nearly 17 m.y. duration as a result of the acquiescence to typology here expressed. Previously the Miocene Epoch had been subdivided into early, middle, and late parts by more or less arbitrary usage in the Pacific Coast area. These subdivisions were provincial in usage, and it was well understood that their application varied with the paleontologic discipline and was not specifically intended as an exact correlation of some archetypal stratigraphic section in Europe. Their usage, nevertheless, was useful in the Pacific Coast Province.

In the chronology of North American vertebrate paleontologists (Wood and others, 1941), as radiometrically calibrated (Evernden and others, 1964), the late Miocene extended from about 16 m.y. ago to about 12 m.y. ago. For the past 10 years at least, (Evernden and others, 1964, p. 147), there has been a growing realization that by this definition, the conclusion of the Miocene as used by North American vertebrate paleontologists was considerably earlier than that of the type Miocene, regardless of the indecision on where the Miocene-Pliocene boundary should be placed in the type section. With the adoption of the recommendation of the Mediterranean Neogene Committee, it appears that the Miocene Epoch persisted about 7 m.y. longer than the Miocene as defined by Wood and others (1941) and as customarily used by most vertebrate paleontologists in North America. A more or less equal change is indicated in the usage of the late Miocene by invertebrate paleontologists in the Pacific Coast area, although historically they have extended the Miocene into rocks slightly younger than those recognized as of this age by vertebrate paleontologists.

Seven million years is a span of time great enough to include several recognizable faunal changes, and hence a span of time for which temporal subdivisions would be useful; to refer to the time from 16 m.y. ago to about 5 m.y. ago as "late Miocene" would result in losing useful precision. On the other hand, to redefine the informal subdivisions early, middle, and late Miocene would be to introduce familiar terms with unfamiliar meaning into the language of Pacific Coast paleontology.

Redefining the informal subdivisions of the Miocene seems to be the most reasonable choice though, regrettably, it will also be the most confusing. Berggren (1971, p. 755) has suggested a threefold subdivision of the Mediterranean Miocene that seems satisfactory for the most part. This subdivision places the Tortonian and the Messinian Stages in the upper Miocene and the Langhian and the Serravallian Stages in the middle Miocene. The

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[2] Based upon an approximately 1.8 m.y.-old Pliocene-Pleistocene boundary as used in Berggren (1971, 1972).

TABLE 1.—*Time correlation chart*

TIME (m.y.)	AGE (this report)			EUROPEAN STAGES [1]	NORTH AMERICAN MAMMALIAN AGE	WEST COAST MARINE STAGES		WEST COAST USAGE	
						MEGAFOSSILS [6]	MICROFOSSILS		
	PLEISTOCENE	Late		Calabrian	Rancholabrean [1]		Delmontian Base *Bolivina obliqua* zone	PLEISTOCENE	Late
1		Early			Irvingtonian [2]				Early
2	PLIOCENE	Late		Astain Placenzian Zanclian	Blancan [3]	"Etchegoin" and "San Joaquin"		PLIOCENE	Late
3									
4		Early			Hemphillian [4]				
5	MIOCENE	Late	Late	Messinian					
6				Tortonian		"Jacalitos"			Early
7									
8			Early		Clarendonian [3]		[7]		
9									
10						"Margaritan"	Mohnian	MIOCENE	Late
11		Middle	Late	Serravallian					
12					Barstovian [5]	"Temblor"			Middle
13			Early	Langhian			Luisian [8]		
14		Early	Late	Burdigalian			Relizian [8]		
15							Saucesian [8]		
16					Hemingfordian [3]				
17			Early						
18						"Vaqueros"			Early
19				Aquitanian					
20									
21					← Arikareean				
22	OLIGOCENE ↓						← Zemorrian		
23									
24									

NOTES

[1] Berggren and Vancouvering, 1974. For exceptions see text.

[2] Addicott, 1972, 1969.

[3] Naeser, Izett, and Wilcox 1971. Johnson, Opdyke, and Lindsay, 1972: based upon the earliest *Lepus*.

[4] Evernden and others, 1964.

[5] Oldest Hemphillian date 8.0 m.y. Ash Hollow Formation, J.D. Boellstorf, written communication to Tedford, 1975.

[6] Pierce, 1970, Barron, 1976: temporal overlap of definitions are involved.

[7] Turner, 1970, KA2127 Barstovian mammals just below, unpublished.

[8] Turner, 1970.

middle-late Miocene boundary falls at approximately 11 m.y., postdating the oldest radiometrically dated record of the horse genus *Hipparion* in Europe, which has been dated at 12.4 m.y. (Lippolt and others, 1963: Howenegg fauna of Germany). In North America the change from the Barstovian to the Clarendonian mammalian ages, marked by the first record of *Hipparion*, also was about 12 m.y. ago (Evernden and others, 1964).

The beginning of middle Miocene is selected to be about 14.5 m.y. ago; this date approximates the beginning of the Langhian Stage in Europe as shown by Berggren and Van Couvering (1974). Berggren (1971, p. 755 and table 52.39, not table 52.40) suggested the base of the Langhian Stage as the base of the middle Miocene, a usage continued here, although Berggren and Van Couvering (1974) place the early-middle Miocene boundary within the Langhian at the base of the planktonic foraminifer zone N9. Following Van Couvering and Miller (1971, p. 562), the late Miocene is believed to have lasted until "something like 5 m.y." Berggren and Van Couvering (1974) review the arguments about the time of the Miocene-Pliocene boundary that further support 5 m.y. This date for the end of the Miocene Epoch falls somewhere within the younger part of the Hemphillian mammalian age in North America and approximates the beginning of the Zanclian Stage in Italy.

By this definition of time, the 3.5-m.y.-long middle Miocene and the 6-m.y.-long late Miocene, span three recognizable stages of otarioid evolution along the Pacific Coast of North America. In order to identify these stages, the middle and late Miocene are here arbitrarily broken into lesser parts: *early middle Miocene,* dominated by the genus *Allodesmus; late middle Miocene and at least part of the early late Miocene,* dominated by the genus *Imagotaria;* and *late late Miocene,* dominated by the new genus *Thalassoleon.* As now understood, the new genus *Thalassoleon* extends throughout the late late Miocene and Pliocene, and some incompletely known genera, among them *Valenictus,* seem to be of both late Miocene and Pliocene age. It is expected that more discoveries, and hoped that more radiometric dates, will better define late Miocene and Pliocene otarioid faunas along the Pacific Coast.

PLIOCENE-PLEISTOCENE BOUNDARY

Probably no chronostratigraphic boundary has received more attention than the Pliocene-Pleistocene boundary. Berggren and Van Couvering (1974), in reviewing and evaluating the highlights of the investigation of the Pliocene-Pleistocene boundary, conclude that the base of the Calabrian deposits in southern Italy, which is equivalent to the base of the Pleistocene as recommended by the Pliocene-Pleistocene Commission of the 18th [1948] International Geological Congress, is between 1.7 and 1.8 m.y. ago. They show it in their charts as a band between 1.7 and 1.8 m.y. ago or as a line 1.8 m.y. ago. The 1.8 m.y. date is used in the present report.

The approximate ages, epochal assignments, and correlation of stages used in this report are summarized in table 1. The antiquity of the fossils discussed will also be stated in years, as an interpretation based upon the best information available to the authors. Because the epochal assignments differ drastically from those customarily used along the Pacific Coast of North America, one column in table 1, "West Coast usage," indicates long-established provincial usage of epoch terminology based upon West Coast marine invertebrates; that by which all previously described fossil otarioid seals from the Pacific Coast have been dated. Present trends seem to indicate that this provincial usage of epoch assignments will be continued along the Pacific Coast of North America for utilitarian considerations, while recognizing that it is not compatible with European usage. Provincial usage of Neogene epochal terminology along the Atlantic Coast has not differed so greatly from European usage, and it seems at this time that the relatively minor adjustments to establish conformity are being incorporated into provincial usage.

ROCK-STRATIGRAPHIC UNITS DISCUSSED

Several rock-stratigraphic units are discussed here in terms of their age and their otarioid pinniped fauna. Because confusion will undoubtedly result from the new age assignments based upon acceptance of the recommendations of the Mediterranean Neogene Committee of the International Geological Congress, it is felt that a tabulation here, in summary, will help the reader retain orientation. Cause for this roughshod revision of formational age assignments lies in the need to discuss chronology when establishing evolutionary sequence. Among fossil otarioids, this need is best illustrated by primitive walruses: *Prorosmarus alleni* is from a formation customarily dated late Miocene, and *Aivukus cedrosensis,* new genus and species, is from a formation customarily dated middle or late Pliocene. Available information now indicates that *A. cedrosensis,* the more primitive genus, is older by as much as 3 m.y. (see table 2).

OTHER TERMINOLOGY

Anatomical terminology follows, as feasible, the usage of Miller, Christensen, and Evans (1965) for the dog. There are a few obvious exceptions, such as the names of the carpals and tarsals for which Miller, Christensen, and Evans use a nomenclature more frequently used for reptiles rather than that derived from human anatomical terminology with which most mammalian paleontologists, at least, are more familiar.

TABLE 2.—*Age assignments of otarioid fauna and their host rocks*

Otarioid Fauna	*Estimated* age (m.y.)[1]	Stage - Age Association[1]	International Epoch Assignment[1]	West Coast usage	Formation or member	Locality	Page Reference
Arctocephaline aff. *Callorhinus*	2 -4	Blancan and "San Joaquin"	Late Pliocene	Late Pliocene	San Diego Formation	San Diego, Calif.	70
Valenictus imperialensis	4	Hemphillian and "San Joaquin"	Early Pliocene	Late Pliocene	San Joaquin Formation	Kettleman Hills, Calif.	54
Prorosmarus alleni	4 - 5	Hemphillian and N18 or N19 zones of Blow	Early Pliocene	Early Pliocene of East Coast usage	Yorktown Formation	Va. and N. Carolina	14
Dusignathus santacruzensis *Thalassoleon* sp. cf. *T. macnallyae*	4 - 6.7	"Etchegoin" and "San Joaquin"	Late late Miocene and Pliocene	Late Pliocene	Purisma Formation	Santa Cruz, Calif.	47, 14-16
?*Dusignathus santacruzensis* *Thalassoleon macnallyae*	4 - 6.7	"San Joaquin"	Late late Miocene or Pliocene	Early Pliocene	Drakes Bay Formation	Point Reyes, Calif.	69, 14-16
Pliopedia pacifica Arctocephaline aff. *Callorhinus*	4 - 7	Hemphillian and "Etchegoin"	Late late Miocene	Middle Pliocene	Etchegoin Formation	Kettleman Hills, Calif.	49, 70
Valenictus imperialensis	4 - 6	None	Late Miocene or Pliocene	Early Pliocene	Imperial Formation	Imperial Valley, Calif.	53
Pliopedia pacifica	5 - 6	"Etchegoin"	Late late Miocene	Early Pliocene	Paso Robles Formation	Santa Margarita, Calif.	49
Pontolis magnus	5 - 7	"Etchegoin"	Late late Miocene	Early Pliocene	Empire Formation	Coos Bay, Oregon	42
Aivukus cedrosensis *Thalassoleon mexicanus* *Disignathus santacruzensis*	6 - 8	None	Late late Miocene	Early Pliocene	Almejas Formation	Isla Cedros, Baja California	14-16
Aivukus cedrosensis	6 - 8	"Etchegoin(?)"	Late late Miocene	Pliocene	Salada Formation	Refugio, Baja California Sur	16
Imagotaria downsi *Pithanotaria starri* Desmatophocine "A" of Barnes	9 - 10	"Jacalitos"	Early late Miocene	Early Miocene	Upper part of Santa Margarita Formation	Santa Cruz, Calif.	24-26
Imagotaria downsi	9 - 11	"Margaritan"	Early late Miocene	Late Miocene	Lower part of the Towsley Formation	Soledad Canyon, Calif.	24
Allodesmus sp.	10 - 12	Clarendonian	Late middle Miocene	Late Miocene	Lower part of the Santa Margarita Fm.	Santa Cruz, Calif.	24, 75
Imagotaria downsi *Pithanotaria starri*	10 - 12	Mohnian	Late middle *Miocene*	Late Miocene	Sisquoc Formation	Lompoc, Calif.	24
Imagotaria sp.	11 - 12	Clarendonian and "Margaritan"	Late middle Miocene	Late Miocene	Santa Margarita Formation	Tejon Hills, Calif.	24
Pithanotaria starri	11 - 12	Mohnian(?)	Late middle Miocene	Late Miocene	Santa Margarita Formation	Seaside, Calif.	59
Allodesmus kernensis *Neotherium mirum* Desmatophocine "B" and "C" of Barnes	13 - 14	Barstovian, Luisian, and "Temblor"	Early middle Miocene	Middle Miocene	Round Mountain Silt	Bakersfield, Calif.	54
Allodesmus packardi	13 - 14	Luisian and "Temblor"	Early middle Miocene	Middle Miocene	Unnamed formation	Menlo Park, Calif.	75
Allodesmus courseni	13 - 14	Luisian	Early middle Miocene	Middle Miocene	Monterey Shale	Torrance, Calif.	75
?*Desmatophoca* sp.	15 - 16	"Temblor"	Late early Miocene	Middle Miocene	Narrow Cape Fm.	Kodiak, Alaska	74
Desmatophoca oregonensis Undescribed enaliarctids	15 - 17	Barstovian, "Temblor," and late Saucesian	Late early Miocene	Middle Miocene	Astoria Formation	Newport, Oregon	74
Enaliarctos mealsi	22 - 23	Arikareean, "Vaqueros," and Saucesian and Zemorrian	Early early Miocene	Early Miocene	Jewett Sand	Bakersfield, Calif.	77

[1] At or near the fossil locality, not necessarily for the entire formation or for other areas.

The following acronyms or abbreviations are used:

Specimen numbers

- CAS—California Academy of Science, San Francisco
- HSC—California State University, Humboldt, at Arcata
- LACM—Natural History Museum of Los Angeles County
- MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
- SBNHM—Santa Barbara Natural History Museum
- SU—Stanford University
- UA—University of Alaska, Fairbanks
- UCMP—University of California Museum of Paleontology, Berkeley
- UCR—University of California at Riverside
- USNM—National Museum of Natural History, Washington, D.C.
- IGCU—Instituto de Geologia, Ciudad Universitaria, Universidad Nacional Autonoma de Mexico.

Locality numbers

- HSC—California State University, Humboldt, at Arcata
- UCMP V—University of California Museum of Paleontology vertebrate locality
- UCR RV—University of California at Riverside vertebrate locality
- USGS M—U.S. Geological Survey vertebrate locality, Menlo Park register

Others

- CBL—Condylobasal length of the skull, measured from the posterior surface of the occipital condyles to the anterior tip of the nasal process of the premaxillae
- m.y.—million years
- B.P.—Before present

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This study of the otarioid seals of the Neogene was begun in 1965 with the description of the female skull of *Imagotaria downsi.* The large collection of fossil pinnipeds from Cedros Island, Baja California, collected by Tedford, Frank H. Kilmer, and associates, was added to the study, as were additional materials from the Santa Margarita Formation in the vicinity of Santa Cruz, Calif., and other formations and localities.

Several years were spent by Repenning on the study of living seals; this work was aided by Francis H. Fay and the late Richard S. Peterson in particular. Many zoologists specializing in the study of seals, in number about 75, from many countries in both the northern and southern hemispheres, were extremely helpful in providing study specimens, information, and discussion. There is a camaraderie among those who study marine mammals that the senior author has not seen matched in any other group of specialists. Whether it derives from the smell of salt air or from the surprises of beaching a rubber raft in the surf, he is most grateful for having experienced this bond.

Because paleontologists specializing in the study of seals are not so numerous as zoologists of the same bent, they can be thanked by name. To Edward D. Mitchell, Clayton E. Ray, Lawrence G. Barnes, and Q. Bret Hendey, we extend our thanks for years of free exchange of ideas and information.

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SUPRAGENERIC DIAGNOSES

Superfamily OTARIOIDEA

Otarioidea Smirnov, 1908, pp. 1, 14: Gregory and Hellman, 1939, p. 313: Scheffer, 1958, p. 52: King, 1964, p. 7.

Otariidae sensu lato: Mitchell, 1968, p. 1897.

Characters.—"Hind legs capable of being turned forward and used in terrestrial locomotion. Neck lengthened*** Skull with mastoid process large and salient (especially in males [and adults]), and with distinct alisphenoid canals." (Allen, 1880, p. 3 [for Gressigrada]). Basal whorl of cochlea directed posterolaterally. Anterior process of malleus present. No head developed on the incus. Internal acoustic meatus present. Adult auditory bulla composed of about three-fourths ectotympanic ossification of the tympanic, the entotympanic ossification largely confined to the formation of the carotid canal. Jugular process of the exoccipital fused to the mastoid in maturity except in the odobenids, where fusion, if it occurs, takes place in old age. Sexual dimorphism great in all members.

Except for the fissipedlike enaliarctids, all otarioids have flat to little-inflated tympanic bullae, no fossa for the origin of the tensor tympani muscle, homodont cheek teeth, and very poorly developed bony external auditory meatuses.

Remarks.—The Phocoidea appear to have originated and diversified in the ancient North Atlantic basin. Enough of the fossil record is now known to be certain that the Otarioidea originated and experienced its major diversification in the North Pacific basin. The record is strongly suggestive that all taxa included in the Otarioidea derive from a common pinniped ancestor. Mitchell and Tedford (1973, p. 278) felt that the pinniped families should be included with their fissiped relatives in the superfamily Canoidea and did not recognize the superfamilies Otarioidea and Phocoidea. The Otarioidea is retained in the present report in recognition of the probable common ancestry of its four included families.

Family ODOBENIDAE

Odobaenidae Allen, J., 1880, p. 5: Smirnov, 1929, p. 242: Ognev, 1935, p. 322.

Odobenidae: Palmer, 1904, p. 833 (emended spelling): Allen, G., 1930, p. 139: Scheffer, 1958, p. 84: Bobrinsky and others, 1965, p. 168.

Odobaeninae: Orlov, 1931, p. 69 (footnote)—Of questionable status as Orlov states, without elucidation, that some workers place the walruses, as a subfamily, in the Family Otariidae but does not do so himself.

Odobeninae, Mitchell, 1968, p. 1897 (as a subfamily of the Otariidae).

Characters—Skull lacking prominent supraorbital process. Occipital condyles widely flaring and in most species they are low relative to the upper margin of the foramen magnum. Jugular process of exoccipital thin and platelike, remaining unfused to the mastoid at least until late adulthood. Basioccipital very broad and roughly pentagonal in form. Tympanic membrane large. Auditory ossicles very large. Internal acoustic meatus very wide and shallow with almost complete separation of canals for vestibulocochlear and facial nerves. Petrosal apex greatly enlarged, broadly rounded, and flat. Bony Eustachian canal of very large calibre. Palate arched. Hypophyseal fossa broad and shallow. Cheek tooth roots simple and peglike at very early stage of evolution. In primitive tooth forms, upper cheek teeth simple with a posterointernal accessory cusp, lower teeth with weak medial anterior and posterior accessory cusps; in forms with greater tooth specialization, these features are greatly subdued (*Odobenus*) or entirely lacking (*Dusignathus*). Lateral lower incisor anterior to lower canine, rather than anteromedial; variably present in some genera. Symphysis of mandible deep, strong, narrowly oval in shape and articulating over the entire depth of the strong chin, completely fusing in the adults of the living genus. Angle of the mandible, where the digastricus inserts, is weak and anteriorly located beneath a point between the last cheek tooth and the coronoid process.

Humerus long, for a pinniped, and slender; distal termination of the pectoral crest about in line with the medial lip of the trochlea of the distal articulation; anteroposterior diameter of the trochlear lip much greater than that of the distal capitulum. Radius with pronator origin at or distal to the midpoint of shaft. Ulna without flat anterior surface of a olecranon above semilunar notch; distal radial articulation distinct and elevated. Scapholunar with deep pit for articulation with magnum.

Femoral head distinctly higher than greater trochanter. Proximal end of fibula not usually fused to the tibia, commonly so even in individuals of great age. Calcaneum with most prominent tuberosity on the medial side of the calcaneal tuber. Astragalus with high and essentially vertical fibular articulation, not flaring distally onto an extended lateral process.

Remarks—Known odobenids are as old as early middle Miocene in the Pacific and early Pliocene in the Atlantic. Much has yet to be discovered regarding their earlier history, as it seems that the family already was sharply divided into two groups by late Miocene time. These two groups are diagnosed as follows.

Subfamily ODOBENINAE

Odobeninae: Mitchell, 1968, p. 1894 (as a subfamily of the Otariidae). See also "Odobaeninae: Orlov, 1931" under Family Odobenidae.

Characters.—Upper canines elongate. Lower canines reduced. Tympanic membrane: oval window area ratio approximating 20:1, suggesting shallow-water feeding (Repenning, 1972, p. 326). Cheek teeth peglike.

Remarks—There is one living genus and species, *Odobenus rosmarus* (Linnaeus), in boreal Atlantic and Pacific. The odobenines were present in the Atlantic at least by early Pliocene time. However, their record in the Pacific extends back possibly to early late Miocene. The presence of older dusignathines only in the Pacific, and the absence of all other otarioids in the North Atlantic, strongly suggest that the odobenines originated in the Pacific.

Subfamily DUSIGNATHINAE

Dusignathinae Mitchell, 1968, p. 1894 (as a subfamily of the Otariidae).

Imagotariinae Mitchell, 1968, p. 1895 (as a subfamily of the Otariidae).

Characters—Upper and lower canines of about equal size. Tympanic membrane:oval window area ratio approximating 10:1 in some genera having sea lionlike teeth with or without multiple roots, suggesting deepwater feeding. Cheek teeth with stout peglike roots in other genera.

Remarks—The extinct dusignathines seem to have been confined to the North Pacific Ocean and to the Miocene and Pliocene Epochs.

Though united by abundant odobenid features of both cranial and postcranial skeletal elements and by the lack of the odobenine character of emphasizing the upper canines while reducing the lower, the dusignathine odobenids include two distinct types. The existence of these two types was recognized by Mitchell in erecting the two subfamilies, one largely or entirely represented by the genus *Dusignathus,* the other largely or entirely represented by the genus *Imagotaria.*

Dusignathus has walruslike stout peglike roots on its cheek teeth and a very large tympanic membrane, suggesting shallow-water habits. *Imagotaria* has sea lionlike teeth and a smaller tympanic membrane with an area ratio to the oval window approximating 10:1 (comparable to the sea lions), suggesting deep-water habits and a fish-cephalopod diet. With further knowledge about this subfamily of odobenids, it is reasonable to suppose that these two dusignathine types may prove sufficiently distinct to merit recognition as separate subfamilies, as was done by Mitchell, but of the Odobenidae, not of the Otariidae.

Family OTARIIDAE

Otariidae Gill, 1866, p. 7: Scheffer, 1958, p. 52: Bobrinsky and others, 1965, p. 166.

Otariinae sensu lato: Mitchell, 1968, p. 1896 (as a subfamily of the Otariidae).

Characters—Supraorbital processes present, very strong in adult males. Occipital condyles high, close together, and parallel or nearly so. Jugular process of the exoccipital knoblike and usually thick, fused to mastoid in adulthood. Basioccipital moderately narrow, parallel sided to trapezoidal in form. Tympanic membrane very small. Auditory ossicles of normal carnivore size. Internal acoustic meatus roundly oval to circular with little or no separation of canals for facial and vestibulocochlear nerves. Petrosal apex pointed or bluntly pointed and relatively little enlarged for a seal. Bony Eustachian tube not conspicuously enlarged. Palate flat to arched. Hypophyseal fossa deep and globose. Teeth consistently double-rooted until the late late Miocene; many living species still retain double-rooted upper molars (Repenning and others, 1971, p. 9). Upper cheek teeth lack any persistent posterointernal cusp. Third lower incisor anteromedial to the lower canine. Symphysis of mandible shallow and weak, broadly oval in shape, usually not articulating over the entire depth of the chin, and never fused. Angle of the mandible, where the digastricus inserts, is weak and anteriorly located.

Humerus short and stout, tending to be more slender in the fur seals; anteroposterior diameter of the trochlear lip about the same as that of the distal capitulum; distal termination of the pectoral crest about in line with the midpoint of the distal articulation except in the fur seals. Radius short with pronator origin proximal to midpoint of shaft. Ulna with flat anterior surface of olecranon above semilunar notch (narrower in more ancient genera), distal radial articulation inconspicuous and united with distal articulation. Scapholunar with facet for articulation with magnum little or no deeper than adjacent facet for unciform.

Femoral head about as high as greater trochanter. Head of the fibula fused to that of the tibia in forms younger than the late Miocene. Calcaneum with medial tuberosity on calcaneal tuber no larger than that on lateral side. Astragalus with low fibular articulation flaring distally and curving toward a paraplantar plane onto an enlarged lateral process.

Remarks—Known otariids are as old as late middle Miocene in the North Pacific Ocean. Although never entering the North Atlantic, they have, in the past 5 m.y., dispersed around the world in the southern hemisphere.

The living Otariidae are subdivided into the subfamilies Otariinae (sea lions) and Arctocephalinae (fur seals) by some workers. Repenning, Peterson, and Hubbs (1971, p. 3) have suggested that the subfamilial distinction is unreal because they were unable to find any consistent osteologic differences in the skull of these groups, and they regarded the presence of abundant underfur in the fur seals as a retention of a primitive otariid feature, possibly in more than one lineage.

In the present study, some differences in the postcranial bones were noted between the fur seals and the sea lions. Together they offer some basis for morphologic separation of living fur seals from sea lions but are of questionable value in diagnosing fossil otariids.

All these differences are here taken to represent retained primitive features in the fur seals either because they more nearly resemble the known Miocene and Pliocene otariids or because they are logically a feature of shallow-water aquatic carnivores, the obvious source of the pinnipeds. As a consequence, the fur seals are presumed to most resemble the ancestral otariids, at least to the extent disclosed by the present fossil record.

As discussed in Part II to follow, the fossil record of the otariids strongly suggests that the lineage leading to the Alaskan fur seal *Callorhinus* diverged from the otariid ancestral group before the sea lions did. Study of their endemic louse fauna and of their bacular morphology supports this suggestion (Kim and others, 1975). It appears most likely that the Subfamily Arctocephalinae, including the two living fur seal genera *Callorhinus* and *Arctocephalus,* is polyphyletic, and it is retained in this report only as a convenience in expression.

The sea lions presumably evolved into their present form with the loss of abundant underfur, increase in average size—particularly body size rather than head size, increase in the rate of development of single-rooted cheek teeth, beginning of the reduction of the number of upper molars, and strengthening of the humerus, possibly in relation to larger body size.

Subfamily "ARCTOCEPHALINAE"

Ouliphocinae Allen, 1870, p. 23.

Arctocephalinae von Boetticher, 1934, p. 359.

Arctocephalini: Mitchell, 1968, p. 1897 (as a tribe of the Subfamily Otariinae s.l. but not Arctocephalina Gray, 1837, p. 582).

Characters—Otariid seals with abundant underfur, usually of small size and relatively large head, third (lateral) upper incisor small and with small root moderately to conspicuously oval in cross section, upper molars usually double-rooted, M^2 usually present, humerus elongate (greatest length/least diameter averaging >5.7, *see* table 3) and with a pectoral crest which terminates distally toward the medial lip of trochlea, anterior part of body and the tip of the os penis (or baculum) transversely very narrow (Morejohn, 1975).

Remarks—The proportions of the humerus tend to make the fur seals appear somewhat more like the odobenids than do the sea lions. The overall difference between the two otariid types is slight, however, and individual or specific exceptions to some of the characters are known.

These characters, with the exception of underfur, are the basis for assigning all pre-late Pliocene otariids to the fur seals. The fossil record here considered is strongly supported by studies of the louse fauna and the bacula of the living otariids (Kim and others, 1975). It seems evident that the sea lions evolved out of the fur seals in very recent time, less than 3 m.y. ago.

Subfamily "OTARIINAE"

Trichophocinae Allen, 1870, p. 23.

Otariinae: von Boetticher, 1934, p. 359.

Otariini: Mitchell, 1968, p. 1897 (as a tribe of the Subfamily Otariinae s.l. but not Otariina Gray, 1825, p. 340).

Characters.—Otariid seals with very sparse underfur, large body size, third upper incisor large with long root of round cross section, cheek teeth single-rooted or nearly so, M^2 frequently missing, humerus stout with pectoral crest directed more or less toward the midpoint of the distal articulation, anterior part of the body and the tip of the os penis transversely broad, triangular to circular (Morejohn, 1975). Stirling and Warneke (1971) discuss vocal and behavioral differences between the sea lions and the fur seals.

Family DESMATOPHOCIDAE

Desmatophocidae Hay, 1930, p. 557.

Allodesmidae Kellogg, 1931, p. 227.

Desmatophocinae: Mitchell, 1966, p. 39 (including *Allodesmus* and *Dusignathus* as well as *Desmatophoca.*

Desmatophocinae: Mitchell, 1968, p. 1839 (excluding *Allodesmus* and *Dusignathus*).

Desmatophocinae: Barnes, 1972, p. 5 (including *Allodesmus* and *Desmatophoca,* excluding *Dusignathus*).

Characters—Supraorbital processes lacking or very weak (no greater than found in some phocids). Jugular process of exoccipital greatly enlarged into a posterolaterally extending process distinct from, but with maturity fused to, the mastoid process. Basioccipital moderately broad and trapezoidal to nearly rectangular in form. Tympanic membrane small. Auditory ossicles large but otherwise not described (Mitchell, 1966, p. 6). Internal acoustic meatus very wide and shallow with almost complete separation of canals for the vestibulocochlear and facial nerves. Petrosal apex very little enlarged. Bony Eustachian canal of very large calibre in *Allodesmus* but not *Desmatophoca*. Palate flat and very broad posteriorly. Mortised jugal-squamosal articulation. Hypophyseal fossa broad and shallow. Cheek tooth roots double-rooted to peglike, evolving single-rooted cheek teeth much earlier than other otarioid families. Upper cheek teeth simple, main cusps may or may not have posterointernal accessory cusps. Third lower incisor anterior to canine. Symphysis of the mandible deep, strong and very narrowly oval in shape, strongly tending to be narrower ventrally than dorsally and not fusing in adults. Angle of the mandible, where the digastricus inserts, deep, strong, and posteriorly located below the apex of the coronoid process or posterior to this point.

At present the postcranial skeleton of the desmatophocid is known only in the genus *Allodesmus* (Downs, 1956; Mitchell, 1966; Barnes, 1972). Relative to *Desmatophoca, Allodesmus* is a very specialized animal in the features of its skull; it is expected that when the postcranial skeletal elements of *Desmatophoca* are known, they will be equally distinct. In general the limb bones of *Allodesmus* appear odobenid in those characters just outlined for the Odobenidae. Although possibly reflecting the specializations of the genus, the limb bones of *Allodesmus* are distinguished by the following unique or otariid-like features of the otherwise odobenid-like skeletal elements:

Humerus elongate with unusually (for a pinniped) weak pectoral insertion; anteroposterior diameter of the trochlear lip about the same as that of the distal capitulum. Radius very elongate with a pronotor origin conspicuously proximal to the midpoint of the shaft. Metacarpals and phalanges very stout. Femur with an unusually deep trochanteric fossa and a greater trochanter which is not conspicuously lower than the head. Tibia short relative to living otarioids. Calcaneum sea lionlike in that the most prominent tuberosity on the calcanear tuber is lateral but marked by overall shortness and broad distal end.

Remarks—Although no specimens included in this family, as here understood, are described in this report, a discussion of familiar characteristics and content is required in explanation of the removal from this family of some genera which are described and which have been considered desmatophocids in some published classifications. As here understood, the characters of this family are based entirely upon the genera *Desmatophoca* and *Allodesmus*. The contents and characters of the family have been most recently reviewed by Barnes (1972).

Morphologically the desmatophocids seem intermediate between the odobenids and the otariids in some characters. Like the otariids, they have minimal development of petrous bone at the apex of the petrosum; thick and knoblike jugular processes of the exoccipital which, however, form distinct posterolaterally directed processes different than the condition found either in the otariids or the odobenids; relatively narrow basioccipital bones; and flat to moderately arched palate. Like the odobenids, the desmatophocids have no supraorbital processes; very greatly enlarged auditory ossicles; a very widely spread internal acoustic meatus (one specimen of *Allodesmus,* UCMP 83363, has an almost phocidlike separation of the facial canal from the vestibulocochlear fossa); a broad shallow hypophyseal fossa; single-rooted teeth early in their history; and deep, strong, and narrowly oval symphysis of the mandible.

Evolution of the living lineages of pinnipeds is marked by a pronounced trend in reducing the length of and increasing the strength of the proximal limb elements and in lengthening the more distal elements. This progressive improvement of flipper strength, leverage, and surface area is at a very primitive stage of development in the genus *Allodesmus,* the most specialized of the known desmatophocids.

Family ENALIARCTIDAE

Enaliarctinae Mitchell and Tedford, 1973, p. 218.

Characters—Supraorbital processes lacking or very weak (no greater than found in some phocids). Jugular process of exoccipital greatly enlarged into a posterolaterally extending process distinct from, but paraoccipital process of the temporal, which, in turn, is connected to the mastoid process by a strong ridge. Basioccipital moderately narrow and nearly parallel sided. Tympanic membrane small. Auditory ossicles of normal carnivore size. Bony Eustachian canal of small calibre. Bullae greatly inflated for an otarioid seal, smooth and flask-shaped because of well-developed external auditory meatus. Tensor tympani originating in a fissipedlike fossa lateral to the promontorium. Lacrimal foramen present. Carnassials present: P^4 three-rooted with protocone, M_1 with talonid; M^{1-2} more or less quadrate, M^1 three-rooted.

Remarks—Although no specimens included in this family, as here understood, are described in this report, a discussion of the ancestral position of this family is included. To date only one species has been described, *Enaliarctos mealsi* Mitchell and Tedford from the early Miocene of California.

PART I: WALRUSES

Family ODOBENIDAE

Subfamily ODOBENINAE

Genus ODOBENUS Brisson

Brisson (1972, p. 30) has been designated author of this genus under the Plenary Powers, Opinion 467, although Linnaeus used the name in his first edition of *Systemae Naturae* (1735, p. 59). In his tenth edition (1758, p. 38), however, Linnaeus used "Phoca rosmarus" and Brisson was the first to use *Odobenus* following this starting point of the Law of Priority. Opinion 467 designated *Rosmarus* Brünnich, 1771, a junior objective generic synonym.

Type species—Odobenus rosmarus (Linnaeus, 1758).

Diagnosis—In the adult, the upper canines are elongate, evergrowing tusks with globular dentine filling the vacated pulp cavity, upper incisors 1 and 2 absent or rudimentary, I^3 well developed and located medial to the tusk and in line with premolars 1-3 forming a continuous cheek tooth arcade of four peglike teeth having essentially equal diameter, upper fourth premolar often present as a greatly reduced and poorly rooted peg, the lower incisors are absent or rudimentary, the lower canine reduced to the size and position of a cheek tooth in line with lower premolars 1-3, mandibular rami firmly fused at the symphysis in adults.

Included species—Odobenus rosmarus (Linnaeus): living in the North Atlantic, North Pacific, and Arctic Oceans. Pleistocene records are known in the Atlantic as far south as North Carolina and Paris (Ray, 1960, p. 137), Michigan (Handley, 1953), and, in the Pacific, San Francisco (R. T. Orr, written commun., 1968).

Odobenus huxleyi (Lankester): Late Pliocene and early Pleistocene of England and Holland and possibly of the United States (Ray, 1960).

This species was originally named by Lankester (1865) under the new genus *Trichecodon*. In 1880 Lankester concluded that the species belonged in the same genus as the living walrus, then called *Trichecus*. This usage has generally been followed by many European workers (Rutten, 1907; Hasse, 1909; Van Deinse, 1964) but *Trichecodon* has generally been retained by American workers. Allen (1880, p. 65) stated that he did not consider *Trichecodon huxleyi* generically separable from the living walrus (in the same year that Lankester published the same opinion) but he retained the generic name (in quotes, p. 14) for the material Van Beneden (1877) described under the name *Trichecodon koninckii*. Rutten (1907, p. 7) did essentially the same thing by referring to *Trichecodon* only with reference to Van Beneden's material, calling *huxleyi* a species of *Trichecus*. Kellogg (1922, p. 49), however, somewhat confusingly mentions that "the figures and descriptions given by Rutten do not warrant his conclusions on the distinctness of the genus *Trichecodon*" and continues usage of this genus for both species *T. huxleyi* and *T. koninckii*.

According to both Lankester (1865, 1880) and Rutten (1907), *Odobenus huxleyi* differs from *Odobenus rosmarus* by its markedly greater tusk curvature. Rutten also discusses other cranial characters, all of which can be matched by extreme individual variations in the living walrus, as he points out. Ray (1960) further discusses the distinctiveness of the tusks and has pointed out (C. E. Ray, written commun., 1975) that Rutten's material is not necessarily *O. huxleyi*.

Genus ALACHTHERIUM DuBus

Type species—Alachtherium cretsii DuBus, 1867, p. 562.

Diagnosis—In the adult, the upper canines are elongate, ever-growing tusks (as inferred from the alveoli; the tusks are unknown, or unrecognized); two well-developed upper incisors are placed medial to the anterior margins of the tusks and do not form part of the cheek tooth row; four upper premolars and one reduced molar are present and are relatively widely spaced in comparison with *Odobenus*. The occiput is markedly rectangular in posterior view. These features are known from *Alachtherium antwerpiensis* of Hasse (1909). From Hasse's illustrations, it would appear that the snout was more elongate and that the tusks were more procumbent than in *Odobenus*.

Two lower incisors are present; the lower canine is positioned as and reduced in size to that of a cheek tooth—in line with the lower premolars 1-4, the mandibular rami are not fused at the symphysis but the symphysis is very elongate—extending posteriorly to the anterior margin of P_4 as projected normal to the alveolar margin, the lower cheek teeth are widely spaced in comparison with *Odobenus*. These features are known from the type species.

***Included species.—Alachtherium cretsii* DuBus, 1867, p. 562: Early Pliocene (Scaldisian) of Antwerp (Mourlon, 1877). The type is a mandibular ramus.** Van Beneden (1877) assigned a braincase, as well as a number of isolated postcranial elements, to this species, these also ostensibly from the Scaldisian of

Antwerp. Rutten (1907, p. 10) questioned Van Beneden's reason for assigning the braincase to *A. cretsii,* pointing out inconsistencies in the configuration of the type mandible and of the referred braincase. He concluded that they are not the same and that the braincase should be given a new name, which he provided: *Trichecus (=Odobenus) antverpiensis.*

Alachtherium antverpiensis (Rutten, 1907, p. 12): Early Pliocene (Scaldisian) and late Pliocene (Poederlain) of Antwerp. Although he pointed to considerable differences between *Trichecus huxleyi* and *Trichecus antverpiensis* to distinguish these two species, Rutten (1907, p. 12) did not deem it advisable to propose a new genus on the basis of the cranium which Van Beneden had referred to *Alachtherium cretsii.* Rather, he elected to put this new species in *Trichecus* (=*Odobenus*).

Hasse (1909) described a new skull, as well as a great number of postcranial bones, from the Poederlian deposits overlying the Scaldisian deposits of Antwerp. He mentioned Rutten's paper in connection with the features of *Trichecus huxleyi,* but he failed to mention Rutten's discussionof *Trichecus antverpiensis.* Although the skull described by Hasse is remarkably similar to that described by Van Beneden (from the older Scaldisian deposits) and named by Rutten, these similarities were not mentioned; rather, Hasse (p. 312) assigned his species to *Alachtherium* on the basis of similarity of dental formula and tooth form with the type mandible of *Alachtherium cretsii* DuBus.

Hasse (p. 312-313) then listed the differences between *A. cretsii* (mandible only) and his species (fewer but not altogether dissimilar to the distinguishing features noted by Rutten), and he concluded that his was a different species of *Alachtherium* than was the type mandibular ramus described by DuBus. He named it, rather prominently pointing out that he was the author, "*Alachtherium antwerpiensis* G. Hasse, 1909."

From the published record, it is not certain that the type of *T. antverpiensis* Rutten, 1907, the cranium from the Scaldisian deposits included in *A. cretsii* by Van Beneden, is the same species as the type of *A. antwerpiensis* Hasse, 1909, the skull from the Poederlian deposits of Antwerp. At present it seems more likely that they are the same species and *Alachtherium antverpiensis* (Rutten) is here used. A review of the European material is needed to eliminate the uncertainties of identification, but such a review is beyond the scope of this report.

Genus PROROSMARUS Berry and Gregory

Plates 2 and 5

Type species.—Prorosmarus alleni Berry and Gregory, 1906; USNM 9343, the left ramus of a mandible.

Diagnosis.—"Two well developed incisors in each ramus*** [lower] canine [reduced] but retains its primitive position [not in line with the cheek teeth] and caniniform shape*** upper jaw must have retained*** functional incisors in the adult [judged by wear on the medial side of the lower canine]* ***symphysial surfaces did not become anchylosed." [*extracted from* Berry and Gregory, 1906, 444-446]. Berry and Gregory infer from the position of the lower teeth that the upper canine was not nearly so enlarged as in living *Odobenus*; this seems unlikely, however, as large isolated walrus tusks have been found in the Yorktown and equivalent formations since 1906 (C. E. Ray, oral commun., 1969). These tusks strongly resemble those of *Odobenus huxleyi* and have globular dentine filling the pulp cavity.

These characters were listed in contrast to *Odobenus.* The resemblances to *Alachtherium cretsii* DuBus, as described by Van Beneden (1877), are greater in some respects but *Prorosmarus* differs by having a mandible more like that of *Odobenus* without the extreme upturn of the jaw found in *Alachtherium,* which, as pointed out by Berry and Gregory (1906, p. 450), "implies a shorter, more upturned facial region." At least in configuration of the mandible, *Prorosmarus* much more greatly resembles *Odobenus* than does *Alachtherium.* And the cheek teeth of *Prorosmarus* are closely spaced as in *Odobenus.* The mandibular symphysis, though unfused and elongate, does not extend nearly as far back as in *Alachtherium* but terminates beneath P_2.

An odobenid humerus from the type area, Yorktown, Va., in the Museum of Comparative Zoology, Harvard, specimen, MCZ 7713, collected by the J. B. Woodworth Expedition, is the size of the humerus of a large male walrus as pointed out by C. E. Ray (oral commun., 1968). Although clearly odobenid, it differs from the humerus of the living walrus in that the deltoid tubercle has not migrated off of the pectoral crest but, rather, is only a prominence on the lateral margin of the crest, as on the sea lion humerus. In this respect, the Yorktown humerus is similar to that of *Alachtherium.* In all other respects this humerus, like that of *Alachtherium,* is quite comparable to that of living *Odobenus,* being elongate for a pinniped, having the medial lip of the trochlea of much greater anteroposterior diameter than the distal capitulum, and having the pectoral crest directed distally toward the medial lip of the trochlea rather than toward the center of the articulation.

Distribution.—The Pliocene of western North Atlantic Ocean. Hazel (written commun., 1971), states that the Yorktown Formation exposed at the type locality belong to his *Orionina vaughani* ostracode assemblage zone; he considers the zone to be upper Miocene, but he suggests (Hazel, 1971, p. 8) that the upper part may be of Pliocene age. Akers (1972) states that the *Orionina vaughani* assemblage zone contains foraminifers indicative of the last half of N18 or N19 zones of Blow (1969) and thus is Pliocene, between 3.5 and 5 m.y. old.

Included species.—The genus is monotypic.

Genus AIVUKUS new genus

Type species.—*Aivukus cedrosensis* new species.

Etymology.—The Inupik-speaking Eskimos of the Bering Strait region call the walrus "Aivuk" and a very similar name is used by all Eskimos according to John J. Burns (written commun., 1972).

Diagnosis.—In the adult, the rostrum is elongate and not massive; the upper canines are elongate and long growing but growth stops when the pulp cavity is filled with annular dentine; the canines have no globular dentine centrally; the lower canines are reduced in size but are 50 percent larger in diameter than the first premolar; the mandibular symphysis is unfused and much less sloping than in *Prorosmarus*, terminating approximately beneath P_1 and P_2. Probable dental formula

$$\frac{2I \cdot 1C \cdot 4P \cdot 1M}{2I \cdot 1C \cdot 4P \cdot 1M} \times 2 = 32$$

Distribution.—Late late Miocene of Baja California.

Included species.—The genus is monotypic.

Aivukus cedrosensis new species

Plates 1–4 and 14; figure 1

Holotype.—A partial skull complete on the right side with associated fragments of the right petrosum, an isolated I^3, fragments of the left mandibular elements, distal part of humerus, parts of radius and ulna, scapholunar, and incomplete metacarpal I, IGCU 901, field No. RHT 1290, collected by David P. Whistler in 1965.

Etymology.—The species is named for Cedros Island, Baja California.

Referred material from Cedros Island.—UCR 15260, Field No. "Cedros 4," collected by Frank H. Kilmer, David P. Whistler, and George T. Jefferson in 1964: associated scapholunar, trapezoid, cuneiform, unciform, metacarpal I, metacarpal II, head of metacarpal IV, and a phalanx. This material is about twice the size of the front limb elements of the holotype and is the basis for assuming that the type is a female. The two sizes are quite comparable to those of male and female of the living *Odobenus rosmarus*.

UCR 15241, Field No. RHT 1312, collected by Richard H. Tedford and Whistler in 1965: male scapholunar fragment, distal articulation of ulna, unciform, and trapezium.

UCR 15242, Field No. RHT 1304, collected by Tedford and Whistler in 1965: isolated female unciform.

UCR 15243, Field No. "Cedros 4, limb C", collected by Kilmer, Whistler, and Jefferson in 1964: female humerus.

HSC 309, collected by Robert E. Jones in 1969 from "coffee-colored marine mammal beds," female metacarpal III.

Referred material from Baja California Sur.—USNM 184045 and 184046, abraded first metacarpal and proximal portion of upper canine, collected by Sr. Felipe Moreno Aviles, Rancho el Refugio, Santiago, Baja California Sur.

Diagnosis.—Only one species is here recognized in the genus *Aivukus*.

Type locality and age.—The type specimen is from UCR locality RV 7309 (Tedford locality 11) approximately 68 feet above the base of the upper Miocene and Pliocene(?) Almejas Formation on Cedros Island, Baja California, Mexico.

As recognized on Cedros Island by F. H. Kilmer, the Almejas Formation (Mina, 1957) is composed of at least 800 feet of yellow and gray sandstone with a few conglomeratic beds, more abundant in the younger half of the section. The basal 200 feet contain fossil marine mammals, and one algal-rich pecten-bearing conglomerate is near the top of this interval. The younger 600 feet of the formation contain a molluscan fauna which is the basis of the following statement by F. H. Kilmer (written commun., 1970) on the age of the formation.

> The precise geologic age of the Almejas Formation on Cedros Island does not appear determinable at the present time, at least on the basis of marine invertebrate fossils. The most refined geologic age interpretation available is that of Jordon and Hertlein (1926), who studied the marine invertebrate fauna of the Almejas in detail and concluded that, with respect to other West Coast marine invertebrate faunas, it bore closest resemblance to the fauna of the San Diego Formation and that it was assignable to the time interval from middle to early late Pliocene. Their usage of the term "Pliocene" is essentially that of the marine

Cenozoic chronology of western North America developed by Weaver and others (1944) and modified for the southern California area by Durham (1954). The Almejas fauna may be at least partially correlative with the marine fauna of the Careaga Formation of California with which it has a number of short-ranging species in common. There appears to be no sound basis, with respect to marine invertebrates, for attempting direct age correlation of the Almejas faunas with those of the European section at the present time. On Cedros Island, the Almejas Formation unconformably overlies diatomaceous rocks of the Tortuga Formation (Mina, 1957). Near the top of the Tortuga, molds of an arcid pelecypod closely resembling *Anadara obispoana*, were collected and this species is common in rocks of Luisian age in the Miocene sequence of California (Reinhart, 1942). The Almejas is unconformably overlain by terrace deposits containing a marine invertebrate fauna of probable late Pleistocene age (Hertlein, 1934).

The referred material with field Nos. RHT 1312 and RHT 1304 was collected from approximately the same part of the stratigraphic section as was the type; those specimens with the field designation "Cedros 4" were collected lower in the formation, from 20 to 30 feet above the basal unconformity. Thus, except for HSC 309, whose locality is unrecorded, all material known of *Aivukus cedrosensis* from Cedros Island was collected from 20 to 70 feet above the base of the 800-foot-thick Almejas Formation; the marine invertebrates from 130 to 730 feet above the base of the formation suggest a middle to late Pliocene age in the usage of Weaver and others (1944) or late late Miocene to Pliocene in the usage of this report; and the unconformably underlying Miocene rocks indicate that the fossil odobenid probably is not so old as middle Miocene.

Howard (1971) has described the avifauna from the beds in the Cedros Island section which contain *Aivukus cedrosensis,* noting that the fauna is quite similar to that from the San Diego Formation "although in no instance are the species the same." She refers to the fauna as being of early Pliocene age, or late Miocene in the usage of this report. Barnes (1973) has described a pygmy sperm whale from these beds and infers a similar age.

The presence of *Dusignathus santacruzensis* about 50 feet above the base of the Almejas Formation, as discussed in a following part of this report, suggests an age comparable to that of the Purisima Formation in the Santa Cruz area of California. This would be Pliocene, younger than the glauconite (minimal) date of 6.7 ± 0.5 m.y. from the base of the Purisima (J. D. Obradovich, written commun., 1964). In addition, fossil remains questionably referred to *Dusignathus* are known from the basal glauconite bed of the Drakes Bay Formation of Galloway (1977), Point Reyes, Calif. This glauconite has been dated at 9.3 ± 0.5 m.y. (A. J. Galloway, oral commun., 1970); however, the glauconite sample contained detrital biotite and may be considerably younger than the date indicates.

Abundant remains of a primitive fur seal, decribed in Part II of this report, are present in the lower part of the Almejas Formation. Remains of this seal have also been found in the glauconite bed of the Drakes Bay Formation and in the Purisima Formation. However, the species from these northern formations seems more modernized than the species from the Almejas Formation. Lawrence G. Barnes, currently studying the cetacean fauna of the Almejas Formation, reports (oral commun., 1974) other similarities with the Drakes Bay Formation: both faunas contain a balaenopterid assignable to *Balaenoptera* sp., a stenodelphine, a phocoenid, and a unique delphinapterine which suggest to him a temporal correlation. He has found the cetacean fauna of the Purisima Formation to be very similar.

The single mollusk known from the Drakes Bay Formation was identified by F. S. MacNeil as *Neptunea colmaensis* (Martin), known elsewhere only from the lower part of the Merced Formation (late Pliocene) of the San Francisco area. This evidence again suggests that the Drakes Bay glauconite age is too old. The Purisima Formation of the Santa Cruz area includes, in its upper part, beds apparently equivalent in age to the lower Merced Formation (Addicott, 1969).

Axelrod (1971, p. 77) mentions cones of Monterey Pine from the Drakes Bay Formation. He notes that the cones resemble those of the modern population at Monterey more closely than the cones from the population living at Waddell Creek, Santa Cruz County, Calif., a population that is much closer to the fossil locality. In all probability the unit containing the cones which Axelrod refers to as the Drakes Bay Formation (without definition or other indication of location) is a surficial Pleistocene deposit and not the Drakes Bay Formation of Galloway (J. A. Wolfe, oral commun., 1976). Axelrod's Drakes Bay Formation is thus interpreted herein as if his wording had been "deposits near Drakes Bay."

Although pinniped remains are abundant in the basal 70 feet of the Almejas Formation, nothing has been found that resembles the primitive otariid *Pithanotaria starri* nor the often associated odobenid *Imagotaria downsi*; these species are from deposits in California believed to be 9-12 m.y. old. The strong faunal similarity shown by the seals and the cetaceans in the lower Almejas, Purisima, and Drakes Bay Formations certainly suggests approximate contemporaneity although the somewhat more advanced fur seal from the Drakes Bay Formation and at least the upper part of the Purisima Formation does suggest that these two units may be somewhat younger than the basal Almejas fauna. As an approximation based upon these similarities, therefore, the basal 70 feet of the Almejas Formation is here taken to be between 6 and 8 m.y. old, late late Miocene. However, the overlying 700 feet of the Almejas, containing the mollusk fauna discussed by Kilmer, may well extend into the Pliocene; conceivably into the late Pliocene as suggested by the similarity of the invertebrate fauna to that of the Careaga and San Diego Formations.

It seems that *Aivukus cedrosensis* is probably at least one million years older than *Prorosmarus alleni,* as would be expected from its less advanced morphology if the two belong to the same odobenine lineage.

USNM 184045 and 184046 are from the Rancho el Refugio locality in the Cape region of Baja California Sur (Hertlein, 1925, p. 3, 7; Lindsay, 1965). The locality is about 3 miles north of Sierrita de la Trinidad and about 12 miles east-southeast of the town of Santiago (roughly one mile north of the ranch house of Felipe Moreno). The locality is in a south-facing slope of the Salada Formation and is an estimated 50 feet below the top of the formation as exposed in this slope. Age assignments of the Salada Formation in this area vary from late Miocene to late Pliocene (see Hertlein, 1925), but there appears to be general agreement that it is more or less contemporaneous with the Almejas Formation. This locality is 8 miles south of the Tropic of Cancer, the southernmost record of any odobenid.

DESCRIPTION

Mandible (pl. 2).—Four fragments of the left mandibular ramus of the type specimen of *A. cedrosensis* were collected as float washing downslope from where the skull was found. The roots of the canine and first two postcanine teeth are in place; parts of the alveolae of the third and fourth postcanine teeth also are preserved. That part of the jaw which would have shown the position of a fifth postcanine is totally missing but wear on the upper dentition suggests that a fifth was present. Enough of the ramus is preserved to indicate that if a fifth postcanine was present it was shallowly rooted, and reduction of the last upper postcanine also suggests considerable reduction in size of the lower. The condyloid and coronoid processes are missing as are all parts of the mandible anterior to the canine. However, the peglike lateral upper incisors both show two distinct facets of wear (pl. 1): a sloping facet on the lateral side from contact against the lower canine and a facet more or less transverse to the axis of the tooth; this wear clearly indicates that at least one large incisor was present in each ramus of the mandible to occlude end-to-end with the two large upper incisors; in order to occlude in this way, the lower incisor must have been essentially anterior to the lower canine.

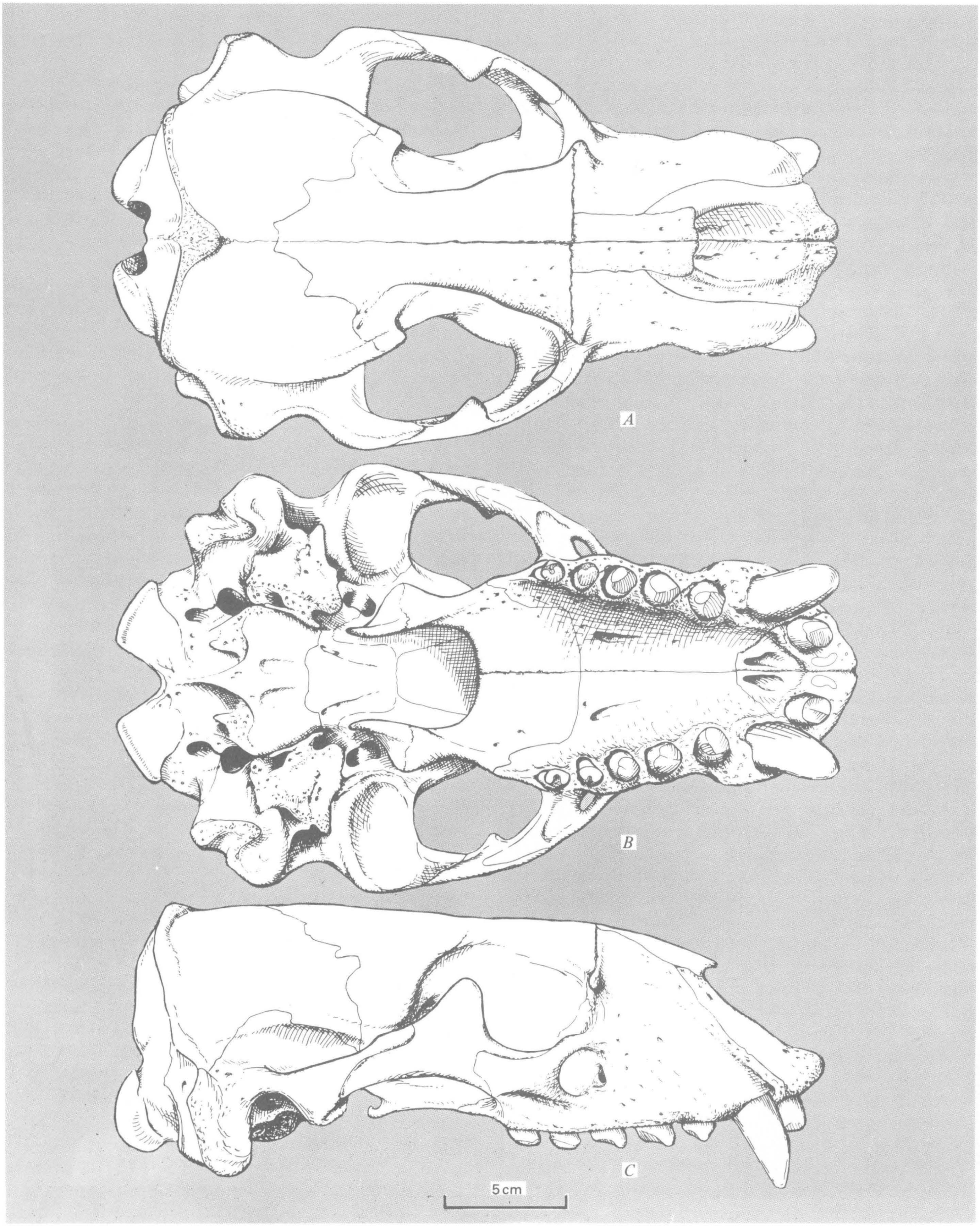
All lower teeth are distinctly single rooted and peglike: solid columns of dentine with a heavy jacket of cementum and nearly circular in cross section. Unlike *Prorosmarus alleni,* the lower canine of *A. cedrosensis* is distinctly larger in cross section than the postcanine teeth, though conspicuously smaller than the upper canine. It is approximately 14.5 mm in anteroposterior diameter at the alveolar margin; the first postcanine is 9.5 mm, the second 8.8 mm, the third about 10 mm, and the fourth very approximately 7.8 in the same dimension. The first postcanine tooth, though of large diameter at the alveolar margin, is the shortest, its root terminating very close to that of the relatively elongate canine. The canine itself extended backward in the jaw to a point between the second and third postcanine roots.

What is preserved of the mandibular ramus exhibits a remarkable similarity to *Prorosmarus alleni.* Behind the symphysis the ramus is conspicuously bowed outward and has a straight inferior margin back to the bladelike angular process. The inferior margin is narrow and forms a rather sharp crest which, anteriorly, begins to drop downward toward an inferior genial eminence, most of which is lost on the specimen. What is preserved of the symphysial surface in *Aivukus cedrosensis* indicates that the articular area was less inclined than in *P. alleni,* possibly in adjustment to the larger canine tooth.

The alveolar distance from the anterior margin of the canine to the posterior margin of postcanine IV is approximately 65 mm, the comparable measurement on *P. alleni* is 104.5 mm. Except for its smaller size the mandible of *A. cedrosensis* differs from that of *P. alleni* by having a relatively much larger canine, presumably by retaining a reduced fifth postcanine tooth, and by having a less procumbent symphysial region. These differences are interpreted as representing a more primitive stage of evolution within the Odobeninae.

Skull (pls. 1 and 2, fig. 1).—The skull of the type

FIGURE 1.—Restoration of the skull of *Aivukus cedrosensis.* Type female skull IGCU 901. *A,* Dorsal view. *B,* ventral view. *C,* Lateral view.


A
B
C
5 cm

specimen of *Aivukus cedrosensis* has been somewhat distorted and fragmented by weathering. The occipital and basioccipital regions are lost, the brain case is partly crushed, and separation of the front and back parts of the skull in the interorbital region has left some question about proper orientation. Nevertheless, most of the right side is present and it is remarkably well preserved when compared with most fossil pinniped skulls. Judged by suture closure and tooth wear, the skull is from a young adult animal.

In general proportions, the skull is quite sea lionlike but in nearly all details it is immediately recognizable as an odobenid. A portion of the occipital crest is preserved indicating a low, broad structure as on living *Odobenus*; however, no trace of a sagittal crest is preserved on the shattered and depressed roof of the brain case, indicating that the braincase was inflated as in the living genus. The lack of a supraorbital process is conspicuous; a prominent preorbital or lacrimal process is present in front of the large orbit; and, walruslike, the maxillary-frontal suture passes through this process and, in a straight line, upward to the nasals. The nasals themselves are not preserved, although the fractures of the skull suggest that their posterior margins, articulating with the frontals, may have formed a straight line continuous with the maxillary-frontal suture. The infraorbital foramen is immense. The palate is conspicuously vaulted. The area between the glenoid fossa and the mastoid is completely filled in with thick ossification of the ectotympanic. The mastoid process itself is knoblike, rather than crestlike, and a thin, platelike jugular process from the missing exoccipital still adheres to its posterior surface.

Consistent with a much more elongate skull than in living *Odobenus,* the interorbital area is narrow and elongate, the ascending ramus of the premaxilla is elongate, and the zygomatic processes of both the squamosal and the maxilla are elongate, though the jugal itself is quite short.

Although the nasal processes of the premaxillae are quite prominent, they protrude anteriorly from just above the alveolar margin rather than being well elevated above this level like those of the square-faced modern *Odobenus*. The palatine fissures of the *Odobenus* premaxillae are extremely reduced, but they are large and well developed in *Aivukus cedrosensis*. Each premaxillae holds two, possibly three, incisors. The medial one or two are small, and their presence on the skull is indicated only by alveoli whose preservation is not distinct. If two medial incisors did exist, the smallest was directly anterior to the other, a situation which seems improbable judging by the dentition of *Odobenus*. The larger, or probably only, medial incisor has an alveolar diameter of about 3.5 mm.

The very large lateral incisor, though more sharply curved and tapering to the root, is about equal to the cheek teeth in size and peglike shape. Its greatest diameter, approximately at the alveolar margin in the type skull, is 14.8 mm; this measurement includes a cementum jacket of about 1 mm thickness. From the nearly closed root to the worn crown, the greatest curvilinear length is 60 mm. No enamel remains on the worn crown. As has been discussed, the wear surface on the crown has two facets (fig. 1B; pl. 1 fig. 10): one lateral and oblique resulting from wear against the lower canine, the other transverse to the long axis of the tooth resulting from attrition with an unknown but presumably equally peglike lower incisor.

The maxilla contains an elongate canine and five postcanine teeth; all are single-rooted pegs except the last, which has a transversely compressed root that might be weakly double-rooted, although the roots are not entirely exposed. The canine is the only tooth in the skull which was still growing at the time of death, and it had not begun to constrict toward root closure. However, it does not appear to have been evergrowing but rather has a shallow conical pulp cavity quite similar to that of the cheek teeth in living *Odobenus*. No globular dentine is developed. The canine is encased in a heavy cementum jacket that is 2 mm thick where the canines are broken off at the alveolar margins. There is no way to judge how far the canines protruded from the skull; from the alveolar margin to the fully open lip of the pulp cavity, they are about 54 mm long with a uniform anteroposterior diameter of 20 mm. In transverse diameter they are slightly narrower, measuring 18 mm. The maxillae are conspicuously swollen, both externally and particularly internally, nearly to the preorbital processes to accommodate these elongate canines.

USNM 184045 is the root of a more mature canine whose pulp cavity is closed. This tooth also is of large diameter, possibly from a male. It has a maximum anteroposterior diameter of 27 mm. Weak longitudinal fluting is evident at the cementum-dentine interface and is present, less distinctly, on the exterior surface of the cementum. The dentine is composed entirely of annular layers and no globular dentine is present.

The roots of all postcanine teeth except the second and the fifth are exposed on one side or the other of the holotype; all are essentially closed. The first four cheek teeth are slightly curved, cementum-encased pegs with an approximately uniform diameter down to the abruptly pinched off root termination, the first three are of approximately equal diameter (about 12.5 mm) and decrease slightly in length to the rear (the first is 43.5 mm long, the third 36.5 mm); the fourth is of noticeably smaller diameter (10 mm). The fifth (last) cheek tooth is not peglike; it has a worn but distinct enamel crown with an almost-doubled shallow root. No cementum is evident on the fifth postcanine (M^1). Two distinct wear facets appear on the first three postcanines: the larger is slightly convex and slopes dorsomedially toward the palate and the smaller is concave and is on the posterior surface. The posterior facet is not evident on the fourth postcanine and an appreciable amount of the thin enamel crown remains on the labial surface. Abrasion on the very small fifth postcanine is essentially horizontal, and a thin rim of enamel is present almost entirely around the base of the crown. From the labial side of the crown of the fifth postcanine, an emargination of the enamel edge crosses half of the preserved crown, suggesting that the crown was originally bicuspid, or perhaps bilophid as in the M^2 of *Imagotaria downsi* (see following section).

By analogy with the tooth wear in living walrus (F. H. Fay, written commun., 1973), the posterior concave wear facet appears to have resulted from end-to-end occlusion with the lower teeth while the lingual convex wear facet seems most likely to have resulted from anterior-posterior motion of the tongue when abrasive material, such as mud, was in the mouth. The similarity of the wear facets and of the vaulted palate to those of living walrus suggest that *Aivukus cedrosensis*, like the living walrus, utilized a tongue-piston type of sucking to extract mollusks from their shells.

The ear region of *Aivukus cedrosensis* is extremely walruslike. The lateral wall of the right middle ear cavity is preserved on the skull and a large part of the right petrosum was recovered from the fragmented debris. The external acoustic meatus is very large in diameter, larger than in most specimens of *Odobenus*, and very closely approximates the size of the tympanic membrane. Only the lateral part of the ectotympanic ossification of the bulla is preserved, but from this it can be seen that the stylomastoid foramen, tympanohyoid fossa, greatly enlarged bony Eustachian canal, and thick bullar wall between the glenoid fossa and the mastoid process are all developed and located very much as in living *Odobenus*. Within the middle ear cavity, the well-preserved crista tympani shows that the tympanic membrane was very large, measuring 10.8 mm in greatest diameter from the tympanic incisure ventromedially to the inward projecting lip of the crista and 6.9 mm in least diameter. No auditory ossicles were recovered but the epitympanic recess is very large, indicating the former presence of ossicles as large as in the living walrus.

Although not so enlarged as in living *Odobenus*, the petrosum of *Aivukus cedrosensis* is larger than that of any otariid or desmatophocid and is characteristically odobenid in the great enlargement of the apex anterior to the promontorium and in the broad internal acoustic meatus, which has wide separation of the passages for the facial and vestibulocochlear nerves (pl. 1, figs 6, 7). The region containing the semicircular canals and the floccular fossa they encircle is not preserved. Approximately one-quarter of the oval window of the cochlea is preserved on the petrosum, but the great uniformity in proportionate shape of this foramen permits an estimate to be made of its size, approximately 2.4 mm and 1.7 mm in maximum and minimum diameters. This size suggests an oval window to tympanic membrane area ratio of 1:28; this ratio is greater than that measured on living *Odobenus* (Repenning, 1972, p. 321) and approaches the minimum reported for fissiped carnivores. Among the living pinnipeds, only the phocid genus *Erignathus* has a greater ratio. This ratio suggests quite shallow-water feeding habits (Repenning, 1972, p. 322) and, in combination with the emphasis on the elongation of the upper canines only, is the basis for the assignment of *Aivukus cedrosensis* to the subfamily Odobeninae as diagnosed earlier.

The elongate facial region, alinement of the canine with the upper cheek teeth, five functional cheek teeth, large external acoustic meatus, great oval window to tympanic membrane area ratio, and less enlarged petrosal apex all are features to be expected in a primitive odobenine. From the apparent greater specialization of *Prorosmarus alleni*, in greater reduction of the lower canine and presumed loss of one lower cheek tooth, it could be inferred that this species had greater enlargement of the upper canine, loss of the fifth upper postcanine, and presumably a more *Odobenus*-like ear region than does *A. cedrosensis*.

With approximate compensation for lost parts, the type skull of *Aivukus cedrosensis* has the following measurements:

	mm
Condylobasal length	295±
Greatest zygomatic width	175±
Length of cheek tooth row	77

TABLE 3.—*Proportions of the humerus in otarioids*

Taxon	Number of Specimens Measured	Average ratio A[1] (Trochlea/capitulum)	Range of ratio A	Average ratio B[2] (Length/least diameter)	Range of ratio B
Arctocephalus pusillus	4	1.01	1.05-1.00	5.77	6.10-5.17
Arctocephalus townsendi	1	.97	---	6.46	---
Callorhinus ursinus	4	.97	1.0-.922	6.41	6.66-5.95
Fur seals	9	.98		6.21	
Zalophus	3	1.03	1.08-.960	5.20	5.47-4.92
Neophoca	2	1.05	1.06-1.03	5.63	5.75-5.51
Phocarctos	4	1.01	1.07-.98	5.63	5.95-5.17
Eumetopias	3	1.06	1.13-1.01	5.67	5.70-5.62
Sea lions	12	1.03		5.53	
Odobenus	11	1.18	1.18-1.39	7.04	8.10-6.26
Aivukus cedrosensis					
type	1	1.34	---	----	---
Cedros 4	1	1.21	---	6.90	---
?*Prorosmarus alleni*	1	1.28	---	7.32	---
Alachtherium	1	1.27	---	6.15	---
"Trichecodon" koninckii	1	1.21	---	----	---

[1] Ratio A = greatest anteroposterior diameter of trochlear lip divided by that of distal capitulum.

[2] Ratio B = greatest length of humerus divided by least transverse diameter of shaft.

Palatal width between canines ..	46
Palatal width between fifth postcanines	32±
Depth of palate from alveolar margins at postcanine 2	22
Minimum interorbital width	47±
Greatest diameter of infraorbital foramen	21

Postcranial skeleton.—Except for a few species with obvious peculiarities in some postcranial skeletal elements, such as the sharply upturned medial epicondyle on the humerus of *Neophoca cinerea,* it is commonly difficult to identify living otarioid species on the basis of postcranial skeletal elements without knowledge of geographic occurrence and differences in size. For example, several species of the genus *Arctocephalus* are difficult or impossible to identify on the basis of postcranial elements, and it is even difficult to separate the humeri of male *Zalophus,* female *Eumetopias,* and perhaps female *Phocarctos:* genera which are quite distinct in their skull morphology. Specific identity of postcranial skeletal elements becomes even less certain in fossil otarioids because of the added problems of the inability to know individual variability or to interpret adequately the stage of evolution.

At the familial and subfamilial levels, however, most postcranial skeletal elements are diagnostic. In the following description of the postcranial skeleton of *Aivukus cedrosenis,* emphasis is placed on those features that identify the species as an odobenine odobenid and upon the stage of evolution of the species represents within this family. At present, no features of the postcranial skeleton are recognizable as being specifically significant without some knowledge of geologic age and geographic distribution.

In the material recovered of the type specimen of *Aivukus cedrosensis* is the distal half of the right humerus. At another locality, Cedros 4, a left humerus (UCR 15243) was collected which is essentially complete and which is identical in all features preserved to the partial humerus belonging to the type. The crest above the external epicondyle, referred to (in phocids) as the supinator ridge by King (1966, fig. 3), is largely lost in the more nearly complete specimen and its configuration is better shown on the partial humerus of the type (pl. 3).

As in all odobenids, and differing from all otariids, the distal articulation of the humerus of *A. cedrosensis* is rotated inward a few degrees such that the antebrachium would be more medially directed than in the otariids. Correlated with this, the greatest anteroposterior diameter of the medial lip of the trochlea is conspicuously greater than that of the distal capitulum, as in the odobenids and differing from the condition in the otariids in which these diameters are about the same (table 3).

As in all odobenids, and differing from the otariid sea lions but overlapping the condition found in the otariid fur seals, the shaft of the humerus of *A. cedrosensis* is relatively slender (table 3), the pectoral crest is directed distally toward the medial lip of the trochlea rather than toward the midpoint of the distal articulation, and the proximal process of the pectoral crest, the greater tubercle, is narrow in proximal aspect. In the living genus *Odobenus,* the humerus is as long as the ulna, rather than being considerably shorter as in the otariids; the *Odobenus* condition appears to exist in *A. cedrosensis,* although the incompleteness of the preserved elements casts some doubt on this observation.

In contrast to living *Odobenus,* but similar to other fossil odobenids, the deltoid tubercle is an integral part of the pectoral crest (as in the otariids) rather than being detached and positioned posterolateral to the crest. The pectoral crest itself is rather unusual in that it drops abruptly to the shaft at its distal termination rather than gradually merging with the shaft as in nearly all odobenids; in this respect the humerus of *A. cedrosensis* resembles that of "*Trichecodon*" *koninckii* Van Beneden (1877, pl. 7, fig. 2) and the otariid humerus. In addition, the medial epicondyle is prominently hooked upward as in *Odobenus,* rather than extending more or less directly medial.

Though much larger, the odobenid humerus from the Yorktown Formation of Virginia (MCZ 7713), presumed to be *Prorosmarus alleni,* is identical in every respect to that of *A. cedrosensis* except that the pectoral crest merges distally with the shaft in a gradual slope, as in modern walrus. Though somewhat less robust, the humerus of *Prorosmarus* strongly resembles the humerus of *Alachtherium cretsii* (Van Beneden, 1877, pls. 3 and 4) from the Scaldisian of the Antwerp Basin.

Though the humerus of *Aivukus cedrosensis* is easily separated from that of modern walrus, the partial radius and ulna found with the type specimen are indistinguishable from these bones of a modern female walrus, at least in those parts preserved. The prominent and elevated distal articular surface for the radius on the ulna and the conspicuously distal position of the insertion for the pronator teres on the radius distinctly mark these bones as odobenid (pl. 2). The distal end of another ulna (UCR 15241) also shows the distinct radial articulation but in size compares to a small male *Odobenus.*

The female scapholunar (radial carpal, pls.2 and 4) of the type skeleton and two male scapholunars (UCR 15260) and (UCR 15241) are identical to that of *Odobenus* and are marked as odobenid by the pocketed articular surface for the magnum. No differences in their structure can be found that are not duplicated in a sample of 16 scapholunars from the living walrus. As in living walrus and "*Trichecodon*" (Van Beneden, 1877, pl. 8, fig. 9), the pitlike articulation for the magnum does not extend nearly as far in a palmar direction as does the articular surface for the unciform.

One trapezium (distal carpal I, pl. 4), from a male to judge by its size, is known (UCR 15241). The trapezium of *A. cedrosensis* differs from that of *Odobenus* by lesser development of the radial-dorsal rugosity for partial insertion of the abductor pollicis muscle, conspicuous enlargement of an ulnar-dorsal process which extends the articular surface for the trapezoid proximally and which produced a pronounced concave articulation for metacarpal I distally. In ulnar view, the facet for articulation with the trapezoid is distinctly more elongate than on the trapezium of *Odobenus.*

One trapezoid (distal carpal II, UCR 15260) was found with other associated male flipper elements. In agreement with the differing articular surface on the trapezium, the trapezium facet on the trapezoid of *A. cedrosensis* is narrower than is that of living *Odobenus.* No magnum (distal carpal III) has been found.

Three unciforms are known, one with the large male manus (UCR 15620), one with the small male material (UCR 15241, pl. 4), and an isolated unciform comparable in size to that of a female *Odobenus* (UCR 15242). Other than in size, these three unciforms are identical in form and are considerably more elongate in the palmar-dorsal dimension than in *Odobenus,* although this dimension is quite variable in the living walrus. One cuneiform (UCR 15260, pl. 4) is with the large male manus and falls well within the range of form and size variation of this bone in the modern walrus.

Metacarpal I is known from the type specimen (pl. 1) and UCR 15260 (pls. 3 and 14) on Cedros Island and from the Rancho el Refugio locality. In size these bones compare closely with the same bone from male and female walrus. In form they differ from this bone of walrus in that the proximal articulation curves onto the dorsal surface, matching the differences noted in the trapezium, and in the relatively slight degree of palmar flattening and broadening of the proximal part of the metacarpal shaft due, in modern walrus, to exaggeration of the insertional area for the functionally important abductor pollicis muscle. These differences are comparable to those noted between the trapezium of *A. cedrosensis* and that of living *Odobenus.* As in the modern walrus, the dorsal surface is marked, near its proximal end, by a prominent rugosity for insertion of the extensor pollicis muscle.

Metacarpal II and the proximal articulation of metacarpal IV are also present with the flipper elements UCR 15260. Though very similar, these metacarpals differ from those of living *Odobenus.* The articular surface for metacarpal III on the ulnar side of metacarpal II is a flat and roughly circular surface in *A. cedrosensis* (pl. 4), whereas it is a convex triangular surface in this bone of modern walrus. As that part of the proximal articular surface of metacarpal IV which contacts metacarpal V is much more salient in *A. cedrosensis* than in *Odobenus,* the head of metacarpal IV in either dorsal or proximal aspect is more nearly an equilateral triangle than in *Odobenus.*

HSC 309 is an isolated metacarpal III, distinguished from that of *Odobenus* by a flat, elevated, and circular facet for articulation with metacarpal II; this shape is consistent with the difference noted in metacarpal II (pl. 4).

Metacarpals II, III, and IV are conspicuously more similar to those of the dusignathine odobenid *Imagotaria* than to these bones in *Odobenus.* The intermetacarpal articulations on these elements in *Odobenus* are broad convexly rounded surfaces but are less extensive, flatter, better delimited and, in some cases, protrude from the head on salient platforms in *Imagotaria. Odobenus*-like broadening and rounding of the articular surfaces between metacarpals III and IV are evident in *Aivukus,* but the surfaces between metacarpals II and III retain the presumably primitive prominence seen in *Imagotaria.*

Except for an isolated terminal phalanx, no elements of the posterior limb of *Aivukus cedrosensis* have been recognized in the collection. This phalanx is identical to the second, third, and fourth terminal phalanges of the pes of *Odobenus* in development of both the attachment for the cartilaginous extension and the bony core for the horny claw.

DISCUSSION

The skull and forelimb of *Aivukus cedrosensis* are obviously odobenid; some of the skeletal elements are inseparable from those of living *Odobenus rosmarus.* Characters that mark *A. cedrosensis* as being less advanced than modern walrus are retention of two, or possibly three, incisors in each premaxilla and at least one functional incisor in each ramus of the lower jaw, of five upper and probably five lower postcanine cheek teeth, of obviously less specialized upper and lower canines, of the less enlarged petrosal apex, of the deltoideus insertion on the humerus, and of the insertion of the abductor pollicis on the trapezium and metacarpal I. Characters that mark *A. cedrosensis* as being more primitive than *Prorosmarus alleni* are the larger lower canine, the caniniform (rather than tusklike) upper canine lacking globular dentine, the probable retention of a reduced fifth lower post-canine, and the less procumbent symphysial region.

The criterion (cited above in "Suprageneric Diagnoses") of enlarging the upper canine while reducing the lower canine places *Aivukus cedrosensis* in the odobenid Subfamily Odobeninae by definition. At this stage of discussion, this definition is arbitrary. In the discussion of the odobenid Subfamily Dusignathinae, the osteologic characters distinguishing the two subfamilies are further described. It will be seen that many of the features of *A. cedrosensis* which mark it as less advanced than modern walrus are even more pronounced in the dusignathine odobenids. Nevertheless some genera of the Dusignathinae have paralleled in their evolution the obvious specializations of the living walrus to a greater extent than *A. cedrosensis* while retaining those primitive features which mark them as an extinct side branch of the odobenid evolutionary lineage. The most notable of the primitive features is the maintenance of an unreduced lower canine while enlarging the upper.

Subfamily DUSIGNATHINAE

Genus IMAGOTARIA Mitchell

Type species.—Imagotaria downsi Mitchell, 1968.

Diagnosis.—A generalized dusignathine odobenid (see section on "Suprageneric Diagnoses") without specialization of the tooth crowns but with a strong tendency to fuse the roots of the cheek teeth. Dental formula:

$$\frac{3I\cdot 1C\cdot 4P\cdot \quad\quad 2M}{2I\cdot 1C\cdot 4P\cdot 1 \text{ or } 2M} \times 2 = 36\text{–}38.$$

Approximate area ratio of oval window:tympanic membrane = 1:10, comparable to living sea lions and deep-diving phocids.

Distribution.—The late middle and early late Miocene of California; by estimation 9-12 m.y. ago.

Imagotaria downsi Mitchell, 1968

Plates 4-15; figure 4

Holotype.—SBMNH 342, parts of an adult male skull and associated anterior postcranial fragments described by Mitchell (1968). From diatomite of the late middle Miocene part of the Sisquoc Formation, Great Lakes Carbon Co. quarry, about 7 miles southeast of Lompoc, Calif.

Referred material from the Santa Margarita Formation, Santa Cruz, Calif.—UCMP 88459, young male mandibular fragments and two small fragments of the skull described by Barnes (1971). Barnes declined assignment of this specimen to species, calling it *Imagotaria* sp., because the lower premolars 2-4 are distinctly two-rooted, whereas in the type of *I. downsi* these teeth have single, bilobed roots with a strong lateral sulcus. As it is from the same area and formation as other material here described which has fused roots, it seems more probable that one species was present which had a high degree of individual variability in root fusion rather than that two very similar species of one genus lived in the same area at the same time. Granite Rock Co. quarry, Olympia, Calif., locality UCMP V-70184.

USNM 23858, female skull and mandible, essentially complete except that the nasals are missing. Skull is crushed dorsoventrally. Parts of the maxillaries, frontals, symphysis of the left mandibular ramus, and some teeth are missing. Four vertebral fragments were found with this specimen and dissection revealed the malleus and incus of both ears. Collected by W. W. Derryberry and C. A. Repenning in the fall of 1963. Abandoned quarry beside Glen Canyon Road near junction with Redwood Drive on the property of Rowland Taylor, formerly of Scotts Valley, Calif., locality USGS M1035.

USNM 184060, juvenile male skull without mandible, essentially complete except that the nasals are missing. The elements of the skull were unfused and are somewhat displaced at time of death; the left side is distorted by crushing. Several teeth are missing. An incomplete scapula was found with the skull. Collected by G. V. Morejohn and students from the Moss Landing Marine Laboratories on April 25, 1973. Same locality as the female skull but about 3 feet lower in the section and 70 feet south along the strike of the beds, locality USGS M1035.

USNM 23859, male right front limb without scapula, proximal part of humerus, trapezium, and some phalanges. Found with the proximal phalanx of the first digit of the left manus. All found within 10-15 feet of the female skull, USNM 23858, in the same stratum and excavation. At least four individuals are represented by material from this single 15-foot excavation, a fifth from the same horizon was found 100 feet away. This material represents a concentration of fossils comparable to the number of dead animals found on beaches in modern rookeries. The elements of this limb were in articulated position in the matrix. Collected by Repenning and W. W. Chamberlain, 1966. Locality USGS M1035.

USNM 23860, immature right metacarpal IV, female(?), found with two phalanges in the same stratum as USNM 23858 but about 100 feet away. Collected by Repenning and J. C. Clark, 1964. Locality USGS M1035.

USNM 23861, left metacarpal III, male, found about 20 feet lower in the section than USNM 23858 at the same locality. Collected by Richard Baker of Santa Cruz, Calif. 1966.

USNM 23862, male right calcaneum from about 10 feet lower in the section than USNM 23858 at the same locality. Collected by Repenning and Chamberlain, 1966.

USNM 23863, left patella and tibia lacking both articulations, large but of uncertain sex, from about 13 feet lower in the section than USNM 28358 at the same locality. Collected by Repenning and Chamberlain, 1966.

USNM 23864, small left tibia, lacking the proximal articulation, from about 18 feet lower in the section than USNM 23858. Collected by Repenning and Clark, 1964.

USNM 23872, small atlas from 10 feet lower in the section than USNM 23858 and about 5 feet from USNM 23862. Collected by Repenning, 1967.

USNM 23865, female right humerus; isolated. Collected by Repenning and Chamberlain, 1966. From palisades along Branciforte Drive, Santa Cruz, Calif., locality USGS M1106.

USNM 23866, male(?) left calcaneum; isolated. Collected a few feet from right trapezium USNM 23875 by Repenning, Clark, and L. C. Smith, 1965. Santa Cruz Aggregate Co. quarry north of Bean Creek, Scotts Valley, Calif., Locality USGS M1104.

USNM 23867, female left calcaneum and astragalus; associated. Collected by Repenning and Clark, 1965. Moore Creek, Santa Cruz, Calif., locality USGS M1108. One vertebra of the giant salmon *Smilodonichtys* was found associated with these elements.

USNM 23868, male mandibular fragment showing symphysis, canine, and I_3 alveolus; associated with a weathered and incomplete metatarsal and isolated canine tooth. Collected by Repenning and Clark, 1964. East side of Bean Creek north of Scotts Valley, Calif., locality USGS M1037.

USNM 184055, very large male left metacarpal V. Collected by Clark, 1968. Same locality as the last mentioned.

USNM 23870, female left humerus and left femur; associated with other fragments presumably of the same individual. Collected by Repenning and Clark, 1965. Nelson Road, Mission Springs, Calif., locality USGS M11015.

USNM 23875, right trapezium; isolated; found in same gravel bed and a few feet from calcaneum USNM 23866 at USGS vertebrate locality M1104. Collected by Repenning, 1965.

USNM 184061, right cuboid, possibly female, found 15 feet lower in the section than the female skull at the same locality, USGS M1035, by Repenning and Morejohn, April 24, 1973.

UCMP 108066, proximal half of a left metatarsal III, from locality USGS M1035 (=UCMP V-6857) found May 5, 1973, by G. McCafferty.

UCMP 102854, head of left metatarsal III lacking dorsal articular surface for metatarsal IV from locality UCMP V-71197, 1900 feet south of M1035, found December 3, 1972, by J. Foote.

UCMP 107752, right female navicular, from locality USGS M1035 (=UCMP V-6857) found March 11, 1973, by J. Lee.

Mr. Gerald Macy of Felton, Calif., has collected four female-sized bones, possibly belonging to one individual, from a locality along Zayante Road, USGS M1243. These are USNM 184084, radius; USNM 184085, astragalus; USNM 184086, trapezoid; and USNM 184087, proximal half of metacarpal III. The first three are shown on Plates 13 and 14.

Material from other localities.—UCMP 34789, proximal half of right metatarsal III, probably male, from UCMP locality V-3916, White-Seale locality below gray sandstone member of the Santa Margarita Formation, about ½ mile up Comanche Creek from mouth of canyon in middle of slope on west side of canyon, Kern County, Calif.; up section from Comanche Point local fauna, probably early but possibly late Clarendonian mammalian age, late middle Miocene, approximately 11-12 m.y. old but possibly somewhat younger; collected by K. A. Richey in 1939.

UCMP 24221, distal end of right tibia described by Kellogg (1925a, p. 93-95), probably male, from UCMP locality 3545, "on opposite side of canyon from Quarry 9 [type locality of *Pithanotaria starri*]***1.5 miles south and east of Lompoc, Santa Barbara County, California," in the same formation as the type specimen of *Imagotaria downsi* but about 5 miles west of the type locality.

USNM 13487, immature skull from the Celite Co. Quarry No. 38, 2.6 miles south and east of Lompoc from within 45 feet of the top of the deposit (*see* Mitchell, 1968, p. 1865).

UCMP 24070-82, right hind flipper of early late Miocene age from the lower part of the Towsley Formation, south of Humphreys, Soledad Canyon, Los Angeles County (not San Diego County), Calif. Kellogg (1925b) described this specimen under the name *Pontolis* cf. *magnus*.

Diagnosis.—Only one species is here recognized in the genus *Imagotaria*. See Mitchell, 1968, p. 1845.

Type locality and age.—See Mitchell (1968, p. 1845). The locality is in the Dicalite quarry of the Great Lakes Carbon Co. 7 miles southeast of Lompoc, Calif. The diatomite in this quarry is the same unit as that in the Celite quarry of the Johns Manville Co. 3 miles south of Lompoc (Dibblee, 1950); the diatomite has been considered to be a facies of both the Monterey Formation and the Sisquoc Formation. Because of a regional unconformity separating the diatomite from the underlying Monterey, here of Mohnian age, Dibblee considers the diatomite to belong to the Sisquoc. Wornardt (1967, p. 11) noted a marked change of the diatom flora in the upper part of the 1,000-foot-thick diatomite and suggested that the Monterey-Sisquoc formational boundary occurs in the upper part of the diatomite.

Based upon Foraminifera in the underlying and overlying units, most workers (Bramlette, 1946, p. 212, and Woodring and Bramlette, 1950, p. 101) consider the diatomite in these quarries to be early Delmontian. More recent correlations have indicated that it is Mohnian (Barron, 1976). Both *Imagotaria downsi* and the primitive otariid *Pithanotaria starri* have been found in the diatomite of the Lompoc area, and these two seals are known in a number of other areas associated with a "Margaritan" or "Jacalitos" invertebrate fauna and with a Clarendonian land mammal fauna. John A. Barron (written commun., 1974) examined the diatomite from the matrix of the type of *Pithanotaria starri* and from a referred skull of *Imagotaria downsi* (USNM 13487) and found the diatoms to belong to Schrader's North Pacific Diatom Zone XI. The age of these fossils from the Sisquoc Formation of the Lompoc area are here estimated to be 9 or 10 m.y. old, or early late Miocene.

Age of the referred material from the Santa Cruz area.—All remains of *Imagotaria downsi* in the Santa Cruz area have been found in the upper 100 feet of the Santa Margarita Formation, which is as much as 430 feet thick in some parts of the area. Many remains have been found in a widespread conglomerate in the upper part of the Santa Margarita in the northern parts of its outcrop area. This bed does not appear to be present to the south at the locality where the two skulls were found. The formation at this locality (USGS M1035) is only about 80 feet thick, and the bones of *Imagotaria* have been found throughout a 30-foot zone approximately 15-45 feet below the overlying Santa Cruz Mudstone of Clark (1966). The Santa Margarita Formation here rests on granite and thins to 5 feet against this underlying granite 4,500 feet to the north and to 2 inches 6,500 feet to the north of the locality (J. C. Clark, oral commun., 1973). The implication of the stratigraphic relations in the vicinity of this locality is that the formation was deposited against the south side of an ancient granitic high and that the 30 feet of fossil-bearing deposits represent a facies, thickened because of its proximity to the highland, of the widespread conglomerate found in the thicker sections to the north of this local granitic mass.

In most areas the Santa Margarita Formation is of late middle Miocene age in the chronology used here, and is a correlative to the Margaritan Stage of Corey (1954). This is true of the lower part of the formation in the Santa Cruz area (Mitchell and Repenning, 1963, p. 9, 12–14). The upper part of the formation in that area, however, contains several mollusks and echinoids generally considered indicative of an early late Miocene age (Clark, 1966); these fossils are characteristic of beds correlative with the lower part of the Jacalitos Formation of former usage (see table 1). Clark (1966, p. 126–131) found his most definitive invertebrate fauna down section from the gravel bed bearing many of the remains of *Imagotaria*. The desmostylian remains reported from this formation (Mitchell and Repenning, 1963, p. 9, 14–15) have been found only well down section in the basal 100 feet or less of the formation and in those areas where the formation approaches 300–400 feet in thickness.

In the Santa Cruz Aggregate Co. quarry on the north side Bean Creek, Scotts Valley (figs. 2 and 3, localities USGS M1104 and UCMP V4004), the Santa Margarita Formation is nearly 400 feet thick and rests on the Monterey Formation of middle Miocene age in this area. Remains of *Imagotaria* have been found in the conglomerate bed here, very close to the top of the Santa Margarita Formation (locality USGS M1104). Two hundred and eighty-five feet lower in the formation the type specimen of the sirenian *Halianassa vanderhoofi* Reinhart was found at locality UCMP V4004. A few feet below this locality, the left M^2 of *Hipparion* cf. *H. forcei* (USNM 23892) has been found. A short distance to the south, on the opposite side of Bean Creek (Locality USMP V5555), a number of horse teeth have been collected from the Santa Margarita Formation that compare best with *Hipparion mohavense*. At this locality specimens are usually collected from a pebbly sand (see fig. 3); the oldest part of the formation exposed in this quarry is at least 75 feet higher in the Santa Margarita Formation than the horse tooth from the north side of Bean Creek.

Hipparion horses comparable to *H. forcei* and *H. mohavense* occur both below and above the Moraga Formation (informally known as the Grizzly Peak Basalt) in the Berkeley Hills, Calif. This unit has been dated at 10 m.y. (G. H. Curtis, oral commun., 1972); a comparable age is suggested for the lower part of the Santa Margarita Formation north of Bean Creek which contains similar horses. Also one tooth of the primitive horse *Archaeohippus* has been found at this locality along Bean Creek, the youngest record of this genus. In the Santa Cruz area, the

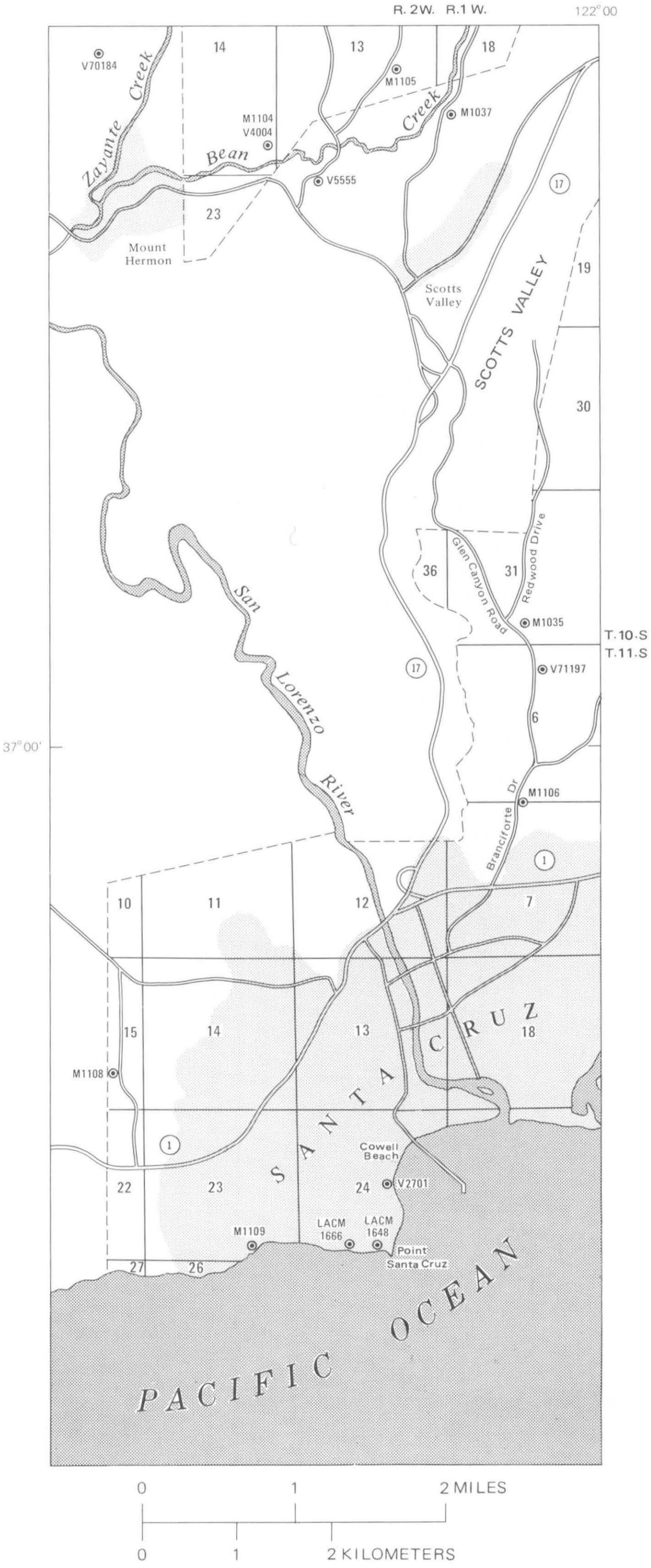
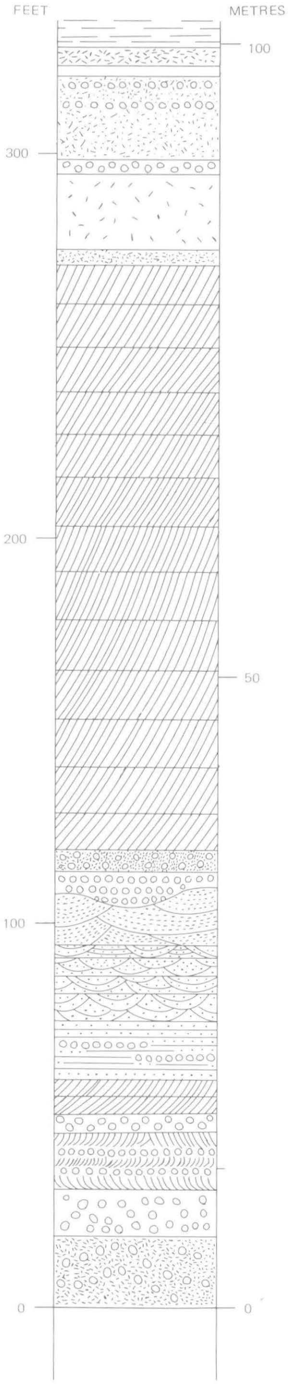


FIGURE 2.—Locality map, Santa Cruz area.



Santa Cruz Mudstone of Clark (1966)

Locality USGS M1104, *Imagotaria downsi*, cetacean, sirenian

Well-sorted pebble bed

Well-cemented *Astrodapsis* bed of early late Miocene age; 2 to 3 feet thick

Fine, well-sorted sand occurring in large-scale (to 8 feet) crossbedding dipping south; burrows increase up section, few cetacean and sirenian fossils

Well-sorted gravel bed, possible source of *Hipparion* sp. cf. *H. mohavense* in Graham quarry to south (locality UCMP V5555)

Sand size decreases up section. Burrows. Approximate floor of Graham quarry to south

Scattered pebbles

Crossbedded sands and planar gravel. Type locality of *Halianassa vanderhoofi* (UCMP V4004) at arrow

Coarse, poorly sorted gravel with abundant bone fragments including *Hipparion* sp. cf. cf. *H. forcei*, desmostylians, cetaceans, sharks, and rays

Approximately 50 feet of cover to underlying Monterey Formation

Section of the Santa Margarita Formation in the Santa Cruz Aggregate Co. quarry. Measured by Larry Phillips, 1973.

FIGURE 3.—Section of Santa Margarita Formation in the Santa Cruz Aggregate Co. quarry.

Santa Margarita is overlain by the Santa Cruz Mudstone of Clark (1966); a glauconite overlying the Santa Cruz Mudstone has been dated at 6.7 m.y. (J. D. Obradovich, written commun., 1964).

Available information thus suggests that the specimens of *Imagotaria downsi* and associated otariid remains referred to *Pithanotaria* are younger than 10 m.y. old, but much older than 6.7 m.y. An early late Miocene age is here assumed, but it is believed that these seals are probably younger than this same pinniped association in the diatomite of the Sisquoc Formation south of Lompoc. The referred specimen (UCMP 34789) from Comanche Creek, Kern County, Calif., appears to be more nearly the age of the type specimen from Lompoc, whereas the referred specimen (UCMP 24070-82) from Soledad Canyon, Los Angeles County, Calif., appears to be more nearly the age of the specimens from Santa Cruz. It is believed that the *Imagotaria-Pithanotaria* pinniped fauna may have existed in the North Pacific from 12 to 9 m.y. ago.

Referral of specimens to the species.—Association of cranial and postcranial bones of the holotype specimen from Lompoc, SBMNH 342, seems unquestionable according to the collector, Phil C. Orr (written commun., 1968, quoted by Mitchell, 1968, p. 1845).

Those specimens from the most productive locality in the Santa Margarita Formation of the Santa Cruz area (USGS M1035) suggest an accumulation of dead animals of varying ages and sexes; the concentration of articulated and disarticulated skeletal elements is very similar to that found on beaches supporting modern rookeries and, as discussed, stratigraphic relations in the area favor the interpretation of deposition adjacent to a beach bordering a granitic highland. One partial mandibular ramus and a first metacarpal of an obviously different pinniped, *Pithanotaria starri,* an otariid smaller than any living genus, was found at this locality, and another mandibular ramus was found 0.4 mile to the south, but no confusion with the walrus-sized *Imagotaria downsi* is possible. All other pinniped remains from this locality fall into two distinct size groups; these size groups are equivalent to those of male and female living walrus.

Of the specimens collected at this locality, indicating a minimum of five individuals, about half are anterior limb elements, which, largely owing to the information provided by the articulated forelimb found here in stratigraphic association with the referred skulls, can be referred to the species by close morphologic similarity with the holotype from Lompoc. The rest, largely posterior limb elements, are referred to the species on the basis of stratigraphic association, size compatibility, and odobenid characters.

Elsewhere in the Santa Margarita Formation of the Santa Cruz area, there are two occurrences of a possible desmatophocid seal (one called "Desmatophocine A" by Barnes, 1972, p. 55) and other fossils of the small otariid seal *Pithanotaria.* These fossils can be eliminated easily from the material assigned to *Imagotaria downsi* from locality USGS M1035 by morphologic differences.

Referral of specimens to *Imagotaria downsi* from other localities in the Santa Margarita Formation of the Santa Cruz area is by morphologic similarity to, and contemporaneity with, the material from locality USGS M1035. The assumption here involved in referral, somewhat enlarging upon that of Scheffer (1958, p. 49), is that in the past, as in the present, two species of the same genus of otarioid seals do not live in the same areas.

In other areas, the assumption of discrete ranges of very similar pinnipeds cannot be used. Referral of this material is considered questionable even though no morphologic differences may be recognizable in postcranial skeletal elements, as specific identity of many living otarioids, based only upon postcranial skeletal elements, is commonly quite uncertain.

DESCRIPTION OF MATERIAL FROM SANTA CRUZ AND COMPARISON WITH THE TYPE

Female mandible (pls. 5 and 7).—The mandible of the female skull, USNM 23858, is most distinctive in its sloping, massive chin with a large, oval symphyseal area over its entire depth. Behind this chin the horizontal ramus appears disproportionately thin and weak; the coronoid process is low with a long anterior margin sloping gradually down to the tooth row; the ramus is markedly bowed outward behind the symphysis; the angular region is narrow and weakly developed; and the pterygoid process is short anteroposteriorly, rounded in form, and does not protrude to the rear much beyond the inferior sigmoid notch.

A small medial incisor lies adjacent to the symphysis in both rami, and a rather large lateral incisor is directly anterior to the medial half of the canine. The canine is fully open at the root and its enamel cap has not completely erupted from the alveolus, indicating some degree of immaturity; it is very long and stout, filling the deep chin and extending behind the symphysis to a point below the third premolar; its enamel crown is rugose and there is a sharp posterior carina. The cheek teeth are quite small, relative to the jaw and the canine, suggesting a female individual. They are much smaller than those of the holotype (Mitchell, 1968). Their crowns are formed by a central primary cusp with a prominent lingual cingulum and a small but persistent anterior cingular secondary cusp. A very poorly developed posterior cingular cusp is present on some lower cheek teeth. P_1 is single-rooted. P_2-P_4 are also single-rooted, but their roots are bilobed with prominent sulci down their length, suggesting that they were derived from a two-rooted condition (pl. 7). M_1 is double-rooted; M_2 is present as a rudimentary small single-rooted peg, as in the holotype. Mitchell (1968, p. 1848) mentions an isolated M_2 found with the type specimen; this M_2 has a small, conical root and a rather globular crown showing a weak central anterior-posterior crest.

The mandible of the female skull differs from that of the holotype by its smaller size, less massive structure, and smaller cheek teeth (both actually and relative to the size of the mandible) with more subdued prominence of their crown structures; all these features are quite compatible with differences in sex and maturity. The M_1 of the type specimen is not as distinctly two-rooted as that of the female skull; rather it has the roots fused nearly to their base (Mitchell, 1968, fig. 9-s, t, u), a variation that is individual in living otarioids (Repenning and others, 1971, p. 9).

The female mandible differs in these same ways from the juvenile mandible UCMP 88459 that is from the Santa Margarita Formation in the Santa Cruz area (Barnes, 1971), except that the ontogenetic differences are not present. And, consistent with individual variation in many living seals as noted by both Barnes (1971, p. 6) and Mitchell (1968, p. 1847), the juvenile mandible shows no sign of the rudimentary second molar; the M_1, P_4 and P_3 are clearly double-rooted. This great difference in root fusion led Barnes (1971, p. 9) to feel that his specimen was of "a more primitive species" than *I. downsi,* but the presence of the female mandible in the same formation of the same area and with P_3 and P_4 root closure comparable to the type but a double-rooted M_1 comparable to the juvenile mandible suggests rather strongly that only one species with great variation in root fusion is present. Because of this, UCMP 88459 is here placed in the species *I. downsi.*

The weak angle of the mandible where the digastricus inserts in combination with a heavy and deep chin with a long oval symphyseal area over its entire depth, the position of the lateral incisor anterior to the canine, the strong but short pterygoid process, and the strong tendency toward single-rooted cheek teeth in early late Miocene time identifies the mandible of *Imagotaria downsi* as odobenid. The presence of a large canine, equal in development to that of the upper canine, identifies the mandible as dusignathine odobenid (table 4).

No mandible was found with the juvenile male skull (USNM 184060) from locality M1035.

TABLE 4.—*Dimensions of the female mandible and teeth of* Imagotaria downsi (*USNM 23858*)

Mandible (right ramus)

Measurements	mm
Greatest length	190
Greatest depth below P_2	47
Least depth at M_2	34
Height, angular process to coronoid process	62
Width of condyle	approx. 33
Width at M_3	13
Width at P_2	22
Greatest length of symphyseal area	65
Greatest width symphyseal area	29
Length P_1 to M_2	63

Mandibular teeth (in mm)

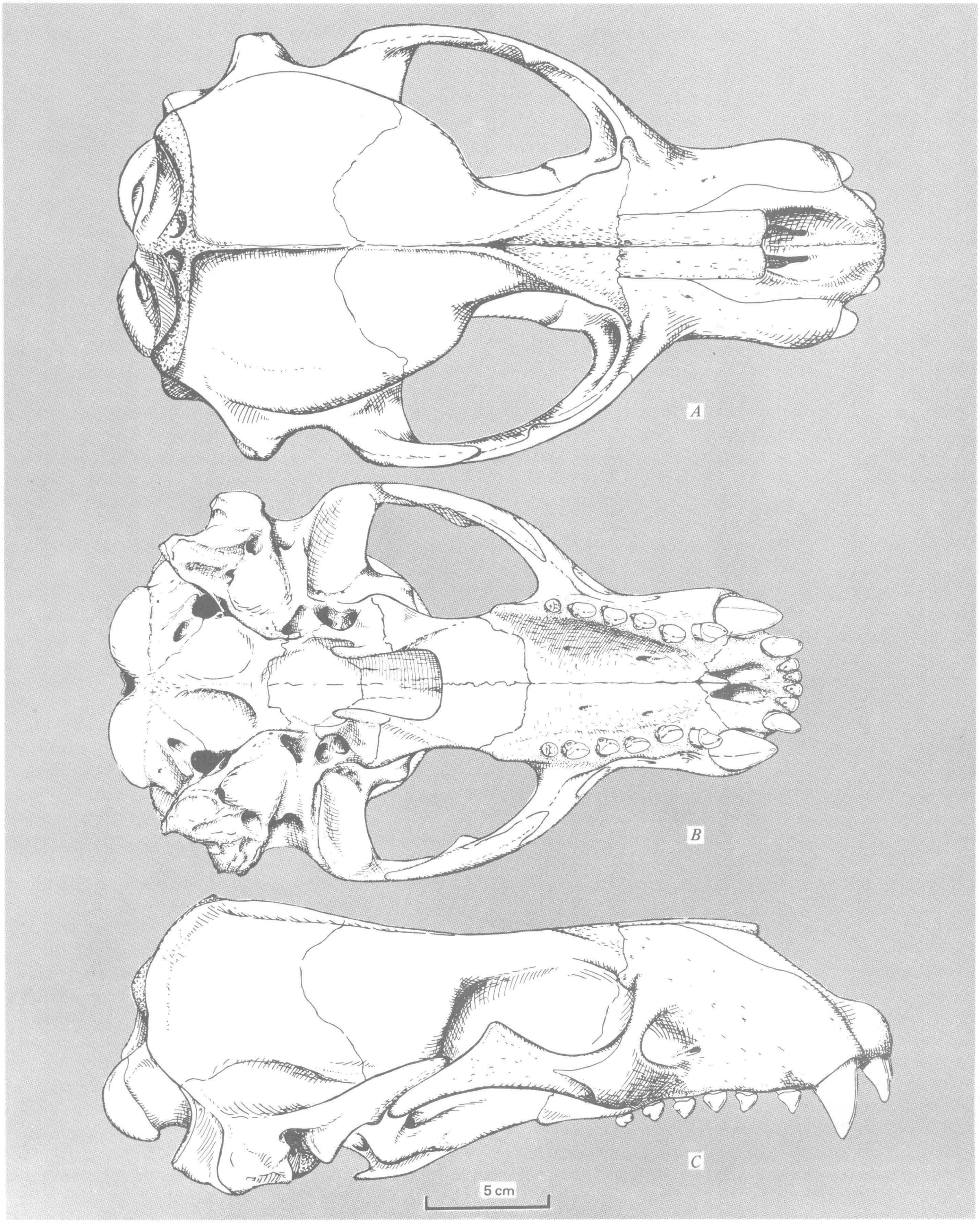
Teeth	Width (transverse at crown base)	Length (longitudinal at crown base)	Height (from crown base)	Root length
I_2	[1]2.0+	[1]4.0	---	---
I_3	[1]5.0	[1]6.5+	---	---
C	13.7	19.3	27.8	47.5+
P_1	[1]4.0	[1]6.3	---	---
P_2	[1]4.2	[1]8.9	---	---
P_3	5.6	8.0	7.5	8.4
P_4	5.2	7.8	6.5	2.8
M_1	5.8	9.4	5.7	---
M_2	[1]2.6	[1]3.8	---	---

[1] Alveolus.

Specimen USNM 23868 from locality USGS M1037 is a right lower canine with enough of the mandible adhering to it to show the large symphysis and the base of the alveolus of I_3 anterior to the canine (pl. 7). The canine, which is as large as that of the holotype, is believed to be from a male individual. The tooth is fully mature, providing one indication of the size range of *Imagotaria downsi.* This tooth is 17.8 mm in transverse diameter and 24.3 mm in anteroposterior diameter at the base of the crown; it has a crown height of 32.7 mm with no correction for moderate tooth wear, and the fully closed root is 69.6 mm long. In crown height it is comparable to an adult male *Eumetopias,* but the root differs in that it is not so bulbous (hence somewhat thinner), is not so curved, and is much longer. The root has a medial and lateral sulcus running its length such that is has a dumbbell-shaped cross section, as noted on the holotype (Mitchell, 1968, p. 1848). It was found with the distal fragment of a badly preserved metatarsal, an extremely large metacarpal V, a large humerus, and a few other scraps from a large-sized individual.

Female skull (pls. 6 and 7).—The female skull, USNM 23858, is most distinctive in its sea lion-like appearance in combination with its broad basioccipital region, vaulted palate, and lack of supraorbital processes (fig. 4). In palatal aspect, the rostrum is long and broad across the muzzle owing to the large canines. The zygomata are rather thin and are arched laterally rather than being flat-cheeked as in modern sea lions. The mastoid process is enlarged, but because it is not combined with an

FIGURE 4.—Restoration of the female skull of *Imagotaria downsi.* Referred skull USNM 23858. *A,* Dorsal view. *B,* Ventral view. *C,* Lateral view.


A
B
C
5 cm

enlarged jugular process, appears to be relatively far forward when compared with modern otariids, and more closely resembles the living walrus. The occipital condyles are large and widely separated dorsally, as in *Odobenus*. The margins of the prominently vaulted palate form conspicuous crests which support the cheek teeth and which continue posteriorly beyond the last cheek tooth (M^2) nearly to the maxilla-palatine suture. The internal pterygoid process on the palatine-alisphenoid suture is very large.

The basicranium is broad between the glenoid fossae, which are transversely shortened. Because of the shortening of the glenoid fossae, the foramen ovale and posterior opening of the alisphenoid canal face more ventrally than in the otariids and are very similar in their orientation to that of *Odobenus*. The eustachian foramen is very large. Relative to living walrus, the middle lacerate foramen is small as a result of an extensive bony floor of the carotid canal; in living walrus, there is a notably short bony bridge beneath the canal between the bulla and the basioccipital. The bulla is otherwise *Odobenus*-like with little inflation apparent on the external surface and essentially no sculpturing so that the stylomastoid foramen opens ventrally with no part of the bulla obscuring it from view in ventral aspect. The hyoid fossa is very large and only slightly concealed in ventral view by a weak lip of the bulla. The wall of the bulla is thick but not so pachyostotic as in *Odobenus* of comparable age. The posterior lacerate foramen is of moderate size, not so enlarged as this foramen in the otariids, nor does it merge surficially with the posterior opening of the carotid canal as in otariids. The mastoid process is enlarged as in all otarioids and is backed by a thin plate forming the jugular process of the exoccipital. The jugular processes of both this female skull and the holotype skull are not fused to the mastoid process, and it is clear that they are not thickened as in living adult otariids but closely resemble the condition in *Odobenus*.

The basioccipital bone is distinctly odobenid in form. It is very broad between the posterior openings of the carotid canal and is pentagonal, rather than rectangular or trapezoidal. The suture of its articulation with the basisphenoid is a straight transverse line medially, but laterally it turns abruptly anteriorly and then turns again transversely in a somewhat irregular pattern to meet the basioccipital-entotympanic suture. The fossae for insertion of the rectus capitis anterior muscles are well developed, as is the sagittal crest separating them, suggesting a fairly mature condition for the animal.

In posterior aspect the female skull of *Imagotaria downsi* is marked by widely spaced condyles, more so dorsally than ventrally; a very large foramen magnum; a low occiput; and flaring mastoid processes joined only by thin jugular processes of the exoccipital.

TABLE 5.—*Dimensions of two skulls of* Imagotaria downsi

Measured parts	mm female young adult USNM 23858	 male juvenile USNM 184060
Condylobasal length (0)[1]	287	327±
Rostral width across canines (12)	77	83±
Palatal width between P^4	47	50±
Palatal arch from alveolus at P^4	19	13±
Length of P^1 to M^2	69	92
Length of palate from back of incisors (10)	134	--
Greatest zygomatic breadth (17)	159	140
Greatest mastoid breadth (20)	158	143
Greatest basioccipital breadth (between posterior openings of carotid canals)	54	57±
Greatest width of occipital condyles	82	87±
Occipital height, subforamenal notch to lambdoidal crest (not corrected for about 15-mm vertical compression)	96	96±
Greatest width foramen magnum	36	43±
Narrowest width between orbits	34	30
Greatest width of braincase, above mastoid processes	124	131±

[1] Numbers in parentheses are those of Sivertsen (1954, figs. 5-7).

In dorsal aspect a very low and short sagittal crest is seen; no supraorbital processes are present on the frontals; and the very large canine teeth are indicated by the swollen maxilla, where they articulate with the premaxilla (pl. 7).

The size of the female skull is comparable to that of an adult male California sea lion (table 5). Although the individual was not fully mature, it does appear to have reached full size. As the enamel cap of the upper canine was nearly filled with dentine at the time of death, the apex of the pulp cavity extended distally only 2 mm into the crown base. Although one upper canine was fractured longitudinally, dental growth lines could not be seen. Comparable measurements of the female skull vary from 65 percent to 72 percent of those of the type male skull.

I^1 and I^2 are not preserved, but their alveoli are distinctly oval. I^3 is larger, with a conical crown, circular alveolus, and a very long root, as in some modern sea lions (not fur seals). The crown of the upper canine is roughly conical with a faintly serrate posterior carina and rugose enamel. Its immature root, with fully open pulp cavity, is distinctly longer than in the modern sea lions; it measures 44 mm. The crown is 32 mm long. P^1 has a single, roughly circular, and posteriorly curved root nearly three times as long as the crown. The crown is a single cusp with nonserrate anterior and posterior carinae and a lingual cingulum which is strongest posteromedially, although no distinct cusp is present here (pl. 7). P^2 has a similar crown except that a minute "cusp" is present on the posterior part of the lingual cingulum and the cingulum is weaker medial to the apex of the principal cusp. This tooth has a single root that is less than twice the height of the crown and roughly triangular in cross section. Slight grooves on the sides of the root strongly suggest that it was derived from the fusion of three roots; two are labial, the third lies below the rudimentary cingular cusp. P^3 is similar to P^2 except that the lingual cingulum is lacking medial to the apex of the principal cusp; there is a small anteromedial cingular shelf and a prominent posteromedial shelf and basin supporting a strong "cusp" which rises out of the medial fused root. The three-rooted nature of P^3 is clear, even though the roots are completely fused (pl. 7). P^4 has a comparable crown but differs in these respects: there is no trace of an anteromedial cingular shelf; the posteromedial cusp is more prominent; and a small cuspule is present on the posterior carina of the principal cusp. Its roots differ, as it is distinctly two-rooted, the posterior root being heavier. M^1 is missing but appears to have been at least weakly two-rooted as judged by its alveolus. M^2 is also missing but appears to have been small and single-rooted. The roots of all upper cheek teeth are progressively and rapidly shortened from P^1 to M^2 (pl. 7). The crown pattern of the upper cheek teeth is similar to that of modern walrus in that it is a simple cusp with a posterointernal cingular cusp. This condition is seen only on fetal or very young walrus because of the rapid destruction of the enamel cap; even when present in modern walrus, the cingular structures cannot properly be called cusps because they are little more than accessory swellings on the side of the swollen enamel cap that forms the tooth crown. Similar swollen areas are seen on unworn crowns of lower teeth in some modern walrus. These are anteromedial and posterior to the principal cusp and are in the position of the secondary cusps on the lower teeth of *Imagotaria*. Dimensions of the upper teeth of three specimens are given in table 6.

TABLE 6.—*Dimensions of the upper teeth of* Imagotaria downsi

[Dimensions measured in mm at crown base unless otherwise noted]

Teeth	Measurements	male		female
		juvenile	adult	young adult
		USNM 184060	SBMNH 342	USNM 23858
I^1	: width, transverse	?	5.2 (root)	3.8 (alveolus)
	: width, longitudinal	(See text)	7.4 (root)	7.5 (alveolus)
I^2	: width, transverse	5.7± (alveolus)	6.9 (root)	4.2 (alveolus)
	: width, longitudinal	7.5± (alveolus)	8.5 (root)	8.3 (alveolus)
I^3	: width, transverse	13.7	11.8	8.2
	: width, longitudinal	18.5	16.4	10.0
	: crown height	26.7	23±	14.5
	: root length	Too immature	45±	35.3
C	: width, transverse	25.2	21.5	15.8
	: width, longitudinal	32.2	26.5	23.1
	: crown height	49.7	42.1	32.0
	: root length	Too immature	73±	44± (root well open)
P^1	: width, transverse	11.9 (alveolus)	10.5	6.2
	: width, longitudinal	12.0 (alveolus)	11.4	7.3
	: crown height	--	10.7	7.9
	: root length	Too immature	--	35.3
P^2	: width, transverse	13.0	10.3	6.9
	: width, longitudinal	17.0	14.5	8.2
	: crown height	16.9	12.2	8.0
	: root length	Too immature	--	21.0
P^3	: width, transverse	10.2 (alveolus)	12.1	7.1
	: width, longitudinal	14.2 (alveolus)	13.9	7.5
	: crown height	--	10.0	6.2
	: root length	--	--	15.5
P^4	: width, transverse	11.5	11.1	6.0
	: width, longitudinal	15.7	13.5	7.5
	: crown height	10.8	9.8	5.7
	: root length	15 (anterior and posterior, not mature)	9.3	10.1 (anterior) 9.2 (posterior)
M^1	: width, transverse	9.9 (posterior alveolus)	--	4.0 (alveolus)
	: width, longitudinal	14.1 (alveoli)	--	8.1 (alveolus)
M^2	: width, transverse	8.5	--	2.9 (alveolus)
	: width, longitudinal	8.5	--	4.6 (alveolus)
	: crown height	6.2	--	--
	: root length	10.0 (anterior medial) 4.9 (anterior lateral) 8.1 (posterior)	--	--

By removal of a section of the roof of the braincase, most of the ventral half of the cranial cavity can be observed. The braincase itself has been partly crushed, the parietals telescoping ventrally between the temporals; only the lower half is well preserved.

In general aspect the braincase is more elongate than that of modern walrus. Two distinct optic foramina are present, differing both from the flattened dumbbell-shaped single foramen of *Odobenus* and from the single round foramen of living otariids. The optic nerves within the brain cavity lie beside each other as in all otarioids, run directly forward from the chiasma, and form what appears as a pedunculate chiasma, that is low and broad as in walrus. Also similar to *Odobenus,* the nerves diverged within the braincase, rather than within the optic canal, to enter the paired optic canals. Because of crushing, only the floors of the optic canals are preserved, and the dorsal part of the rather small cribriform fossae are superimposed on these.

The hypophyseal fossa, which is very *Odobenus*-like, is a broad, shallow basin with poorly defined lips quite unlike the deeply pocketed fossa of the otariids (pl. 10). The bony tentorium lies directly on the petrosum at the rather large cerebellar fossa, the internal acoustic meatus is quite broad with almost complete separation of the canals for the facial and vestibulo-cochlear nerves, and the petrosal apex is enlarged and flat; all features are very similar to those of *Odobenus*. In its relative enlargement, the petrosal apex is actually more like living walrus than that of *Aivukus cedrosensis,* but the internal acoustic meatus is rather far back from the apex, more resembling *A. cedrosensis* than *Odobenus*.

The sylvian sulcus was remarkably deep and long and was supported by an extensive plate of bone from the temporal that unites with the tentorium directly above the oval foramen. The development of this plate to support the anterior ectosylvanian gyrus is greater than in any modern pinniped examined. The sylvian sulcus ran posterodorsally at an angle approximating 45° from the vertical to the floor of the braincase.

Within the middle-ear cavity, the structure of the female skull, though somewhat smaller, is essentially identical to that of the holotype (pl. 10), described in detail by Mitchell (1968, p. 1854-1863). Most conspicuous are the very large epitympanic recess housing *Odobenus*-sized ossicles and the very large tympanic membrane. The bony ring of the tympanic membrane of the type skull measures 9.3 mm in its largest diameter, 7.5 mm in its smallest. That of the female skull is nearly as large, measuring 8.3 and 7.2 mm for the same dimensions. The oval window of the holotype has maximum and minimum diameters of 3.2 and 2.1 mm, resulting in an approximate membrane:window-area ratio of 10:1. Comparable measurements of the female oval window are 2.8 and 1.5 mm, also resulting in a membrane:window-area ratio of approximately 10:1. These ratios are quite comparable to those of living sea lions but not to those of living walrus; they suggest that *Imagotaria downsi* was consistently a deeper diving odobenid than was or is any other known member of the Odobenidae (see Repenning, 1972).

This ratio, with such a large tympanic membrane, is the result of a large oval window; this large window, in turn, suggests an enlarged basal whorl of the cochlea. Although the cochlea was not dissected in either the holotype skull nor in the skulls here described, all specimens are characterized by a remarkably high and globular promontorium; this shape also suggesting that the basal whorl is enlarged (pl. 10). Enlargement of the basal whorl appears to have a specific purpose in improvement of underwater hearing and is present in varying degrees throughout the pinnipeds (Repenning, 1972); this specialization in *Imagotaria* is greater than in living otarioids and parallels that of the phocids.

Though differently formed than in any other pinniped, the tympanic cavity is basically *Odobenus*-like (pl. 10). Most distinctive is a posterolateral inward swelling in accommodation of the deep hyoid fossa; Mitchell (1968, p. 1855) noted this and called it the eminentia vagina processus styloidei. This swelling into the tympanic cavity is variably developed in *Odobenus* and partially isolates the posteromedial part of the cavity as a somewhat globose space into which the round window of the cochlea, and its fossa, face. A comparable structure has not been noted in the otariids.

The tympanic bulla of the female skull appears to be slightly more inflated than that of the holotype, and it is distinctly less rugose, there being no posterior spur below the hyoid fossa, no spine or fossa in the meatal region, nor an underhanging lip to form a canal for the auricular branch of the vagus nerve between the hyoid fossa and the stylomastoid foramen. Such differences are typically sexual and ontogenetic in living otarioids.

The head of the malleus is large and swollen, and its articular surfaces are flat, as in all odobenids. The angle between medial and lateral articular facets is about 130° as compared with about 115° in *Odobenus* and 100° in otariids and most terrestrial carnivores (pl. 10). The lamina between the head and the anterior process (processus gracilis) is reduced (this process was broken before the plate was made). The neck of the malleus is short, much shorter than in *Odobenus*. The manubrium is long and is flattened only distally, as in the otariids, rather than along its entire lateral margin from the tip to the short process as in *Odobenus*. Curvature of the manubrium is slight, as in otariids and terrestrial carnivores; this slight curvature indicates a nearly flat tympanic membrane rather than a somewhat conical membrane as in *Odobenus*.

The anterior face of the head of the malleus is somewhat swollen and the anterior process originates from it, as in both odobenids and otariids, rather than having a flat or concave anterior face on the head of the malleus as in phocoids. Vertically, the malleus measures 8.79 mm from the extremity of the manubrium to the top of the head.

The proportions of the incus are more *Odobenus*-like. Although relatively short, the posterior process (short crus) of the incus is placed very low relative to the articulation with the malleus, and the body is large and inflated as in *Odobenus*. Except for the wide angle between articulations, the incus greatly resembles that of the phocids. Vertically, the incus measures 6.20 mm from the distal end of the ventral process (long crus) to the top of the body. Horizontally, the incus measures 3.38 mm from the tip of the posterior process to the angle of the mallear articular surface on the lateral side.

In summary, the female skull (USNM 23858) from the Santa Margarita Formation of the Santa Cruz area differs from the holotype (SBMNH 342) of *Imagotaria downsi* from the Sisquoc Formation of the Lompoc area by its smaller size, smaller and less ornamented cheek teeth, and less rugosity of the tympanic bulla. The postglenoid lip of the ectotympanic of the type specimen does not ride forward beneath the postglenoid process as much as in the female skull, and Mitchell (1968, p. 1850) noted a postglenoid foramen at their union on the holotype that is not present on the female skull. A foramen in this superficial position is sometimes present in modern otarioids, usually unilaterally, and its significance in the present comparison is not known. These differences appear to be either sexual or individual.

Juvenile male skull (pls. 8 and 9).—A very immature male skull and scapula (USNM 184060) were found at locality M1035 about 3 feet lower in the section than the female skull. Most of the elements of the skull are unfused and displaced by varying amounts. Two-thirds of the crown of the large lateral incisors and about one-third of the crown of the canines had erupted at the time of depth. The pulp cavity extended to within 10.4 mm of the apex of the 49.7-mm-high enamel crown of the canine. All cheek teeth were fully erupted but had, except for the small M^2, widely open pulp cavities in the roots and showed no signs of wear on the crowns (pl. 8).

By analogy with the tooth eruption and suture fusion of living otariids, the individual was between 1 and 2 years old. The right canine had been broken off roughly 2.6 cm above the crown apex and about 2.4 cm below the base of the enamel cap. The break exposed 3.9 mm of dentine deposited inside the enamel crown. Mineral deposits on the fracture were cleaned off with a micro sand blaster, and the fracture surface was examined under 30 x magnification. Interpreted according to the findings of Kubota, Nagasaki, Matsumoto, and Tsuboi (1961, pl. 7), the following deposits were found across the fracture:

Growth layers, male upper canine, Imagotaria downsi, *USNM 184060*

Enamel	0.15 mm
Prenatal dentine	.72
Double neonatal line	.13
First year dentine	3.05

It is concluded from this depositional sequence that the individual died at about 1 year of age.

TABLE 7.—*Number of roots on the upper cheek teeth,* Imagotaria downsi

	Male	Female	Male
Tooth	USNM 184060	USNM 23858	SBMNH 342
P^1	one	one	one
P^2	one: one lateral sulcus	one: two sulci suggesting 3-rooted origin	one: one lateral sulcus
P^3	one: one lateral sulcus	one: two sulci suggesting 3-rooted origin	one: one lateral sulcus
P^4	two	two	one: one lateral sulcus
M^1	two: the posterior one much broader	two: possibly only separate distally	?
M^2	three: two anterior, one posterior	one: small	?

The cause of the double neonatal line is not known, but examination of the upper canine of a one-year-old male *Eumetopias jubata* revealed the same double structure (deposited entirely within the enamel crown). Comparable growth layer measurements show a few interesting differences. The *Eumetopias* tooth was considerably smaller than that of the immature male *Imagotaria*; the measurements were made at a point 1.9 cm above the crown apex and 1.2 cm below the base of the enamel.

Growth layers, male upper canine, Eumetopias jubata

Enamel	0.32 mm
Prenatal dentine	.32
Double neonatal line	.05
First year dentine	1.05

Although the enamel crown was nearly twice as large in *Imagotaria,* the enamel was less than half as thick as in *Eumetopias.* And dentine deposition during the first year of life was three times greater in *Imagotaria.* All known odobenids are characterized by thin or no enamel and by excessive dentine deposition in their tusks or upper canines.

The juvenile male skull, though of a much younger individual, is considerably larger than the female skull, having a CBL of 327+ mm (40 mm longer than the female skull). The premaxillae were at least partially fused to the maxillae, although their mutual sutures appear open, but the two sides of the rostrum were not fused together at the median palatine suture and, as it was buried, were considerably displaced; several teeth had fallen out and been lost. Restoration along this suture is not certain; part of the palate obviously was lost from the left maxilla and possibly from the right. And the premaxillae anterior to the incisors are abraded. The CBL length, therefore, was somewhat greater than measured.

The specimen appears to have only two incisors in each premaxilla, but because of the nature of damage during burial, it is not possible to be certain what incisors were present.

As with the lower teeth in other specimens, the condition of the roots of the upper teeth appears individually variable (table 7). Those of the juvenile male skull show a greater development of multiple roots than those of the female skull or the holotype.

Despite its immaturity, the juvenile male skull shows several features of greater similarity to the type specimen than does the female skull. These similarities strengthen the interpretations of specific identity and female sex of the associated smaller but more mature skull from the Santa Cruz area. Most obvious is the large size of the cheek teeth of the juvenile male, actually larger than those of the holotype, supporting the interpretation that the relatively small size of the teeth of the female skull is a sexual feature not to be considered in specific assignment. The crowns of the cheek teeth are more ornamented, particularly in the more prominent lingual cingulum, than the teeth of the female individual, and they more closely resemble the teeth of the type specimen. The M^2, known only on the juvenile male skull, has a roundly triangular crown above the three roots with a low transverse loph anteriorly and a slightly higher posterior cusp above the posterior root.

Even though clearly not fully developed, the ear region of the juvenile skull has a well-developed inframeatal spine and an apical bullar fossa which are comparable to these structures on the type specimen but lacking on the female skull. In addition, the form and ventral projection of the mastoid process are more similar to that of the holotype. Ossification of the ectotympanic was obviously very incomplete on the juvenile skull, and the floors of the middle-ear cavities must have been very thin and fragile, for they are broken away on both sides and were lost prior to burial. Similarly, both entotympanic ossifications were lost, and the petrosal on each side was broken from the mastoid, the left being lost and the right being disoriented but present in its approximately correct position at the time of burial. All features of the middle ear otherwise conform to both the holotype and the female skull except that the prominently intruding crista tympanica is not as well developed and measurement of the size of the tympanic membrane is accordingly uncertain.

In dorsal aspect (pl. 9), the juvenile male skull is markedly more elongate than the female skull, particularly in the interorbital region. This difference appears to be the most marked of the sexual dimorphic features in the skull of *Imagotaria downsi*, although the small size of the cheek teeth in the female is nearly as conspicuous. The interorbital elongation of the juvenile male skull is particularly striking in view of its youth, because facial-interorbital elongation correlated with maturation is particularly marked in the living otariids.

An approximation of what might have been the size of the juvenile male skull (USNM 184060), had it grown to maturity, can be made from the mandibular length and cheek tooth size of the specimen (UCMP 88459) described by Barnes (1971) and the size of the cheek teeth of the holotype and of the immature male skull. Although the cheek teeth of UCMP 88459, undoubtedly a young male, are essentially the same size as those of the holotype, the length of its cheek tooth row is only 91 percent of that of the holotype because of its immaturity (see Barnes, 1971, table 1). Barnes reconstructed a complete dentary on the basis of the two incomplete rami available (1971, fig. 3); the restoration is about 220 mm in length, which is 30 mm longer than the female mandible. From this, the mandible of the holotype is estimated at 241 mm long, essentially the length of the missing mandible of the juvenile male (USNM 184060) judged by the measurement from the glenoid fossa to the anterior end of the premaxilla. Because the cheek teeth of the juvenile male average 121 percent of the size of those of the holotype, it is assumed that as an adult its mandible would have been 291 mm long and its adult CBL 377 mm, a 50 mm additional elongation in the skull. Therefore an adult male of *Imagotaria downsi* would seem to have had an extremely elongate skull, particularly in the interorbital region, possibly one-third (or 90 mm) longer than the female skull for essentially the same sized braincase (table 5).

Scapula (pl. 8).—Mitchell (1968, p. 1864), in describing two fragments from the glenoid region of the left and right scapulae of the type specimen, noted that the glenoid fossa was shallow and that the coracoid process was very large. These features help distinguish the scapula of *Odobenus* from those of the living otariids. A prominent nutrient foramen is present 15 mm posterior to the ventral termination of the base of the scapular spine.

An incomplete left scapula was found in association with the juvenile male skull from the Santa Cruz area. The epiphyseal elements of the glenoid and coracoid had not fused to the body of the scapula and were lost, but the symphyseal surface on the body is curved ventrally in the coracoid region, suggesting a prominent coracoid process. In addition, a prominent nutrient foramen is present in the same position posterior to the termination of the spine base. The position of this foramen is more ventral and posterior than in *Odobenus* and living otariids (pl. 8).

The caudal border, caudal angle, and infraspinous fossa of the body more resemble those of the otariid scapula than they do those of *Odobenus*; the infraspinous fossa is distinctly broader, particularly dorsally, than in *Odobenus*, and the caudal angle is located more ventral relative to the dorsal extent of the vertebral border. Anteriorly, the scapular notch is extremely ventral in position and has a very short radius of curvature; these characteristics resemble neither *Odobenus* nor the living otariids but are reminiscent of the Antarctic monachine seal, *Hydrurga*. The scapulae of *Allodesmus* (Mitchell, 1966, pls. 15, 16; Downs, 1956, pl. 26) and that of *Pithanotaria starri* (Kellogg, 1925a, fig. 1) both appear to share some similarities with that of *Imagotaria downsi*. All have a low scapular notch with a short radius of curvature, suggesting that this is a primitive condition.

Humerus (pls. 11 and 12).—The associated male right front limb (USNM 23859, pl. 11) from locality USGS M1035, found a few feet from the female skull, lacks the proximal part of the humerus. In those measurements that can be compared, the humerus of USNM 23859 is 10 percent larger than the humeri of the type (Mitchell, 1968, table III), and is therefore from a very large male (table 8). In other respects, it is identical.

The humerus of *I. downsi*, which is rather robust for an odobenid, is characterized by a pronounced curve of the medial outline from the head to the epicondyle, a transversely short medial epicondyle, an elongate pectoral crest that gradually tapers distally to the shaft almost to the medial lip of the trochlea (toward which it is clearly directed), a very prominent medial lip of the trochlea that has an anteroposterior diameter up to 32 percent greater than the greatest anteroposterior diameter of the distal capitulum, and a deltoid tubercle that is on the pectoral crest.

The humerus of *Imagotaria downsi* differs from that of *Aivukus cedrosensis* most conspicuously by lacking the abrupt distal termination of the pectoral crest.

Ulna (pls. 11 and 13).—This bone, known only from USNM 23859, is characterized by its remarkably deep olecranon process and short, stout shaft. In other respects, it is odobenid in nature. The anterior margin of the olecranon, dorsal to the greater sigmoid cavity (in the orientation here used the shaft axis is considered to be dorso-ventral), has been damaged, as well as the dorsal lip of the humeral articulation. Enough is preserved, however, to indicate that this margin was narrow and not a broad anterior-facing surface as in the living sea lions.

The greater sigmoid cavity for articulation with the humerus has its transverse axis between 15° and 25° from normal to the shaft axis, and in this orientation, as well as in other features, resembles *Odobenus*. The lesser sigmoid cavity for articulation with the radius is nearly flat and circular in shape. As in all otarioids, the anterior end is heavier than the posterior end of the olecranon crest but there is no lateral process at the approximate midpoint of the crest. The distal articulation for the radius is distinctly separated from the styloid process as in *Odobenus*.

TABLE 8.—*Dimensions of three humeri of* Imagotaria downsi *from the Santa Margarita Formation*

Measured parts	mm		
	USNM 23959	USNM 23870	USNM 23865
Greatest length, greater tuberosity, to radial capitulum	---	265	226
Greatest width across epicondyles	113	88	71
Transverse width at narrowest part of shaft	51	42	37
Transverse width across tuberosities	---	85	65
Anteroposterior width midshaft	101	76	62
Greatest anteroposterior diameter of medial edge of trochlea	77	50+	43
Greatest width of distal articulation	80	66	53
Greatest anteroposterior diameter of radial capitulum	52	42	34

Radius (pls. 11 and 13).—Two specimens of this bone are known, USNM 23859 (a male) and USNM 184084 (a female). As is the ulna, the radius is marked by its shortness and stoutness, more pronounced on the male specimen. Walrus-like, the prominent process for the insertion of the pronator teres lies distal to the midpoint on the anterior margin of the shaft rather than distinctly proximal to the midpoint, as in the otariids. Unlike the sea lion, the anterodistal crest between the pronator teres process and the distal articulation, the radial crest as here used (see pl. 2), is low and not prominent. The lowness of this radial crest is comparable to the odobenids, but in *Imagotaria* the distal termination, the radial process as here used (see pl. 2), is notably medial in position relative to the shaft axis (pls. 12 and 13).

In distal view the extreme medial position of the radial process is the most conspicuous feature of the radius of *Imagotaria*. The grooves for the extensor tendons of the manus are quite shallow; however, the groove for the extensor metacarpi pollicis, like the radial process, is notably medial of the position found in *Odobenus, Aivukus,* or the otariids; the radius of *Imagotaria* is comparable in this respect to the radii assigned to *Dusignathus* and *Pliopedia,* as will be discussed in a later section. The articular facet for the scapholunar is nearly square but has a convex lateral margin in *Imagotaria.* Walrus-like, there is no articular facet for the cuneiform on the ulnar side of the distal termination of the radius. In all otariids the cuneiform articulation on the radius is on a slightly elevated platform and visible in distal, as well as ulnar, or posterior, views of the radius.

The articular surface on the sides of the head of the radius, for articulation with the lesser sigmoid cavity, or radial notch, of the ulna, are much more extensive in *Imagotaria* than in *Odobenus.* On the medial side of the head, this articular surface is much like that of *Odobenus,* but it continues around the posterior side onto the lateral side of the head as a well-developed surface in *Imagotaria.* Among eight *Odobenus* radii, only one approached this condition, whereas six clearly had no continuation of this articular surface onto the lateral surface. It appears that pronation of the manus of *Imagotaria* was about as functional as it is in *Odobenus* but that supination was much greater in *Imagotaria* than it is in at least most *Odobenus.*

The dimensions of the male ulna and of male and female radii are given in table 9.

Scapholunar (pl. 13).—The scapholunar from limb USNM 23859 articulates with the radius, trapezoid, trapezium, magnum, and unciform, but it has no facet for articulation with the cuneiform. The counterpart facet is missing on the cuneiform. Examination of 16 *Odobenus* scapholunars shows that although the size of the cuneiform facet varies, it is always present, suggesting that its lack on the scapholunar of USNM 23859 may be of significance taxonomically. This surface, on the ulnar end of the scapholunar, is continuous with the distal surface for articulation with the unciform in *Odobenus* and *Aivukus,* and the opposing surface is large and well developed along the distal margin of the radial side of the cuneiform. In the scapholunar of the otariids, the ulnar termination of the articular facet for the unciform is a sharp lip and there is no cuneiform articular surface. Similarly, the radial side of the sea lion cuneiform shows no articulation with the scapholunar along its distal margin, rather it has a large surface along its proximal margin for articulation with the radius. This surface is not present in *Odobenus* or *Imagotaria.*

The pocketed articulation for the magnum on the scapholunar of *Imagotaria* is about as long as that for the unciform, and this articulation extends about as far in a palmar direction. Sixteen scapholunars of *Odobenus,* three of *Aivukus,* and one of *"Trichecodon"* (Van Beneden, 1877, pl. 8, fig. 9) have a magnum articulation on the scapholunar that is considerably shorter than the unciform articular surface and it terminates in the palmar direction far short of the termination of the unciform articular surface.

TABLE 9.—*Dimensions of a radius and ulna of* Imagotaria downsi

Measured parts	mm male USNM 23859	mm female USNM 184084
Ulna:		
Length, anterior end of olecranon to styloid process	340	---
Depth, humeral sigmoid notch to posterior end of olecranon	143	---
Depth, narrowest part of shaft	48	---
Width, narrowest part of shaft	25	---
Radius:		
Length	260	181
Greatest width, proximal articulation	76	47
Greatest width, distal termination	95	66
Least width, proximal articulation	54	37
Depth of shaft at pronator teres origin	58	35
Width of shaft at pronator teres origin	32	17

In all other respects, the scapholunar of *Imagotaria downsi* is odobenid. In distal aspect the articulation for the magnum is deeply pocketed; it does not resemble this articular surface in the otariids, which has nearly the same surface curvature as the adjacent articular facet for the unciform. Dorsally, in the sense opposite to palmar and as though the flipper were prone on the substrate, there is a round lip terminating the articular surface for the magnum which curves slightly over the dorsal surface; the termination of this facet in otariids is a sharp lip facing distally. From ulnar to radial sides, the common facet for the trapezium and trapezoid is strongly curved, rather than slightly so as in the otariids.

Cuneiform (pl. 13).—This bone, from limb USNM 23859, differs from that of *Odobenus* largely by lacking an articular surface for contact with the scapholunar, as has been discussed. It is otherwise most similar to *Odobenus.* It lacks the articular surface for contact with the radius found in all otariids. The palmar process is long in comparison with either *Odobenus* or living otariids, and there is a distinct pisiform articulation. Continuous with this articulation, the surface on the ulnar side for articulation with the styloid process of the ulna is not so flat as that in *Odobenus* but not nearly so cupped as is this articulation in the otariids. *Odobenus*-like, the articulation with metacarpal V is triangular and is present only on the palmar process, whereas in otariids it is continuous across most of the body of the cuneiform.

Pisiform (pl. 11).—This bone, from limb USNM 23859, is large and has a well-defined articular surface for both the cuneiform and the styloid process of the ulna. It does not appear clearly odobenid except that it is long relative to that of the otariids.

Trapezium (pl. 11).—This bone was not represented in the articulated limb USNM 23859. An isolated trapezium (USNM 23875) was found a few feet laterally from the left calcaneum (USNM 23866) at locality M1104. These two bones were from the 2- to 3-foot thick gravel bed in the upper part of the Santa Margarita Formation. The isolated trapezium conforms closely to what could be expected for the trapezium missing from the referred articulated limb and it actually articulates well in the limb (pl. 11). It is referred to the species on the basis of both its odobenid morphology and its stratigraphic association.

This trapezium is very distinctive in form. Most conspicuous is a dorsal-ulnar projection of the distal articulation which conforms to the prominent dorsal-palmar convexity of the proximal articulation of metacarpal I. This articulation surface for contact with the metacarpal I is very concave, not moderately so as in sea lions, and very different from the flat surface in *Odobenus.*

In living walrus the proximal articulation of the trapezium is concave in a palmar-dorsal direction, a shape reflected in the rounded articular surface on the scapholunar. In otariids this surface is slightly concave to flat in this direction. On the trapezium of *Imagotaria,* this proximal articulation is convex in a palmar-dorsal direction, a shape reflected in the flat articular surface on the radial process of the scapholunar. Comparing these differences, the trapezium of *Aivukus cedrosensis* is intermediate between those of *Imagotaria* and *Odobenus.*

Trapezoid (pl. 13).—Based upon two available specimens, male limb (USNM 23859) and a female specimen (USNM 184086), this bone, in dorsal aspect, is narrow between the trapezium and scapholunar facets, as in *Odobenus.* As in *Aivukus cedrosensis,* this bone has a narrower facet for contact with the trapezium than in *Odobenus.* The facet for contact with metacarpal II is triangular in outline rather than nearly rectangular as in both *Aivukus* and *Odobenus,* and it is more deeply concave than the facet on this bone of those genera.

Magnum (pls. 14 and 15).—This bone, available only from the limb USNM 23859, is very *Odobenus*-like: the surface for articulation with the scapholunar is high toward the palmar side, reflecting the pocketed articulation for the magnum on the scapholunar, and extends farther toward the palmar projection than in *Odobenus.* In addition, that part of this articular surface on the dorsal part of the radial face of the magnum is deeply pocketed (more so than in walrus) to receive the rounded lip of the scapholunar. The articular area for contact with the scapholunar is continuous along the proximal margin to its dorsal termination, rather than being entirely on the radial surface at its dorsal termination as in otariids. In otariids, the surface for articulation with the unciform faces more or less proximally at its dorsal termination, whereas in *Odobenus* and *Imagotaria* this surface remains on the ulnar side of the bone. The small articulation for the metacarpal IV on the ulnar side of the magnum in *Imagotaria* faces more distally than either *Odobenus* or otariids, narrowing the dorsal half of the distal articulation for metacarpal III.

In dorsal view, using the surface of articulation for metacarpal III for dorso-ventral orientation, there is seen the most marked difference recognizable between the magnum of *Imagotaria* and that of *Odobenus* (pl. 15). In this view, the proximal crest of the *Imagotaria* magnum appears to have the form of a sigmoid curve; it inclines first in an ulnar direction and curves smoothly toward the radial side as it extends back toward the palmar process. The inclination of this crest appears to be entirely in a radial direction in *Odobenus,* and this inclination is consistently so in all modern *Odobenus* magna. The appearance is largely due to the more distal orientation of the articular facet for metacarpal IV in *Imagotaria*; the angle on the magnum of *Odobenus,* formed by the intersection of the articular surfaces for metacarpals III and IV, varies from 72° to 90°, and on the single known magnum of *Imagotaria* this angle is 123°.

Unciform (pl. 14).—The unciform of *Imagotaria downsi,* known only from the referred front limb USNM 23859, is essentially identical to those of *Aivukus cedrosensis,* except that it is somewhat narrower between the radial and ulnar sides and has a sharper proximal crest between the scapholunar and cuneiform articular facets. In these features the unciform of living walrus varies greatly with the individual. Like that of *A. cedrosensis,* the unciform of *Imagotaria downsi* differs from modern walrus by being elongate in the palmar-dorsal dimension.

Metacarpals (pls. 11 and 14).—As a group, the metacarpals of the male limb of *Imagotaria downsi* (USNM 23859) are very *Odobenus*-like but very slender. They closely resemble the metacarpals of *Aivukus cedrosensis* except that in those features of the latter that differ from the metacarpals of living *Odobenus,* the metacarpals of *Imagotaria downsi* differ more extremely. In size the metacarpals of male *Imagotaria* are very similar to those from males of the two other genera.

Compared to that of *Aivukus,* metacarpal I of

Imagotaria downsi is very slender, has virtually no flattening of the palmar surface of the shaft nor broadening of the proximal part of the shaft to form a crest on the anterior (radial) edge for insertion of the abductor pollicis (pl. 14). Although a raised area on the dorsal surface of the shaft is present for insertion of the extensor pollicis, it is separated from the proximal articulation by a distinct depression which is unknown in the Odobeninae and which appears diagnostic of the Dusignathinae. The proximal articulation is saddle-shaped, extends well onto the dorsal surface (somewhat more so than in *Aivukus*), and is distinctly different than in *Odobenus*.

Metacarpals II, III, and IV are more slender shafted than the comparable elements of *Aivukus cedrosensis*; otherwise they are identical (pls. 4 and 14).

Metacarpal V is unknown in *Aivukus*; in *Imagotaria downsi* it is known from the limb USNM 23859 and from a very large isolated specimen USNM 184055. It strongly resembles *Odobenus,* particularly because the shaft is not flattened as in the otariids.

The dimensions of the metacarpals are given in table 10.

Phalanges (pl. 11).—The proximal phalanges of all digits were recovered with the articulated anterior limb, although the distal half of the proximal phalanx for the third digit was lost in collecting. The distal phalanx of the first digit, lacking the proximal articulation, and one complete and two incomplete middle phalanges of the other digits were also recovered. In addition, the proximal phalanx of the first and second digit of the opposite forelimb (left) were found in the same excavation.

The phalanges are not so flattened as in the living otariids, but they are distinctly more flattened than in the living walrus. On all phalanges the processes for insertion of the flexor tendons are more pronounced than in either of the living otarioids; they more closely resemble those of land carnivores. The only terminal phalanx found, from the first digit, suggests a reduction in nail development comparable to that otariids, and it has a widened and abrupt termination which clearly supported a cartilaginous extension for flipper elongation in typical otarioid manner. Proximal phalanges of the fourth and fifth digit have a slightly developed palmar curvature comparable to some degree with the curvature found in land carnivores.

TABLE 10.—*Dimensions of the metacarpals of* Imagotaria downsi, *transverse diameters*

Measurements (mm)	USNM 23859					USNM 23861	USNM 23860	USNM 184055
	I	II	III	IV	V	III	IV	V
Length	147	103	94	89	91	86	--	115
Minimum diameter	21	16	16	16	20	14	13	28
Proximal diameter	46	25	26	35	26	26	28	42
Distal diameter	30	30	27	27	28	25	--	36

Femur (pl. 15).—Skeletal elements of the hind limb of *Imagotaria downsi* are poorly represented in the collections from the Santa Margarita Formation near Santa Cruz. Their reference to this species is based upon the following circumstances:

1. Size bimodality of specimens comparable in actual size to front limb elements from the same and other beds as the referred female skull, and also to the holotype and the referred mandible already discussed.
2. Odobenid structure.
3. Close stratigraphic association with anterior limb elements identical to others belonging to the genus, or stratigraphic bracketing of hind limb elements between specimens clearly assignable to *Imagotaria downsi,* or similarity to other hind limb elements less questionably referred to the genus and from strata from which no other odobenid is known.

The material thus referred to *Imagotaria* includes one poorly preserved femur, three calcanea, two astragali, one patella, and two tibia. The femur was found with a humerus. The three calcanea were found at three localities, one at USGS locality M1035 down section from the female skull and male front limb but up section from an unquestionably referred metacarpal and at the same horizon and a few feet away from an atlas which conforms to the fragments of the atlas found with the female skull. One astragalus was found with one calcaneum and a second was found with a female radius and a metacarpal III. One patella was found up section from a referred metacarpal III. One tibia was found with the patella, and an isolated tibia was found at the same horizon as referred metacarpal III but about 20 feet away.

The single femur referred to *Imagotaria* (USNM 23870) is very poorly preserved but shows some unique features (pl. 15). Most conspicuous is the extreme flatness of the shaft, not only distally as in *Odobenus* but also proximally. The lesser trochanter is extremely well developed, more so than in living otariids and contrasting even more strongly with living walrus; the head is short necked but clearly higher than the greater trochanter.

Patella (pl. 11).—A single patella and associated immature shaft of a tibia, USNM 23863, were collected at the same locality but about 15 feet down section from the female skull and 5 feet up section from a referred metacarpal III. The patella does not have a distinctly conical shape with the greatly protruded apex seen in otariids, and is flatter and more like that of *Odobenus* and land carnivores.

Tibia.—The lateral condyle on the average is much larger than the medial, and its supporting crest on the shaft is more extended laterally in *Odobenus* than it is in the otariids. As a result the fossa for the origin of the tibialis cranialis is broader and in some cases deeper in *Odobenus*. The tibia found with the patella and referred to *Imagotaria* (USNM 23863) shows this lateral-cranial crest to be produced equally as much as in any of seven *Odobenus* tibiae available for comparison and far greater than in any living otariid. The shaft is remarkably straight but within the range of variation in modern walrus. This specimen lacks both distal and proximal articulations, but it is large and stout, presumably from a young male. This tibia and the associated patella were found in the same bed less than 4 feet from the immature male skull.

An isolated tibia, USNM 23864, was found at the same horizon as referred metacarpal III at USGS locality M1035. This bone, though poorly preserved, is recognizably from a mature animal about one-fourth smaller than the immature tibia and patella found 5 feet up section and is assumed to be female. As is the other tibia, this bone is characterized by a prominent lateral-cranial crest and prominent fossa for origin of the tibialis cranialis. The proximal articulation was weathered away. Although somewhat abraded, the distal articulation shows the weak grooves above the medial malleolus for flexor tendons that characterize the tibia of walrus; these grooves are uniformly double, long, and strong in otariids. The greater extent of preservation, in comparison to the tibia described above, emphasizes the straightness of the shaft.

Kellogg (1925a, p. 94-95) has described the distal part of a tibia (UCMP 24221) from the Sisquoc Formation south of Lompoc, Calif. He noted odobenid similarities in this bone, and it is possible that it belongs to *Imagotaria downsi*. Though larger, it is comparable in form to the smaller tibia from the Santa Cruz area (USNM 23864) by having the weak flexor grooves on the medial malleolus and by the presence of a long narrow facet along the anterior border of the distal articulation. On the tibia from Lompoc, the medial malleolus is separated from the astragalar articular facet, a condition not evident on the tibia from Santa Cruz; the difference may correlate with greater size.

Calcaneum (pl. 15).—Four calcanea, all mature and with a range in size comparable to this bone in living male and female *Odobenus*, have been collected from the upper part of the Santa Margarita Formation in the Santa Cruz area. The two most nearly complete, USNM 23862 (male) and UCMP 107759 (female), were collected at USGS locality M1035, where the female skull, juvenile male skull, and male limb were found. The male calcaneum was found at the same horizon and a few feet from an isolated atlas which matches the fragments of the atlas found with the female skull and very close to the juvenile male skull.

Walrus-like, the calcanea referred to *Imagotaria* have a very prominent internal tuberosity on their calcaneal tuber. They differ from the calcanea of *Odobenus* by having a cuboid facet that is between 10° and 15° from normal to the long axis of the bone in dorsal aspect (rather than between 30° and 35° as in walrus) and by the lack of a medial-distal extension of the body beyond the limits of the distal astragalar articulation, the secondary shelf of the sustentaculum of Robinette and Stains (1970, fig. 1), as found in the calcaneum of both *Odobenus* and otariids. In distal aspect, the cuboid facet is rectangular in outline and the calcaneum body is deep on the medial side below this facet.

A third calcaneum, USNM 23866, of slightly smaller size than the male calcaneum, displays these characters except that the cuboid articulation and peroneal tubercle have been destroyed. This bone, from locality USGS M1104, was not associated with other elements of *Imagotaria*, although it was found near the trapezium referred to the genus. A fourth calcaneum, with associated astragalus and partial navicular and other tarsal fragments forming USNM 23867, was found at USGS locality M1108. These bones are of distinctly small size, identical to the female calcaneum from USGS locality M1035. Damage to the calcaneum is similar to that described above, and in addition the internal tuberosity has been broken off. In features that are preserved, in particular the lesser process and distal astragalar articulation, this calcaneum matches the other three and falls within the size variation evident in other specimens of *Imagotaria*.

A right hind flipper, UCMP 24070-82, from the Towsley Formation (Winterer and Durham, 1962) of early late Miocene age was assigned to *Pontolis* cf. *magnus* by Kellogg (1925b). The partial astragalus (pl. 14), partial calcaneum (pl. 15), cuboid (pl. 9, fig. 4), and metatarsal III of this specimen are identical to elements of *Imagotaria downsi* from the Santa Margarita Formation. The flipper from the Towsley Formation is here identified as *Imagotaria* sp. because of these similarities.

Astragalus (pl. 14).—One of the two complete astragali referred to *Imagotaria downsi* was associated with the calcaneum, USNM 23867. It has a nearly vertical fibular articulation which is normal to the trochlear surface for articulation with the tibia and a lateral process which is small, in line with the lateral crest of the trochlea, and does not flare widely in a distal-lateral direction; these two features characterize the astragalus of *Odobenus.* It lacks an astragalar foramen, as do most astragali of *Odobenus.* In addition, the process medial to the posterior calcanear articulation and extending posteromedial from the plantar side of the body of the astragalus, the calcanear process which is greatly enlarged in phocids, is enlarged. Examination of 27 *Odobenus* astragali suggests that these features are probably quite constant. The configuration of the astragalus would require that the astragalar articulation on the fibula would be a nearly vertical surface alined with the long axis of the fibula, and distinctly different from that of the otariids.

The second known astragalus, USNM 184085, found with a female-sized radius and metacarpal III by Gerald Macy, is identical in size and configuration to USNM 23867 except that the lateral process is more bluntly terminated and a well-developed astragalar foramen is present (pl. 14). The fragment of the astragalus with the pes described by Kellogg (1925b) from the Towsley Formation and here called *Imagotaria* sp. is identical in those parts preserved, but it is much larger and is considered to be from a male individual.

Navicular.—A female navicular, UCMP 107752, is known from USGS locality M1035, and another incomplete one was associated with the pes, USNM 23867, from USGS locality M1108. No significant difference is evident, although the complete specimen is either abraded or immature as several features are obscure, particularly the entocuneiform facet.

A series of 11 naviculars from *Odobenus* indicates considerable variation in the cuneiform facets and the astragalar fossa, and no consistent differences between the naviculars of *Odobenus* and *Imagotaria* have been noted in these articulations. However, among the *Odobenus* naviculars, the plantar process is consistently on the fibular side of the center of the navicular, and on the two naviculars of *Imagotaria,* the plantar process is on the tibial side of the center. The same condition is evident on the navicular of *Imagotaria* sp. from the Towsley Formation (UCMP 24072) (see Kellogg, 1925b, fig. 10).

On the tibial side of the dorsal margin of the astragalar fossa of the *Imagotaria* navicular, there is a conspicuous lip on all three specimens which is developed on only one of the 11 *Odobenus* naviculars available for comparison. Kellogg (1925b) described how this bone differs from the otariids.

It may be noted here that the minute navicular attributed to *Neotherium mirum* by Kellogg (1931) has the plantar process centrally located.

Cuboid (pl. 9).—One well-preserved female cuboid, USNM 184061, was recovered from USGS locality M1035. It compares most favorably with that from the pes described by Kellogg (1925b) from the Towsley Formation, and those differences which can be seen can be equaled in the available series of nine cuboids from *Odobenus.* It also is identical to the cuboid of *Neotherium mirum* (Kellogg, 1931) except for its larger size; Kellogg noted this similarity in describing *Neotherium.*

In odobenids the angle formed, in dorsal aspect, by the navicular facet and the calcanear facet on the cuboid is never less than 75°. The astragalar facet, near the apex of this angle, may lie in the plane of the navicular facet (in which case it is hard to recognize) or may assume an intermediate orientation. In otariids this angle varies from 48° to 70°. By this criterion, *Imagotaria downsi, Imagotaria* sp. from the Towsley Formation, and *Neotherium mirum* are odobenids.

The cuboid of *Imagotaria* differs from that of *Odobenus* by the marked prominence of its plantar process, a fissipedlike feature lost in most living otarioids but present in extinct forms, both otariid and odobenid, but presumably lost in desmatophocids judged by *Allodesmus kelloggi* (Mitchell, 1966).

Kellogg (1925b, p. 106) commented on the small size of the astragalar facet on the cuboid of the pes from the Towsley Formation. This facet is usually smaller in odobenids than in otariids, with which Kellogg was comparing the fossil, and it is not uncommonly small (for an odobenid) in *Imagotaria.* Its limits, however, are usually difficult to judge without having the adjacent navicular in articular position. Kellogg (1925b) described the plantar process in unfortunate terms; it is present across the entire plantar surface but the pronounced process on the fibular side of this face makes the remainder seem insignificant; hence Kellogg refers to the process as being reduced and restricted to the fibular side, which is exactly the opposite of its condition.

Cuneiform bones.—None of these three elements have been found in the Santa Margarita Formation of the Santa Cruz area. They are described by Kellogg (1925b) from the pes collected in the Towsley Formation. In general Kellogg understated their odobenid nature as his primary comparison was with the otariid *Eumetopias.*

Metatarsals.—No metatarsal I of *Imagotaria downsi* has been found in the Santa Cruz area. Kellogg (1925b, p. 111-113) decribed a complete first metatarsal from the Towsley Formation that he compared only with *Eumetopias,* as he did all metatarsals. This was unfortunate, as they all compare more closely with the metatarsals of *Odobenus*.

Metatarsal I from the Towsley Formation is more elongate than that of *Odobenus,* has a moderate plantar-dorsal curvature not seen in *Odobenus,* and has a pointed dorsal apex on the proximal articulation. When compared with otariid metatarsals, it is conspicuously odobenid in its elongate, slender, and unflattened shaft.

The proximal half of metatarsal II is known from both the Santa Cruz area (USNM 23868, found at locality M1037 with a humerus, a mandibular fragment, and a fifth metacarpal) and the pes from the Towsley Formation. Both specimens are badly preserved. Both differ from *Odobenus* by having a more elliptical cross section at about the midpoint of the shaft, the shaft being compressed in a dorso-tibial and palmar-fibular direction.

Metatarsal III is known from four individuals: two (UCMP 108066 and UCMP 102854) from the Santa Margarita Formation in the Santa Cruz area, one from the pes from the Towsley Formation, and one (UCMP 34789) from the Santa Margarita Formation in Tejon Hills, Kern County, Calif. All specimens are only the proximal half or less. All are essentially identical to metatarsal III of *Odobenus*. Kellogg has compared the specimen from the Towsley Formation with the third metatarsal of *Eumetopias*. Assignment of the specimen from the Tejon Hills to *Imagotaria* is made only on the basis of its geologic age and geographic proximity, as it is obvious that other odobenids will be similar in the configuration of the proximal part of metatarsal III.

Metatarsals IV and V are known only from the pes from the Towsley Formation. As described by Kellogg (1925b, p. 115-116), they are very poorly preserved.

Vertebrae.—Several fragments of vertebrae were found with the female skull of *Imagotaria downsi* but only one nearly complete vertebra is known. This is an atlas (USNM 23872) found near the right calcaneum (USNM 23862) and 10 feet lower in the section than the female skull (pl. 7). The atlas is distinctive in several features, including the widely spaced anterior articulations, a very large vertebral foramen, an antero-posteriorly narrow neural arch, the lack of a ventral notch between the anterior articular surfaces, the small transverse processes which are less ventrally directed than in otariids, and, most conspicuously, the position of the canal for the vertebral artery which, in posterior aspect, is seen to be ventral to the lateral part of the articular surface for the axis, rather than lateral to it, and hence to lie on the postero-medial surface of the transverse process.

The transverse processes of an atlas were found in direct association with the female skull (pl. 7). In the position of the arterial canal relative to the posterior articulation and the unexpanded condition of the transverse processes, these fragments agree exactly with the nearly complete atlas found 10 feet lower in the section. Because the nearly complete atlas is about one-third smaller than the fragments found with the type skull, it is assumed to be from a young individual. Except for size and features of immaturity, the atlas is identical with the fragments found with the holotype of *Imagotaria downsi* described by Mitchell (1968, p. 1863).

USNM 13487

Mitchell (1968, p. 1865-1868) described an unprepared skull from the same diatomite quarry as, but about 800 feet farther west of, the referred "Individual II" and "Individual III" of *Pithanotaria starri* (Kellogg, 1925a, p. 84, 87). This locality is roughly 1½ miles south of the type locality of *P. starri* and the locality of the distal end of the tibia discussed and referred to *Imagotaria downsi.* The locality is about 5 miles west of the type locality of *I. downsi.* All are from the same stratigraphic unit and are essentially of the same age.

The specimen is embedded in a block of diatomite which has been fractured in a way that exposes a frontal section of the skull at the palate. According to Mitchell (1968, table 2), the CBL is 340 mm, 13 mm longer than the juvenile male skull (USNM 184060); other measurements are quite comparable. Elongation of the interorbital region suggests a male individual.

The lateral incisors of this specimen seem very large; Mitchell discusses the possibility that they actually represent still-retained milk canines, but he rejects the possibility. The explanation for what appear to be extremely large lateral incisors is evident upon examination of the juvenile male skull from the Santa Cruz area: the lateral incisors are nearly or completely erupted but the canines are only one-third erupted or less. Mitchell notes that P^4 is double-rooted; the posterior root is larger, as in the juvenile male skull from Santa Cruz, but differing from the condition of the P^4 roots of the holotype.

The resemblance of this specimen to the juvenile male skull and to the holotype, as discussed by Mitchell, and its close stratigraphic association with the holotype certainly indicate that Mitchell's referral of this specimen to *Imagotaria downsi* is correct.

DISCUSSION

The mandible, skull, and postcranial skeleton of *Imagotaria downsi* all show decidedly odobenid features. In general appearance, however, it would seem that the species was adapted for a sea lion-like existence. Sea lions that were contemporary with *Imagotaria,* as will be discussed, had cheek teeth that were entirely double-rooted and were small animals. The only known genus, *Pithanotaria,* was smaller than the smallest living otariid, the Galapagos fur seal. By contrast, *Imagotaria downsi* had the dimensions of the living walrus. This great size difference suggests that *Imagotaria* and contemporary otariids were not in direct competition; a suggestion strengthened by their joint occurrence in several late Miocene deposits of California, including the Santa Margarita Formation at Santa Cruz and the Sisquoc Formation at Lompoc.

From both *Odobenus* and *Aivukus,* as well as from other extinct odobenine genera, *Imagotaria* differs by having more slender metacarpals with a distinct pit on the proximal dorsal surface of metacarpal I, a wide (123°) metacarpal III and IV facet angle on the magnum, a magnum articulation on the scapholunar that is extended in the palmar direction, a conspicuously medial location of the radial process of the radius (pls. 12 and 13), a notably short and stout shaft on both radius and ulna, and, dubiously, a relatively weak medial epicondyle on the humerus in addition to the lack of reduction of the lower canines mentioned in the diagnosis of the Dusignathinae. The bones of the rear limb of *Aivukus* are not known. However, *Imagotaria* also differs from *Odobenus* in the very prominent lesser trochanter and proximally flattened shaft of the femur and the rectangular articular facet for the cuboid on the calcaneum, which has less inclination from normal to the long axis of this bone. These differences appear to be of use in distinguishing between the odobenid subfamilies Odobeninae and Dusignathinae.

Genus PONTOLIS True

Plates 10 and 18

Type species.—Pontolis magnus True (1909); USNM 3792, the basicranium and occiput of a skull that was badly shattered and incompletely repaired and prepared at the time of True's description (1905 and 1909).

DISCUSSION

This genus was based upon the above specimen collected before the turn of the century in beds of late Miocene age that are exposed near Empire, Oreg. Based upon its invertebrate fossils (Glen, 1959, fig. 5), the Empire Formation appears to be similar in age to the Purisima Formation, possibly 4-6.7 m.y. old. In June of 1973, C. E. Ray and D. R. Emlong collected the premaxillary "Sabertooth" breeding tooth of *Smilodonichthys* from the Coos Conglomerate Member of the Empire Formation, at or very near to the type locality of *Pontolis magnus.* This giant salmon is also known from the Drakes Bay Formation of Galloway and the Purisima and the Santa Margarita Formations of the Santa Cruz area.

Shotwell (1951) mentioned a mandibular ramus from the type locality of *Pontolis magnus*; he believed it was most likely that this ramus represented this species. Unstudied material from this locality at the Smithsonian Institution indicates that at least two types of large odobenids are present in this formation at this locality.

True believed that there were similarities between *Pontolis magnus* and the living otariid genus *Eumetopias,* but incomplete preparation misled him into believing that the auditory bullae were "completely obliterated" (1909, p. 144) and "crushed and splintered off down to the level of the basioccipital and so mingled with the matrix that their form is lost" (1905). Consequently, he derived almost no comparative information from the ventral surface of the basicranium.

The floor of the brain cavity was quite well exposed and here True noted considerable difference between *Pontolis magnus* and *Eumetopias jubata* (1909, p. 147). However, he did not compare these structures with any other pinniped. The floor of the braincase of *Pontolis magnus* (pl. 10) is marked by the broad and shallow hypophyseal fossa of the odobenids, which contrasts markedly with the deep globular fossa of the otariids. Much of the right petrosum is preserved on the specimen. It has a broad and flat apex, and the internal acoustic meatus is very broad with almost complete separation of the canals for the facial and vestibulocochlear nerves. The cerebellar fossa is small, and the bony tentorium is closely appressed to the petrosum in this region. These features are diagnostic of the odobenids. There appears to have been formed a rather strong bone plate to conform to the sylvian sulcus, much as in the female skull of *Imagotaria downsi.*

Further preparation of the type skull (pl. 18) shows that both middle ear cavities were shattered and had been repaired with much fragmentation and dislocation of bone prior to True's examination; the nature of the middle ear cavity, tympanic membrane, epitympanic recess, and promontorium of *Pontolis magnus* remains unknown. Externally, however, the basicranial area is not badly damaged. Major breaks cut across the mastoid-bulla region of both sides and were partly offset in repairing. However, most external features are discernible on one or the other side of the specimen. Contrary to True's impression, the bulla and basioccipital are largely intact. However, they are not at all typical of *Eumetopias* nor any otariid seal. The bullae are very flat and smooth. Associated foramina and canals are very large. The basioccipital is extremely broad with an equidimensional pentagonal form. These all are features of the Odobenidae, but none at present clearly distinguish the Odobeninae from the Dusignathinae. As with *Imagotaria,* development of the petrosal apex is more advanced toward the *Odobenus* condition than in *Aivukus cedrosensis,* suggesting greater parallel adaptation in this specialization than in contemporary odobenines and more resembling the condition in *Imagotaria.*

The resemblance of *Pontolis magnus* to *Imagotaria downsi* is exceedingly great. In the material available for comparison, the most dissimilar feature is the smoothness of the fusion of the posterior parts of the bulla to the mastoid process in *Pontolis*; in the type specimen of *Imagotaria,* this region is marked by a prominent groove (for the auricular branch of the vagus) between the stylomastoid foramen and the hyoid fossa, as well as other underhanging irregularities such as the small posterior bullar projection. However, these structures are not present on the female or juvenile male skull of *Imagotaria downsi.* In addition, these structures are not present on the fragment of the temporal of the holotype of *Dusignathus santacruzensis,* although virtually nothing else of this specimen can be compared with *Pontolis magnus.* Without further knowledge about *Pontolis magnus* or *Dusignathus santacruzensis,* it does not seem advisable to consider synonymy. Mitchell (1968, p. 1877) concluded, from differences in proportions, that the two species, *Imagotaria downsi* and *Pontolis magnus* (and genera, by inference), are distinct. *Pontolis magnus* is here considered a dusignathine odobenid, but generically and specifically it is a *nomen dubium.*

cf. Pontolis magnus, Lyon, 1941

A badly distorted skeleton from the Valmonte Diatomite Member of the Monterey Shale, of early late Miocene age (upper Mohnian, Kleinpell, 1938) was compared to this species by Lyon (1941). The locality is near Lomita, on the north side of the Palos Verdes Hills, Los Angeles County, Calif. Mitchell (1968, p. 1879-1800) discussed it in some detail and concluded that it is "clearly related" to *Imagotaria downsi,* remarking that the specimen should be further prepared and studied. The specimen was not further examined for the present report. We concur with Mitchell's conclusion and consider "cf. *Pontolis magnus*" of Lyon a dusignathine odobenid of unknown generic affinity.

Genus DUSIGNATHUS Kellogg

Type species.—Dusignathus santacruzensis Kellogg, 1927.

Diagnosis.—A specialized dusignathine odobenid with elongate upper and lower canines: the upper canines apparently did not occlude with any lower teeth because they show little or no wear from this cause; the lower canines are very close together because of an extremely narrow symphyseal region and apparently occluded only with the elongate lateral upper incisors—they exhibit considerable anteromedial wear from this occlusion. Cheek teeth have stout peglike roots and simple almost conical crowns including a fully developed and peg-rooted P_4 and M_1, crowns are capped by thin smooth enamel and show wear entirely on their anterior and posterior surfaces. Palate not greatly vaulted; infraorbital foramina of moderate size. Braincase has both sagittal and lambdoidal crests but they are low. Mandibular rami very deep, narrow, and upturned. Probable dental formula:

$$\frac{1I\cdot 1C\cdot 4P\cdot 1M(?)}{0\cdot 1C\cdot 4P\cdot 1M} \times 2 = 24\text{–}26$$

Distribution.—Late late Miocene and Pliocene of California and Baja California, by estimation 4-8 m.y. ago.

Dusignathus santacruzensis Kellogg, 1927

Plates 5, 15, 16, and 18

Holotype.—UCMP 27131, left and right dentaries, part of the right maxilla, dorsal fragment of the occiput, incomplete right temporal and isolated teeth including two upper incisors. From UCMP locality V-2701 in the late late Miocene or early Pliocene part of the Purisima Formation, Santa Cruz, Calif. The specimen is apparently a young adult individual to judge from moderate development of the sagittal and lambdoidal crests, tooth wear, and incomplete fusion between maxilla and premaxilla.

Referred material.—LACM 3011, "parts of an associated right antebrachium and manus including the following: ulna, radius, cuneiform, unciform, trapezoid, metacarpals 4 and 5, and the proximal ends of metacarpals 1 and 3" (Mitchell, 1962, p. 4, under the name "Odobenid, possibly new genus and species"). From LACM locality 1181 in the Purisima Formation, within 20 feet of the stratigraphic horizon of the type, and about 3,000 feet S. 25° W. of the point herein presumed to be the type locality.

LACM 4342, a complete right fibula. From LACM locality 1666 (fig. 2) which is the same or nearly the same locality as LACM 1181 (Mitchell, 1962, fig. 1).

UCR 15244, the right half of a snout bearing lateral I, C, P^1, P^2, and half of P^3. From UCR locality RV-7312 in the late late Miocene part of the Almejas Formation, Cedros Island, Baja Calif. Collected by R. H. Tedford (field number RHT 1294) about 50 feet above the base of the formation and in the same beds as *Aivukus cedrosensis.*

USNM 23869, associated left scapholunar and magnum from the base of the Purisima Formation 5,500 feet southwest of the presumed type locality and possibly 40 feet lower in the section. Collected by C. A. Repenning and J. C. Clark in 1965. USGS locality M1109 on seacliff west of Point Santa Cruz (fig. 2). These specimens are from a glauconite bed which has been dated at 6.7 ± 0.5 m.y. (J. D. Obradovich, written commun., 1965, KA 396).

Questionably referred material.—UCR 15245, a fragment of a large right mandibular ramus having the pterygoid process, articular process, and part of the coronoid process. Collected by R. H. Tedford (field number RHT 1309), at UCR locality RV-7313, about 15 feet above the base of the Almejas Formation.

UCMP 83370, associated elements of a left forelimb from the Drakes Bay Formation of Galloway (1977) (pl. 15). Collected by J. H. Hutchison, D. P. Domning, and L. G. Barnes, 1968. Drakes Beach, Point Reyes, Calif., UCMP locality V-6930. This material is from a glauconite bed which has been dated by Geochron Laboratories at 9.3 ± 0.5 m.y. (A. J. Galloway, oral commun., 1970). The magnum of this specimen is the only bone well enough preserved to recognize.

USNM 23891, an immature right radius lacking the distal articulation from the Purisima Formation (Glen, 1959, p. 160) at Moss Beach, San Mateo County, Calif. Collected by Evelina Dunton of San Mateo, Calif., in March 1970, at USGS locality M1245, a point about 100 feet west of the bluff at the mouth of San Vincente Creek in rocks exposed only at low tide. This locality is about 50 miles northwest of Santa Cruz, and the strata may be somewhat older than those included in the Purisima Formation at Santa Cruz for Glen (1959, p. 164) suggests that they are "probably middle or perhaps even early Pliocene"; late late Miocene in the usage of the present report and possibly from 6 to 8 m.y. old.

UCMP 65318, an adult right humerus from the same locality as the preceding specimen at Moss Beach, Calif., UCMP locality V-6531.

Type locality.—Considerable question exists as to the exact locality from which the type specimen was collected (*see* Mitchell, 1962, p. 20-21). The locality map in UCMP shows the locality, V-2701, to be about 1,350 feet north of Point Santa Cruz lighthouse along the seacliff. On the other hand, the original description is rather explicit in latitude and longitude and in its description of the lithology at the locality. These facts seem to designate the seacliff along East Cliff Drive in the Seabright District of the City of Santa Cruz as the locality. This would be 1.3 miles east-northeast of the locality shown on the UCMP locality map and higher in the Purisima Formation where the sandstone "becomes quite soft when weathered." At some points in this locality, the seacliff has receded as much as 200 feet since 1925 and East Sea Cliff Drive is no longer a continuous street. Remains of cetaceans are relatively abundant in the seacliff.

Kellogg (1927, p. 28) describes the type locality as being between Seabright and "the lighthouse." The only lighthouse that appears on old maps is at Point Santa Cruz, and, as pointed out by Mitchell (1962, p. 21), this description covers about 1½ miles of coast adjacent to the City of Santa Cruz. A further complication, but one which greatly reduces the extent of coastline covered by the words "between Seabright***and the lighthouse" was discovered by Jane Knapp, of the Remington Kellogg Library of Marine Mammalogy in the National Museum of Natural History. This complication was a sketch map of the locality in a manuscript of Kellogg's marked "Geological Correlations." On this map Kellogg mislocated "Seabright" at the headland above Cowell Beach just west of the present Municipal Pier (fig. 2), 3,700 feet north of the lighthouse on Point Santa Cruz, and indicated the type locality of *Dusignathus santacruzensis* as being along the seacliff, just below West Cliff Drive, approximately 2,800 feet north of the lighthouse, roughly 1,500 feet north of the locality on the map filed at UCMP (fig. 2).

There appears, at present, to be no way to determine which of the three possible localities is more nearly correct. Arbitrarily, the middle one, shown on Kellogg's sketch, is here considered most likely.

DISCUSSION OF THE TYPE

In describing the type specimen, Kellogg (1927) failed to note that the very long and relatively slender canines show a remarkable difference in wear: the upper ones show virtually no wear and the one lower canine whose crown is preserved is worn completely beyond the base of the enamel on its anteromedial side. The extreme tips of the upper canines are truncated, whether from wear or fracture is difficult to determine, and there is a slight wear facet, not cutting through the thin enamel, on the anteromedial base of each upper crown which is matched by a slight wear facet on the posterolateral base of the crown of the lower canine. The great wear of the lower canine was obviously against one or more upper incisors.

Kellogg does not mention the extreme narrowness of the mandible at the symphysis: when the two rami are placed together, there is barely 5 mm between the two lower canines at the alveolar margin. If lower incisors were present, they were anterior to the canines, certainly not between them. The combination of a very narrow chin, occlusion of the lower canines against the upper incisors, and lack of normal wear of the upper canines against the lower indicates that *Dusignathus santacruzensis* had an unusual dentition in which the upper canines were laterally displaced from the lower dental arcade and hung, tusk-like, beside the lower jaw. Despite the equally elongate lower canines, the muzzle of *Dusignathus* must have been very reminiscent of a walrus.

The mandibular rami (pl. 5) are deep and narrow and are bent dorsally at the region between the anterior termination of the coronoid process and the digastricus insertion. The condyloid processes are missing, but a sharp crest extends from the lateral termination of the condyle anteriorly along the inferior margin of the masseteric fossa forming a prominent lateral shelf for insertion of the masseter. A comparable but less prominent shelf is present on the mandible of *Imagotaria downsi.*

Kellogg (1927, p. 32) notes that the enamel on all teeth is thin and very smooth. Most teeth show evidence of corrosion or imperfect deposition of enamel, mainly near the base of the crowns. The roots of all cheek teeth are short, curved, swollen pegs whose greatest diameter exceeds that of the crown. The poor deposition or the corrosion of the enamel near the crown bases makes it difficult to be certain, but there appears to be no indication of lateral or medial cheek tooth wear; all clear evidence is on the anterior and posterior faces of the cheek teeth. Although the crowns are nearly conical and roundly lanceolate, their sharpness is increased by this wear, which contrasts markedly with the wear seen on *Aivukus cedrosensis* and *Odobenus*. It appears that the lower cheek teeth of *Dusignathus* occluded between their upper counterparts as in some phocids, particularly *Halichoerus,* without any placement medial to their upper counterparts as is common in the otarioids.

The temporal of the type of *Dusignathus santacruzensis* is very walruslike. Kellogg compared the fossil with *Eumetopias, Zalophus, Mirounga,* and *Cystophora*. In view of the walruslike temporal and peglike teeth, it is rather remarkable that possible odobenid relationships did not occur to him.

In those parts preserved, the temporal of *Dusignathus* is nearly identical to *Imagotaria,* particularly the female skull. This similarity has been noted and described by Mitchell (1968, p. 1885–1886), along with some dissimilarities. Odobenid features include an extremely large tympanic membrane (measuring nearly 12 mm in its greatest diameter), a very large epitympanic recess (indicating the former presence of walrus-sized ossicles), a tentorium that must have been closely appressed to the now missing capsule of the semicircular canals, and a large bony eustachian canal. The hyoid fossa was very deep, extending upward nearly to the epitympanic recess, and there must have been a well-formed eminentia vagina processus styloidei protruding into the middle ear cavity although this wall of the fossa has been destroyed and all that remains is the trace of the fossa on the medial side of the mastoid process. These features, the deep symphysis of the mandible, and single-rooted cheek teeth in late late Miocene time, when all known otariids had double-rooted teeth, indicate that *Dusignathus santacruzensis* is an odobenid. Failure to reduce the lower canine while enlarging the upper is characteristic of the dusignathine odobenids.

The dorsal fragment of the occiput and adjacent parts of the parietals show a weak sagittal crest and a strong but low occipital crest which, except for larger size, is quite similar to this area on the female skull of *Imagotaria downsi.*

DISCUSSION OF REFERRED SPECIMENS

LACM 3011, which is an incomplete anterior limb, was described by Mitchell (1962). He fully recognized the odobenid nature of the limb bones but, following Kellogg, did not then recognize the odobenid nature of *Dusignathus* and hence did not suggest an association between the two, even though they appear to have come from the same stratigraphic interval and from localities about 1,800 feet apart as he judged the position of the type locality, or about 3,000 feet apart as the position of the type locality is herein arbitrarily selected.

Except for general odobenid features, which Mitchell clearly defines, these bones are significant in the following features: radius and ulna short and stout; radius with the radial process (distal termination of the radial crest) radial and medial to the distal articular surface—conspicuously medial in location in distal aspect; ulna without the prominent olecranon of *Imagotaria* and the proximal radial articulation long and narrow; metacarpal I elongate, not flattened proximally, with proximal articulation saddleshaped and extending onto the dorsal surface, and with a distinct basin on the dorsal surface proximal to the insertion for the pollical extensor. These limb bones bear a far greater resemblance to those of the dusignathine *Imagotaria downsi* from older strata than they do to those of the odobenine *Aivukus cedrosensis* of more comparable age or to those of living *Odobenus*. They are, however, not identical to those elements of *Imagotaria*.

The most conspicuous differences from the comparable elements of *Imagotaria* are the lesser development of the olecranon and the long radial notch of the ulna, distal narrowness of the trapezoid, distal broadness of the unciform, presence of an articular surface for the scapholunar on the cuneiform, and shorter and more robust metacarpals IV and V; all of which enhance the similarity of these elements to those of *Odobenus*.

In view of the stratigraphic association with the type of *Dusignathus* and their great similarity to other dusignathine limb elements, this material is here referred to *Dusignathus santacruzensis*.

LACM 4342, described by Mitchell in the same paper as an odobenid fibula, cannot be compared to any dusignathine odobenid as no unquestionably dusignathine fibula is known. Its stratigraphic association, however, at or very near to the point of discovery of LACM 3011, and its odobenid nature certainly suggest referral to the same animal, as was done by Mitchell (1962, p. 12). This fibula has the proportions of living *Odobenus*, however, and does not show the short, stocky nature of the anterior limb elements. A fibula from the Etchegoin Formation, questionably referred to *Pliopedia* in the following pages, does show an extremely short and stocky nature.

USNM 23869 is an associated left scapholunar and magnum from USGS locality M1109 in the glauconite bed at the base of the Purisima Formation at a point 3,300 feet farther west than the anterior limb LACM 3011. These two bones are also referred to *Dusignathus santacruzensis* on the basis of dusignathine characters in combination with some features more similar to *Odobenus* than *Imagotaria* and because of stratigraphic and geographic association. This locality may be as much as 40 feet stratigraphically lower in the Purisima Formation and is about 1 mile from where Kellogg indicated the type locality on his manuscript map previously referred to. We believe that this association is close enough to rely upon the assumption that "similar species are allopatric" and that one species is represented.

This scapholunar appears dusignathine in that the pocketed articulation for the magnum is long and extends about as far in a palmar direction as does the articular surface for the unciform. This condition matches that of the scapholunar of *Imagotaria downsi,* and, as there noted, is consistently different from 16 *Odobenus,* 3 *Aivukus,* and 1 "*Trichecodon*" scapholunars. And this scapholunar has a pronounced facet for articulation with the cuneiform, matching the presence of the opposing facet noted on the cuneiform of the anterior limb discussed above and referred to *Dusignathus santacruzensis.*

The associated magnum of USNM 23869 has an angle of 109° between the two articular facets for metacarpals III and IV (pl. 15), greater than the range or 72° to 90° found in the magnum of *Odobenus* and less than the 123° found in *Imagotaria.* The dorsal face of the *Odobenus* magnum is triangular in outline, that of *Imagotaria* narrowly trapezoidal because the dorsal edge of the scapholunar articulation parallels and is close to the dorsal edge of the metacarpal IV articulation. Although the metacarpal IV articular surface on the magnum of USNM 23869 faces less distally than does that of *Imagotaria,* the dorsal part of the articular surface for the scapholunar also faces less proximally and the two surfaces remain approximately parallel. The surfaces are farther apart than in *Imagotaria,* however, and the dorsal face of the magnum of USNM 23869 is broadly trapezoidal and quite intermediate between *Odobenus* and *Imagotaria.* In other respects, this magnum is identical to that is *Imagotaria*: most notably the scapholunar articular surface extends completely to the palmar surface, reflecting the elongate articular pocket on the scapholunar.

UCR 15244, a portion of a pinniped snout from the lower part of the Almejas Formation of Cedros Island, is from one of the largest known otarioid pinnipeds (pl. 18). It is distinguished by an extremely long and slender canine (to judge by the long and slender root) whose alveolar diameter is no greater than that of P^1; by smallcrowned cheek teeth with very thick and swollen, curved, peglike roots; by very thin and smooth enamel crowns on the cheek teeth of essentially conical form; by cheek tooth wear only on the anterior and posterior surfaces; by a lateral incisor that, while not equaling the canine in diameter, is stout and extremely long-rooted; and by an extremely small incisor-canine diastema, suggesting that the lower canine occluded with this large incisor rather than fitted into the diastema between the incisor and canine. The palate is not markedly arched nor is the infraorbital foramen greatly enlarged for a pinniped.

Although generally quite similar to the type of *Dusignathus santacruzensis,* this specimen from Cedros Island does differ by having much greater size, stouter cheek tooth roots, more nearly conical crown on the cheek teeth, and longitudinal fluting on the very dense cementum and dentine of both the canine and lateral incisor, similar to that on the tusks of "*Trichecodon.*" These differences are here believed to be the expression of sexual dimorphism; the larger specimen from Cedros Island is believed to be a male and the holotype is believed to be a female.

The dimensions of UCR 15244 are given in table 11.

TABLE 11.—*Dimensions of* Dusignathus santacruzensis, *referred specimen UCR 15244*

Measured parts	mm
Canine root, apex to alveolus	104
Canine diameter at alveolus, anteroposterior	30.0
Canine diameter at alveolus, transverse	22.8
Laminated cementum of canine, thickness	1.5±
Canine-incisor diastema at alveoli	5.2
Lateral incisor alveolar diameter	18.9
P^1 alveolar diameter, anteroposterior	22.8
P^1 alveolar diameter, transverse	24.0
P^1 diameter at base of crown	16.2
P^1 height, lateral alveolar lip to apex	24.4
Rostral width across canines	118.2±
Rostral width across P^3	120.6±
Root length P^3, alveolus to apex	26.8

DISCUSSION OF QUESTIONABLY REFERRED SPECIMENS

Those specimens questionably referred to *Dusignathus santacruzensis* are, for the most part, so questioned because they are sufficiently removed from the type, both in distance and in stratigraphic correlation, that the assumption of "different species being allopatric" cannot be used in defense of specific identity. The single exception is UCR 15245, which will be discussed first. All specimens are odobenid, some are demonstrably dusignathine, but none can be assigned to the other odobenid species previously discussed.

UCR 15245 is a gigantic mandibular fragment from UCR locality RV-7313 in the lower part of Almejas Formation on Cedros Island. The condyle measures 107 mm in width, and the largest modern male *Eumetopias jubata* available for comparison measures 57 mm in the same dimension. This specimen is questionably referred to *Dusignathus santacruzensis* because of general stratigraphic association, very large size, and the suggestion of dusignathine affinity in the very broad and sharp-edged shelf (where the superficial masseter inserts) that extends anteriorly from the lateral end of the condyloid process to the horizontal ramus, and the anteroposteriorly short pterygoid process that extends only slightly posterior to the inferior sigmoid notch.

UCMP 83370, a partial anterior limb from the glauconite at the base of the Drakes Bay Formation at Point Reyes, Calif. (pl. 15), contains a rather well-preserved magnum. In those features considered to be dusignathine characters and in those considered different from the magnum of *Imagotaria downsi,* as well as other features except size, this magnum is identical to the magnum of USNM 23869 that was discussed and referred to *Dusignathus.* The angle of the dorsal face formed by the facets for metacarpals III and IV is 116°; it is somewhat more similar to that of the *Imagotaria* magnum, but the dorsal face is broadly trapezoidal. Judged by the other bones of this limb, the specimen appears to be from an adult animal and because of its smaller size is believed to be female.

The glauconite from which this specimen was collected has had a K/A age determination of 9.3 ± 0.5 m.y. according to A. J. Galloway (oral commun., 1970), and thus the rock unit appears to be older than the Purisima Formation in the Santa Cruz area 100 miles farther south. However, the identity of the fur seal found in this same unit, associated fossil cetaceans being studied by L. G. Barnes, and the available fossil invertebrate evidence all suggest a considerably younger age than indicated by the K/A date, as will be discussed in connection with the description of the fur seal from the same locality (see also the section "Type locality and age" of *Aivukus cedrosensis*).

USNM 23891 is a small immature odobenid radius lacking the distal epiphysis; the distal position of the pronator origin on the anterior surface marks it as an odobenid (pl. 16). The articular surface on the sides of the head, for articulation with the radial notch of the ulna, is continuous from medial to lateral sides, indicating a high degree of supination relative to the great majority of known odobenines and equaling the condition found in *Imagotaria.* This characteristic suggests that the specimen is that of a dusignathine odobenid. The occurrence of this specimen in the Purisima Formation at Moss Beach, San Mateo County, Calif., suggests the possibility that it represents a juvenile *Dusignathus santacruzensis* and it is questionably referred to this species. The specimen was found 50 miles northwest of the type locality, and about an equal distance southwest of the anterior limb from the Drakes Bay Formation discussed.

UCMP 65318 is a stout, adult, odobenid humerus also from the Purisima Formation at Moss Beach, Calif. (pl. 16). The combination of a pectoral crest directed distally toward the medial lip of the trochlea and an anteroposterior diameter of this lip far exceeding that of the distal capitulum marks this specimen as an odobenid. It is further distinguished by a distinct lateral bowing of the shaft, by a moderately broad U-shaped bicipital groove, by a greater tubercle which is about the same height as the head, by a very prominent medial epicondyle, by remarkably weak development of the insertional area for the deltoideus muscle on the lateral side of the pectoral crest, and by a conspicuously short shaft relative to the size of the head and the distal structures. These features distinguish this humerus from other odobenid humeri thus far considered.

The greatest length of this specimen is 271.6 mm, the greatest transverse width across the epicondyles 122.8 mm, and the greatest anteroposterior width across the head to greater tubercle 130.0 mm. Although the distal termination of the pectoral crest has been lost because of the midshaft fracture, it would appear to have dropped rather abruptly, distally, to the shaft. Because of its odobenid nature, occurrence in the Purisima Formation, dissimilarity to other known fossil odobenids so far discussed, and shortness of the shaft (which might well parallel the shortness of more distal elements referred to *Dusignathus*), this specimen is also questionably referred to *Dusignathus santacruzensis*. Though not identical, this humerus is similar to the humerus of *Pliopedia* and *Valenictus* in several characters, discussed under these genera, in particular the extremely low greater tubercle.

CONCLUDING DISCUSSION

Stratigraphic and geographic association in combination with uniqueness of structure have here been relied upon to refer, with varying degrees of doubt, several dusignathine postcranial skeletal elements to *Dusignathus santacruzensis*, the holotype of which consists entirely of cranial elements. As with the cranial elements, the postcranial elements show some specializations paralleling those of the odobenines and some unique features which sharply separate them from the older dusignathine genus *Imagotaria*.

Those features of the holotype and referred specimens which appear to characterize the Subfamily Dusignathinae, insofar as it presently is known, are: (1) lower canine not reduced relative to upper canine, (2) radius and ulna short and stout with a conspicuously medial position of the radial process at the distal end of the radial crest of the radius, (3) a pocketed articular surface for the magnum on the scapholunar that is elongate and extends about as far in a palmar direction as the articular surface for the unciform, (4) in agreement with the last, a scapholunar articular crest on the magnum which continues in a palmar direction to the palmar process without break, a metacarpal III to IV articular facet angle of 110°-130° on the magnum, and a dorsal surface on the magnum that is trapezoidal rather than roughly triangular, and (5) slender metacarpal I with pronounced basin on the dorsal surface between the head and the insertional spur for the pollical extensor.

Those features of the holotype and referred specimens of *Dusignathus santacruzensis* which appear to represent specializations paralleling those of the odobenine odobenids which are not so conspicuously developed in the older dusignathine genus *Imagotaria* are (1) cheek teeth with stoutly peglike roots, (2) tympanic membrane very large, (3) medial epicondyle of the humerus prominently pointed and upturned, (4) olecranon of ulna not greatly enlarged, (5) cuneiform articular facet on the scapholunar and scapholunar articular facet on the cuneiform, and (6) proportions of the distal articulations of the trapezoid and unciform.

Those features of the holotype and referred specimens which at present appear unique to *Dusignathus santacruzensis* are: (1) enlarged upper lateral incisor which occludes with the lower canine, (2) very narrow mandibular symphysis, (3) distinctive cheek tooth occlusion and wear that is restricted to anterior and posterior surfaces, and (4) short stocky humerus with very conspicuous lateral bow to the shaft and very weak anconeal crest and deltoideus insertion.

Dusignathus santacruzensis lived in association with *Aivukus cedrosensis* in the southern waters of Baja California, but nothing has been found in the more northerly deposits of central and northern California which could be assigned to the primitive odobenine *Aivukus*. In Baja California, the Santa Cruz area, and the Point Reyes area, *Dusignathus* is found associated with a primitive otariid genus to be described in Part II of this report. If all referrals to this species are correct, there appears to have been only one dusignathine odobenid living along the California and Mexican open coast of the North Pacific Basin from questionably 8 to less than 5 m.y. ago. It replaced the earlier dusignathine genus *Imagotaria*. Two possible exceptions are the genera *Pliopedia* and *Valenictus*. Northward along the Oregon coast, *Dusignathus* is either replaced by or equal to the genus *Pontolis*.

Genus PLIOPEDIA Kellogg

Type species.—Pliopedia pacifica Kellogg, 1921.

Diagnosis.—The dentition and facial portion of the skull are unknown; sagittal and lambdoidal crest lacking and supraoccipital area for insertion of neck muscles low and broad; carotid canal very large, and petrosum and bulla as in *Odobenus.* Humerus with greater tubercle no higher than head; lesser tubercle large, curved medially, and sloping distally; bicipital groove deep and narrow; deltoid tubercle not on pectoral crest but on lateral surface of shaft; internal epicondyle directed posteriorly as well as internally; shaft straight and not shortened or curved. Ulna short and stout with moderate depth of olecranon process. Radius short and stout with radial process medial in position. Metacarpal I with dorsal depression distal to proximal articulation; more slender than in *Imagotaria.*

Distribution.—Known only from the late late Miocene inland sea of central California and possibly restricted to this body of water as the contemporaneous genus *Dusignathus* appears to have occupied the open coasts of California and northern Mexico at this time.

Pliopedia pacifica Kellogg, 1921

Plates 4, 14, 16, 17, and 24

Holotype.—USNM 13627 (formerly SU537): portions of both left and right forelimbs collected by Robert Anderson in 1909.

Referred material.—USNM 187328, portions of left and right forelimbs, braincase of the skull and one rib collected by W. P. Woodring in 1932 and C. A. Repenning in 1974 (Woodring and others, 1940, p. 98, their locality 350). USNM 187337, a fibula, and USNM 187338, a phalanx, are questionably referred to *Pliopedia pacifica* because they are odobenid elements found in the same stratigraphic zone as was USNM 187328.

Type locality and age.—From the basal conglomeratic member of the Paso Robles Formation "on summit of hill, one mile southeast of the town of Santa Margarita" (Kellogg, 1921), San Luis Obispo County, Calif. Marine mollusks from the same unit 8 miles to the north suggest an early Pliocene age according to Addicott and Galehouse (1973), late late Miocene in the usage of this report.

Addicott and Galehouse (1973) found the invertebrate fauna of the Paso Robles Formation unique in that is has some seemingly late Pliocene forms as well as forms known from the lower part of the Pliocene of the Kettleman Hills, Calif. Because of a previously established extreme variability of the apparent late Pliocene form, they placed more reliance on the early Pliocene form. Woodring, Stewart, and Richards (1940, chart following p. 78) show this early Pliocene form, *Ostrea atwoodi* Gabb, as occurring from the Upper *Pseudocardium* zone to the *Macoma* zone of the Etchegoin Formation in the Kettleman Hills. Within this stratigraphic range of *Ostrea atwoodi,* Woodring collected, in 1932, an odobenid radius and fragments of its humerus which were identified by Remington Kellogg as an "eared seal***wholly unlike any known extinct and living otarid***" (Woodring and others, 1940, p. 98, their locality 350). Excavation of this old locality in 1974 produced a complete humerus, two ulnae, and a brain case. Largely on the strength of unique features of the humerus, these are identifiable as *Pliopedia pacifica* Kellogg. The fragments of the radius and ulna of the holotype are also identical to those of the specimen from the Etchegoin Formation. A tooth of the horse *Pliohippus* sp. is known from this zone (J. W. Durham, oral commun.), and other teeth have been found in other parts of the Etchegoin of the Kettleman Hills (Durham and others, 1954).

The upper *Pseudocardium* zone of the Etchegoin Formation lies roughly 400 feet down section from the *Neverita* zone of the overlying San Joaquin Formation in which Woodring collected a different odobenid (Woodring and others, 1940, table on page 46). This odobenid is identifiable as *Valenictus imperialensis* Mitchell, 1961. Midway between the *Neverita* zone and the younger *Pecten* zone of the San Joaquin Formation, a tuff bed occurs along Arroy Doblegado on the east side of North Dome of the Kettleman Hills. This tuff has been dated as 4.3 m.y. old (J. D. Obradovich, oral commun., 1975). The *Pecten* zone contains a Blancan mammalian fauna.

Valenictus is thus older than 4.3 m.y., and *Pliopedia* is considerably older than *Valenictus,* though distinctly younger than the *Imagotaria-Pithanotaria* seal fauna which is found in rocks that appear to be as young as 9 m.y. As will be discussed, the similarities between *Pliopedia* and *Valenictus* are such that the possibility exists that *Valenictus* evolved directly from *Pliopedia* in the inland sea of California. The presence of *Pliopedia* in the Etchegoin and the suggestion of a rather short temporal range for this genus in this stratigraphic succession strongly supports the age assignment of the basal Paso Robles Formation by Addicott and Galehouse (1973). The type specimen of *Pliopedia pacifica* is here considered to be from 5 to 6 m.y. old, late late Miocene in the usage of this report.

DISCUSSION

Kellogg (1921) noted odobenid similarities in this fossil, although he tentatively referred it to the Otariidae. Mitchell (1962, p. 22) also recognized odobenid relationships and later regarded it as an odobenid (1966, p. 38-39). In 1968 Mitchell (p. 1880-1881) pointed out differences between the humerus of *Pliopedia pacifica* and *Imagotaria downsi.* These differences showed that "the two species are clearly distinct" although he did not mention why they were generically distinct.

Humerus (pl. 17).—Kellogg (1921) failed to note that the preserved distal half of the left humerus of the type, as well as the fragments of the radius and the ulna, are badly crushed; in fact he stated (p. 219) that the "most striking general characteristic [of the humerus] is the antero-posterior compression of the distal end***" This compression is obviously a result of the overall crushing and distortion of the specimen whereby the distal articulation and the medial epicondyle have been rotated forward and upward approximately 30° such that the medial lip of the trochlea is actually pressed against the distal end of the pectoral crest. The distance from the region of the pectoral insertion to the trochlear crest has been halved by this rotation. The supinator crest, leading distally to the medial epicondyle, seems remarkably well developed and flaring, as noted by Kellogg, and it appears that this feature has been accentuated by the anteroposterior crushing.

Kellogg did note a "lateral compression of the shaft in the deltoid region." The anteroposterior diameter of the shaft near the most prominent part of the pectoral crest is 86 mm, whereas the lateral diameter at the same point is about 50 mm, without compensation for the anteroposterior compression of the proximal root of the supinator crest, which somewhat exaggerates these measurements. The insertion for the deltoideus muscle is not evident. Correcting for the distortion of the specimen, the distal half of the humerus of *Pliopedia pacifica* is essentially identical in size and form to UCMP 65318 from the Purisima Formation at Moss Beach which has been questionably referred to *Dusignathus santacruzensis* with one conspicuous exception: the medial epicondyle is directed medially and posteriorly, as noted by Kellogg (1921, p. 220 and fig. 1d). This posterior orientation of the internal epicondyle is typical of *Odobenus,* but not of most odobenids including the humerus referred to *Dusignathus.*

Though weathered and leached by root action, the right humerus of USNM 187328 from the Etchegoin Formation of Middle Dome, Kettleman Hills, Calif., is complete and undistorted. It is a long and moderately stout humerus not showing the shortening of the humeri of *Dusignathus* and *Valenictus,* and the shaft is not curved as is the humerus of *Dusignathus.* The humeri of all three genera are distinguished by an exceptionally low greater tubercle which does not protrude dorsally beyond the humeral head; this feature is unique among the humeri of odobenids, although it is present in at least some desmatophocids. The lesser tubercle of *Pliopedia* is unique in that its dorsal crest slopes distally and the tubercle is curved prominently medially. The bicipital groove is very narrow and has a nearly V-shaped cross section, comparable only to *Valenictus.* The insertion of the deltoid muscle is not obviously marked on the humerus of *Dusignathus,* but, because of the rather sharp lateral margin of the pectoral crest, it appears most likely to have inserted on that crest. Except for the genus *Odobenus* (including *Trichecodon*), *Pliopedia* and *Valenictus* are unique among odobenids in that the tubercle for insertion of the deltoid muscle is clearly removed from the pectoral crest and is on the lateral surface of the shaft.

Except for those features obviously caused by distortion of the humerus of the type specimen, the humerus of the specimen from the Etchegoin Formation is identical. Most distinctive is the posterior curve of the medial epicondyle. This condyle otherwise looks quite usual, being triangular with its lower margin directed dorsomedial, rather than like the swollen knob seen on *Valenictus.* This humerus measures 306 mm in greatest length from head to distal articulation, 80 mm in head diameter, 133 mm in greatest transverse diameter from the posterior margin of the head to the anterior border of the pectoral crest, and 129 mm across the epicondyles.

Ulna (pl. 24).—A fragment of the left ulna of the type specimen, preserving much of the proximal articulation, appears to have been buried beneath the humerus in a position such that the ulnar shaft posterior to the anconeal process lay beneath the olecranon fossa of the humerus; compaction of the deposits forced the supinator crest of the humerus downward onto the trochlear notch of the ulna and the entire proximal articulation of the ulna is displaced medially relative to its shaft. Possibly the missing olecranon process of the ulna was responsible for the displacement of the distal articulation of the humerus.

The depth, or anteroposterior diameter of the ulna shaft below the trochlear notch, indicates that the olecranon was not the deep, hatchetlike process as in *Imagotaria,* instead it must have been much like *Odobenus* and *Dusignathus.* Also *Dusignathus*-like, the radial notch is narrow, rather than being nearly circular as in *Imagotaria.* In regard to these features, the ulnae of the specimen from the Etchegoin Formation match the holotype and, in addition, the ulnae are seen to be short and stout as are those of *Imagotaria.*

The distal tip of the right ulna of the type and those of the ulnae from the Etchegoin Formation show the distinctly odobenid separation of the distal radial articulations and also a greater development of a pisiform articular surface than has been seen in *Odobenus.*

Radius (pl. 24).—The fractured and distorted head of the left radius of the holotype has the ulnar articulation very well developed on the lateral side of the head; it is quite comparable to the radius of both *Imagotaria* and *Dusignathus.* This articular surface is less developed on the radius from the Etchegoin Formation, a variation common in the radii of *Odobenus.*

The complete radius from the Etchegoin Formation is 22.5 cm long, has a greatest proximal diameter of 6.95 cm, and an anteroposterior distal diameter of 8.73 cm. This bone is clearly that of a dusignathine odobenid, but it cannot be separated definitely from the radii of either *Imagotaria* or *Dusignathus,* although the distal articulation for the scapholunar is more oval, as in *Dusignathus,* rather than roundly rectangular as in *Imagotaria.* The radii of *Pontolis* and *Valenictus* are unknown.

Right trapezoid.—This nearly complete bone from the type specimen, called the fifth metatarsal by Kellogg (1921, p. 226), lacks the palmar process but appears more similar to those of *Imagotaria* than *Dusignathus* (judged by the published sketch, Mitchell, 1962, fig. 4) in that the distal articulation is broad dorsally but narrows in a palmar direction. It is less similar to that of *Odobenus* than to either of these, but it is quite comparable to the trapezoid of *Aivukus cedrosensis.* A reasonably large sample of trapezoids of *Odobenus* was not available to evaluate individual variation.

Right metacarpal I (pl. 14).—This bone of the type specimen was broken, and the distal part was considered questionably the right metacarpal IV while the proximal part was recognized as the right metacarpal I by Kellogg (1921, figs. 7 and 10). It bears a marked similarity to both *Imagotaria* and *Dusignathus* in being slender, having a saddle-shaped proximal articulation, and in having a basin on the dorsal surface proximal to the insertion of the pollical extensor. This bone is somewhat smaller and much more delicate than the first metacarpal of a male *Imagotaria.* Because the first metacarpal of *Dusignathus* is not complete, its relative slenderness cannot be compared.

Right metacarpal II.—Called "right metatarsal II?" by Kellogg (1921, fig. 9): this bone of the type specimen is represented only by its head, which is quite similar to this bone in *Imagotaria,* narrower in proximal aspect than this bone in *Aivukus cedrosensis,* and very narrow in comparison with metacarpal II of *Odobenus.* The bone is not present in the specimens referred to *Dusignathus santacruzensis.*

Right metacarpal III (pl. 4).—Called "left" by Kellogg (1921, fig. 8) and differing from this bone in *Imagotaria* in that the articular surface for metacarpal II is smaller, though largely broken on the specimen and best judged by the counterpart on the head of metacarpal II. It differs in the same way from metacarpal III of *Aivukus cedrosensis,* and it cannot be compared with the weathered metacarpal III here referred to *Dusignathus* from the published description (Mitchell, 1962, p. 11). This bone has a head that is much more rounded and indistinct in structure in *Odobenus,* but this element of *Pliopedia, Imagotaria,* and *Aivukus* cannot be differentiated between these genera.

Metacarpal proportions (table 12).—*Pliopedia pacifica* has a smaller and more delicate metacarpal I than *Imagotaria downsi.* Although metacarpal III of *Pliopedia* measures 90 mm in greatest length and is only 4 mm (4 percent) shorter than the same element of *Imagotaria* (male articulated limb, USNM 23859), the greatest length of the *Pliopedia* metacarpal I is only 123.5 mm and is 24 mm (16 percent) shorter than this element in the articulated limb of *Imagotaria.* Except for this difference in metacarpal proportions, the metacarpus of *Pliopedia* falls well within the range of variability of *Imagotaria,* in both size and morphology. This difference, in combination with the strong differences in the skull, humerus, radius, and ulna, appears to separate *Pliopedia* from *Imagotaria.*

Because metacarpal I is not complete in the limb referred to *Dusignathus santacruzensis* (LACM 3011), it is not possible to judge whether its metacarpal proportions are more like those of *Imagotaria* or *Pliopedia.* It is to be noted, however, that the differences in relative lengths of metacarpals I and III between *Pliopedia* and *Imagotaria* are exactly those which exist between *Eumetopias* and *Odobenus.* It would appear that the relatively longer metacarpal I of *Imagotaria* indicates the sea lionlike adaptations already suggested for *Imagotaria* by such features as the dentition and tympanic membrane:oval window area ratio. Conversely, the proportionately shorter first metacarpal of *Pliopedia pacifica* would suggest more walrus-like adaptations, theoretically including dentition and ear ratio, such as are present in the type of *Dusignathus*

TABLE 12.—*Metacarpal measurements of three dusignathine genera*

Species	*Imagotaria downsi* referred (males)								*Dusignathus santacruzensis* referred				*Pliopedia pacifica,* type		
Specimens	USNM 23859[1]					USNM 23860	USNM 23861	USNM 184055	LACM 3011[2]				USNM 13627		
Greatest measurement	MC I	MC II	MC III	MC IV	MC V	MC IV	MC III	MC V	MC I	MC II	MC IV	MC V	MC I	MC II	MC III
Length	147	104	94	89	91	--	86	114	--	--	71	78	122	--	89
Proximal width	46	26	26	35	26	28	25	40	38	20	28	21	41	26	±26
Proximal height	32	35	30	31	43	25	31	50	28	24	26	34	29	39	33
Distal width	30	30	26	27	28	--	23	30	--	--	24	25	24	--	20
Distal height	25	21	20	21	23	--	18	28	--	--	19	21	23	--	17
Minimum shaft width	21	18	16	16	19	14	14	27	--	15	17	17	18	<18	15

[1] Limb.

[2] Mitchell, 1962, p. 14.

santacruzensis.

Skull (pl. 24).—A very badly weathered and fragmented braincase was discovered with the limb bones from the Etchegoin Formation which, together with one rib, make up USNM 187328. Only the dorsal part of the braincase is intact, but recovered fragments of the basicranial area include part of the right auditory bulla with the petrosal in place.

The braincase is low and rounded, strongly resembling that of *Odobenus.* No sagittal crest is present; elongate parallel grooves, presumably leading posteriorly to nutrient foramina, are present on either side of the midsagittal suture approximately at the juncture of the frontals and parietals. The occipital crest is a broad rugose area very much like *Odobenus* except that it is straighter and more transverse because of the less swollen braincase. The auditory bulla is low and rugose and has a broad surface for articulation with the basioccipital, and the carotid canal is very large, measuring 7.5 mm in diameter. The petrosal is also very similar to that of *Odobenus,* the internal acoustic meatus is very wide with almost complete separation of the facial and vestibulocochlear foramina.

Possible rear limb elements (pl. 16).—From their *Macoma* zone in the lower part of the Etchegoin Formation, Woodring, Stewart, and Richards (1940) collected a walrus fibula and phalanx (USNM 187337 and 187338, from their locality 302a). These specimens were not mentioned in their report. The fibula is most remarkable in its stoutness; its length is 26.8 cm, the greatest proximal diameter 4.8, and the greatest distal diameter 5.2 cm. Fibulae from living *Odobenus* with comparably large distal and proximal diameters have total lengths that are about twice as great.

This extreme massiveness of the pelvic limbs seems to parallel the massiveness of the humerus and radius noted for both *Dusignathus* and especially *Valenictus.* However, the fibula from the Purisima Formation at Santa Cruz, herein referred to *Dusignathus santacruzensis* because of close stratigraphic and geographic proximity to the type specimen, is of *Odobenus*-like proportions and could not be the same species as that from the Etchegoin Formation. Because the fibula (USNM 187337) is within the recorded range of *Ostrea atwoodi,* from which the second specimen (USNM 187328) of *Pliopedia pacifica* was collected, it is possible that it represents this species.

Possible synonymy.—*Pliopedia pacifica* seems to be of the same approximate age as *Dusignathus santacruzensis,* and in the Central Valley of California, *Valenictus imperialensis* seems to be only slightly younger than *Pliopedia pacifica.*

Pliopedia pacifica differs from *Dusignathus santacruzensis* by having a more elongate and straighter humerus which has the deltoid insertion on the shaft rather than on the pectoral crest, a narrow bicipital groove, and in a backward bend of the medial epicondyle. In addition, the skull of *Pliopedia* lacks a sagittal crest, which is moderately developed in *Dusignathus,* and its occipital crest is a low broad rugose area as in *Odobenus* and not the actual crest of *Dusignathus.* Other known elements are very similar, with the possible exception of the fibula.

Valenictus imperialensis, as will be discussed, is a genus and species known only from its humerus. Of all known odobenid humeri, only the humeri of *Valenictus, Pliopedia,* and *Odobenus* have the tubercle for insertion of the deltoid muscle on the lateral surface of the shaft; in all other genera, the insertion is either obscure or clearly on the lateral margin of the pectoral crest. Of all known odobenid humeri, only those of *Valenictus, Pliopedia,* and *Dusignathus* do not have a greater tubercle that is distinctly higher than the humeral head. The unique features shared between *Valenictus* and *Pliopedia* and, to a lesser extent, *Dusignathus* strongly suggest affinity between these dusignathine odobenids. When they are better known, it may be reasonable to classify all three species, which are distinct, under the senior generic name *Pliopedia.*

Genus VALENICTUS Mitchell

Plate 16

Type species.—Valenictus imperialensis Mitchell (1961); LACM (CIT) 3926, a left humerus from the Imperial Formation on the east side of Coyote Mountains, Imperial County, Calif.

DISCUSSION

The age of the Imperial Formation was considered early Pliocene by Durham (1954, p. 27); it is considered late Miocene in the usage here used. As discussed under the section "Type locality and age" of *Pliopedia pacifica,* the referred incomplete humerus of *Valenictus,* USNM 13643, is from the *Neverita* zone of the San Joaquin Formation, Kettleman Hills, Calif., and is a short distance down section from a tuff bed in the San Joaquin Formation which was dated 4.3 m.y. and up section from Hemphillian land mammals. This would suggest an age of from 5 to 6 m.y., late late Miocene or early Pliocene as used herein.

Mitchell (1961) compared the type humerus in detail with the humeri of living and fossil otarioids. His report omitted comparison with UCMP 65318 from the Purisima Formation here questionably referred to *Dusignathus,* USNM 187328 from the Etchegoin Formation here referred to *Pliopedia,* USNM 13643 from the San Joaquin Formation here referred to *Valenictus,* and MCZ 7713 from the Yorktown Formation presumably referable to *Prorosmarus.* These specimens were unknown to Mitchell at the time of his study. The odobenid affinities of *Valenictus imperialensis* were clearly defined by Mitchell.

The humerus of *Valenictus imperialensis* is as markedly distinct from that of *Prorosmarus* as it is from the odobenid humeri considered by Mitchell. Most conspicuous of its features are the distinct lateral bowing of the shaft, an extremely prominent and distally positioned medial epicondyle, a very low greater tubercle, and a very short shaft relative to the size of the head and distal structures (compare Mitchell's illustrations). In some of these features, it is similar to the humerus of *Dusignathus* from the Purisima Formation, and the two are easily separable from all other known odobenid humeri except that of *Pliopedia.*

However, the humerus of *Valenictus* is not identical to that questionably referred to *Dusignathus* (pl. 16). Although of equal length, the shaft of the humerus of *Valenictus* is thicker, the pectoral crest has an indistinct lateral margin, the deltoid insertion is marked with a prominent swollen area on the lateral side of the shaft, and the medial epicondyle is a distally located large round knoblike structure dissimilar to that known on any other odobenid humerus. The lesser tubercle is more massive on the humerus of *Valenictus,* and the bicipital groove is relatively narrower, though as deep as on the humerus of ?*Dusignathus.* In addition, the distal articulation is relatively small, having a transverse diameter about 12 percent less than that of the distal articulation on the humerus questionably referred to *Dusignathus.* Because of this small distal articulation and the very large medial epicondyle, the distal articulation of the humerus of *Valenictus* has a transverse diameter that is only about half the diameter across the epicondyles. The lateral epicondyle is notably small and inconspicuous on the humerus of *Valenictus,* the entire distal end of the bone giving the impression that the articular surface has been shifted laterally.

A close relationship between *Valenictus* and ?*Dusignathus* seems obvious, but the differences between the two humeri are much greater than those known to be a result of individual or sexual variation. In its distal structures, the humerus of *Valenictus* differs from that of *Pliopedia* (pl. 17) in the same ways that it differs from that of ?*Dusignathus.* In addition, *Pliopedia* lacks the shortening and bowing of the shaft seen in *Valenictus* and *Dusignathus,* but it does have the deltoid insertion on its shaft as in the humerus of *Valenictus,* and the humeri of the two genera have equally narrow bicipital grooves.

It is to be noted that *Dusignathus, Pliopedia, Pontolis,* and *Valenictus* are all of the same approximate age, late late Miocene and (or) early Pliocene. These facts suggest either an appreciable variety of dusignathine odobenids in the North Pacific at this time or a considerable synonymy resulting from unfortunate application of new names to specifically indeterminate specimens.

USNM 13643 (pl. 16), the distal part of a humerus, was collected by Woodring, Stewart, and Richards (1940, p. 98) in the Kettleman Hills, Calif., from their *Neverita* zone of the San Joaquin Formation. The locality was approximately 700 feet down section from their *Pecten* zone, which contains land mammals of early Blancan age [comparable to the Hagerman fauna of Idaho, radiometrically dated at 3.5 m.y. (Evernden and others, 1964)] and approximately 300 feet down section from a tuff bed dated 4.3 m.y. Woodring, Stewart, and Richards quote Remington Kellogg's comments about the fossil in which he noted the narrowness of the distal articulation and the distal position of the knoblike medial epicondyle, features known only in *Valenictus*. The lateral epicondyle, while larger than that of the holotype, is noticeably less produced than that on the humerus referred to *Dusignathus*.

The Purisima Formation of the Santa Cruz area includes deposits equivalent in age to both the Etchegoin and San Joaquin Formations of the Kettleman Hills area. Not only are they of the same age but they were also depositionally continuous (Addicott and Galehouse, 1973). The inland Etchegoin-San Joaquin sea extended northward in a valley following the San Andreas fault, a valley now occupied by the San Benito River, and left this valley in the vicinity of Santa Cruz to merge with the open ocean. In the San Benito River area, the Etchegoin Formation contained odobenid remains which were collected by C. J. Bleifus and deposited now in UCMP (UCMP 112806—proximal end of a large femur, and UCMP 112806—proximal epiphysis of a large tibia).

Southward the Etchegoin sea was connected by a second passage to the open ocean in the Santa Maria area by way of the region of Santa Margarita, where the type specimen of *Pliopedia pacifica* was found in the basal Paso Robles Formation. The overlying beds of the Paso Robles appear to be entirely continental in origin, however, and there is no known record of the inland sea connecting to the open ocean by this route during the later time that the San Joaquin Formation was deposited.

We are forced to conclude that three large odobenids of markedly different limb proportions lived during the late late Miocene and Pliocene in central California, one known from the open coast and the other two in chronologic succession from the warmer inland sea then present in the San Joaquin Valley. The younger of the two inland sea forms (*Valenictus*) must have frequented the open coast, as its type specimen is known from deposits of the ancient Gulf of California.

Genus NEOTHERIUM Kellogg

Plates 9 and 11

Type species.—Neotherium mirum Kellogg, 1931; USNM 11542, a right calcaneum which Mitchell and Tedford (1973, p. 266) have selected as the lectotype. Kellogg originally included this calcaneum and an astragalus, a cuboid, and a navicular as the hypodigm, but Mitchell and Tedford have restricted the lectotype to the calcaneum on the grounds that the original material was not necessarily associated. The lectotype and referred material are all from the Sharktooth Hill bone bed in the Round Mountain Silt, Kern County, Calif. The deposits are of the Luisian Stage (Beck, 1952) and are estimated to be about 13-14 m.y. old; early middle Miocene.

DISCUSSION

Kellogg clearly recognized the pinniped identity of the "type material" and compared it with skeletal elements from some living otariids as well as with the sympatric *Allodesmus kernensis* and his *"Pontolis* cf. *magnus"* (Kellogg, 1925b, pes from Towsley Formation). The latter is referred to *Imagotaria* sp. in the present report. Kellogg (1931, p. 302) noted that the cuboid of *Neotherium* was more like that of his *"Pontolis* cf. *magnus"* than that of any living otariid.

The lectotype calcaneum is more similar to that of *Imagotaria downsi* than it is to any other known pinniped, fossil or living. From this species it differs by being much smaller and more slender and the distal astragalar, or sustentacular, articular facet projects more medially. Most typically odobenid is the prominent internal tuberosity on the calcanear tuber. Typical of all primitive otarioids so far known, no sustentacular shelf is present, as was noted by Kellogg.

Compared with fissipeds, the calcaneum is more bearlike than otterlike in that the sustentacular articulation is very near the distal end of the bone, at the cuboid articulation. It is otarioid in that the sustentacular articulation meets and merges, over a sharp crest, with the cuboid articulation, and the calcanear tuber is quite short relative to bears and is transversely broad at the heal. The calcanear process of the astragalus, extending posteriorly from the trochlea and so greatly enlarged in the phocids, is typically otarioid in form and characteristically is much larger than in the canoid fissipeds.

The astragalus of the hypodigm also is odobenid character in its nearly vertical fibular articulation and relatively small lateral process that is alined with the lateral trochlear crest, rather than flaring outward in a distal-lateral direction. The head is transversely narrow relative to that of *Imagotaria* *downsi,* otherwise the astragalus appears to be a miniature replica of that of *Imagotaria.*

Mitchell and Tedford (1973) illustrate other limb elements from the type locality of Neotherium mirum; they suggest that these elements may belong to *Neotherium.* A navicular, LACM 4733 (their fig. 20), strongly resembles this element in Kellogg's "type material" of *Neotherium* in that the plantar process is centrally located. However, because it is about twice the size of the navicular described by Kellogg, it thus suggests sexual bimodality and that the type material is from a female individual. Mitchell and Tedford illustrate a left metacarpal IV, LACM 4360 (their fig. 21), which is a miniature of that from *Imagotaria downsi,* as are some other elements referred to *Neotherium mirum.*

An isolated right radius lacking the distal epiphysis, USNM 187377 (pl. 11), found in the Round Mountain Silt in the bed of Kelley Canyon, 3 miles north of Sharktooth Hill, by M. N. Alling in 1927, was associated with a fifth metatarsal of *Allodesmus kernensis.* This small radius, measuring 11 cm in length without correction for the missing epiphysis, is distinctly odobenid in that the pronator teres insertion is distal to the middle of the shaft. In addition the radial process at the distal termination of the anterior or radial crest is located conspicuously medial to the center of the shaft. Like other skeletal elements that presumably belong to *Neotherium,* this radius is a miniature replica of that of *Imagotaria,* differing only by being relatively less massive and one-half the size of the radius of a male *Imagotaria downsi.*

That *Neotherium mirum* is a pinniped seems certain, and the features of the few known bones, especially those of the lectotype calcaneum, all appear to be odobenid. The resemblances are greatest when compared with *Imagotaria downsi,* and it is here considered a dusignathine odobenid. However, the small size, the relatively elongate calcaneum, and the relatively small head on the astragalus all suggest a more primitive form than that represented by *Imagotaria.* It may be that it is an enaliarctid ancestor to the odobenids. Mitchell and Tedford (1973, p. 279) referred *Neotherium* to their Enaliarctinae. The discovery of the rest of the animal promises to reveal much about the unknown earlier history of the odobenids.

CLASSIFICATION OF THE WALRUSES

As herein defined, the walruses now known are classified as follows:

Family ODOBENIDAE
  Subfamily ODOBENINAE
    Genus *Aivukus* new genus
      Aivukus cedrosensis new species
        Late late Miocene, Baja California
    Genus *Prorosmarus* Berry and Gregory
      Prorosmarus alleni Berry and Gregory
        Early Pliocene, Virginia
    Genus *Alachtherium* DuBus
      Alachtherium cretsii DuBus
        Early Pliocene, Europe
      Alachtherium antverpiensis (Rutten)
        Early and late Pliocene, Europe
    Genus *Odobenus* Brisson
      Odobenus huxleyi (Lankester)
        Late Pliocene and Pleistocene, Europe and possibly the USA
      Odobenus koninckii (Van Beneden), *nomen dubium*
        Late Pliocene, Europe
      Odobenus rosmarus (Linnaeus)
        Pleistocene and living, N. Atlantic and N. Pacific
  Subfamily DUSIGNATHINAE
    Genus *Neotherium* Kellogg
      Neotherium mirum Kellogg
        Early middle Miocene, California
    Genus *Imagotaria* Mitchell
      Imagotaria downsi Mitchell
        Late middle and early late Miocene, California
    Genus *Pontolis* True
      Pontolis magnus (True), *nomen dubium*
        Late late Miocene, Oregon
    Genus *Dusignathus* Kellogg
      Dusignathus santacruzensis Kellogg
        Late late Miocene and Pliocene, California and Baja California
    Genus *Pliopedia* Kellogg
      Pliopedia pacifica Kellogg
        Late late Miocene, California
    Genus *Valenictus* Mitchell
      Valenictus imperialensis Mitchell
        Late late Miocene and Pliocene, California

SUMMARY OF THE HISTORY OF THE WALRUSES

Insofar as they are presently recognizable, the earliest known walruses are of early middle Miocene age in the North Pacific basin and of Pliocene age in the North Atlantic basin. At least by late Miocene time, the family was clearly divided into two groups; one seems to have become extinct by the end of the Pliocene; the other leads to the living walrus. Both of these subfamilies were well along the road of adaptive specialization in the late Miocene.

With the exception of the poorly known *Neotherium mirum,* which may well be the enaliarctid ancestor of the odobenids, the dusignathine genus *Imagotaria* is the most generalized genus included in the family. However, it already had a strong tendency, in the late middle and early late Miocene, toward single-rooted cheek teeth, had enlarged ear ossicles and other auditory features which today characterize the walrus, and had other peculiarities of the cranial and postcranial skeleton which clearly mark it as an odobenid.

There is very little about *Imagotaria* which precludes the supposition that it is prototypic of the stem odobenid from which both subfamilies evolved. Perhaps the feature of *Imagotaria* most objectionable to such a supposition is the development of a tympanic membrane:oval window area ratio of around 10:1, a far greater divergence from the range of ratios found in other carnivores than that present in the living walrus. From this specialization, it seems possible that so primitive a walrus as *Imagotaria* survived until approximately 9 m.y. ago by occupying the realm now occupied by the sea lions and extending its range of feeding to depths not regularly frequented by living walrus. During the temporal range of *Imagotaria,* the known otariids were small- to medium-sized animals; the earliest large-sized otariid is from the late late Miocene, as will be discussed, perhaps 8 m.y. ago. This otariid is found with the *Odobenus*-like genus *Dusignathus* in deposits from northern California to Mexico and, in the southern part of this range, with the primitive odobenine genus *Aivukus.*

The late late Miocene genus *Dusignathus,* while retaining several primitive features characterizing its subfamily, was clearly advanced in other features which suggest parallel specialization with the contemporary odobenines. In the Almejas Formation of Cedros Island, Baja California, *Dusignathus* occurs with the odobenine *Aivukus;* this fact suggests that this parallel specialization was not enough to cause a great amount of ecologic competition. It is difficult to judge whether the distinctively different cheek-tooth wear shown by these genera was caused by a difference in diet or simply resulted from the unusual geometry of the mandible of *Dusignathus.* The lack of a greatly arched palate and of lingual tooth wear in *Dusignathus* suggests that it was not a tongue-piston sucking feeder as was *Aivukus* and as is *Odobenus.*

Pliopedia pacifica was a contemporary of *Dusignathus,* but present records suggest that it was an inhabitant only of the warmer inland sea then occupying the Central Valley of California. In the Pliocene *Valenictus* inhabited both the Central Valley and Gulf of California inland seas, but there is no clear evidence that *Dusignathus* survived until so recent a time as the only records from the Purisima Formation in the Santa Cruz area are from low in the formation, a short distance stratigraphically above a 6.7-m.y. glauconite date. Only otariids more advanced than those from the Almejas Formation have been found in the upper Pliocene, part of the Purisima Formation in the Santa Cruz area, as discussed under the consideration of the otariid seals to follow.

Aivukus cedrosensis is the most primitive known odobenine. Some postcranial elements are inseparable from living *Odobenus,* whereas others are intermediate between the dusignathines and *Odobenus.* Although the skull is intermediate between the dusignathines and *Odobenus* in the loss of the posterior cheek teeth and reduction of the lower canines, the completely odobenine nature of the cheek teeth indicates a major step toward *Odobenus* from the condition of *Imagotaria.* From this, one may surmise that the odobenine odobenids were a distinct lineage at least as long ago as the early late Miocene.

Prorosmarus alleni is more advanced toward *Odobenus* than is *A. cedrosensis* by the loss of an additional posterior lower cheek tooth, further reduction of the lower canines, and enlargement of the upper canines. This species may be as much as 3 m.y. younger than *A. cedrosensis.*

It seems quite plausible that a species of *Aivukus* comparable to *A. cedrosensis,* or perhaps somewhat more similar to *Imagotaria,* was the emigrant from the North Pacific, perhaps as long ago as 9 m.y., and that the rate of odobenine evolution accelerated in the North Atlantic in the absence of the dusignathine odobenids and the otariids.

The failure of the dusignathine odobenids and of other otarioids to enter the Atlantic may be related to the southerly distribution of *Aivukus cedrosensis* in the late Miocene; possibly it was then the only otarioid whose range extended as far south as the Central American Seaway. Paradoxically, it seems to be the northerly distribution of *Odobenus* which accounts for its reentry into the Pacific during the Pleistocene without permitting the otariids access to the Atlantic.

The absence of any otariids in the North Atlantic suggests that this group, to be discussed next, did not expand their southerly distribution until after the effective closure of the Central American Seaway and after the Atlantic invasion by the odobenine odobenids. Most critical to establishing the date of this event, therefore, is the report of late Miocene or early Pliocene otariids from Sacaco, Peru (Robert Hoffstetter, written commun., 1973) and it is here presumed, on the basis of this tentative age, that the Central American Seaway was effectively closed to otariid crossing by about 5 m.y. ago. This closure could have been an ecologic barrier as easily as it could have been a land bridge; Savage (1974, p. 26) suggests strong currents through the narrowing straits although very warm waters in the shallowing straits seem a more likely barrier.

The presence of the varied late Miocene and Pliocene phocid seals of the North Atlantic (Van Beneden, 1877) would have an orienting effect on the North Atlantic odobenines toward benthonic feeding. This would explain the progressive morphology of *P. alleni* and the longer and more varied record of odobenine odobenids in younger deposits of the North Atlantic. In the odobenine record of the North Pacific, *A. cedrosensis* is succeeded only by late Pleistocene *Odobenus,* largely from Alaskan latitudes, and it is highly probable that these actually derive from the North Atlantic as no morphologically intermediate forms are known from the North Pacific region.

PART II: FUR SEALS AND SEA LIONS

Family OTARIIDAE

Genus ARCTOCEPHALUS F. Cuvier

Type species.—Phoca ursina Linnaeus [*fide* F. Cuvier, 1826] = *Arctophalus antarcticus* (Thunberg, 1811) [*fide* Allen, 1905, there being no doubt in his mind that Cuvier's description and illustration were of a South African specimen] = *Arctocephalus pusillus* (Schreber, 1776), Peters, 1877.

Diagnosis.—Fur of the forelimb extends distally past the wrist onto the dorsum of the foreflipper, and facial angle is always greater than 125° (Repenning and others, 1971, p. 3). Premolars single-rooted, molars usually retain double roots; basioccipital parallel-sided or nearly so. Dental formula

$$\frac{3I \cdot 1C \cdot 4P \cdot 2M}{2I \cdot 1C \cdot 4P \cdot 1M} \times 2 = 36.$$

Os penis transversely narrow at apex and in anterior part of shaft (Morejohn, 1975).

Included species.—Arctocephalus pusillus (Schreber): living along shores of southern Africa and southeastern Australia; late Pleistocene, South Africa (Hendey, 1974, p. 189).

Arctocephalus townsendi Merriam: living along Pacific shores of Mexico and California, late Pleistocene, San Miguel Island, Calif., (Repenning unpubl. data, 1969).

Arctocephalus gazella (Peters): living on oceanic islands in and south of the Antarctic Convergence. No fossil record.

Arctocephalus forsteri (Lesson): living on islands of southern New Zealand waters and along coast of South Australia and southern Western Australia. No fossil record although known from aboriginal sites.

Arctocephalus tropicalis (Gray): living on islands north of Antarctic Convergence. No fossil record.

Arctocephalus australis (Zimmerman): living along Atlantic and Pacific shores of South America from Brazil to Peru. No fossil record although *Arctocephalus fischeri* (Gervais and Ameghino, 1880) may belong to this species; the published description (Ameghino, 1889, p. 342–343) is not adequate for identification and the specimen is now lost (D. E. Russell, written commun., 1972).

Arctocephalus galapagoensis Heller: living in the Galapagos Islands. No fossil record.

Arctocephalus philippii (Peters): living in the Juan Fernandez Islands. No fossil record.

Genus CALLORHINUS Gray

Type species.—Phoca ursina Linnaeus, based upon Steller's *Ursus marinus* from Bering Island (Gray, 1850, p. 359).

Diagnosis.—Fur of the forelimb extends only to the wrist, where it terminates in a sharp, straight line,[3] facial angle always less than 125° (Repenning and others, 1971, p. 3). Premolars single-rooted, M^1 usually double-rooted, M^2 single- or double-rooted, and basioccipital parallel-sided or nearly so. Dental formula

$$\frac{3I \cdot 1C \cdot 4P \cdot 2M}{2I \cdot 1C \cdot 4P \cdot 1M} \times 2 = 36.$$

Ventral processes of bacular apex very broad relative to dorsal process and base flattened dorsoventrally (Morejohn, 1975).

Included species.—Callorhinus ursinus (Linnaeus): living along shores of North Pacific from southern California, to central Japan. Late Pleistocene, Seward Peninsula, Alaska (Repenning unpubl. data, 1968).

As here conceived, *Arctocephalus* is the genus most like the ancestral otariids and both the sea lions and the genus *Callorhinus* diverged from this lineage leading to *Arctocephalus.* By reason of some *Callorhinus*-like features of late late Miocene and

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[3] R. L. DeLong (written commun., 1973) has recently shown us photographs of a pup born (in 1972) on San Miguel Island, Calif., with fur extending down the flipper below the wrist in *Arctocephalus* fashion. This example is the only known exception to this most conspicuous character of *Callorhinus.* As *Arctocephalus townsendi* also frequents San Miguel Island, the possibility of a natural hybrid exists.

Pliocene otariids from California, described below, and because the earliest recognized sea lions are of late Pliocene age, it is herein suggested that *Callorhinus* diverged from the *Arctocephalus* lineage before the time of divergence of the sea lions.

A recent study of the endemic louse fauna of living sea lions, of *Arctocephalus,* and of *Callorhinus,* in combination with a study of the bacula of these living forms and of their fossil history (Kim and others, 1975) strongly supports this interpretation of the greater antiquity of the *Callorhinus* lineage.

Genus PITHANOTARIA Kellogg

Type species.—Pithanotaria starri Kellogg, 1925a.

Diagnosis.—A small genus of fur seal with M^2 missing, M^1 to P^4 diastema, double-rooted cheek teeth except P^1 and presumably P$_1$, cheek teeth simple with a sharply pointed crown having very weak internal cingula and no secondary cuspules, third (lateral) upper incisor with a distinct postero-internal cuspule rather than being simple and nearly conical as in most modern otariids. Dental formula

$$\frac{3I\cdot 1C\cdot 4P\cdot 1M}{2I\cdot 1C\cdot 4P\cdot 1 \text{ or } 2M} \times 2 = 34 \text{ or } 36.$$

Os penis unknown.

Distribution.—Known only from the late middle and early late Miocene of California, perhaps from 12 to 9 m.y. ago.

Included species.—The genus is monotypic.

Pithanotaria starri Kellogg, 1925

Plate 19

Holotype.—SU Museum No. 11, now CAS 13665, the impression of a nearly complete, somewhat crushed young individual from the late middle Miocene Sisquoc Formation 1.4 miles south of Lompoc, Calif.; in the same formation but about 5 miles west of the type locality of *Imagotaria downsi.*

Referred material.—UCMP 74813, impression of the inferior surface of a skull showing primarily the palate and one zygomatic arch with one mandibular ramus and one vertebra from the Santa Margarita Formation about 6 miles east of Seaside, Calif., locality UCMP V-6627. Collected by Keith Stafford, Piedmont, Calif., in 1964.

UCMP 26785, "Individual III" of Kellogg (1925a, p. 87-93), a cast of right and left hind limbs from the Celite Co. quarry No. 15, 2.5 miles south of Lompoc, Calif. Same formation and age as the type. The present condition of this specimen is such that much of the original detail appears to have been lost through spalling of the diatomite, although enough is still preserved to unquestionably identify it as Kellogg's specimen.

UCMP 26784, "Individual II" of Kellogg (1925a, p. 84-87), a cast of a left forelimb from the same locality as "Individual III." In its present condition, this specimen is nearly completely lost through fracturing and spalling of the diatomite. The only distinctive feature remaining is the somewhat unusually oriented lesser tubercle of the humerus noted in Kellogg's description.

UCMP 108069, a portion of a right mandibular ramus bearing P$_3$ from UCMP locality V71197, 1,900 feet south of locality M1035 along Glen Canyon Road, Santa Cruz, Calif. Santa Margarita Formation. Collected by D. P. Domning, May, 1973.

USNM 184062, left metacarpal I from USGS locality M1035, 12-15 feet south and 8 feet lower in the section than the juvenile male skull of *Imagotaria downsi,* along Glen Canyon Road, Santa Cruz, Calif., Santa Margarita Formation. Collected by G. V. Morejohn, April 1973.

USNM 184056, the proximal three-quarters of an adult humerus from the upper part of the Santa Margarita Formation, Santa Cruz area, locality USGS M1036 on the west side of Bean Creek along fence marking north boundary of Canada del Rincon en el Rio land grant in NE¼ sec. 13, T. 10 S., R. 2 W. Collected by C. A Repenning and J. C. Clark in 1965.

Diagnosis.—Only one species of the genus *Pithanotaria* is recognized at this time (1976). See diagnosis of the genus.

Type locality and age.—"No. 9 quarry of the Celite Co. [purchased by Johns Manville Corp. in the late 1920's] 1.4 miles south of the intersection of Ocean Ave. and 'C' Street, Lompoc, San Bernardino [actually Santa Barbara] County, California" (Kellogg, 1925a, p. 74). Although no other mention of a quarry No. 9 that is 1.4 miles south of Lompoc has been found in the literature, the same diatomite unit being mined at the modern Celite Co. quarries of the Johns Manville Corp., which are 1 to 2 miles farther south, is present at this locality. There seems to be no reason to suspect that the mileage was incorrect in the description of the type locality nor that the type was from the main quarries of the modern Celite Co.

The type description mentions that the specimen was found 200 feet above the base of the 1,400-ft-thick diatomite unit. Bramlette (1946, p. 212) places the Mohnian-Delmontian boundary somewhere in the lower part of the diatomite unit on the basis of Mohnian foraminifers in the underlying unit. The estimated age is 10-12 m.y., late middle or early late Miocene. John A. Barron has examined the diatoms in the matrix of the type specimen and reports that they are equivalent to Schrader's North Pacific Diatom Zone XI.

DISCUSSION

Kellogg's description of the holotype and of his two referred specimens leaves little need for additional comment. The type is an immature individual and possibly also a female, for there is no indication of an os penis although the skeleton is nearly complete and nearly completely articulated; such bones as the sternebrae and a hyoid element are preserved in approximately the normal position. As Kellogg notes, there is very little in the postcranial skeleton of this most ancient of now known otariids to separate it from the living eared seals.

From a comparison of the humerus of the type and that of the articulated forelimb UCMP 26784, which show impressions of lateral and medial sides, respectively, it appears that the humerus is relatively more slender than that of the sea lions and that the distal termination of the pectoral crest is directed toward the medial lip of the trochlea for articulation with the ulna, as in living fur seals. Relative to the size of the canine, the lateral upper incisor is distinctly smaller than that of living sea lions. To the extent that the skeletal elements of the living fur seals can be separated from those of sea lions, it appears that *Pithanotaria starri* should be considered a fur seal.

Considering the primitive nature of comparably ancient odobenids, it is surprising to see so modern-looking an otariid contemporary with them. All that separates the skull of *Pithanotaria starri* from the modern otariids are double-rooted cheek teeth and an ursine-like cingular cusp on the medial side of the lateral upper incisor; both features are not mentioned by Kellogg and are not clearly shown on the type specimen but are evident on the referred skull. Double-rooted cheek teeth, except P^1, are indicated on the type specimen, however, and though the medial side of the lateral upper incisor is not shown, the posterior broadening of the crown near its base suggests that this is a weak development of a cingulum and not a more nearly conical crown as found in modern otariids. The posteromedial cingular cusps on the lateral incisors are well shown on referred skull UCMP 74813 (pl. 19) from the Santa Margarita Formation east of Seaside, Calif., a deposit of an age presumably similar to that in which the type specimen was found.[4]

Regarding the skull of the type specimen, Kellogg indicates that the braincase is deeper than that of *Callorhinus* of comparable age and that the rostrum is relatively short and low. This description may be correct but these features are certainly not recognizable on the type specimen which, owing to crushing, shows largely the dorsal aspect of the braincase, rather than the lateral, and which shows so much crushing and distortion of the rostrum that no judgment of the height of the rostrum can be made.

At the generic level, *Pithanotaria starri* is distinguished by small size, apparently five postcanine cheek teeth in each upper tooth row rather than six as in modern fur seals, a small diastema between the upper premolars and the single molar, and by a simple cheek-tooth crown consisting of a single narrowly pointed cusp with very weak internal cingulum. Although a small genus, it is not unusually small and is roughly comparable in size with the smallest of living fur seals, *Arctocephalus galapagoensis,* assuming that the type specimen is a female. The type clearly shows five upper postcanine teeth with a small diastema between the molars and premolars. The crowns are very simple with no external cingula, and the impression of the lingual surface of the last cheek tooth on the left mandibular ramus of the holotype clearly indicates a very weak internal cingulum; the crowns are identical to those of some living species of *Arctocephalus,* particularly *A. galapagoensis, A. tropicalis,* and the more simple variation of the cheek teeth of *A. forsteri.*

It is not possible to maintain that there was no sixth postcanine (second molar) in the upper jaw of the holotype; it may have been present and lost, for at least two of the lower cheek teeth have fallen out of the right mandibular ramus and P^1 is preserved in a position half out of its alveolus. Because the type is an impression, the possible presence of an alveolus cannot be checked. However, there is no indication that the second upper molar was present on the type and it is clearly not present on referred specimen UCMP 74813. Because the lack of a second upper molar is very unusual, it is the strongest basis for generic distinction. In their review of the living fur seals Repenning, Peterson, and Hubbs (1971, p. 22) noted only one individual in all the specimens examined in which the second upper molar was missing; this was CAS 1185, a female Galapagos fur seal (pl. 19). The loss of the second upper molar is common in living sea lions.

The impression of the left mandibular ramus is present with the palate of UCMP 74813. No indication of the lower teeth is preserved. The ventral margin shows a rather sharp crest in the region of

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[4] No associated fossils are known from the Santa Margarita Formation east of Seaside, but the unit at this location represents only the lower part of the formation recognized elsewhere and intertongues with the underlying Monterey Formation (J. C. Clark, oral commun., 1973).

the digastricus insertion. This crest is formed by the lateral surface curving ventrally and medially to meet the nearly planar medial surface. Anterior to the digastricus insertion, both surfaces are curved and the ventral margin is rounded. In addition, the inferior pterygoid process beneath the lower sigmoid notch, though damaged, is shown to be notably elongate. Although elongation of this process is not visible on the lateral impression of the mandible of the type, the process can be seen to protrude posteriorly beyond the notch; preservation of the type is such that the inferior margin in the region of the digastricus insertion is not well defined.

UCMP 108069, from the Santa Margarita Formation of the Santa Cruz area, does not show the posterior mandibular structures but does show the sharp ventral margin in the region of the digastricus insertion and the rounding of the margin anteriorly. In addition, it shows a deepening of the jaw toward the symphysis beneath P_3 and the development of a similarly sharp ventral margin from this point anterior to the symphysis. The deepening of the ramus below P_3 is evident in the mandible of the type specimen. All cheek teeth of this specimen except P_1 were two-rooted, and the crown of P_3 is identical to that of the type and has a very weak and rounded lingual cingulum (pl. 19).

USNM 184056 is the proximal three-fourths of a right humerus comparable in size to a small living fur seal, though larger than that of the type of *Pithanotaria starri*; this size suggests that the type specimen may be a female. It is from the Santa Margarita Formation of the Santa Cruz area and is referred to *Pithanotaria* because of stratigraphic and geographic association. It is inseparable from the humerus of any similarly sized otariid except by a single criterion. As on the type specimen, the crest for insertion of the deltoideus muscle on the lateral side of the pectoral crest is very weakly developed, conspicuously less prominent than in any other known otariid, fossil or living.

An isolated first metacarpal, USNM 184062 (pl. 19), was collected at USGS locality M1035; it has the same proportions as that of the holotype but it is somewhat larger. Its length is 62 mm, that of the metacarpal I of the type specimen about 54 mm. The bone is from a fully mature individual, differing in this respect from the holotype. The articular surface for contact with metacarpal II, if present, is very inconspicuous, suggesting an otariid; the stratigraphic association in the area with both *Imagotaria* and *Pithanotaria,* as well as general similarity to this bone of the type, indicate assignment to *P. starri.*

The bone is remarkably dissimilar to the first metacarpal of living otariids in that it shows no flattening of the shaft. And a prominent fossa is present on the proximal dorsal surface for insertion of the extensor. In fact, its general appearance is that of a miniature metacarpal I of *Imagotaria,* it differs from it largely by lacking a prominent articulation for the second metacarpal and by having a flatter proximal articulation.

In summary, *Pithanotaria starri* is the oldest known otariid, but it is remarkably like living otariids except that the cheek teeth are double rooted and primitive structures characterize at least some of the limb bones. It is generically distinct from the living fur seals in the above features and in having lost M^2 (if this is not a variation in the individual specimen showing no M^2), and in having a cingular cusp on the anteromedial side of the I^3. It is also characterized by a P^4 to M^1 diastema, present in some living fur seals.

The loss of M^2 would seem to preclude *Pithanotaria starri* being ancestral to the living fur seals, and it may be assumed, therefore, that there were other otariids living 12-10 m.y. ago. Nearly all known records of *Pithanotaria* are stratigraphically associated with specimens of the primitive odobenid *Imagotaria downsi.*

Genus THALASSOLEON new genus

Type species.—Thalassoleon mexicanus new species.

Etymology.—Gr. *Thalassa,* the sea; and *Leon,* lion, masculine; hence, "sea lion."

Diagnosis.—A large otariid genus with short rostrum, exceedingly broad nasals, a facial angle (see Repenning and others, 1971, fig. 1) of about 150° in adult males, M_2 lost, M^2 present, all cheek teeth (except P^1) double-rooted, persistent diastema between M^1 and M^2 and a lesser and variably present diastema between P^4 and M^1, cheek tooth crowns form a single lanceolate cusp with moderate and rounded internal cingulum and no accessory cusps, trapezoidal basioccipital that is very broad posteriorly (for an otariid), coronoid process of the mandible very broad and its posterior margin not undercut, pterygoid process of the mandible is shallow with very little shelflike medial protrusion, vertebral foramen of all vertebrae small relative to living species, specifically variable primitive structures of limb elements. Dental formula:

$$\frac{3I{:}1C{:}4P{:}2M}{2I{:}1C{:}4P{:}1M} \times 2 = 36.$$

Os penis very long without forked apex, dorsal process of apex small, base flattened dorsoventrally.

Distribution.—Late late Miocene and Pliocene, Pacific coast of Baja California and California.

Included species.—Thalassoleon mexicanus n. sp., late late Miocene, Baja California. *Thalassoleon macnallyae* n. sp., late late Miocene and Pliocene, California.

Thalassoleon mexicanus new species

Plates 20–23; figure 5

Holotype.—IGCU902, adult male skull with some postcranial elements, collected from UCR locality RV-7301, about 15 feet above the base of the upper Miocene Almejas Formation, Cedros Island, Baja California, by R. H. Tedford and D. P. Whistler on August 4, 1965; field No. RHT 1273.

Etymology.—The specific name is given in appreciation of the cooperation shown by the Government of Mexico and particularly by the Instituto de Geologia, Universidad Nacional Autonoma de Mexico.

Diagnosis.—Ectotympanic ossification of the tympanic bulla lacking conspicuous medial ornamentation in mature males, fibula not fused to tibia with maturity, metatarsal I is stout and short, distance from lambdoidal crest to midpoint of frontal-parietal suture (in young individuals) more than half the distance to the anterior limits of the braincase.

Type locality and age.–From about 8 feet to about 104 feet above the base of the Almejas Formation, Cedros Island, Baja California, Mexico. By estimation, between 6 and 8 m.y. old. This material was found in stratigraphic association with both the odobenine odobenid *Aivukus cedrosensis* and the dusignathine odobenid *Dusignathus santacruzensis*. The age of this part of the Almejas Formation is more fully discussed under *Aivukus cedrosensis* n. sp. and *Thalassoleon macnallyae* n. sp.

Referred material.— Thalassoleon mexicanus is the most abundant pinniped in the UCR collection from the Almejas Formation. This collection includes 2 complete skulls, 5 shattered and/or significantly incomplete skulls, 5 skull fragments of significance to the understanding of individual and sexual variation, 25 complete or incomplete mandibular rami, 10 isolated cheek teeth, and about 300 postcranial elements. Of these, the following are considered most informative.

UCR 15252, crushed juvenile male skull collected from UCR locality RV-7302, by G. T. Jefferson in 1964 from 20-30 feet above the base of the formation; field No. Cedros 4E (pl. 22).

UCR 15253, rostrum and temporal of an adult female skull, collected from UCR locality RV-7303 by R. H. Tedford on August 9, 1965, from about 25 feet above the base of the formation; field No. RHT 1295 (pl. 22).

UCR 15251, partial adult male skull collected from field locality Cedros 4A by Jefferson in July 1964, from 20-30 feet above the base of formation.

UCR 15258, hind quarters, including the os penis, of an adult male skeleton, collected from UCR locality RV-7307 by D. P. Whistler on August 14, 1965, about 70 feet above the base of the formation; field No. RHT 1321 (pls. 21 and 23).

UCR 15254, most of two anterior limbs, vertebrae and ribs, collected from UCR locality RV-7304 by Juan Felix and Tedford, August 15, 1965, about 104 feet above the base of the formation; field No. RHT 1324 (pl. 22).

UCR 15255, fragments of skull, mandible, two anterior limbs, and vertebrae collected from UCR locality RV-7305 by Whistler on August 11, 1965, about 70 feet above the base of the formation; field No. RHT 1307.

UCR 15256, female humerus collected from UCR locality 7306 by Juan Felix and Tedford on August 11, 1965, between 40 and 60 feet above the base of the formation; field No. RHT 1322 (pl. 22).

UCR 15249, astragalus collected about 60–70 feet above the base of the formation by Whistler on August 8, 1965; field No. RHT 1288 (pl. 23).

UCR 15250, radius collected about 40 feet above the base of the formation by the UCR party; field No. RHT 1320 (pl. 22).

UCR 15257, male humerus, ulna, and distal termination of radius collected from UCR locality 7306 by Juan Felix and Tedford on August 11, 1965, between 40 and 60 feet above the base of the formation; field No. RHT 1312 (pl. 22).

DESCRIPTION OF SKULL

Thalassoleon mexicanus is equal in size to the largest of the living fur seals, *A. pusillus* from South Africa and southeastern Australia. The skull of the holotype, an old male,[5] has a condylobasal length of 272 mm; that of the referred adult male skull UCR 15251 is 259 mm in the same dimension. King (1969, p. 844) found a range of condylobasal length in 42 male skulls of *A. pusillus* (her *A. doriferus*) from 254 to 304 mm. The largest skull of all other living species of *Arctocephalus* seen by Repenning, Peterson, and Hubbs (1971, p. 23) had a condylobasal length of 268 mm. Although no complete female skull of *T. mexicanus* is known, incomplete female skull UCR 15253 is comparable in size to female skulls of *A. pusillus*.

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[5] The left upper canine was removed from the skull of the type and was found to have a nearly closed root. In addition, cementum annuli are present on the root, as on modern otariids, indicating that the individual was at least 8 years old (pl. 21). These cementum annuli and the marked sexual dimorphism suggest that intraspecific behavior patterns of *Thalassoleon mexicanus* were very similar to those of living otariids. Repenning (1976) discusses this and other aspects of the behavioral evolution of the otarioid seals.

TABLE 13.—*The skull and humerus length and proportions of mature specimens of* Thalassoleon mexicanus, Arctocephalus pusillus, *and* Arctocephalus forsteri

Species	Specimen	CBL = A (mm)	Humerus length[1] = B (mm)	B/A (percent)
A. pusillus	USGS 7008	287	234	81.5
T. mexicanus	IGCU 902 + UCR 15257 [2]	272	215	79.3
A. forsteri	USGS 7107	246	188	76.5

1. Most distal part of capitulum to most proximal part of greater tubercle.
2. Largest available male specimens but not from same individual.

Possibly of even greater significance is the similarity in size of the postcranial elements of *T. mexicanus* and *A. pusillus,* for *A. pusillus,* unlike other living fur seal species, has sea lion-like proportions in that its body is large relative to its head. As an approximation of this similarity, the condylobasal length of the skull is compared (table 13) with the greatest length of the humerus for *A. pusillus, A. forsteri,* and *T. mexicanus.* The proportions suggest that *T. mexicanus* is intermediate in this feature. Judged by the size of postcranial elements, males of *T. mexicanus* attained a weight of at least 650-700 lbs (295-318 kg).

Dorsally, the adult male skull is distinctive in its extreme development of the sagittal crest (fig. 5a), which extends anteriorly to a point about midway between the brain case and the supraorbital process (seen on two male specimens), very widely flaring nasal bones, located far to the rear such that they extend behind the anterior limits of the supraorbital processes (evident on three male skulls and the female rostrum), premaxillae whose ascending or nasal processes form essentially no part of the lateral surface of the rostrum in the region just below the termination of the nasal bones (shown on three adult male skulls, one juvenile male skull, and one adult female rostrum) but rather lie entirely within the large piriform aperture (juvenile male skull) or form broad anterior-facing surfaces on the lateral margins of the aperture (four adults), and extremely large preorbital processes (both sexes). On the juvenile male skull, the distance from the rudimentary lambdoidal crest to the parietal-frontal suture at its midline is over half the distance to the front of the brain case as determined by the squared anterior corners housing the sigmoid gyri.

In lateral aspect (fig. 5c) the skull is most distinctive in the posterior position of the nasals such that a line from the tip of the nasals to the gnathion makes an angle of 45° or less with the line of the alveolar margins of the cheek teeth. Measured by the method employed by Repenning, Peterson, and Hubbs (1971, fig. 1), the facial angle of the three adult male skulls is between 150° and 151°. In anterior aspect, the prominent preorbital ("lacrimal") processes and very broadly oval infraorbital foramina are distinctive. In ventral aspect (fig. 5b) the basioccipital is trapezoidal in form and unusually broad posteriorly compared with *Arctocephalus* and most living otariids. This bone is essentially rectangular and has parallel lateral margins in living fur seals, but comparably broad and trapezoidal basioccipital bones are present in some of the living sea lions, notably *Neophoca* and *Zalophus.* The double-rooted cheek teeth and the M^1-M^2 diastema also are distinctive in ventral aspect.

The auditory region of *T. mexicanus* is distinctively otariid. Externally the bulla is possibly more rugose than those of the average living fur seals, and it is moderately inflated but certainly within the range of variation in these features. Within the middle ear, the elongate promontorium, the very small tympanic membrane, the very small epitympanicum, and the lack of a prominence on the posterior wall (caused by the deep hyoid fossa characteristic of the odobenids) are all clearly otariid features and differ in no way from living species. Within the brain cavity (pl. 22), the apex of the petrosum has minimal enlargement, the internal acoustic meatus is essentially circular in cross section with no separation of the passages for the facial and vestibulocochlear nerves, and the prominent floccular fossa is detached from the bony tentorium, which arches distinctly above the petrosum rather than being closely appressed and fused to it. In all features the auditory region of *T. mexicanus* is clearly otariid, remarkably so for such an ancient species, and it has no differences which could separate it from that of the living otariids. No auditory ossicles have been found.

The mandible closely resembles that of living *A. pusillus* in that the coronoid processes are very broad and not undercut and overhanging along their posterior margins. (See fig. 7 in Repenning and others, 1971.) The pterygoid process, also similar to *A. pusillus,* is long and shallow and projects only slightly as a medial shelf.

Skull dimensions are given in table 14.

Although larger, the general proportions of the skull and particularly the short broad rostrum and flaring nasal bones bear a strong resemblance to the living *A. forsteri* and *A. australis.* In size and in the morphology of the mandible, *T. mexicanus* is most

FIGURE 5.—Restoration of the male skull *Thalassoleon mexicanus.* Holotype IGCU 902. *A,* Dorsal view. *B,* Ventral view. *C,* Lateral view.

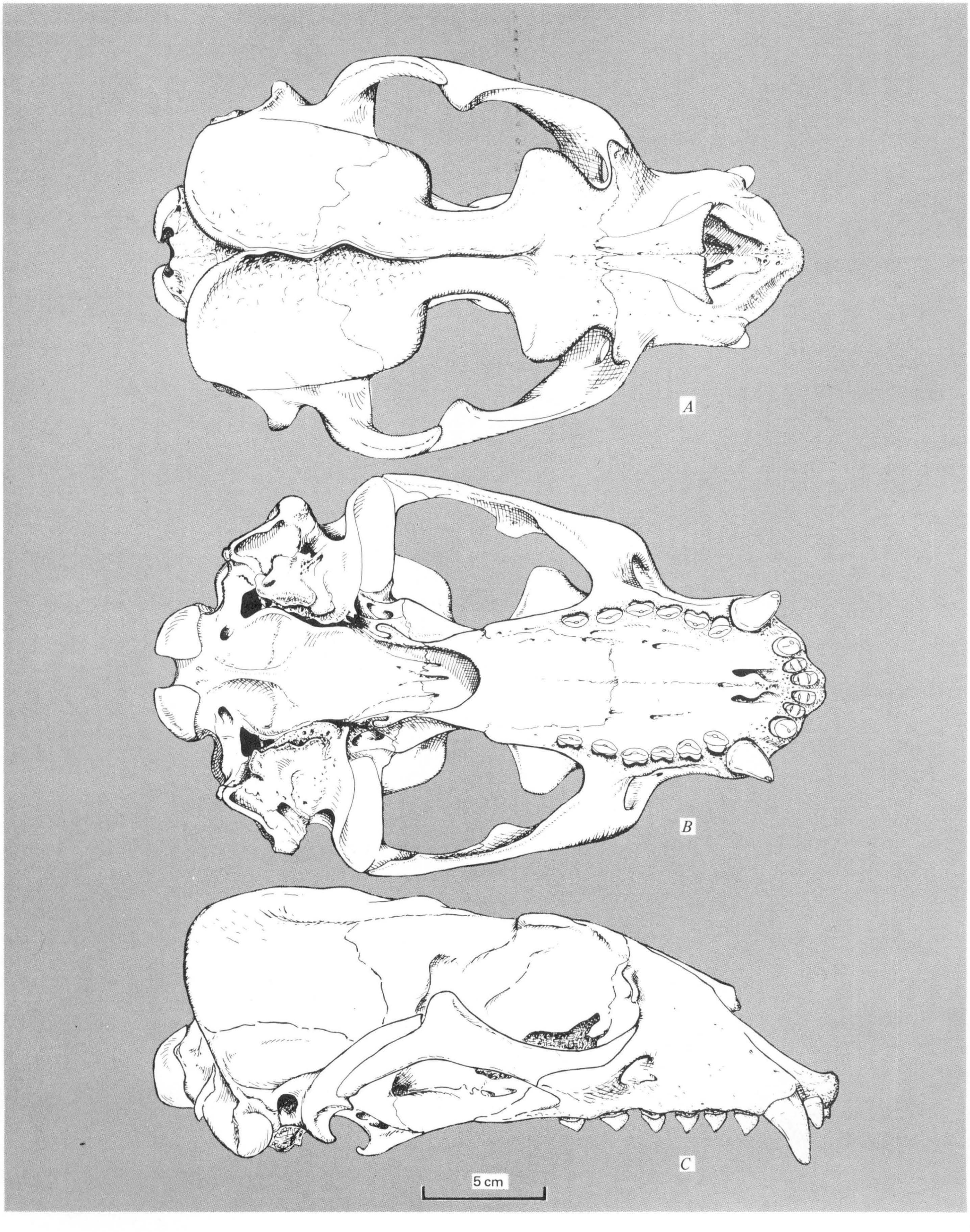
A
B
C
5 cm

TABLE 14.—*Dimensions of the skulls of* Thalassoleon mexicanus *and* Thalassoleon macnallyae

Specimen	Sex	Suture age[1]	CBL	Greatest zygomatic width	Greatest mastoid width	Width across canines	Least intra-orbital width	Nasal length	Upper row post-canines length	Greatest basi-occipital width	Upper canine alveolar diameter
T. mexicanus:											
IGCU 902 (Type)	M	36	272	167	147	69	29	44	70	51	14.5
UCR 15251	M	36	259	[3]156	[3]144	62	29-	43	64	--	14.5
HSC 310	M	[3]34	[3]267	[3]170	---	61	30	44	65	--	14.6
UCR 15252	M	[3]15	207	104	89	33	[3]32	[3]18	54	40	[2]10.0
UCR 15253	F	[3]36	---	---	---	38	--	[3]30	[3]53	--	8.5
T. macnallyae:											
UCMP 112809	M	[3] 36	---	---	134	--	-	--	--	47	----

[1] From Sivertsen, 1954.

[2] Crown only about half erupted.

[3] Approximation because of incomplete specimen.

comparable to the living *A. pusillus.* The cheek tooth crowns most resemble the living *A. philippii* and *A. townsendi.* The double-rooted premolars, very large preorbital processes, very broad infraorbital foramina, and very broad basioccipital bone are not known in the living fur seals.

DISCUSSION OF THE POSTCRANIAL SKELETON

The vertebrae of *Thalassoleon mexicanus* are very similar to those of the living otariids. The principal difference appears to relate to a lesser specialization of the venous system. With the type specimen, IGCU 902, all cervical and most thoracic vertebrae were collected. Although the last cervical and more posterior vertebrae are distorted, the other cervical vertebrae exhibit essentially no distortion, and from these, it is apparent that the vertebral foramina are small relative to that of living otariids (pl. 23). The small size is primarily expressed in the narrowness of the ventral part of each foramen. From this relation, it is presumed that the right and left vertebral sinuses of *T. mexicanus* were smaller than those of living otariids, a condition indicating a more restricted ability to remain underwater (Harrison and Kooyman, 1968, p. 240).

Four complete male scapulae from two individuals (UCR 15254 and UCR 15255) are in the collection from Cedros Island. They are basically otariid with two-thirds of the external surface occupied by the supraspinous fossa, but, unlike nearly all living otariids, they have no straight anterior or cranial border with a more or less distinct cranial angle. Instead, the cranial border and the vertebral border form one arc continuous posteriorly to the caudal angle. Further, the entire blade is less elongate, measuring about 1:1 in height from the glenoid cavity to the vertebral border relative to the length from the cranial border to the caudal angle. The difference in the *T. mexicanus* scapula would seem to indicate the lack or rudimentary development of the distinctive otariid muscle, the episubscapularis (Howell, 1929, p. 70).

Two female and six male humeri in reasonably complete condition from Cedros Island are in the UCR collection and a third female humerus is in the HSC collection. In all features except one, these are identical to the humeri of living *A. pusillus doriferus* from southeastern Australia. None of the specimens is quite as large as the largest of the humeri of the living species of comparable sex, but they are larger than any known humerus of other living species of *Arctocephalus.* On all specimens, the insertion for the deltoideus is less prominent on the fossil than on the humerus of this large living fur seal but this feature is comparable to that of other living species. The humeri are distinctly like those of living fur seals in that they are more elongate than those of the sea lions, and the pectoral crest is directed distally toward the medial lip of the trochlea.

One reasonably complete left ulna from the Almejas Formation is in the UCR collection, UCR 15257. The epiphysis of the olecranon is much less inclined posteroventrally than in living fur seal species so that its posterior process for the triceps is notably higher than the trochlear notch. In addition, the cranial or anterior surface of the olecranon, dorsal to the trochlear notch, is very narrow, and the lateral crest of this surface, for insertion of the anconeus muscle and marking the anterior limit of the dorsal part of the origin of the long pollical abductor, is positioned posteriorly such that there is considerably more relief to the dorsal margin of the lateral

TABLE 15.—*Hind limb proportions of fossil and living otariids*

Species, in order of greater CBL	A—length pelvic girdle	B—length acetabulum-ilium	C—Ischial depth[1]	D—length femur	E—length tibia	A/B	A/C	A/D	A/E
Adult males:									
E. jubata									
CBL 385	355.0	150.5	101.5	192.5	314.0	2.36	3.50	1.84	1.13
P. hookeri									
CBL 333	264.0	116.5	74.3	126.0	281.0	2.26	3.55	.08	.94
A. pusillus									
CBL 287	230.0	96.0	71.8	123.5	247.5	2.40	3.21	1.87	.93
Z. californianus									
CBL 276	239.5	95.0	74.0	126.0	257.5	2.51	3.24	1.89	.87
T. mexicanus									
CBL±270	269.5	107.5	83.5	127.0	239.0	2.52	3.22	2.11	1.12
A. forsteri									
CBL 244	204.0	85.0	58.5	99.5	212.5	2.40	3.49	2.05	.96
Young males:									
C. ursinus									
CBL 184	143.5	59.0	34.2	83.5	165.0	2.52	4.19	1.78	.90
N. cinerea									
CBL 263	217.5	90.0	61.2	109.0	208.5	2.42	3.55	2.00	1.04

[1] Ischial depth is measured from ischiatic tuberosity to ventral margin of pubis normal to this margin.

half of the trochlear notch than is found in living otariids. These features suggest that extension leverage for the triceps and possibly the anconeus was not so well developed as in living otariids, an important feature because the otariids swim primarily with their front flippers.

Four essentially complete male and two female radii are in the UCR collection from Cedros Island. Their proportions are similar to the radius of living *Eumetopias,* though smaller. From those radii of the living species of *Arctocephalus* that have been examined, the radius of *T. mexicanus* differs by being broader over its distal half because of a much more prominent radial crest. The radial crest itself arises at the pronator origin (pronator teres process of Howell, 1929, p. 32) somewhat more distally than in the living fur seals and most living sea lions, though still proximal to midshaft. As with living species of *Arctocephalus,* the extensor grooves at the distal extremity of the radius are deeper and more distinct than they are on the radii of living sea lions; this distinctness applies particularly to those extensor grooves other than the most prominent and anterior one for extensor metacarpi pollicis which lies on the lateral side of the radial crest and process.

No difference considered significant was observed in the carpals and metacarpals between *T. mexicanus* and these bones in the living species of *Arctocephalus.* It should be noted, however, that the carpals differ in detail from those of most living genera of sea lion; the sea lion carpals most similar to those of *Thalassoleon* and *Arctocephalus* are those of the genus *Zalophus.* In many features, including form of the baculum (Kim and others, 1975), the genus *Zalophus,* of all sea lion genera, is the most like the fur seals.

The pelvis of *Thalassoleon mexicanus* is proportionately very large; it is longer than the tibia (pl. 23), a condition seen only in *Eumetopias* in the living otariids (table 15). However, the other bones of the posterior limb are roughly proportional in length to those of the living otariids.

There appear to be no significant differences between the femora of *T. mexicanus* and those of the living otariids. Similarly the tibia and fibula show no distinguishing features with one exception. On each of the nine tibiae from Cedros Island in the UCR collection, there is a prominent proximal articular surface for the fibula and a comparable articular surface on the head of the three known fibula. This condition is unknown in the living otariids in which the fibula is firmly fused to the proximal end of the tibia.

The patella is typically otariid in its conical form.

There are very subtle differences between the form of the tarsals of *T. mexicanus* and those of the living otariids which appear to be distinctive. On the astragalus, the tibial articulation surface does not flare so widely nor extend as far onto the lateral process; on the plantar surface, the posterior calcaneal articular surface is much more extensive, extending nearly to the end of the lateral process. These conditions appear constant on six astragali from Cedros Island. The astragalar foramen is well

developed on all known astragali; this feature differs from those of living otariids, where it is variably developed. On the calcaneum, the posterior articular surface for the astragalus is much longer than in most living genera except *Zalophus* (which has less curvature of this surface) and *Eumetopias*. In all living genera (minimal on *Callorhinus* as noted by Robinette and Stains, 1970, p. 583), the anterior or distal articular surface for the astragalus on the medial process of the calcaneum, or sustentaculum, is smaller than the process itself and the process protrudes farther distally than the articular surface, forming what Robinette and Stains (1970, fig. 1) call the secondary shelf of the sustentaculum; this secondary shelf is essentially lacking in the 11 calcanea from Cedros Island.

Four cuboids, one navicular, one entocuneiform, and one ectocuneiform of *T. mexicanus* from Cedros Island seem to show no distinctive characters which would separate them from the living otariids. All metatarsals are represented in the collection; they are uniformly short and stout. With one exception, the metatarsals of the living otariids are at least one-third longer, proportionate to basal and shaft diameters, than those of *T. mexicanus* (pl. 23). The single exception is the sea lion genus *Neophoca* that has remarkably short metatarsals in comparison with other living otariids.

A single os penis, from specimen UCR 15258, was collected on Cedros Island. This specimen is less like this bone of any known otariid than any other skeletal element. Although measuring 162.2 mm in length, nearly twice as long as that of an adult *Arctocephalus pusillus,* it has the appearance of a juvenile in that the ventral knob of the apex projects forward as a continuation of the shaft and the dorsal knob is expressed only as a small spur (see Morejohn, 1975). The base is equally distinct; it is dorsally depressed and flattened and ends caudally in two lateral knobs. Among living otariids such dorsal-ventral flattening of the bacular base is known only in *Callorhinus*. The shaft, though nearly oval in cross section, does have a slight ventral flattening; no urethral groove is present. The entire shaft is quite narrow except near the base.

SUMMARY AND DISCUSSION

Thalassoleon mexicanus is very well represented by fossil remains from the late late Miocene of Cedros Island. The species is a very large, but otherwise primitive otariid.

Compared with living fur seals, the genus *Thalassoleon* **is characterized by the combination of very large size, short rostrum, broad and posteriorly placed nasals, double roots on all cheek teeth except the first premolars,** M^1-M^2 **diastema, trapezoidal** basioccipital that is broad posteriorly, very large preorbital ("lacrimal") processes, broadly oval infraorbital foramina, broad coronoid processes on the mandible, small size of the vertebral foramina, lack of a distinctly straight cranial border on the scapula, weaker deltoideus insertion on the humerus, weaker triceps and other extensor insertions on the olecranon of the ulna, relatively broad distal half of the radius, long innominate, minor differences in the articulation of the tarsus, notable shortness of the metatarsus, relatively large postcranial skeletal elements, and a unique os penis.

Some of these features, most presumed to be primitive, are retained in living otariid genera, most notably the genus *Eumetopias,* although the shortness of the metatarsus is found only in *Neophoca* and the posteriorly broad basioccipital is found in *Neophoca* and *Zalophus.*

The species *Thalassoleon mexicanus* is distinguished from the other known species, to be discussed next, on the basis of the combination of a lack of fusion of the fibula to the tibia, notably lesser ornamentation of the medial edge of the ectotympanic, the anterior position of the parietal-frontal suture, somewhat less metatarsal elongation, and possibly smaller vertebral foramina.

In their review of the living species of *Arctocephalus,* Repenning, Peterson, and Hubbs (1971, p. 32) suggested that most insular species may have evolved from a mainland form similar to *A. australis* and appear to have one feature in common—cheek tooth simplification. The simple cheek tooth pattern of the late late Miocene *T. mexicanus* and of the late middle Miocene *Pithanotaria starri* suggest, to the contrary, that cheek tooth complication, best seen in the living *A. australis* and *A. pusillus* in the form of well-developed anterior and posterior cingular cusps, is the advanced condition. Those living species associated with continental shores, South America, Africa, and Australia, now appear to be the most advanced of the living fur seals, and insular species, with simple cheek tooth crowns, appear to retain a primitive condition. This conclusion is in agreement with several sea lion-like features of *A. pusillus,* referred to in the review of Repenning and coworkers 1971, (p. 9 and 10).

Thalassoleon macnallyae new species
Plates 23 and 24

Holotype.—UCMP 112809, fragments of an adult male skeleton including basicranium, maxillary fragment, vertebral and costal fragments, and anterior and posterior limb elements collected from UCMP locality V66128 by Kathleen McNally, then of San Francisco State College, in the fall of 1965.

Etymology.—The species is named in honor of Kathleen McNally Martin of Fremont, Calif., who collected the type specimen.

Diagnosis.—Ectotympanic ossification of the tympanic bulla with conspicuous medial ornamentation in the form of an elevated ornate ridge as generally found on adult male *Callorhinus ursinus,* fibula fused to the tibia proximally, metatarsal I slender and somewhat elongate, possibly larger vertebral foramina than present in *T. mexicanus,* and parietal-frontal suture posteriorly located.

Type locality and age.—UCMP locality V66128; from the basal glauconite bed of the Drakes Bay Formation of Galloway (1977), 1,350 feet east of the end of the road to Drakes Beach, Point Reyes National Seashore, Calif., below high-tide level. This glauconite has been dated at 9.3±0.5 m.y., as discussed under *Aivukus cedrosensis* n. sp., and contains an odobenid questionably referred to *Dusignathus santacruzensis.* As discussed below, it seems improbable that this locality could be as old as 9.3 m.y.

Questionably referred material.—LACM 4343 is the proximal end of a right ulna from the Purisima Formation near Point Santa Cruz, Santa Cruz, Calif. (Mitchell, 1962, p. 18-20). This specimen is from the lower part of the formation as exposed in the area and is no more than 20 feet stratigraphically above the basal glauconite bed, which has been dated at 6.7 m.y. (J. D. Obradovich, written commun., 1964).

Santa Cruz City Museum specimen No. 9975.1 is the partial cranium and frontal region of an immature fur seal from the Purisima Formation near Soquel Point, City of Santa Cruz. It was collected by Gerald Macy. The deposits exposed in the Soquel Point area are stratigraphically considerably higher in the section of rocks included in the Purisima Formation than those at Point Santa Cruz.

USNM 184076 (pl. 24) is the posterior half of the skull of a juvenile from the Purisima Formation along Capitola State Beach. It was collected in 1974 by L. J. Macdonald and Steve Turner, then of Foothill College, Santa Clara County, Calif. The deposits exposed at Capitola State Beach are stratigraphically the highest known rocks included in the Purisma Formation. This locality (USGS M1241) is 1.9 miles northeast of Point Soquel. The molluscan fauna from this part of the formation is considered by W. O. Addicott (1969, fig. 2, locality 4) to be of late Pliocene age and to be correlative to the lower part of the Merced Formation of the San Francisco Peninsula. The lower part of the Merced Formation has been recognized by marine molluscan fossils beneath the continental Santa Clara Formation in the vicinity of Stanford University, Santa Clara County (Addicott, 1969), and 11 miles to the southeast of there a Blancan mammalian locality (C. A. Repenning, unpubl. data, 1973, USGS vertebrate locality M1219) occurs approximately in the middle of the Santa Clara Formation. By these extended correlations, it is judged that the upper part of the Purisima Formation, as exposed at Capitola State Beach, is of latest Hemphillian or Blancan age, and latest early Pliocene or late Pliocene.

DISCUSSION

The fragmentary specimen UCMP 112809 from the Drakes Bay Formation of Galloway is that of a male individual as large as male specimens of *T. mexicanus*; it includes the basicranial region of the skull, showing a posteriorly broad, trapezoidal basioccipital bone, a maxilla fragment showing the alveoli of a double-rooted P^4, M^1, and M^2, and an M^1 to M^2 diastema, and a mandibular fragment bearing a double-rooted P_4 with a simple crown having a moderately strong internal cingulum and the posterior root of P_3. The P_4 preserved in the mandibular fragment measures 8.40 mm in antero-posterior diameter at the crown base and is slightly smaller than the P_4 of six male individuals of *T. mexicanus* which average 9.26 mm in this measurement with a range of 8.45-9.82 mm. The mandible, however, is as massive as any from *T. mexicanus.* In these preserved parts, *T. macnallyae* differs from *T. mexicanus* only by possibly smaller cheek teeth and the greater ornamentation of the medial lip of the ectotympanic bone. These particular features are quite similar to the living genus *Callorhinus,* and it seems possible that a larger sample from Point Reyes might provide evidence for the origin of the genus *Callorhinus* out of *Thalassoleon macnallyae.* The questionably referred specimens from the Purisima Formation at Santa Cruz also strongly resemble *Callorhinus.*

In addition to the greater ornamentation of the ectotympanic, the specimen from Point Reyes differs from those from Cedros Island in that the fibula is fused proximally to the head of the tibia in both hind limbs of the specimen, as in all living otariids. All tibiae from Cedros Island show an articular surface for the fibula on their heads and none show a fusion with the fibula.

The holotype includes two fragmental vertebrae, one of the more anterior thoracics, and a lumbar vertebra. Although their incomplete preservation precludes confident assignment to a position in the vertebral series and the size of the foramen varies greatly with position in otariids, these specimens appear to have larger vertebral foramina than *T. mexicanus*. A final difference is seen in the single preserved first metatarsal of the holotype, which is identical to male first metatarsals from Cedros Island in dimensions of the base but is somewhat more slender distally and 6.5 mm (8 percent) longer (pl. 23). The larger sizes of the vertebral foramina and first metatarsal suggest that this species is somewhat more advanced than *T. mexicanus* from Cedros Island.

Questionably referred specimen LACM 4343, the proximal end of a right ulna from the Purisima Formation near Point Santa Cruz, was described by Mitchell (1962, p. 18-20). He noted that this ulna differs from those of living otariids by the narrow anterior margin of the olecranon, and, further, the epiphysis of the olecranon is much less inclined posteroventrally than in living fur seal species and many sea lion species, the conspicuous exception again being *Eumetopias*. In these features, the ulna from the Purisima Formation agrees with that of *Thalassoleon mexicanus.*

Questionably referred specimen Santa Cruz City Museum No. 9975.1, the partial cranium and frontal region of an immature individual from the Purisima Formation near Soquel Point, is distinctive in the posterior position of the parietal-frontal suture at the midline of the skull roof. The suture is less than half the distance that the front of the braincase is from the lambdoidal crest. This position greatly resembles the position of the suture in immature *Callorhinus ursinus* and differs from that of *T. mexicanus* and living *Arctocephalus*. The presence of this *Callorhinus*-like feature in *Thalassoleon* sp. from the Purisima Formation of Santa Cruz suggests a closer affinity to *T. macnallyae* from Point Reyes than to *T. mexicanus* from Cedros Island.

In the material from this locality at the Santa Cruz City Museum is a very immature left metatarsal IV noteworthy for the relative shortness of its shaft in comparison with this element of living fur seals.

USNM 184076, the posterior half of the skull of a juvenile individual from Capitola State Beach, is moderately crushed dorsoventrally. The bone was removed from the right side of the skull, revealing a well-preserved endocranial cast (pl. 24) which shows good detail except in its ventrolateral area, where the vertical crushing has confused or destroyed the detail of the major neopallial convolutions.

The parietal-frontal suture crosses the midline of the skull roof at a point which is less than half the distance that the front of the braincase is from the lambdoidal crest and the stylomastoid foramen opens widely anteroventrally as in young *Callorhinus,* rather than being partially obscured in ventral view by an underhanging lip of the bulla.

Brain casts of *Zalophus* and *Callorhinus,* prepared by W. I Welker, and endocranial casts of *Zalophus, Eumetopias, Callorhinus,* and *Arctocephalus forsteri* were available for comparison. In addition, skulls of juvenile individuals of four other species of *Arctocephalus* were available for checking the variability of some features. From the comparison possible with these specimens, it appears that the cerebrum of the fur seals is characterized by many fewer convolutions of the neopallium than that of the sea lions, a situation in agreement with the inferred primitive status of the fur seals. However, the basic pattern of sulci and gyri is the same in all otariids and is very similar to that of the bears except that the olfactory bulbs are greatly reduced and the anterior region of the cerebral hemispheres has been pushed backward, forcing the sigmoid gyri outward and downward and the coronal gyri, pseudosylvian sulci, and the posterior ectosylvian gyri into a near-vertical position.

Among the fur seals, *Callorhinus* appears distinct by having an unconvoluted and notably narrow gyrus ectosylvius posterior relative to the width of the adjacent gyrus supersylvius posterior. Dorsally, a prominent sulcus, the postcruciate, connects the longitudinal fissure to the sulcus lateralis, separating the postcruciatus and lateralis gyri, which appears to be unique to the genus. In these features of *Callorhinus,* the juvenile endocranial cast from Capitola State Beach is very similar. Although the posterior ectosylvian gyrus is broader than in three specimens of *Callorhinus,* it is relatively narrow for an otariid and distinctly less convoluted than this gyrus in available specimens of *Arctocephalus.* The dorsal aspect (pl. 24) shows a very *Callorhinus*-like postcruciate sulcus running transversely from the longitudinal fissure to the lateral sulcus.

Greater ornamentation of the ectotympanic, fusion of the fibula to the head of the tibia, elongation of the metatarsals, and enlargement of the venous sinuses all increase the resemblance of *Thalassoleon macnallyae* to living otariids and are presumed to indicate that the species was more advanced, at least in these respects, than *T. mexicanus.* The glauconite in which the type specimen of *T. macnallyae* was found has been dated at 9.3 m.y. and is associated with foraminifers believed indicative of the Delmontian Stage (Galloway, 1977). The only mollusk from this unit was identified by F. S. MacNeil as *Neptunea colmaensis* (Martin), known elsewhere only from the lower (Pliocene) part of the Merced Formation. Material questionably referred to *T. macnallyae* from the Purisima Formation at Santa Cruz is younger than a glauconite bed dated at 6.7 m.y. One referred specimen of *T. macnallyae* is from the youngest part of the Purisima in beds correlative to the lower Merced Formation. No direct dating is available for the lower part of the Almejas Formation of Cedros Island containing *T. mexicanus,* but its age is here judged to be between 6 and 8 m.y.

As mentioned in the discussion of the age of *Aivukus cedrosensis,* the dated glauconite from the Drakes Bay Formation of Galloway (1977) contained detrital biotite and may be younger than the date indicates. Also mentioned were the cetacean faunas of the Drakes Bay Formation, the Purisima Formation, and the Almejas Formation, which have a high degree of similarity at the generic level according to Lawrence G. Barnes. With the differences already noted, the pinniped faunas are equally similar. The only mollusk from the Drakes Bay Formation appears to be Pliocene, probably late Pliocene. Finally, the glauconite date of 9.3 m.y. is extremely close to the youngest age inferred for the pinniped fauna characterized by *Imagotaria downsi* and *Pithanotaria starri,* seals considerably more primitive than those from the Almejas, Purisima, and Drakes Bay Formations. It is therefore concluded that the Drakes Bay Formation of Galloway must be younger than the glauconite date indicates and that it probably is about the age of the Purisima Formation of the Santa Cruz area, between 4 and 6.7 m.y. old.

The lower part of the Almejas Formation of Cedros Island may or may not be older than the Drakes Bay Formation of Galloway, depending upon which of two interpretations of the species of *Thalassoleon* is correct. Either the two species lived at the same time along more than 1,000 miles of the Pacific Coast, the present range of the California sea lion, and the northern species was more advanced in several respects, or the modernization of *Thalassoleon macnallyae* actually represents a later historic event and *T. mexicanus* and the lower part of the Almejas Formation are older than the Drakes Bay Formation of Galloway and the Purisima Formation near Santa Cruz.

OTHER FUR SEALS

A few other fragmentary otariid fossils are known from late late Miocene and Pliocene deposits that are generically indefinable but appear to record a significant stage in otariid evolution: the first development of single-rooted cheek teeth.

This development takes place first in the most anterior cheek teeth. Although the holotype of *Thalassoleon macnallyae* is relatively complete in comparison with many types of named fossil seals, unfortunately the more anterior cheek teeth are not known. Whether the following specimens belong to this species, to other unnamed species of the genus, or should be recognized as distinct genera cannot be judged at least until the anterior cheek teeth of *T. macnallyae* are known.

Specimens from the San Diego Formation.—LACM 4323 (formerly UCLA 2282), a mandibular ramus described by Burleson (1948); LACM 16062, proximal epiphysis of a humerus; LACM 16063, an astragalus, and LACM 16064, a single-rooted cheek tooth, possibly P^2 from a somewhat larger individual. Burleson noted that the mandibular fragment matches closely a female specimen of *Callorhinus ursinus* in size, slenderness, position of the P_4 and M_1 on the dorsal crest of the dentary rather than on the medial side of the crest as in *Arctocephalus townsendi* and in tooth crown form. She suggested that the mandible is that of a fur seal intermediate between *Pithanotaria starri* and living *Callorhinus,* and she named it *Pithanotaria* sp. She did not mention what now appears to be the most significant feature of the specimen—that P_3, P_4, and M_1 are double rooted. P_2 is single rooted with a lateral sulcus on the root and is set in the ramus slightly out of alinement with the tooth row, being directed anterolaterally.

The crown of the isolated tooth, LACM 16064, is better preserved than the three present in the mandibular fragment, and in form it is identical to *C. ursinus* in that it is a simple cusp with a fairly prominent internal cingulum. The crown of the tooth is larger than those of the mandible and those of male *C. ursinus,* which do not appear to have cheek teeth noticeably larger than females. The presence of the tooth from the same (or nearly the same, see below) locality suggests that the mandible is that of a female.

The mandible differs from that of *Pithanotaria starri* by having a more rounded inferior margin in the region of the digastricus insertion and beneath P_2, in addition to having a single root on P_2. The singlerooted second premolar and small size of the teeth clearly separate this fur seal from *Thalassoleon mexicanus.* The P_2 of *T. macnallyae* is unknown.

LACM 16062, the humerus head, provides no useful information. LACM 16063, the astragalus, is identical to those of female *T. mexicanus* from Cedros Island and, except in size, to that of the type of *T. macnallyae*; it differs from the astragali of living otariids by the lesser degree of lateral-distal flaring of the tibial articular surface onto the lateral process and, on the plantar side, by the much greater extent of the posterior articular surface for the calcaneum, which extends well out toward the end of the lateral process. Though distinguishable from living otariids, this astragalus could not be separated from those of female *T. mexicanus.*

The locality of the mandible is LACM loc. 1072 and that of the other remains is questionably LACM 1073 along Reynard Way between Eagle Street and Redwood Street, San Diego, Calif. This locality is known primarily for its fossil birds (Howard, 1949, p. 180) and the question about the locality seems to be whether the material was collected on the east side of Reynard Way (LACM loc. 1072) or on the west side (LACM loc. 1073). The LACM records indicate that the specimens of questionable locality were entered into the museum on May 25, 1947; that is the same date when George P. Kanakoff, of the LACM staff, collected the localities for the bird remains described by Howard, but catalog records in the museum do not include the collector's name, only that they were from the "bird locality." UCLA 2282 (now LACM 4323) was collected on the east side of Reynard Way by C. W. Kennell (Burleson, 1948, p. 247).

This locality is a short distance from a locality where an undescribed fossil tapir was found in strata of the San Diego Formation, which E. C. Allison believed to be "probably below rocks containing *Patinopecten healeyi* and other characteristic San Diego formation marine fossils***" which may "correspond to the *Plesippus*-bearing rocks between similar marine Pliocene faunas on Soledad Mountain." (*in* Leffler, 1964, p. 58-59). The age almost certainly would be Blancan, late Pliocene, comparable in age to, or only slightly younger than, the specimen from Capitola State Beach in the youngest part of the Purisima Formation. Significantly, Howard has found the avifauna associated with the pinnipeds of the Almejas Formation of Cedros Island to be similar in composition to that associated with the fossil otariid of the San Diego Formation "but in no instance are the species the same" (Howard, 1971, p. 14-15). The avian fauna thus is evidence permissive of the conclusion that the pinniped bearing strata of the Almejas Formation are older than the San Diego Formation and the younger part of the Purisima Formation.

Specimen from the Etchegoin Formation.—USNM 184065 is the anterior part of a mandibular ramus collected by J. R. Macdonald and Kent Krispin at USGS locality M1220, about 50 feet below the *Pseudocardium* bed of the Etchegoin Formation exposed in North Dome of the Kettleman Hills, Kings County, Calif. This locality is in the same approximate part of the formation as the locality in which *Pliopedia pacifica* was found, possibly 5-6 m.y. old. This specimen is larger and more robust than that from the San Diego Formation. While not so robust a jaw as that of a male *Callorhinus ursinus,* the length of the tooth row alveoli from the anterior surface of the canine to the midpoint of P_4 is well within the range of living male *Callorhinus.* P_4 was distinctly two-rooted, P_3 was two-rooted for at least two-thirds of the root length, although the separating alveolar septum was broken out during preparation, and P_2 was single-rooted and was oriented out of alinement with the tooth row, being directed anterolateral. The only tooth present is the canine; it has a distinct trefoil cross section of the root near the base of the crown produced by prominent posterior and lateral sulci; such a lower canine is very typical of male *C. ursinus.* The mandibular fragment, however, is much less massive than that of the holotype of *T. macnallyae* (obviously a male) and somewhat more massive than the known mandibles of female specimens of *T. mexicanus.*

This mandibular fragment was found about 30 feet above the *Siphonalia* zone of Woodring, Stewart, and Richards (1940) from which these workers report (p. 98) a Hemphillian-age horse tooth and about 1,290 feet down section from the Blancan mammalian fauna of their *Pecten* zone of the San Joaquin Formation. This fossil was roughly contemporaneous with the older late late Miocene part of the Purisima Formation in the Santa Cruz area. However, if the specimen is a fragment of a male individual, it is of an individual smaller than any fur seal yet discovered in the Purisima.

FOSSIL SEA LIONS

Earlier it was stated that certain features of *Pithanotaria starri,* from the late middle Miocene, suggested that this species and genus was not directly ancestral to the living fur seals. As small size is herein considered a primitive condition of the Otariidae, the large size of *Thalassoleon mexicanus* suggests that this late late Miocene genus might already have evolved in the direction toward the sea lions to a point beyond that from which most living fur seals could be derived. Both of these suggestions imply the possible existence of other middle and late Miocene and Pliocene otariids as yet unknown. This possibility, in combination with the scarcity of fossil sea lions, hinders interpretation of the origin of the sea lions. The development of modern sea lions out of the fur seals would appear to have taken place in the late

Pliocene or more recently, an interpretation supported by the endemic louse fauna on the living otariids and by the otariid bacular forms, as well as the present fossil record (Kim and others, 1975).

In the section on "Suprageneric diagnoses" it was stated that loss of abundant underfur, increase in body size, increase in rate of development of single-rooted cheek teeth, and beginning of the reduction in the number of upper molars were the principal criteria whereby the divergence of the sea lions from the fur seal lineage might be recognized. The first, loss of abundant underfur, is not recognizable in the fossil record; the rest are qualitative, particularly because *Thalassoleon mexicanus* is a large fur seal. Along the Pacific coast of North America, the oldest known otariid with any single-rooted cheek tooth other than the first premolars is a small form resembling *Callorhinus* of late late Miocene age, and the oldest known otariids of large size and morphologically comparable to the living sea lion genera are from beds containing land mammals of Irvingtonian (early Pleistocene) age. From late Pleistocene deposits, a number of fossil otariids have been recovered along the west coast of North America, in Japan, and in the western South Pacific which rather clearly belong to extant species. On the whole, Pleistocene records are few and very incomplete.

Pliocene record.—"Allodesmus(?)" sp. of Kaseno (1951) = "*Eumetopias* sp. cf. *E. jubata*" of Shikama (1953, p. 11) = "*Eumetopias* sp.?" of Mitchell (1968, p. 1882); this specimen is a very large and massive mandibular ramus with unusual teeth from the Omma Formation of Ishikawa Prefecture, Japan. Ikebe, Takayanagi, Chiji, and Chinzei (1972, fig. 2) consider this formation as being roughly between 2.5 and 3.5 m.y. old (late Pliocene as here used).

Nirei (1969) has discussed the age of the Omma in more detail and believes that the Pliocene-Pleistocene temporal boundary is to be found within it, probably within its upper half (personal communication to Kiyotaka Chinzei). As Kaseno's specimen came from near the middle of the Omma Formation, it would appear to be very near that boundary or about 2 m.y. old, and probably somewhat younger than the fur seal from the San Diego Formation.

Because of its large size and advanced root fusion, this specimen is a good candidate for a very early sea lion. The cheek teeth all have fused roots except for M_1, which retains a two-rooted condition over half the root length. This clearly represents a greater rate of development of single-rooted cheek teeth than is exhibited by the San Diego fossil if their geologic ages are comparable. The cusp of the cheek tooth crown, though pointed, is notably low, and the base of the crown is somewhat larger than in living *Eumetopias*. As with all otariids younger than *Pithanotaria,* but not all odobenids or desmatophocids, only one molar is present in the lower dentition.

Kaseno's *Eumetopias* sp. from the Omma Formation is the only sea lion described in publication that may be as old as latest Pliocene. In the eastern Pacific a single femur, now in the University of California Museum of Paleontology, from deposits at Capitola, California (D. Domning, oral commun., 1975), may represent a similarly ancient large sea lion. The femur is very large, is between 4 and 3 million years old, and was found in association with the ancestors of the Alaskan fur seal.

Early Pleistocene record.—Leffler (1964) has described a large isolated otariid tooth, evidently a lower cheek tooth judged by the length and straightness of the root, from the Elk River Formation of Cape Blanco, Oreg. He compared this tooth with those of living *Zalophus* and *Eumetopias,* noting greater similarity in structure to *Zalophus* and in size to *Eumetopias.* Packard (1974a) has described an otariid radius from the uppermost unit of the underlying Port Orford Formation of Baldwin (1945)[6] of the same approximate area which he felt was most similar to *Eumetopias.* An immature otariid radius (USNM 184057), lacking both epiphyses, was recently found by R. J. Janda in the same area in the *Clinocardium*-bearing pebble and cobble gravel of the Port Orford Formation; this radius also is most similar to *Eumetopias* in size, distal broadness, and relatively distal position of the pronator teres process. In addition, a nearly complete skull (USNM 187108) and left mandibular ramus (USNM 187109) are known from the Port Orford Formation. The specimens appear to represent an extinct species of the genus *Eumetopias* (C. E. Ray, written commun., 1975).

The *Clinocardium* beds of the Port Orford Formation have been considered to be of about the same age as deposits in Humboldt County, Calif., known as the "Moonstone Beach" locality (Allison and others, 1962); here a number of postcranial bones similar to those of living *Eumetopias jubata* have been found. The specimens, which are in the Geology Department, Humboldt State College, catalogued under locality 205, consist of a proximal phalanx of the first digit of the manus, a scapholunar, and a metacarpal III. This material, though long considered middle to late Pliocene in age, was found associated with a scaphoid from a large species of *Mammuthus,* also in

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[6] Formational nomenclature for this section is currently in a state of flux. Most investigators agree that there is little difference in age between what is here called the Elk River Formation and the underlying Port Orford Formation.

the collection in Humboldt State College. This scaphoid indicates that the deposit is at least as young as early Pleistocene.

A picture comparable to that of the Pacific coast of North America is found in Japan. A few early Pleistocene specimens are known which have been assigned to extinct species of living genera including *Eumetopias watasei* Matsumoto (1925), part of a rostrum, and *Zalophus kimitsensis* Matsumoto (1939), fragment of a mandible. These two were considered to be of Calabrian (early Pleistocene) age by Matsumoto, coeval with his *Paralephas protomammonteus* zones. Teilhard de Chardin and Leroy (1942, p. 55) consider this species of mammoth to be of post-Villafranchian Pleistocene age, probably early Pleistocene as used herein. Shikama and Takayasu (1971) indicate that *Z. kimitsensis* is of this ("Günz-Mindelian") age and state that it cannot be separated from the living species. Mitchell (1968, p. 1881-1883) questioned the specific distinction of *Z. kimitsensis* from living *Zalophus californianus* and was unable to recognize *E. watasei* as any living otariid species; accordingly, he placed the specimen assigned to *E. watasei* in a new genus as *Oriensarctos watasei* (Matsumoto). Admittedly the specimen differs from known specimens of the living species, but it is hardly complete enough to dismiss the possibility that it is an extinct species of the genus *Eumetopias*.

Eumetopias(?) *kishidae* Shikama (1953) = *Zalophus californianus* of Mitchell (1968, p. 1882); it is a very *Zalophus*-like rostrum of uncertain provenance, but reportedly is from Pleistocene deposits of Tokyo. The specimen has a single-rooted P^2; the more posterior teeth are lost. More recently Shikama and Takayasu (1971) have described a fragmentary mandible from the Shibikawa Formation of the Oga Peninsula under the name of the living species, *Zalophus lobatus* (= *Z. californianus japonicus*). They state that these beds are about 2.2 m.y. old, which, in the usage of the present report, is close to the temporal limit between late Pliocene and early Pleistocene; all teeth appear to be single-rooted.

It appears that *Zalophus kimitsensis* of Matsumoto from the early Pleistocene and *Zalophus lobatus* of Shikama and Takayasu from the late Pliocene or early Pleistocene of Japan are indistinguishable from the living (or recently extinct) *Zalophus californianus japonicus*. This suggests that the evolution of at least one living species took place earlier in Japan than along the eastern North Pacific shores. Both specimens, however, are mandibular fragments and may not be specifically identifiable. Further evidence from the early Pleistocene of both western United States and Japan would be most useful.

Late Pleistocene record.—A number of published and unpublished records of late Pleistocene sea lions are known from North America all of which appear to represent the living species *Eumetopias jubata* and *Zalophus californianus*. In the South Pacific the Ohope Skull from the late Pleistocene (Castlecliffian) deposits near Whakatane, New Zealand, was described in manuscript as an extinct species of *Neophoca* by J. A. Berry (Fleming, 1968, p. 1185). However, most late Pleistocene records around the margins of both North and South Pacific oceans appear to represent living species of sea lions.

Arctocephalus caninus Berry (1928) from North Island, New Zealand, reported to be of Pliocene age (Fleming, 1968), is now recognized to be *Phocarctos hookeri* (Berry and King, 1970) and to be less than 1,000 years old (Weston and others, 1973). *Arctocephalus williamsi* McCoy (1877) from the mouth of Melbourne harbor, originally described as of Pliocene age, has long been known to be *Neophoca cinerea* (Allen, 1880, p. 770; King, 1964, p. 129) and seems to be of late Pleistocene age (Gill, 1968)

CLASSIFICATION OF FUR SEALS AND SEA LIONS

As herein defined, the otariid seals now known are classified as follows:

Family OTARIIDAE
  Genus *Pithanotaria* Kellogg
    Pithanotaria starri Kellogg
      Late middle and early late Miocene, California
  Genus *Thalassoleon* new genus
    Thalassoleon mexicanus new species
      Late late Miocene, Baja California
    Thalassoleon macnallyae new species
      Late late Miocene and Pliocene, California
  Genus *Arctocephalus* F. Cuvier
    Arctocephalus pusillus (Schreber)
      Late Pleistocene, South Africa; historic, South Africa and southeastern Australia
    Arctocephalus gazella (Peters)
      Historic, subantarctic islands of Atlantic and Indian Oceans
    Arctocephalus forsteri (Lesson)
      Historic and pre-historic, southern New Zealand and Australia
    Arctocephalus tropicalis (Gray)
      Historic, islands of South Atlantic and southern Indian Oceans

    Arctocephalus australis (Zimmermann)
      Historic, Atlantic and Pacific shores of South America, roughly south of lat 15° S.
    Arctocephalus galapagoensis Heller
      Historic, Galapagos Islands

Arctocephalus philippii (Peters)
Historic, Juan Fernandez Islands
Arctocephalus townsendi Merriam
(?)Early Pleistocene, California (J. Firby, oral commun., 1972); late Pleistocene, California; historic, Pacific coast of North America from about lat 20° N. northward to Point Conception, California
Genus *Callorhinus* Gray
cf. *Callorhinus ursinus* but retaining two roots on most teeth
Late late Miocene and Pliocene, California
Callorhinus ursinus (Linnaeus)
Late Pleistocene, Alaska; historic, circum-North Pacific north of about lat 33° N.
Genus *Phocarctos* Peters
Phocarctos hookeri (Gray)
Historic, New Zealand region
Genus *Neophoca* Gray
Neophoca sp.
Late Pleistocene, New Zealand (Fleming, 1968, p. 1185)
Neophoca cinerea (Peron)
Late Pleistocene and historic, Australia (including *Arctocephalus williamsi* McCoy)
Genus *Otaria* Peron
Otaria byronia (Blainville)
Late Pleistocene, Argentina (Ameghino, 1889, p. 343); historic, Atlantic and Pacific shores of South America south of about lat 10° S.
Genus *Zalophus* Gill
Zalophus kimitsensis Matsumoto, nomen dubium
Early Pleistocene, Japan
Zalophus californianus (Lesson)
Possibly early Pleistocene, Japan; late Pleistocene and historic, eastern and western North Pacific shores between lats 20° and 45° N. Historic, Galapagos Islands
Genus *Eumetopias* Gill
Eumetopias sp.
Latest Pliocene or earliest Pleistocene, Japan; early Pleistocene, Oregon and California
Eumetopias jubata (Schreber)
Late Pleistocene and Holocene, circum-North Pacific north of about lat 33° N.
?Otariid, incertae sedis
Genus *Oriensarctos* Mitchell
Oriensarctos watasei (Matsumoto)
Early Pleistocene, Japan

SUMMARY OF THE HISTORY OF FUR SEALS AND SEA LIONS

The earliest known otariids, insofar as they are recognizable at the present time, appear to have been small fur seals of late middle Miocene age (*Pithanotaria*). The lineage leading to modern *Callorhinus* appears to have diverged from the main otariid line by late late Miocene time. The sea lions appear, on the basis of a meager fossil record, to have evolved from the *Arctocephalus* lineage in the later Pliocene of earliest Pleistocene in the North Pacific Ocean, possibly the western North Pacific.

The wider distribution of the fur seals in the southern hemisphere, in comparison with sea lions, seems to suggest an earlier crossing of the equator. However, the total absence of otariid seals in the North Atlantic suggest that both must have crossed the equator after effective (for pinnipeds) closure of the Central American Seaway; this closure may have occurred in late late Miocene time—5-6 m.y. ago (Repenning and others, in press). Robert Hoffstetter reports (written commun., 1973) rare otariid remains in the Miocene or Pliocene deposits (about 5 m.y. ago) of Sacaco, Peru. The Central American Seaway appears to have been the avenue of introduction of the monachine phocid seals to the Pacific (Hendey, 1972) and of the sirenian genus *Hallianasa,* found in association with *Pithanotaria* in the California area in late middle and early late Miocene deposits.

It therefore is suggested that the fur seals originated in the North Pacific and dispersed into the South Pacific at a late date, probably late late Miocene time, and that the development of the sea lions out of the fur seals in late Pliocene and early Pleistocene time was either shortly followed by their dispersal to the southern hemisphere, before the late Pleistocene when living genera and species are known in both hemispheres, or was an event which took place independently in both northern and southern hemispheres from the already endemic fur seals. Contradicting the latter possibility is the evidence of the endemic lice found on living sea lions of both northern and southern hemispheres (Kim and others, 1975).

Except for the late appearance of the sea lions, the fossil history of the otariid seals is remarkably simple when compared with that of the walruses. All that seems to separate the earliest known members of the family from the living species are such minor features as double-rooted cheek teeth, plainer crowns on the cheek teeth, broader basioccipital bones, smaller vertebral foramina, unfused fibula, and minor differences in muscular attachments, articular patterns, and proportions of the limbs. Many of these differences slightly increase the similarity of these earlier otariids to the walruses, but the increase is slight and the oldest known otariid, *Pithanotaria,* is clearly an otariid. There obviously is a considerable history of the pre-late middle Miocene Otariidae that is yet unknown.

PART III: DESMATOPHOCIDS, ENALIARCTIDS, AND FAUNAS

Family DESMATOPHOCIDAE

As indicated in the introductory section, "Suprageneric Diagnoses," the desmatophocid otarioid seals are distinguished by several features; the more conspicuous are: lack of supraorbital processes, nasals penetrating the frontals, posterolaterally projecting jugular processes of the exoccipital, moderately broad basioccipital widening posteriorly, posteriorly very broad and flat palate, mortised jugal-squamosal articulation, and the development in some of single-rooted cheek teeth very early in the known history of the otarioid seals.

In the genus *Allodesmus* there is minimal enlargement of the petrosal apex, wide separation of passages for the vestibulocochlear and facial nerves on the medial surface of the petrosal, a broad, shallow hypophyseal fossa, rather small tympanic membrane, and large ossicles. These features are either not known or not described in the genus *Desmatophoca*.

As noted in the original description of *Desmatophoca*, and in its name (Condon, 1906, p. 13), the desmatophocid seals are phocidlike in a number of features, though clearly otarioid in most. In addition to characters unique to this family such as the distinctive jugular process, they possess features found in the odobenids, as the lack of supraorbital processes, and in the otarioids, as the narrow basioccipital bone.

Only two genera are currently included in the Desmatophocidae. Mitchell has variously placed these genera, *Desmatophoca* and *Allodesmus*, in either the same subfamily (1966, p. 40; Subfamily Desmatophocinae of the Family Otariidae—in the sense here used) or in separate subfamilies (1968, p. 1897; Subfamilies Desmatophocinae and Allodesminae of the Family Otariidae—in the sense of Otarioidea as here used). Barnes (1972, p. 61), in a recent review, placed *Desmatophoca* and *Allodesmus* in the Subfamily Desmatophocinae of the Family Otariidae—in the sense of Otarioidea as here used. This grouping is followed here, and the group is given familial status, equivalent in morphologic and phylogenetic distinctiveness to the Otariidae and Odobenidae.

Genus DESMATOPHOCA Condon

Type species.—Desmatophoca oregonensis Condon, 1906.

Diagnosis.—A large desmatophocid with double-rooted cheek teeth, well-developed internal cingulum on the cheek teeth, incisive foramina large for a desmatophocid, mortising of the jugal-squamosal articulation weak, orbits relatively small for known desmatophocids, about 17 percent of the CBL. Dental formula:

$$\frac{3I:1M:4P:2M}{2I:1C:4P:1M} \times 2 = 36$$

Os penis unknown.

Included species.—Desmatophoca oregonensis Condon. Known only from the late early Miocene Astoria Formation of coastal Oregon (Saucesian and Relizian Stages or more likely only Saucesian according to Snavely, Rau, and Wagner, 1964, estimated age about 15-16 m.y.). Packard (1974b) has described a humerus assigned to this species, and a number of unstudied specimens from the type area are in the collection of the National Museum of Natural History.

An otarioid rib, University of Alaska Department of Geology No. UA 2420, may belong to an individual of the genus *Desmatophoca*. The rib was found in Astoria-equivalent deposits of the Narrow Cape Formation on Kodiak Island and is characterized by a large head and tubercle and by a more elongate neck than known from otariid seals. The head, however, is not so swollen as those known for *Allodesmus* (Mitchell, 1966, pl. 13).

Desmatophocine A of Barnes (1972, p. 55) from the upper part of the Santa Margarita Formation of the Santa Cruz area, California, is part of a mandible that bears a strong resemblance to that of *Desmatophoca oregonensis*. The specimen was collected higher in the section than some remains of *Imagotaria downsi*. Similarities to *Desmatophoca oregonensis* include a transversely compressed canine and doubly rooted P_2 and P_3, as well as other desmatophocid characters mentioned by Barnes. The specimen is somewhat smaller than the mandible of the type of *Desmatophoca oregonensis*, but it could well equal in size the mandible of a female individual if the type is a male. Its more recent geologic age and more nearly coalesced cheek-tooth roots suggest that it may be an unknown species, possibly assignable to the genus *Desmatophoca*.

Genus ALLODESMUS Kellogg

Type species.—Allodesmus kernensis Kellogg, 1922.

Diagnosis.—Large to small desmatophocids "***with crowns of teeth bulbous and smooth; lingual cingulum of cheek teeth reduced and smooth***," (quotes from Barnes, 1972, p. 5), incisive foramina very reduced, mortising of the jugal-squamosal articulation greatly expanded, orbits very large relative to *Desmatophoca,* between 20 and 25 percent of the CBL. Dental formula:

$$\frac{3I \cdot 1C \cdot 4P \cdot 2M}{2I \cdot 1C \cdot 4P \cdot 1M} \times 2 = 36$$

Os penis (of *A. kernensis*) recurved as in *Odobenus,* circular in cross section except for slight ventral flattening, one ventral and one larger and slightly bilobed dorsal process on the apex (Barnes, 1972, p. 34).

Included species.—Allodesmus kernensis Kellogg, 1922 (including *Allodesmus kelloggi* Mitchell, 1966, following Barnes, 1972): very large species with "***premaxillae expanded into prenarial shelf*** premolars deep rooted with single bilobed root; ventral margin of dentary concave dorsally***" (extracted from Barnes, 1972, p. 6). See Mitchell (1966) and Barnes (1970 and 1972) for more details.

This species is known entirely, or almost entirely, from early middle Miocene deposits (Luisian Stage according to Beck, 1952, estimated age about 13-14 m.y.) near Bakersfield, Calif. Mitchell (1966, p. 25 and 26) lists some specimens from other sites in southern California of questionable specific assignment.

Mr. and Mrs. Martin R. Sorenson have collected an isolated cheek tooth, USNM 184058, from the Santa Margarita Formation of the Santa Cruz area which greatly resembles those of *Allodesmus kernensis.* This locality (UCMP V5555), an active sand quarry where most fossil material is found after slumping down the cut face, is difficult to assign to a stratigraphic horizon. However, the fauna found thus far includes *Desmostylus, Paleoparadoxia,* and *Hipparion,* genera which elsewhere in the area characterize the older part of the Santa Margarita Formation. It is therefore believed that *Allodesmus* sp. cf. *A. kernensis* from UCMP V 5555 is from strata older than local records of *Imagotaria downsi, Pithanotaria starri,* and "Desmatophocine A" of Barnes.

Mitchell (1968, p. 1881) has assigned *Eumetopias sinanoensis* Nagao (1941) to *Allodesmus kernensis.* Although the Japanese specimen is of near record size and very robust, particularly in the size of the cheek teeth, this generic assignment certainly appears to be correct. Without additional information, it is questionable whether specific synonymy can be demonstrated. The specimen is from middle Miocene rocks in Nagano Prefecture and indicates the extent of the former range of this genus.

Allodesmus courseni (Downs, 1956): a small species lacking a prominent prenarial shelf, with double-rooted cheek teeth, and lacking a dorsally concave inferior margin of the mandible. For more details see Downs (1956) and Barnes (1972, p. 39-40). The type specimen was collected from early middle Miocene (Luisian) deposits in Los Angeles County, Calif.

In the National Museum of Natural History there is a cast of a Japanese fossil skull (USNM 24915) questionably referable to *Allodesmus courseni* (pl. 9). According to Tokio Shikama (written commun., 1967), the specimen was probably destroyed during World War II; it "was found in late 19th century and stored in a shrine of Utsunomiya***The formation north of Utsunomiya (area of Hachimanyama) is middle Miocene Kanomata-zawa formation." Shikama also states that the matrix, according to Dr. J. Suzuki, who purchased the specimen from the shrine in 1927, was a green tuff containing Tertiary mollusks.

From the cast, the specimen measured 23.9 cm from the anterior tip of the rostrum to the most posterior part of the backward-projecting lambdoidal crest (comparable to a CBL of 27.7 cm for the type of *Allodesmus courseni*). The cast shows a very low sagittal crest, narrow interorbital area with no supraorbital process, a somewhat procumbent canine and greatly enlarged third incisor, and one cheek tooth with bulbous and smooth crown. Although it appears to have a better developed prenarial shelf than *A. courseni,* the shelf is not so accentuated as in *A. kernensis.*

Allodesmus packardi Barnes, 1972: a medium-sized (or large, as Barnes suggests that the type may be a female individual) species with broad skull, apparently with reduced prenarial shelf, single-rooted cheek teeth with marked anterolateral orientation, palate very broad with widely diverging cheek tooth rows. For more details see Barnes (1972). The type and only specimen is from early middle Miocene deposits in Menlo Park, Calif. A femur (USNM 23881) from the same formation and same general area may belong to this species; it is relatively more elongate but otherwise identical to the femur of *Allodesmus kernensis* as described by Mitchell (1966, p. 16 and pl. 20).

Barnes (1972) has described, as Desmatophocine B and Desmatophocine C, two additional partial mandibles which differ from known mandibles of named species, but which are not adequate for definition of a new species. Desmatophocine B is questionably and

Desmatophocine C certainly from the middle Miocene rocks from which *Allodesmus kernensis* is known. For further discussion see the report by Barnes (1972).

CLASSIFICATION OF THE DESMATOPHOCIDS

Only two desmatophocid genera are currently recognized; one *Desmatophoca,* is monospecific. Following Barnes (1972), except that the group is retained as a distinct family, they are here classified as follows:

Family DESMATOPHOCIDAE
  Genus *Desmatophoca* Condon
    Desmatophoca oregonensis Condon
      Late early Miocene, Oregon and Alaska(?) (rib)
    ?Desmatophocine A of Barnes
      Early late Miocene, California
  Genus *Allodesmus* Kellogg
    Allodesmus kernensis Kellogg
      Early and late(?) middle Miocene, California
    Allodesmus sinanoensis (Nagao)
      Early middle Miocene, Japan
    Allodesmus courseni (Downs)
      Early middle Miocene, California, ?Japan (Utsunomiya shrine)
    Allodesmus packardi Barnes
      Early middle Miocene, California
  Desmatophocid incertae sedis
    ?Desmatophocine B of Barnes
      Early(?) middle Miocene, California
    Desmatophocine C of Barnes
      Early middle Miocene, California

DISCUSSION OF THE DESMATOPHOCIDS

From approximately 16 m.y. ago to possibly 9 m.y. ago, there seems to have been a variety of desmatophocids in all the coastal waters of the North Pacific Ocean. Although the variety is not large, most species now known show extremely high specialization compared with the contemporary primitive otariids (*Pithanotaria*) and odobenids (*Neotherium* and *Imagotaria*).

Unlike the odobenids and the otariids, the desmatophocids seem to have appeared rather abruptly in the late early Miocene, to have acquired full diversification by early middle Miocene, and to be quite rare in the late Miocene. There are no younger records. At present the record appears to be insufficient to attempt any phylogenetic interpretation. By reason of its somewhat greater age and less specialized skull, however, *Desmatophoca oregonensis* may be assumed to approximate the ancestral desmatophocid from which *Allodesmus* evolved.

Mitchell (1968, p. 1888 [lines 6, 7, 12–14] and fig. 16) considered *Desmatophoca* an approximation of the ancestral form for all otarioids (his "otariids"), but Barnes (1972, p. 62) rejects this suggestion on the grounds that the genus is far too specialized, a rejection with which we are in agreement. The familial characters of the Desmatophocidae, as outlined in the introductory section of the present report, are much too distinctive and specialized even to suggest that the very different odobenids and otariids could have been derived from this family. Mitchell (1968, p. 1888 [lines 9, 10, 14–17]) seems inclined to agree with this. Moreover, Mitchell and Tedford (1973) have recently documented an ancestral group from which all otarioid families could have been derived.

Family ENALIARCTIDAE

Mitchell and Tedford (1973) have erected the Enaliarctidae (their subfamily Enaliarctinae) to include otarioid (their otariid) pinnipeds of hemicyonine ursid derivation which, because of their primitive structure, cannot be assigned to other otarioid families. Although they strongly favored the interpretation that *Enaliarctos mealsi,* or a closely related member of the same family, was ancestral to some of the otarioids (p. 278), they expressed strong reservations about the derivation of the desmatophocids from the enaliarctids, specifically stating that *E. mealsi* was not ancestral to *Desmatophoca oregonensis* (p. 254).

In terms of the characters adopted in this paper for diagnosis of the Desmatophocidae, most, perhaps, represent conditions theoretically derivable from the more primitive (that is, more canoidlike) features of *Enaliarctos.* Few of the derived features that characterize the Desmatophocidae are possessed or hinted at in *Enaliarctos mealsi.* On the other hand, as Mitchell and Tedford had concluded, the observable cranial features of *E. mealsi* do agree well with those displayed by the Otariidae, as seen by comparing the family diagnoses presented herein (see section on "Suprageneric Diagnoses"). Other features such as the shape of the auditory bullae, presence of a tensor tympani fossa, and carnassial cheek teeth are clearly arctoid characters retained in *Enaliarctos* that emphasize the primitive nature of this genus.

In sum total, it cannot be fairly argued that the close resemblance of *Enaliarctos* to the otariids rules out relationship of other unknown members of the Enaliarctidae with other otarioid families. The lack of derived characters typical of specific otarioid families only reinforces the morphologically central position of *Enaliarctos mealsi.*

Although the geologically younger *Neotherium mirum* is here considered a primitive odobenid, as discussed, morphologic data are not yet available to debate the stand that it was not an enaliarctid greatly advanced over the condition of *E. mealsi* toward the odobenids. There is no doubt that other enaliarctids existed which more closely resemble the Otariidae and Desmatophocidae as these are recognizable in unstudied material in the National Museum of Natural History. Therefore, it is here maintained, in the absence of contradictory evidence, that the enaliarctids are an ideal group from which all other otarioid families, Desmatophocidae, Otariidae, and Odobenidae, could easily have been derived.

The enaliarctids are characterized as a group distinct from the other known otarioids by the combination of the following conspicuous features: lack of supraorbital processes, nasals penetrating the frontals, ursidlike mastoid and jugular processes, narrow basioccipital, unspecialized jugal-squamosal articulation, inflated and flask-shaped bullae, fissipedlike tensor tympani muscle, and hemicyoninelike dentition. Mitchell and Tedford enumerate the pinnipedlike features that distinguish this group from contemporary hemicyonine ursids.

Genus ENALIARCTOS Mitchell and Tedford

Type species.—Enaliarctos mealsi Mitchell and Tedford, 1973.

Diagnosis.—At present only the genotypic species has been described and generic and specific diagnoses necessarily follow the familial diagnosis (see section on "Suprageneric Diagnoses"). For details see Mitchell and Tedford (1973, p. 218).

Included species.—Enaliarctos mealsi Mitchell and Tedford, from early Miocene deposits on Pyramid Hill, Kern County, Calif. The deposits are believed to be about at the temporal limit separating the Zemorrian and Saucesian Stages (Beck, 1952) and are approximately 22.5 m.y. old (Turner, 1970, p. 101). This age is early early Miocene; in fact, Berggren (1972) would place this age at the Oligocene-Miocene boundary. It is evident that a considerable record of otarioid evolution is still unknown between 22 and 16 m.y. ago.

This species was described on the basis of two skulls, a braincase, and some isolated teeth, including lower carnassials associated with *E. mealsi* on the basis of their occlusal relations with the corresponding upper teeth. The lower jaw, anterior cheek teeth, and the postcranial skeleton are unknown. Mitchell and Tedford (1973, p. 272-275) illustrate and discuss the pinniped and limb axial elements in the L. E. Wilson collection at Yale University. These remains, obtained near Woody in the Kern River district, constitute part of the Woody local fauna and were collected from the outcrops of the Pyramid Hill Sand Member of the Jewett Sand at that locality. In Mitchell and Tedford's (1973, p. 275) view, this local fauna is only slightly younger than the Pyramid Hill local fauna, which includes the type of *E. mealsi*. The importance of the fragmentary Woody pinniped fauna lies in its indication that more than one kind of pinniped was in existence in early Miocene time. Knowledge of the exact nature of these pinnipeds will have to await further evidence from the Pyramid Hill Sand Member or other contemporaneous deposits, but limbs of appropriate size for association with *Enaliarctos* are present along with specimens of larger forms attributed by Wilson to the desmatophocid *Allodesmus*. If these identifications are correct (the latter doubted by Mitchell, 1966, p. 20), stocks ancestral to the enaliarctids and desmatophocids may already have diverged from a common ancestor prior to early Miocene time.

FAUNAS

The Neogene record of the otarioid pinnipeds, though far from complete, is sufficiently well known to recognize lineages and to specify the general composition of faunas during different temporal intervals. Some suggestion of latitudinal ranges in the North Pacific Ocean is evident as well as the approximate times of dispersal to the southern hemisphere by the otariids and to the Atlantic by the odobenids. To this time (1977), the desmatophocids and the enaliarctids are known only from the North Pacific.

In the faunal record of the North Pacific basin, there are two major gaps. The longest, just mentioned, is that between *Enaliarctos mealsi* of about 22 m.y. age and *Desmatophoca oregonensis* of about 16 m.y. age. Within this time span, or possibly earlier, evolution of the enaliarctids into the desmatophocids and possibly the odobenids took place. Further information regarding otarioid evolution during the interval between 22 and 16 m.y. ago will be most rewarding.

The second major gap, that between 5 and about 2 m.y. ago, clouds the history of the Otariidae between *Thalassoleon* spp. and the early Pleistocene otariids apparently assignable to extinct species of living genera. At the present time, only the fragmentary remains from the San Diego and Purisima Formations and the mandibular ramus, *Eumetopias* sp., described by Kaseno (1951), are known during this time span. Kim, Repenning, and Morejohn (1975) have suggested that divergence of the lineage leading to *Callorhinus* may be of greater antiquity than that leading to the living sea lions because of species differentiation in the sucking lice endemic on modern otariids and because of bacular morphology. *Callorhinus*-like features of *Thalassoleon macnallyae* and of the fragmentary late late Miocene and Pliocene specimens here discussed may record the beginnings of this early differentiation, but the major features of this history, yet to be discovered, must lie in this second major gap.

In generalized outline, the desmatophocids, odobenids, and otariids all experienced three major stages in their evolution but at distinctly different times in each lineage. The first, which is not yet documented in any lineage, consists of the evolution of homodont dentition out of the heterodont, fissiped-like dentition of the enaliarctids. This first stage appears to be the most reasonable criterion for future separation of advanced enaliarctids from the most primitive members of the three derived otarioid families.

The second major evolutionary stage is the evolution of single-rooted cheek teeth, presumably in response to simplification of crown pattern. In the desmatophocids, this stage was achieved in some species of *Allodesmus* 13–14 m.y. ago. In the odobenids, the oldest genus in which the dentition is known, *Imagotaria,* appears to have such variation in the presence of double-rooted or single-rooted cheek teeth that it seems reasonable to suppose that the single-rooted stage was achieved in this odobenid about 9 m.y. ago; all younger odobenids have single-rooted cheek teeth. In the more slowly evolving otariids, some single-rooted cheek teeth are not known before about 5 m.y. ago; all cheek teeth were not single-rooted in any form before 3 m.y. ago; and living fur seals, as well as some sea lions, still retain some posterior cheek teeth having double roots.

The third major evolutionary stage of the otarioids is best called diversification. This stage seems to follow shortly upon the development of single-rooted cheek teeth and shortly follows the extinction of the preceding diverse family. While only one species of *Desmatophoca,* with double-rooted cheek teeth, is known about 16 m.y. ago, one or two million years later three species of *Allodesmus* and "Desmatophocine B" of Barnes had evolved. All of these had rather distinct specializations of the head, three had single-rooted cheek teeth, and two appear to have dispersed around the North Pacific to Japan. In one to two more million years, 11-12 m.y. ago, the supremacy of the desmatophocids appears to have come to an end, and undiversified but more abundant odobenids (*Imagotaria)* and otariids (*Pithanotaria*) are found in the same deposits as the last known remains of *Allodesmus* and possibly *Desmatophoca* ("Desmatophocine A" of Barnes).

Geographic distribution and ecologic restriction of the several desmatophocids of the middle Miocene are not clearly evident in the present record. Although many or all seem to have lived at the same time in various parts of California, in general, only one species is found at one locality. It seems evident that *Allodesmus kernensis* and Desmatophocine "B" of Barnes lived in the inland Temblor Sea of the southern San Joaquin Valley, as no specifically identifiable specimens have been found outside this area. *Allodesmus packardi* and *Allodesmus courseni* seem to have lived along the open coast, possibly with latitudinal differences in ranges. Both *A. courseni*? and *A. sinanoensis* are represented in Japan, indicating that the genus was widespread in the North Pacific.

Although the otariids remain undiversified, all later odobenids from possibly 8 to about 4 m.y. ago have single-rooted cheek teeth and are diverse. Two subfamilies are recognizable during this time interval, the Odobeninae and the Dusignathinae; the genera *Aivukus, Dusignathus, Pliopedia,* and *Valenictus* and the problematical *Pontolis* are known from the North Pacific. The odobenids seem to have been quite abundant; they are known from south of the Tropic of Cancer (*Aivukus*) to almost 45° N. lat (*Pontolis*). However, the present record suggests that the odobenines, at this time, were distributed more southerly than the dusignathines because the odobinines are not certainly known north of 29° N. lat while the dusignathines are not known south of this latitude. Before 5 m.y. ago, the odobenines succeeded in invading the North Atlantic, and, because of their southerly distribution, it seems most probable that they did so by the Central American Seaway. Failure of contemporary otariids to invade the Atlantic suggests that they had a more northerly distribution than the odobenines, comparable to that of the dusignathine odobenids.

Within the Dusignathinae, the poorly known genus *Pliopedia* may have been coeval with the genus *Dusignathus* for 1 or 2 m.y., between 5–7 m.y. ago. *Pliopedia* seems to have preferred the warmer waters of the then existing inland sea of central California. From at least 5 to possibly 8 m.y., *Dusignathus* inhabited the waters of the open coast at least from lat 38° N. to 28° N. Depending upon the correct age of the Drakes Bay Formation, the youngest record of *Dusignathus* may be the type specimen, something less than 6.7 m.y. In the central Californian sea, *Pliopedia* is succeeded by *Valenictus* whose age is more than 4.3 m.y. *Valenictus* is also known in the Imperial Valley of California in deposits of the ancient Gulf of California, and it may be that this poorly known genus gained access between these two inland seas by occupying the open coast environment vacated by *Dusignathus.* Thus part of the Imperial Formation may be only 4-6 m.y. old.

As mentioned, single-rooted cheek teeth (other than the first premolar) are not known in the Otariidae until about 5 m.y. ago. A separate lineage leading to living *Callorhinus* may have been established at this time, and the fur seals seem to have dispersed south of the equator shortly thereafter. However, it seems evident that major diversification of the otariids began about three million years ago and that the diversity of the living fur seals and particularly the living sea lions represents the same sort of diversity seen in the odobenids from 6-9 m.y. ago and in the desmatophocids from 13-14 m.y. ago.

In summary (fig. 6), the Neogene pinniped faunas of the Pacific coast of North America have, or can be expected to have, the following composition:

Oligocene (pre-22.5 m.y. B.P.).—Published record: None. Undoubtedly the enaliarctids were present in the Oligocene (following Berrgren's usage of this time term), but judged by the cranial features of *Enaliarctos mealsi,* without evidence of the nature of their feet or flippers, it may be difficult to decide whether they are fissipeds or otarioid pinnipeds. At this time, it seems most reasonable to separate the Enaliarctidae from the hemicyonine ursids at that point where they become obviously aquatic in habit.

Early early Miocene (about 22.5-17 m.y. B.P.).—Published record: *Enaliarctos mealsi* from the beginning of this time. This species shows greatest similarities to the Otariidae or, conversely, the Otariidae show the least modification of the features of this primitive type of otariioid. It is to be expected that other early Miocene enaliarctids, some already known but unstudied, will show features indicating evolution toward the other two otarioid families. Because of its complete homodonty in the late early Miocene, *Desmatophoca* suggests that the enaliarctine-desmatophocine transition took place in the early early Miocene or before; this suggestion is corroborated by the postcranial elements from the early early Miocene Woody local fauna, as pointed out by Mitchell and Tedford (1973, p. 274).

The only described enaliarctid is associated with land mammals believed to indicate a late Arikareean age and with mollusks of the "Vaqueros Stage" (Mitchell and Tedford, 1973).

Late early Miocene (about 17-14.5 m.y. B.P.).—Published record: *Desmatophoca oregonensis* from Oregon and probably Alaska. It is probable that early forms of *Allodesmus,* resembling *A. courseni,* also evolved in this period because of the high degree of specialization of other species known from the early middle Miocene. Though poorly known, the primitive nature of the few known bones of the early middle Miocene odobenid *Neotherium* suggests that there were enaliarctids in the late early Miocene immediately ancestral to the odobenids, unless *Neotherium* itself proves to be such an enaliarctid. The complete homodonty, loss of the upper second molar, and general otariid appearance of the late middle Miocene *Pithanotaria* suggests that a considerable gap separates it from the immediate enaliarctid ancestor of otariids. Hence, such an ancestor may also have lived during the late early Miocene, and in fact such forms are already recognizable in unstudied specimens in the National Museum of Natural History.

From near the type locality of *Desmatophoca oregonensis,* as nearly as it can be determined, a relatively large rhinoceros maxilla has been collected which is tentatively assigned to the genus *Aphelops* and appears to be identical to specimens from Mascall-equivalent beds in southeastern Oregon. The specimen is now in the National Museum of Natural History (USNM 187123). A Barstovian land mammal age, possibly early Barstovian, is indicated. Megainvertebrate and microinvertebrate faunal control, which is excellent, indicates that "Temblor" and Saucesian Stages are represented.

Early middle Miocene (about 14.5-13 m.y. B.P.).—Record: *Allodesmus packardi, Allodesmus courseni, Allodesmus kernensis,* "desmatophocine B" and "C" of Barnes, and *Neotherium mirum,* all from California but also two *Allodesmus* records from Japan. If *Neotherium* does not prove to be an enaliarctid, the enaliarctids may be extinct by this time except that there is no known record of an otariid from this time interval, so the enaliarctid immediately ancestral to the otariids may have been of this age.

The renowned Sharktooth Hill locality of Kern County, Calif., is the most productive of marine mammals of this age. *Allodesmus kernensis, Neotherium mirum,* "desmatophocine C" of Barnes, and presumably "desmatophocine B" of Barnes are known from this locality. A few land mammals have been found in this locality (listed by Mitchell, 1966, p. 29); they are of Barstovian age. The fossil beds are closely tied into the late "Temblor" megainvertebrate stage and the Luisian microinvertebrate stage.

Late middle and early late Miocene (about 13-8.5 m.y. B.P.).—Record: *Imagotaria downsi, Pithanotaria starri, ?Allodesmus* sp., and *?Desmatophoca*

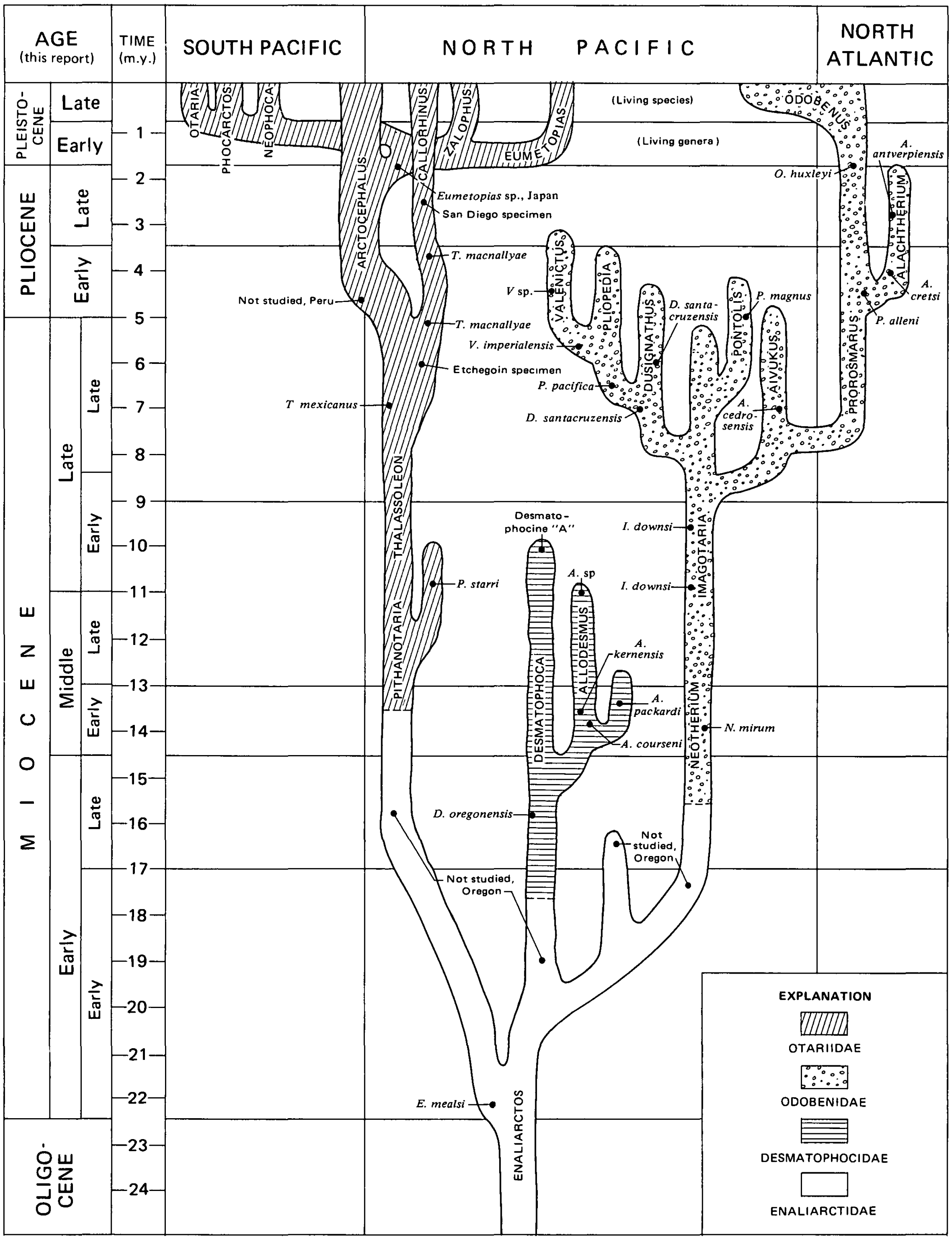

FIGURE 6.—Phylogenetic diagram of the Otarioidea.

sp. ("desmatophocine A" of Barnes). The primitive odobenid and otariid seem to have been fairly common seals in California, but the two questionably assigned desmatophocids are represented by only one record each.

Hendey (1972) has suggested that the monachine phocids entered the North Pacific through the Central American Seaway at this time, although there is no conclusive fossil evidence as yet known. Repenning and Ray (1977) give reasons for believing that this happened at an earlier date.

As nearly as available correlations indicate, this otarioid fauna seems to correlate closely with the Clarendonian land mammal age and with the "Margaritan" and earlier "Jacalitos" megainvertebrate stages. The association of *Imagotaria* with *Pithanotaria* is remarkably persistent. Records from the inland sea area in the southern San Joaquin Valley do not include *Pithanotaria,* however, and thus they offer a very weak suggestion that this primitive fur seal may have preferred the cooler waters of the open sea.

There exists at present considerable doubt about the temporal extent of this fauna into the late Miocene. The very large sample from the Santa Margarita Formation of the Santa Cruz area is at least largely, and possibly entirely, from rocks containing invertebrates of the "Jacalitos" stage and thus the fauna is presumably younger than 10 or 11 m.y. In contrast, the fossil pinnipeds from Point Reyes, Calif., represents the next younger fauna, which is distinctly different than that containing *Imagotaria* and *Pithanotaria.* This fauna from Point Reyes has been directly dated, however, at 9.3 m.y. As discussed, the pinnipeds, the cetaceans, and the only mollusk known from the Drakes Bay Formation of Galloway at Point Reyes all suggest a considerably younger age than the radiometric date seems to indicate. In the present report, the pinniped fauna from Point Reyes is considered as being late late Miocene or Pliocene, possibly no older than 6 m.y. and possibly as young as 4 m.y.

Late late Miocene and early Pliocene (about 8.5-about 3.8 m.y. B.P.).—Record: *Thalassoleon mexicanus, Thalassoleon macnallyae, Aivukus cedrosensis, Dusignathus santacruzensis, Valenictus imperialensis, Pontolis magnus, Pliopedia pacifica,* and a poorly known fur seal possibly representing the lineage leading to *Callorhinus.*

Both latitudinal and environmental differentiation of faunas seems to be apparent during this time. The only Tertiary odobenine odobenid of the Pacific, *Aivukus,* seems to have been restricted to southern latitudes from Cedros Island southward at least to the Tropic of Cancer. The dusignathine *Dusignathus* extended its range from Cedros Island northward to at least Point Reyes, and the dusignathine *Pontolis* may have represented still another faunal differentiate from Oregon. The warm inland seas seem to have been favored by the dusignathine genera *Pliopedia* and *Valenictus* over the latitudinal range of *Dusignathus.* The two species of *Thalassoleon* seem to have been either separated on a north-south basis or the northern species represented a somewhat later and more advanced species (contrary to the radiometric date of the Drakes Bay Formation of Galloway). Within the northern of the two then existing interior seas, the San Joaquin-Etchegoin sea, the otariids are represented by a single mandibular fragment of a small fur seal which may represent the beginning of the *Callorhinus* lineage.

Toward the end the early Pliocene, *Prorosmarus alleni* is known from the Atlantic coast of North America, but the history of the odobenines of the North Pacific largely began and ended in the late Miocene; *Dusignathus* and *Pliopedia* may have lived until the beginning of the Pliocene, and *Valenictus* may have survived until the late Pliocene.

According to Robert Hoffstetter (written commun., 1973), late Miocene or early Pliocene collections from Sacaco, southern Peru, contain a few remains provisionally identified as postcranial elements of an otariid. From this it would appear that the otariids first dispersed to the South Pacific Ocean about 5 m.y. ago, presumably of the *Thalassoleon* stage of evolution.

Late Pliocene (about 3.8-1.8 m.y. B.P.).—Record: a small fur seal from the San Diego Formation, resembling *Callorhinus* but with a primitive astragalus and some teeth still double rooted, probably "*Allodesmus* sp." of Kaseno (1951) from Japan, which seems to be the earliest record of the sea lion stage of otariid evolution. The San Diego specimen could be the same species as that known from the late late Miocene of the Etchegoin Formation, and if it is, shows little difference and a slow rate of evolution in what is presumed to be the early stages of the lineage leading to modern *Callorhinus.* On the other hand, the Japanese sea lion described by Kaseno and currently included in the genus *Eumetopias* shows a comparatively sudden development of single-rooted cheek teeth and of large size, both features considered to be characteristic of the sea lions.

The late Pliocene history of the otarioid seals is obviously very incomplete. There is no record of any odobenid, and it is reasonable to suspect that this ancient, abundant, and diversified family became extinct in the North Pacific. Also from rocks of late Pliocene age, 5,000 feet below the top of the Yakataga Formation in the Malaspina District of Alaska, is the oldest record of a phocoid seal in the North Pacific (Repenning and others, in press), a phocine radius of very modern aspect (USNM 23876, pl. 16), most similar to that of *Pusa sibirica* among the radii of living phocids.

Early Pleistocene (about 1.8-0.7 m.y. B.P.).—Early Pleistocene records consist largely, but not entirely, of postcranial elements from California, Oregon, and Japan, which are, in contrast to the San Diego fossil, indistinguishable from living genera; however, a few specimens of dentition and one undescribed skull from North America indicate extinct species. Mitchell (1968) has placed a partial rostrum from Japan in an extinct genus, *Oriensarctos*. Very limited, but quite indicative, terrestrial mammals are associated with these early Pleistocene otarioids which indicate this age but, in North America, these mammals do not exclude a younger age.

Although there are no early Pleistocene records in the Southern Hemisphere, the presence of the living species of the three southern sea lion genera in the late Pleistocene of Australia, New Zealand, and Argentina suggests that they had evolved in place for some time. As the earliest known sea lion seems to be only about 2 m.y. old, it is assumed that southern dispersal was in the early Pleistocene. The possibility that southern and northern sea lion genera evolved independently, each in its own hemisphere, from the then native fur seals seems to be ruled out by the nature of their endemic sucking lice; both northern and southern sea lions are host to the same endemic species of louse, a species not known from any other host, including the northern and southern fur seals (Kim and others, 1975).

Late Pleistocene (about 0.7-0.01 m.y. B.P.).—Late Pleistocene records also are fragmentary but are known from California, Oregon, Alaska, and Japan. Many records, particularly in Alaska, are associated with terrestrial mammals. Only living otariid species are known; the oldest North Pacific record of *Odobenus rosmarus* is a humerus (USNM 184059) dug from a fossil beach ridge of the Pelukian (Sangamon) transgression 5-6 miles up the Kokolik River northeast of Point Lay, Alaska. Because of the lack of any record of an odobenine odobenid in the North Pacific between the late late Miocene and the late Pleistocene, it is presumed that *Odobenus* entered the North Pacific at this time from the North Atlantic. As presently known, the late Pleistocene record of otarioid seals is identical to that of today except for changes of ranges associated with glaciation and the influence of man.

By late Pleistocene time the fur seals had crossed the South Atlantic and are known from South Africa; presumably they had already established their present circumpolar distribution. In addition, the fossil record of *Otaria* from Argentina would indicate that this sea lion had entered the western South Atlantic, but the southern distribution of the sea lions has not enlarged since that time, and they still are basically animals of the North and South Pacific.

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PLATES 1–24

[Contact photographs of the plates in this report are available, at cost, from U.S. Geological Survey Library, Federal Center, Denver, Colorado 80225]

PLATE 1

[Abbreviations: OW—oval window. RW—round window. P—promontorium. A—apex. F—floccular fossa. V—vestibulocochlear canal. FN—facial canal. ICM—internal acoustic meatus]

FIGURES 1,3,6,7,10. *Aivukus cedrosensis* n. gen. and n. sp.

Holotype, IGCU901. Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico.

1. Palatal view of skull, ×0.73.
3. Right metacarpal I, dorsal view, ×0.50.
6. Right petrosum, ventral view, ×1.
7. Right petrosum, medial view, ×1.
10. Left third upper incisor, posterior view showing cementum coat and two wear facets, ×1.0.

2,4,5. *Odobenus rosmarus* (Linnaeus).

Recent.

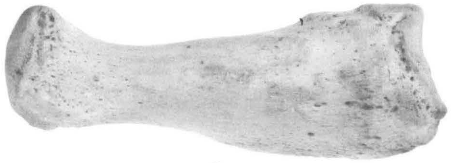
2. Female right metacarpal I, dorsal view, ×0.50; for comparison.
4. Male right petrosum, ventral view, ×1; for comparison.
5. Same, medial view.

8,9. *Neophoca cinerea* (Peron).

Recent.

8. Male right petrosum, ventral view, ×1; for comparison.
9. Same, medial view.

1



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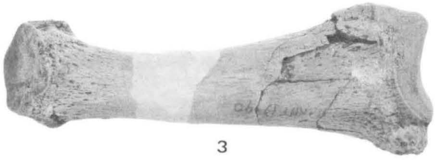

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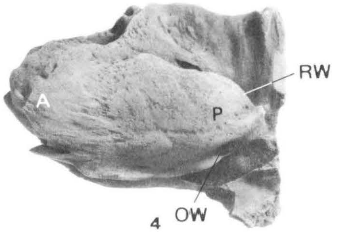

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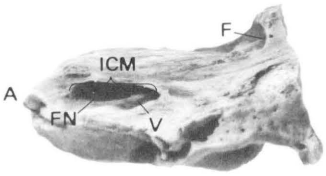

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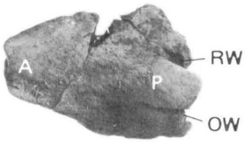

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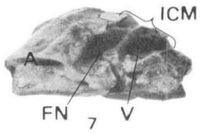

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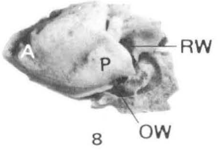

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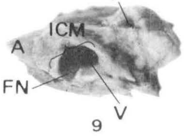

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AIVUKUS, ODOBENUS, NEOPHOCA

PLATE 2

[Abbreviations: A—articular surface for cuneiform. B—articular pit for magnum. C—canine tooth. D—radial crest. E—radial process. PT—insertion for pronator teres on the proximal end of the radial crest]

FIGURES 1-3, 5, 7, 9-11. ***Aivukus cedrosensis* n. gen. and n. sp.**

Holotype, IGCU901. **Late Miocene,** lower part of the Almejas Formation, Cedros Island, Mexico.

1. Right side of skull, ×0.66.
2. Fragments of left mandibular ramus, medial view, ×0.66.
3. Same, occlusal view.
5. Distal half of right radius, lateral view, ×0.31.
7. Distal three-quarters of right ulna, lateral view, ×0.31.
9. Right scapholunar, ulnar view, ×0.45.
10. Right scapholunar, proximal view, ×0.45.
11. Right scapholunar, distal view, ×0.45.

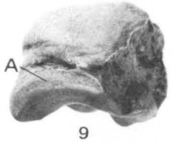
4. *Prorosmarus alleni* Gregory and Berry.

Holotype, USNM 9343. Pliocene, Yorktown Formation, Yorktown, Va. Left mandibular ramus, cast of type, medial view, ×0.50.

6, 8. *Odobenus rosmarus* (Linnaeus).

Recent.

6. Right female radius, ×0.31; for comparison.
8. Right female ulna, ×0.31; for comparison.



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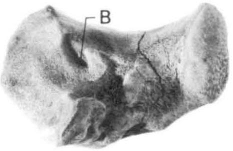

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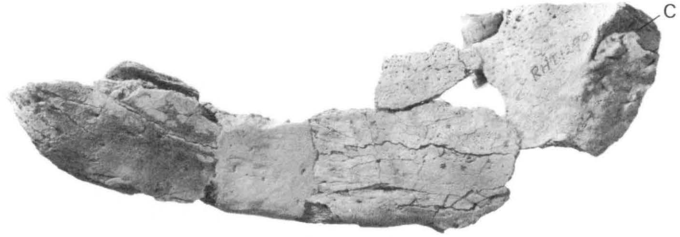

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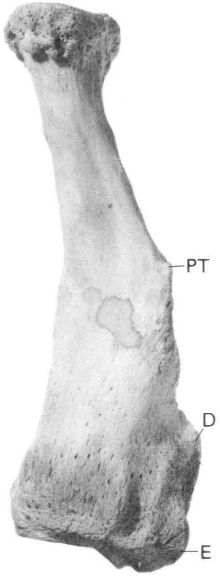

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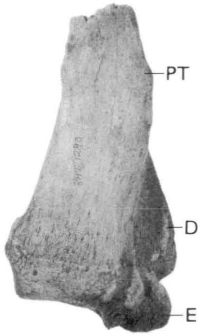

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AIVUKUS, PROROSMARUS, ODOBENUS

PLATE 3

[Abbreviations: DT—deltoid tubercle. PC—pectoral crest.]

FIGURES 1–8. *Aivukus cedrosensis* n. gen. and n. sp.

Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico.

1, 2. Referred male left first metacarpal, UCR 15260, ×0.53.
  1. Dorsal view.
  2. Palmar view.

3–5. Partial female right humerus, type, IGCU 901, ×0.48.
  3. Medial view.
  4. Posterior view.
  5. Anterior view.

6–8. Referred female left humerus, UCR 15243, ×0.42 (reversed).
  6. Medial view.
  7. Posterior view.
  8. Anterior view.

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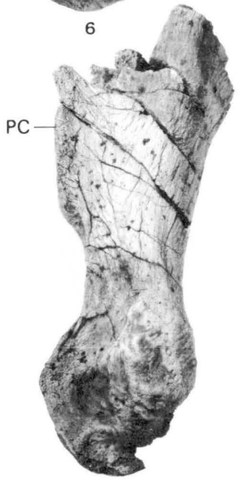

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AIVUKUS

PLATE 4

FIGURES 1–21. *Aivukus cedrosensis* n. gen. and n. sp.

Referred male carpal elements. Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico.

1–4. Left scapholunar from UCR 15260 (reversed), ×0.45.
  1. Ulnar view; A-cuneiform articulation.
  2. Proximal view.
  3. Distal view; B-pocketed articulation for magnum.
  4. Dorsal view.

5–7. Right trapezium from UCR 15241, ×0.47.
  5. Ulnar view.
  6. Distal view.
  7. Dorsal view.

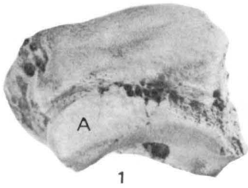
8–11. Left trapezoid from UCR 15260 (reversed), ×0.50.
  8. Ulnar view.
  9. Distal view.
  10. Dorsal view.
  11. Radial view.

12–15. Left unciform from UCR 15260 (reversed), ×0.43.
  12. Ulnar view.
  13. Distal view.
  14. Proximal view.
  15. Radial view.

16–18. Left cuneiform from UCR 15260 (reversed), ×0.50.
  16. Ulnar view.
  17. Proximal view.
  18. Radial view; C-scapholunar articulation.

19–21. Left metacarpal II from UCR 15260 (reversed), ×0.48.
  19. Dorsal view.
  20. Ulnar view.
  21. Proximal view.

22–25. Right metacarpals III of *Aivukus, Pliopedia, Imagotaria,* and *Odobenus,* dorsal views, × 0.50.
  22. *Imagotaria downsi* Mitchell. Referred male limb, USNM 23859. Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.
  23. *Pliopedia pacifica* Kellogg. Type, USNM 13627. Late Miocene, basal Paso Robles Formation, Santa Margarita, Calif. The platformed articulation for metacarpal II has been roughly restored with clay.
  24. *Aivukus cedrosensis* n. gen. and n. sp. Referred specimen, H.S.C. 309. Late Miocene, lower part of Almejas Formation, Cedros Island, Mexico.
  25. *Odobenus rosmarus* (Linnaeus). Recent male.



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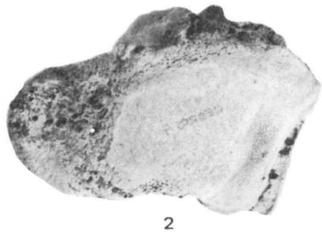

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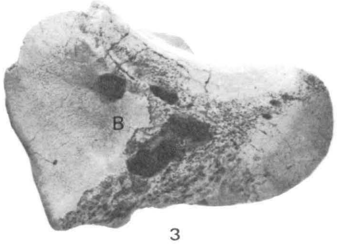

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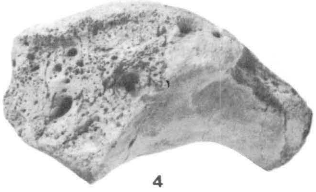

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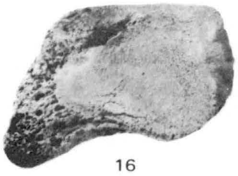

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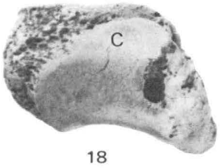

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AIVUKUS, PLIOPEDIA, IMAGOTARIA, ODOBENUS

PLATE 5

Lateral (a) and medial (b) views of mandibular rami, ×0.50.

FIGURES 1. *Zalophus californianus* Lesson.
Recent, for comparison

2. *Imagotaria downsi* Mitchell.
Referred female specimen, USNM 23858. Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

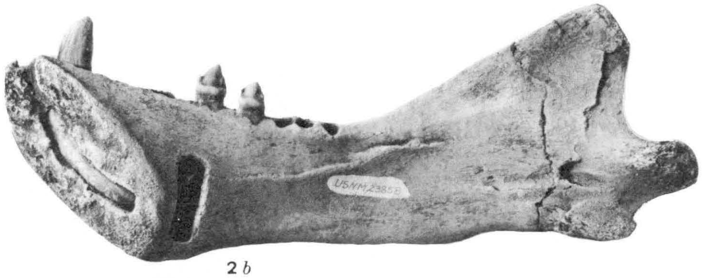
3. *Dusignathus santacruzensis* Kellogg.
Holotype, UCMP 27121. Late late Miocene, **Purisima Formation.** Santa Cruz, Calif.

4. *Prorosmarus alleni* Gregory and Berry.
Holotype, USNM 9343. Pliocene, Yorktown Formation, Yorktown, Va (photo of cast.)

1*a*

1*b*

2*a*

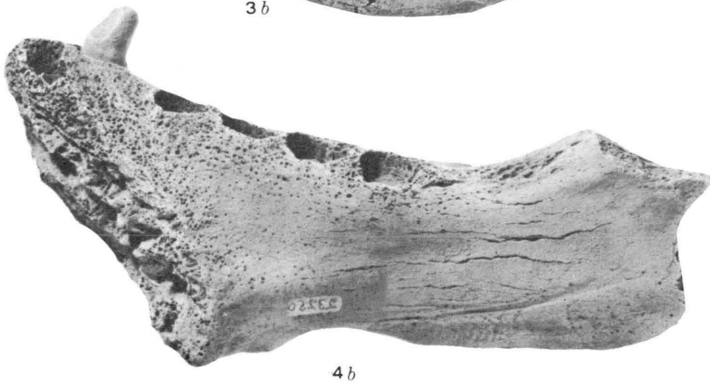


2 *b*

3*a*

3 *b*

4*a*



4 *b*

ZALOPHUS, IMAGOTARIA, DUSIGNATHUS, PROROSMARUS

PLATE 6

Imagotaria downsi Mitchell. Referred female skull, USNM 23858. Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif., ×0.77.

IMAGOTARIA

PLATE 7

FIGURES 1-11. *Imagotaria downsi* Mitchell.

Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

1-5. Referred female skull, USNM 23858.

  1. Right side of skull, ×0.59.
  2. Dorsal view of skull, ×0.59.
  3. Fragments of atlas, ×0.40.
  4. Lingual view of left upper premolars, ×1.
  5. Lingual view of left lower P_{3-4} and M_1 showing premolar roots, ×0.50.

6, 7. Referred male lower canine with mandibular fragment, USNM 23868, ×0.47.

  6. Symphyseal view.
  7. Anterior view.

8-11. Referred immature atlas, USNM 23872, ×0.37.

  8. Posterior view.
  9. Anterior view.
  10. Dorsal view.
  11. Left lateral view.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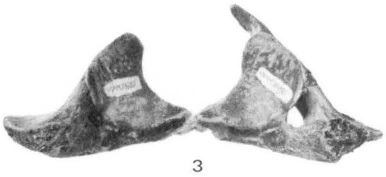
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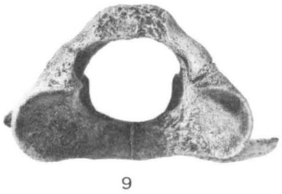
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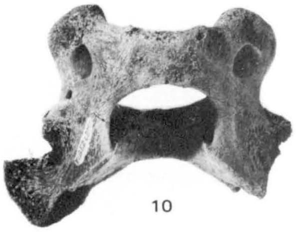
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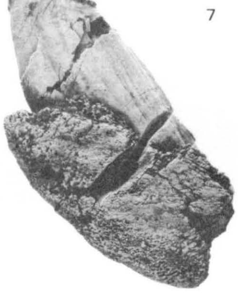
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IMAGOTARIA

PLATE 8

FIGURES 1, 2. *Imagotaria downsi* Mitchell.

Referred juvenile male skull and scapula. USNM 184060.

Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

1. Palatal view of skull, ×0.66.
2. Lateral view of scapula, ×0.50.

3. *Imagotaria downsi* Mitchell.

Late middle Miocene, Sisquoc Formation, Lompoc, Calif. Holotype, SBMNH 342.

3. Lateral view of portion of scapula, ×0.50.

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IMAGOTARIA

PLATE 9

FIGURES 1, 2, 5. *Imagotaria downsi* Mitchell.

Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

1. Referred juvenile male skull, USNM 184060. Lateral view of skull, ×0.53.
2. Same. Dorsal view of skull, ×0.53.
5. Right cuboid, USNM 184061, ×0.48.

3\. *Allodesmus courseni* Downs.

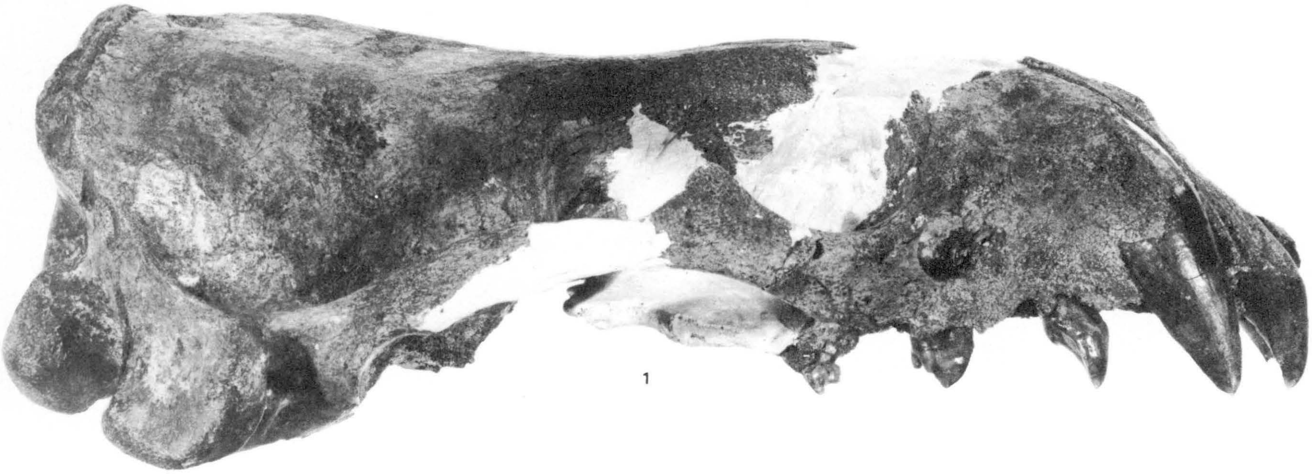
Middle Miocene, Kanomata-zawa Formation, Utsonomiya, Japan. Cast, USNM 24915, of lost specimen, ×0.50.

4\. *Imagotaria* sp.

Early late Miocene, Towsley Formation, Soledad Canyon, Calif. Right cuboid, UCMP 24073, ×0.48.

6\. *Neotherium mirum* Kellogg.

Early middle Miocene, Round Mountain Silt, Bakersfield, Calif. Right cuboid, USNM 11552, ×0.48.



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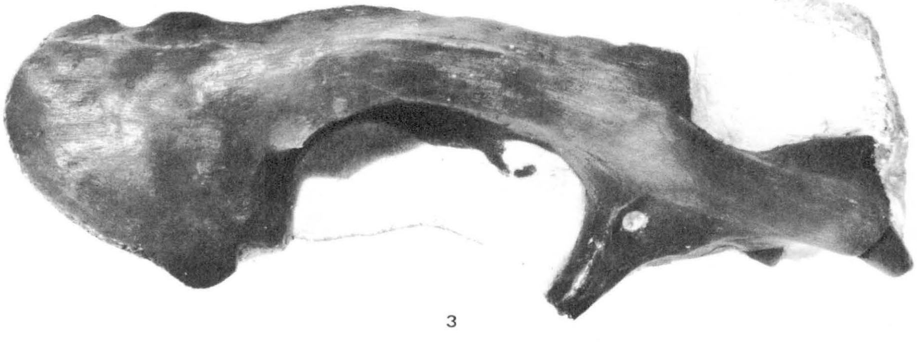

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IMAGOTARIA,? ALLODESMUS, NEOTHERIUM

PLATE 10

[Abbreviations: RW—round window. P—promontorium. A—apex. F—floccular fossa. V—vestibulocochlear canal. FN—facial canal. JP—jugular process of the exoccipital. T—position of tympanic membrane. HF—hyoid fossa. EHF—internal swelling of the hyoid fossa. SM—stylomastoid foramen. JF—jugular foramen. IC—internal carotid foramen. OF—oval foramen. OR—truncated passageway to round foramen and orbital fissure. X—sylvian sulcus. H—hypophyseal fossa. E—epitympanic recess]

FIGURES 1,3–6,9,11. *Imagotaria downsi* Mitchell.

Late middle and early late Miocene, Santa Cruz and Lompoc, Calif.

1. Latex mold of the floor of the braincase of the female skull, USNM 23858, ×0.5.
3. Left temporal of holotype (male) SBMNH 342, medial view, ×1.
4. Same, ventral view.
5. Latex mold of the left middle ear cavity of female skull, USNM 23858, lateral view, ×1.
6. Latex mold of left middle ear cavity of male skull, type, SBMNH 342, lateral view, ×1.
9. Right malleus and incus of female skull, USNM 23858, lateral aspect, ×3.
11. Left middle ear cavity of female skull, USNM 23858, ventral view, ×2.

2. *Pontolis magnus* True.

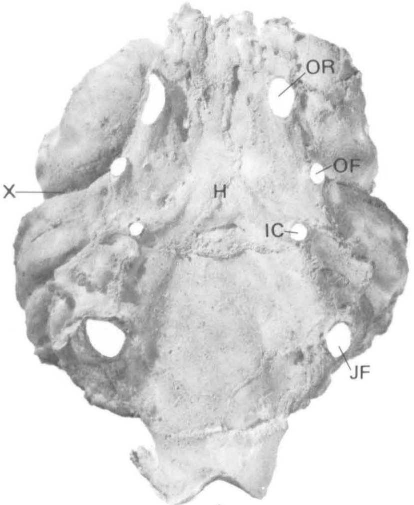
Holotype, USNM 3792. Late Miocene, Empire Formation, Oreg. Latex mold of floor of braincase, ×0.50.

7,8. *Odobenus rosmarus* (Linnaeus), for comparison.

7. Latex mold of left middle ear cavity of female skull, lateral view, ×1.
8. Right malleus and incus, lateral aspect, ×3.

10. *Zalophus californianus* (Lesson).

Right malleus and incus, lateral aspect, ×3, for comparison.



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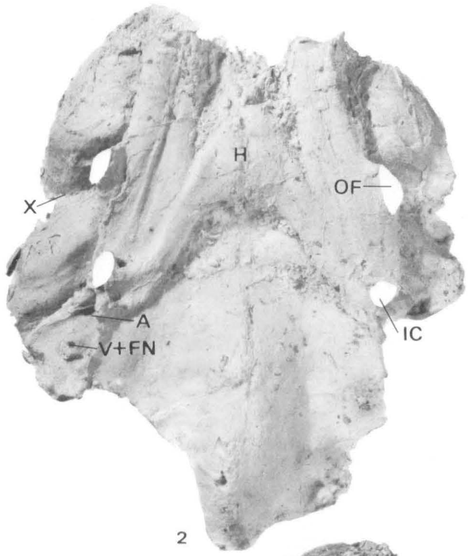

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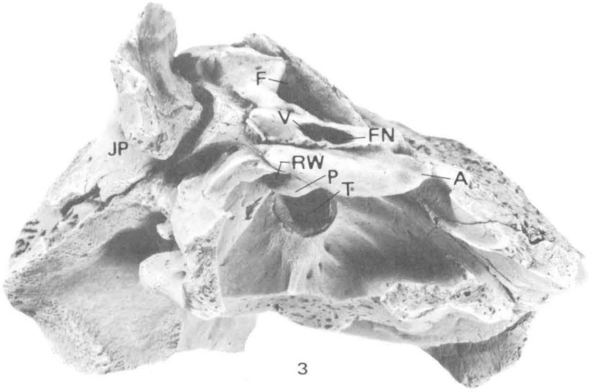

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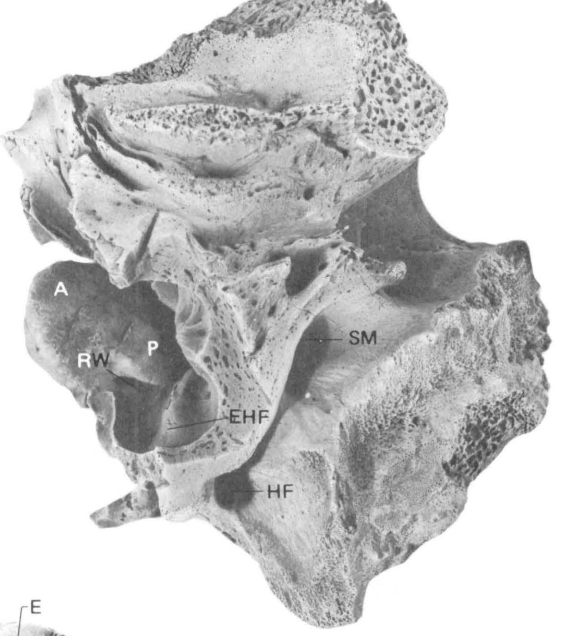

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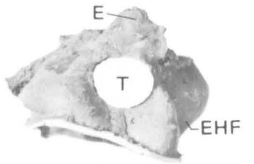

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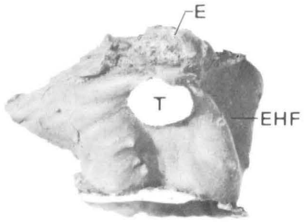

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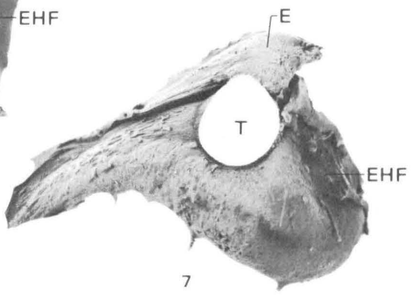

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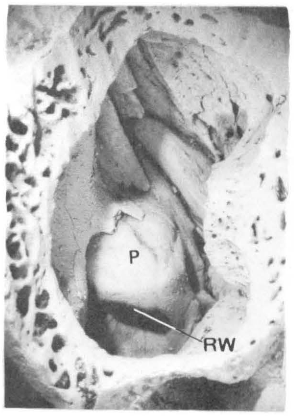

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IMAGOTARIA, PONTOLIS, ODOBENUS, ZALOPHUS

PLATE 11

FIGURES 1-8. *Imagotaria downsi* Mitchell.

Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

1, 2. Referred male right anterior limb, USNM 23859.
  1. Articulated limb, lateral view, ×0.31.
  2. Articulated carpals and metacarpals with referred trapezium USNM 23875 inserted in position of trapezium missing in limb, dorsal view, ×0.40.

3–5. Referred male right trapezium, USNM 23875, ×0.47.
  3. Ulnar view.
  4. Dorsal view.
  5. Distal view.

6–8. Referred female patella, USNM 23863, ×0.47.
  6. Anterior view.
  7. Posterior or proximal view.
  8. Lateral view.

9. ?*Neotherium mirum* Kellogg.

Early middle Miocene, Round Mountain Silt, Bakersfield, Calif.

Right radius lacking distal epiphysis. USNM 187377, ×0.33.

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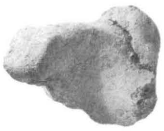

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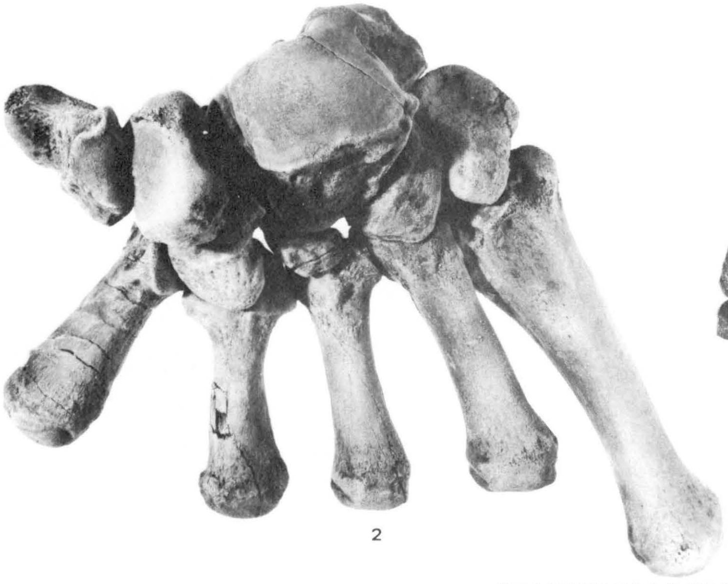

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IMAGOTARIA, ? NEOTHERIUM

PLATE 12

[Abbreviation: RP—radial process of the radius]

FIGURES 1-7. *Imagotaria downsi* Mitchell.
Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.
Referred anterior limb elements.
1,2,5–7. Elements from male right limb, USNM 23859.
1. Partial humerus, lateral view, ×0.48.
2. Same, posterior view, ×0.48.
5. Same, distal view, ×0.45.
6. Ulna, distal view, ×0.48.
7. Radius, distal view, ×0.48.
3,4. Referred female left humerus, USNM 23870.
3. Posterior view, ×0.45.
4. Lateral view, ×0.43.


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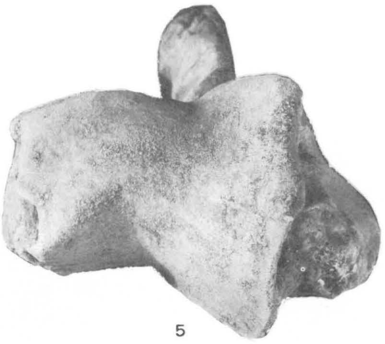
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IMAGOTARIA

PLATE 13

[Abbreviation: RP—radial process of the radius]

FIGURES 1–17. *Imagotaria downsi* Mitchell.
Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.
Referred anterior limb elements.
1–3,6–16. Elements from male right limb, USNM 23859.
1. Ulna, anterior view, ×0.43.
2. Same, lateral view.
3. Radius, lateral view, ×0.48.
6. Scapholunar, proximal view, ×0.45.
7. Same, distal view.
8. Same, ulnar view.
9. Same, dorsal view.
10. Cuneiform, ulnar view, ×0.45.
11. Same, distal view.
12. Same, radial view.
13. Trapezoid, radial view, ×0.43.
14. Same, ulnar view.
15. Same, distal view.
16. Same, dorsal view.
4,5,17. Female elements.
4. Left radius, USNM 184084, lateral view, ×0.48.
5. Same, distal view.
17. Right trapezoid, USNM 184086, dorsal view, ×0.48.

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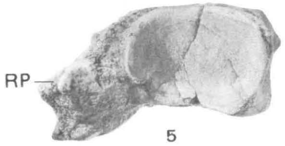

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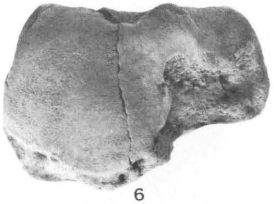

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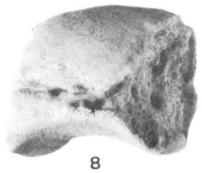

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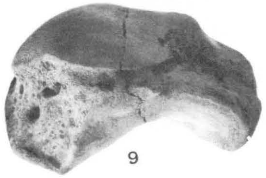

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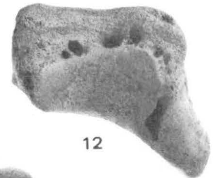

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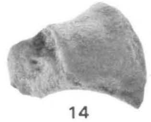

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IMAGOTARIA

PLATE 14

FIGURES 1–17. *Imagotaria downsi* Mitchell.

Early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

Referred male right forelimb, USNM 23859, carpals and metacarpals.

1. Magnum, radial view, ×0.45.
2. Same, ulnar view.
3. Same, proximal view.
4. Same, dorsal view.
5. Same, distal view.
6. Unciform, proximal view, ×0.47.
7. Same, dorsal view.
8. Same, distal view.
9. Same, ulnar view.
10. Same, radial view.
11. Metacarpal I, palmar view, ×0.47.
12. Metacarpal I, dorsal and proximal view, ×0.47.
13. Metacarpal II, dorsal and proximal view, ×0.47.
14. Metacarpal III, dorsal and proximal view, ×0.47.
15. Metacarpal IV, dorsal and proximal view, ×0.47.
16. Metacarpal V, dorsal and proximal view, ×0.47.
17. Metacarpal V, radial view, ×0.50.

18–21. Comparison of dorsal view of male right first metacarpals of four odobenids.

18. *Imagotaria downsi* Mitchell. Referred, USNM 23859, same as figure 12, ×0.50.
19. *Pliopedia pacifica* Kellogg. Holotype, USNM 13627, late Miocene or Pliocene, Paso Robles Formation, Santa Margarita, Calif., ×0.50.
20. *Aivukus cedrosensis* Repenning and Tedford. Referred, UCR 15260, late Miocene, lower Almejas Formation, Cedros Island, Mexico, ×0.45.
21. *Odobenus rosmarus* (Linnaeus). Recent, ×0.48.

22–26. Right astragali referred to *Imagotaria downsi* Mitchell.

22. "*Pontolis* cf. *magnus*" of Kellogg. Fragment of male astragalus UCMP 24071, late Miocene, Towsley Formation, Los Angeles County, Calif., proximal view, ×0.48.
23. Female astragalus, USNM 184085, early late Miocene, Santa Margarita Formation, Santa Cruz, Calif., proximal view, ×0.48.
24. Female astragalus, USNM 23867, early late Miocene, Santa Margarita Formation, Santa Cruz, Calif., proximal view, ×0.48.
25. Same, calcanear view.
26. Same, fibular view.


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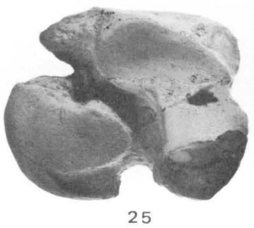
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IMAGOTARIA, PLIOPEDIA, AIVUKUS, ODOBENUS

PLATE 15

FIGURES 1-7,9,18. *Imagotaria downsi* Mitchell.

Referred hind limb elements, early late Miocene, Santa Margarita Formation, Santa Cruz, Calif.

1. Female left femur (reversed), USNM 23870, found with humerus (pl. 12, figs. 3-4), anterior view, × 0.52.
2. Same, posterior view.
3. Probable male incomplete left calcaneum (reversed), USNM 23866, found with male trapezium (pl. 11, figs. 3-5), astragalar view, × 0.48.
4. Same, plantar view.
5. Male right calcaneum, USNM 23862, astragalar view, × 0.48.
6. Same, plantar view.
7. Same, distal view.
9. Partial female left calcaneum (reversed), USNM 23867, found with articulated astragalus (pl. 14, figs. 24-26), astragalar view, × 0.45.
18. Right magnum (reversed) from limb USNM 23859, dorsal view, for comparison, 0.48.

8. "*Pontolis* cf. *magnus*" of Kellogg.

Fragment of male right calcaneum, UCMP 24070, early late Miocene, Towsley Formation, Los Angeles County, Calif., distal view, × 0.50.

10-16,19. *Dusignathus santacruzensis* Kellogg.

Referred left scapholunar and magnum, USNM 23869, late late Miocene, Purisima Formation, Santa Cruz, Calif.,

10. Scapholunar, dorsal view, × 0.48.
11. Same, distal view.
12. Same, ulnar view; A—articular surface for cuneiform.
13. Same, proximal view.
14. Magnum, distal view, × 0.48.
15. Same, proximal view.
16. Same, ulnar view.
19. Same, dorsal view.

17,20,22. ?*Dusignathus santacruzensis* Kellogg.

Questionably referred left forelimb elements, UCMP 83370, late late Miocene or Pliocene, Drakes Bay Formation of Galloway (1977), Point Reyes, Calif.

17. Magnum, ulnar view, × 0.50.
20. Magnum, dorsal view, × 0.50.
22. Entire specimen with magnum in radial view (next to figure number), × 0.42.

21. *Odobenus rosmarus* (Linnaeus).

Living. Left magnum, adult male, dorsal view, for comparison, × 0.48.

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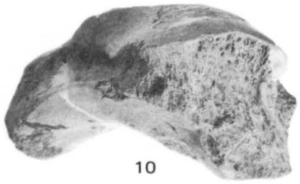

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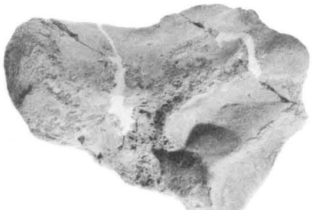

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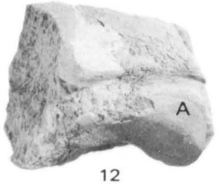

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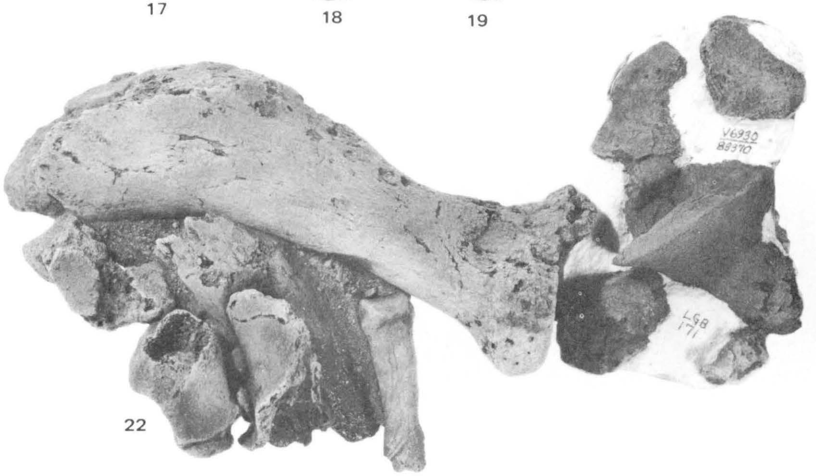

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IMAGOTARIA, DUSIGNATHUS, ODOBENUS

PLATE 16

FIGURES 1,3,5. ?*Dusignathus santacruzensis* Kellogg.

Humerus, UCMP 65318, and immature radius, USNM 23891, late Miocene, Purisima Formation, Moss Beach, Calif., ×0.50.

1. Humerus, anterior view.
3. Humerus, lateral view.
5. Immature radius lacking distal epiphysis, lateral view.

2,4,7. *Valenictus imperialensis* Mitchell.

Cast of holotype humerus, LACM (CIT) 3926, late Miocene, Imperial Formation, Imperial County, Calif., × 0.50.

2. Anterior view.
4. Lateral view.

Fragment of humerus, USNM 13643, early Pliocene, San Joaquin Formation, Kings County, Calif., × 0.50.

7. Anterior view.

6. Phocid cf. *Pusa sibirica* (Gmelin).

Late Pliocene, Yakataga Formation, Malaspina District, Alaska. Immature radius, × 1.

8. ?*Pliopedia pacifica* Kellogg.

Fibula, USNM 187337, late late Miocene, Etchegoin Formation, Kings County, Calif., × 0.40.


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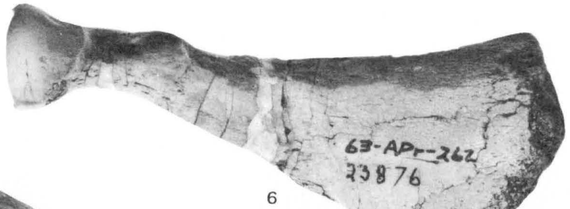

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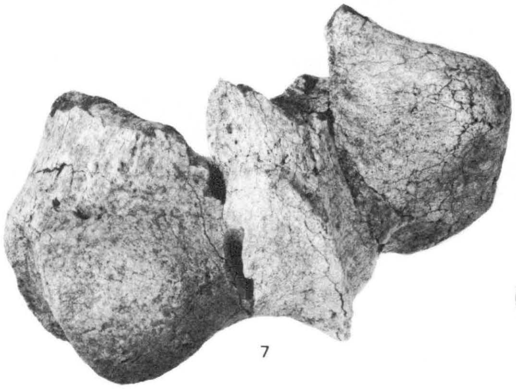
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?*DUSIGNATHUS*, *VALENICTUS*, ?*PLIOPEDIA*, PHOCID

PLATE 17

FIGURES 1-3. Right humerus of *Pliopedia pacifica* Kellogg, USNM 187328, late late Miocene, middle part of Etchegoin Formation, Kettleman Hills, Calif., × 0.50.

1. Medial view.
2. Anterior view.
3. Lateral view.

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PLIOPEDIA

PLATE 18

FIGURES 1,3. *Dusignathus santacruzensis* Kellogg.

Referred snout, presumably male, UCR 15244, late Miocene, lower part of Almejas Formation, Cedros Island, Mexico.

1. Palatal view, ×0.62.
3. Lateral view, ×0.48.

2,4. *Dusignathus santacruzensis* Kellogg.

Snout of holotype, presumably female, UCMP 27121, Pliocene, Purisima Formation, Santa Cruz, Calif.

2. Palatal view, ×0.62.
4. Lateral view, ×0.48.

5. *Pontolis magnus* True.

Holotype, USNM 3792, late Miocene, Empire Formation, Coos Bay, Oreg., ventral view of prepared basicranium, ×0.66.


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DUSIGNATHUS, PONTOLIS

PLATE 19

FIGURES 1-3. *Pithanotaria starri* Kellogg.

1. Referred mandibular fragment, UCMP 108069, early late Miocene, Santa Margarita Formation, Santa Cruz, Calif., medial view, ×1.
2. Referred first metacarpal, USNM 184062, early late Miocene, Santa Margarita Formation, Santa Cruz, Calif., dorsal view, ×1.
3. Referred palate, UCMP 74813, late middle Miocene, Santa Margarita Formation, Seaside, Calif., ×1.

4. *Arctocephalus galapagoensis* Heller.

Young female skull, CAS 1185, suture age 22, a unique individual in not having the second molars. For comparison, ×0.90.

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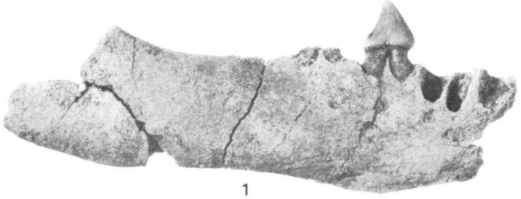

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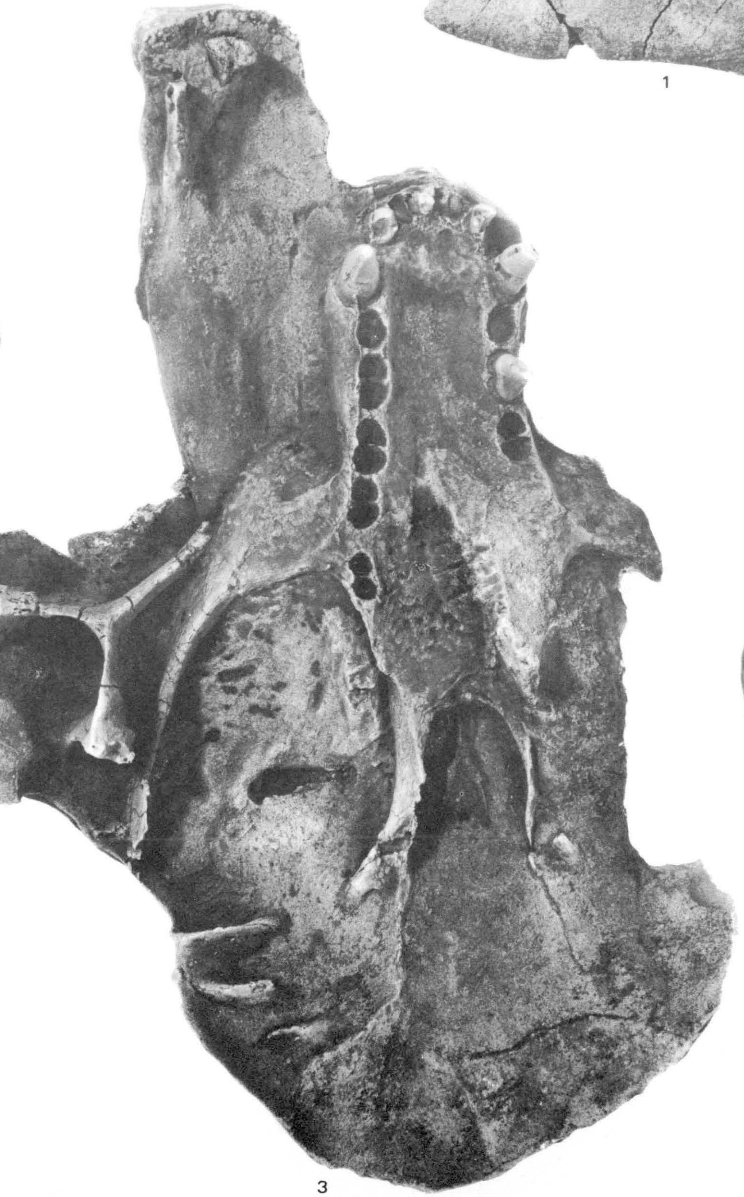

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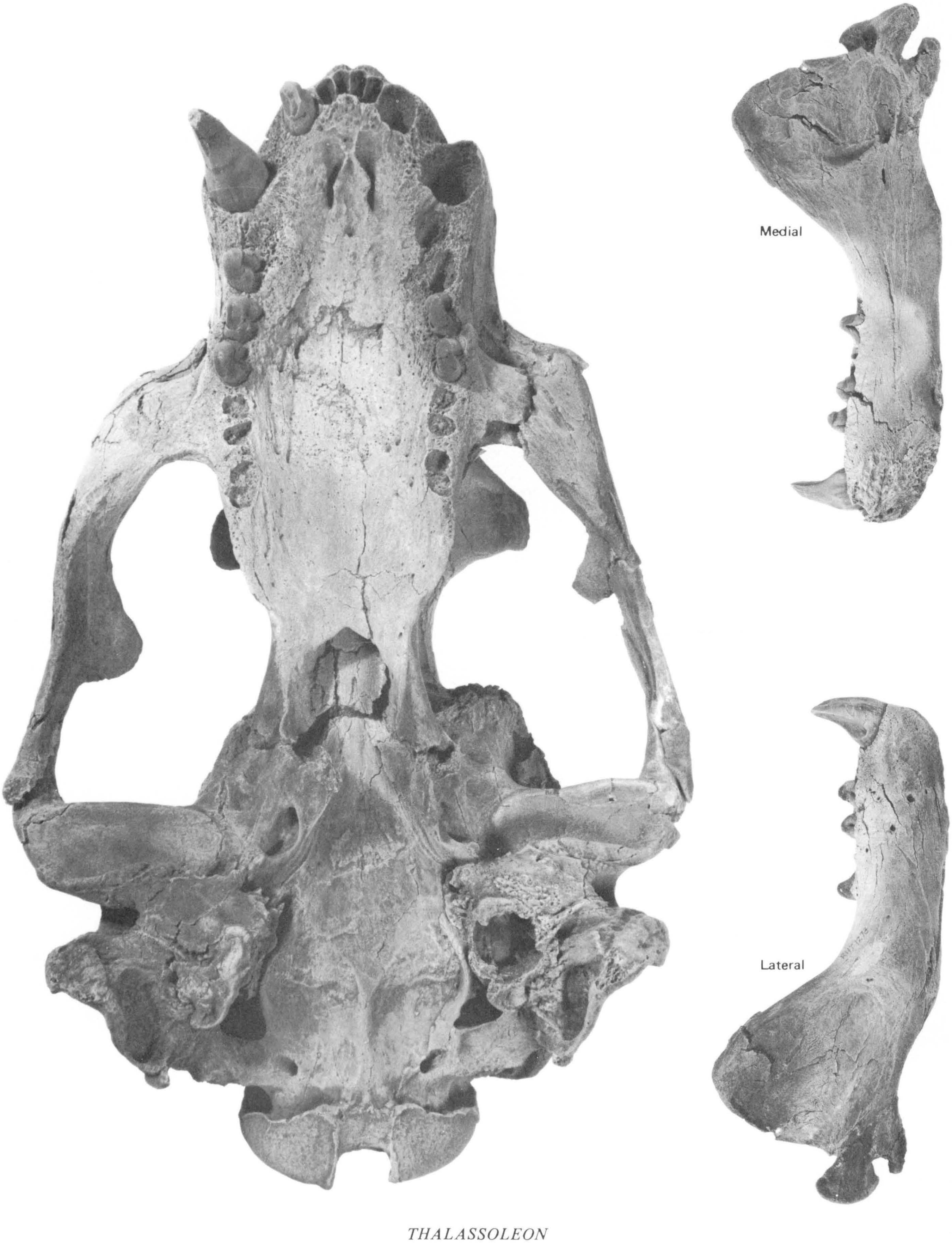
PITHANOTARIA, ARCTOCEPHALUS

PLATE 20

Thalassoleon mexicanus n. gen. and n. sp.

Holotype, IGCU 902. Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico. Ventral view of the skull, ×0.77, and medial and lateral views of the right mandibular ramus, ×0.50.



THALASSOLEON

PLATE 21

FIGURES 1-4. *Thalassoleon mexicanus* n. gen. and n. sp.

Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico.

1. Right side of skull, holotype, IGCU 902, ×0.62.
2. Dorsal view of skull, holotype, IGCU 902, ×0.62.
3. Left lateral view of os penis, referred, UCR 15258, ×0.52.
4. Left upper canine of holotype, IGCU 902, showing growth annuli, ×1.

5-7. Left lateral views of os penis of living otariids for comparison.

5. *Neophoca cinerea* (Peron). South Australia, juvenile, to show early ontogenetic similarity of apex, ×0.52.
6. *Callorhinus ursinus* (Linnaeus). Alaska, old age adult, to show similarity of apex and base, ×0.52.
7. *Arctocephalus pusillus* (Schreber). South Africa, young adult (suture age 26) to show differences in apex, ×0.52.

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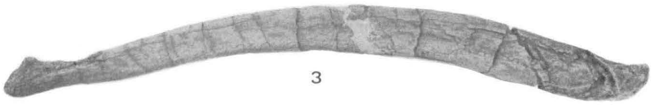

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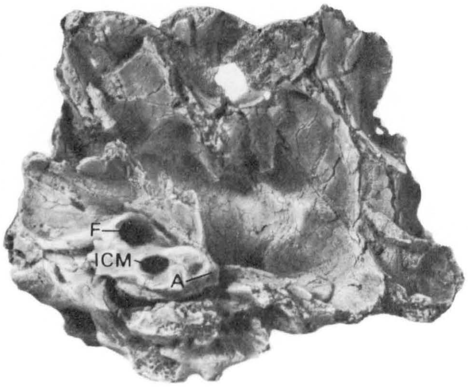
THALASSOLEON, NEOPHOCA, CALLORHINUS, ARCTOCEPHALUS

PLATE 22

FIGURES 1-9. *Thalassoleon mexicanus* n. gen. and n. sp.

Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico. Referred specimens.

1. Temporal bone of female individual, UCR 15253, medial view, ×1. Abbreviations as on plate 1.
2. Juvenile male skull, UCR 15252, ventral view, ×0.53.
3. Right mandibular ramus of figure 2, UCR 15252, lateral view, ×0.53.
4. Calcaneum, UCR 15248, astragalar view, ×0.53.
5. Radius, UCR 15250, lateral view, ×0.53.
6. Ulna, UCR 15247, lateral view, ×0.53.
7. Humerus, UCR 15254, anterior view, ×0.50.
8. Same, lateral view.
9. Scapula, UCR 15254, lateral view, ×0.33.



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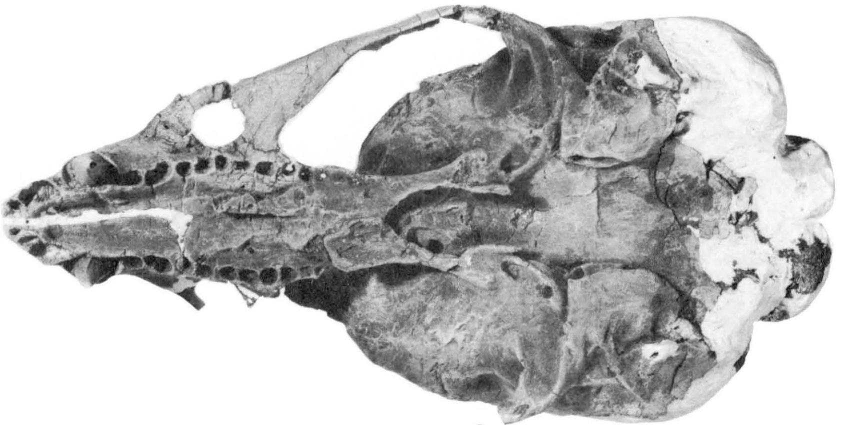

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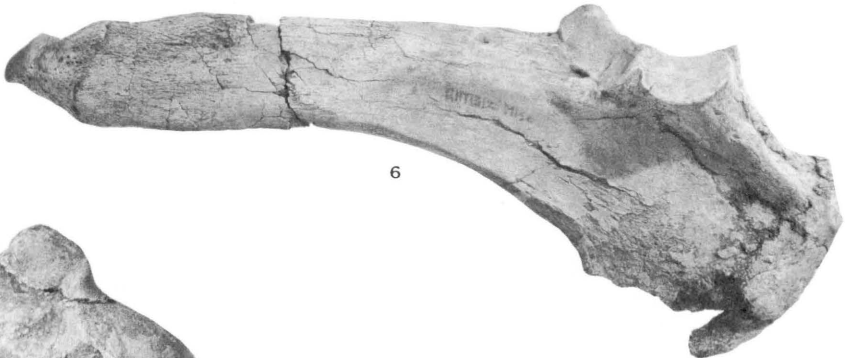

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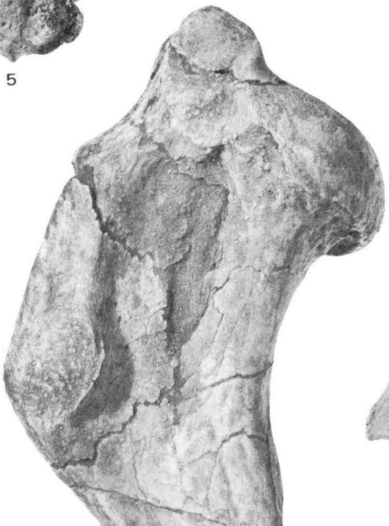

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THALASSOLEON

PLATE 23

FIGURES 1,3,5–9,15. *Thalassoleon mexicanus* n. gen. and n. sp.

Late Miocene, lower part of the Almejas Formation, Cedros Island, Mexico. Holotype and referred specimens.

1. Astragalus, UCR 15249, tibial view, ×0.50.
3. Same, calcaneal view.
5. Femur, UCR 15258, anterior view, ×0.53.
6. Axis, type, IGCU 902, anterior view, ×0.53.
7. Fibula, UCR 15258, anterior view, ×0.50.
8. Tibia, UCR 15258, anterior view, ×0.50.
9. Innominate, UCR 15258, lateral view, ×0.50.
15. Metatarsal I, UCR 15246, dorsal view, ×0.50.

2,4. *Zalophus californianus* (Lesson).

2. Astragalus, tibial view, ×0.50, for comparison.
4. Astragalus, calcanear view, ×0.50, for comparison.

10,18. *Arctocephalus pusillus doriferus* Wood Jones.

Adult male.

10. Axis, anterior view, for comparison, ×0.53.
18. Metatarsal I, dorsal view, for comparison, ×0.50.

11–14,17. *Thalassoleon macnallyae* n. gen. and n. sp.

Late Miocene, lower part of the Drakes Bay Formation of Galloway (1977), Point Reyes, Calif. Holotype specimen, UCMP 2535.

11. Mandibular fragment, medial view, ×0.53.
12. Maxillary fragment, palatal view, ×0.66.
13. Mandibular fragment, lateral view, ×0.53.
14. Basicranium, ventral view, ×0.66.
17. Metatarsal I, dorsal view, ×0.53.

16. *Neophoca cinerea* (Peron).

Metatarsal I, dorsal view, for comparison, ×0.50.


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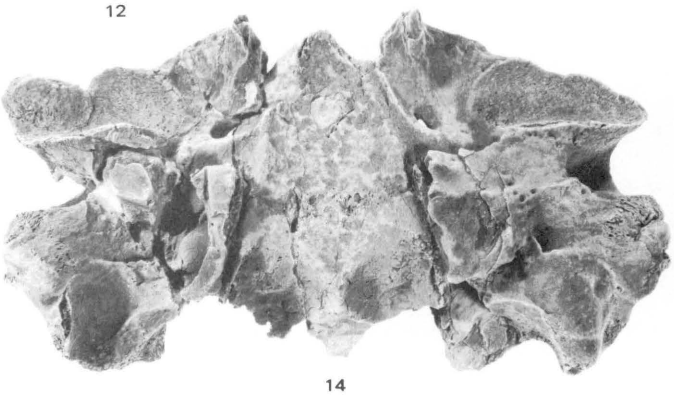
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THALASSOLEON, ZALOPHUS, ARCTOCEPHALUS, NEOPHOCA

PLATE 24

[Abbreviations: X—sulcus postcruciatus. O—gyrus ectosylvius posterior]

FIGURES 1-3. *Thalassoleon macnallyae*? n. sp.

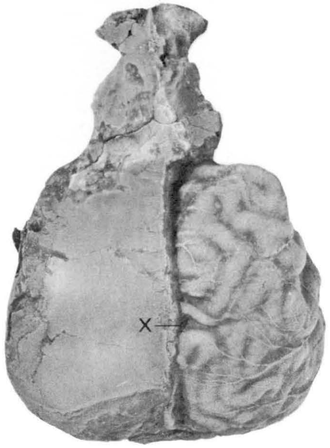
Immature female brain case, USNM 184076, late Pliocene, Purisima Formation, Capitola, Calif., ×0.50.

1. Dorsal view.
2. Right lateral view.
3. Ventral view.

4-6. *Pliopedia pacifica* Kellogg.

USNM 187328, late late Miocene, middle part of Etchegoin Formation, Kettleman Hills, Calif., ×0.50.

4. Left radius, external view.
5. Left ulna, external view; olecranon process restored from right ulna.
6. Weathered brain case, dorsal view.



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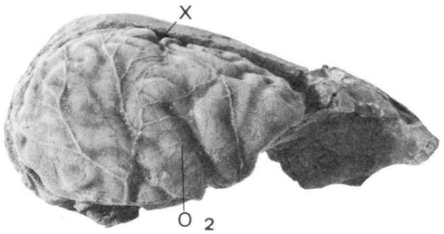

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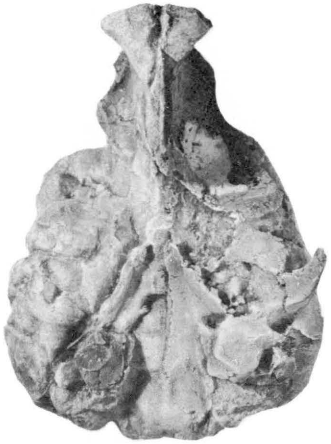

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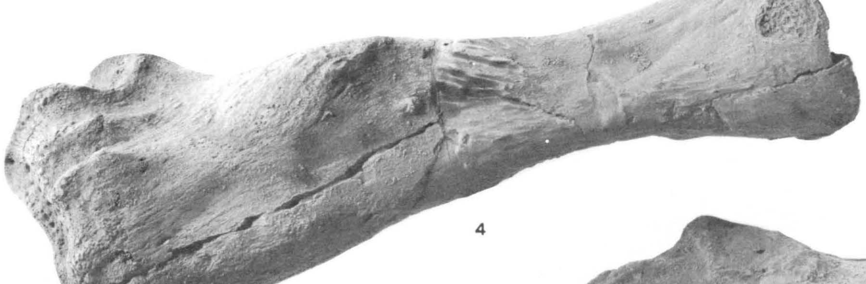

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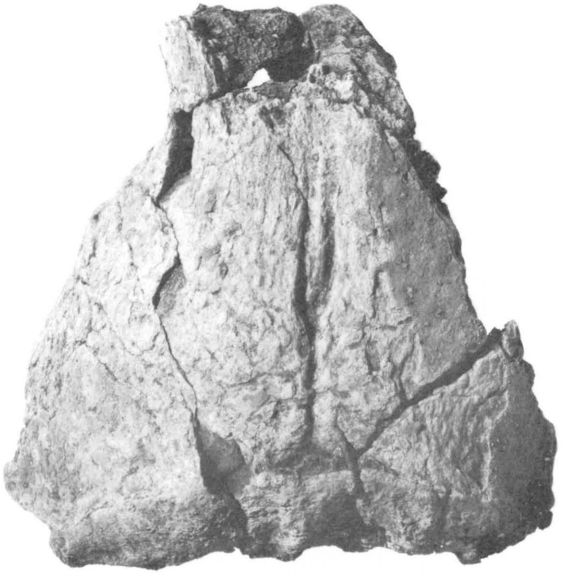

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THALASSOLEON, PLIOPEDIA

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